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MR. SIMON THORN (Orcid ID : 0000-0002-3062-3060)

PROFESSOR DAVID B LINDENMAYER (Orcid ID : 0000-0002-4766-4088)

MR. SEBASTIAN SEIBOLD (Orcid ID : 0000-0002-7968-4489)

DR JÖRG MÜLLER (Orcid ID : 0000-0002-1409-1586)

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Impacts of salvage logging on biodiversity – a meta-analysis

Simon Thorn. Field Station Fabrikschleichach, Department of Animal Ecology and Tropical Biology (Zoology III), Julius-Maximilians-University Würzburg, Glashüttenstraße 5, 96181 Rauhenebrach, Germany. simon@thornonline.de

Claus Bässler. Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany. Claus.Baessler@npv-bw.bayern.de, Tel.: +4985529600179.

Roland Brandl. Department of Ecology, Animal Ecology, Faculty of Biology, Philipps-Universität Marburg, Karl-von-Frisch-Str. 8, 35032 Marburg, Germany. brandlr@mailer.uni-marburg.de, Tel.: +496421 2823386.

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Philip J. Burton. University of Northern British Columbia, 4837 Keith Ave., Terrace, B.C., V8G 1K7, Canada. phil.burton@unbc.ca, Tel.: +12506153333.

Rebecca Cahall. Department of Forest Ecosystems and Society, Oregon State University, 321 Richardson Hall, Corvallis, OR 97331, USA. beccacahall@gmail.com, Tel.: +13528460552.

John L. Campbell. Department of Forest Ecosystems and Society, Oregon State University, 321 Richardson Hall, Corvallis, OR 97331, USA. john.campbell@oregonstate.edu, Tel.: +15417378426.

Jorge Castro. Department of Ecology, University of Granada. Campus Fuentenueva s/n, 18071 Granada, Spain. jorge@ugr.es, Tel.: +34958241000.

Chang-Yong Choi. Department of Forest Sciences, Seoul National University, Seoul 08826, Korea. subbuteo95@ gmail.com, Tel.: +8228804766.

Tyler Cobb. Royal Alberta Museum 12845 – 102nd Ave, Edmonton, Alberta, T5N 0M6, Canada. tyler.cobb@gov.ab.ca, Tel.: +17804539197.

Daniel C. Donato. University of Washington, School of Environmental & Forest Sciences, Seattle, WA 98195, USA. donato.danc@gmail.com, Tel.: +13609021753.

Ewa Durska. Department of Ecology and Biodiversity, Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, 00-679 Warsaw, Poland. edurska@miiz.waw.pl,

Tel.: +48608495928.

Joseph B. Fontaine. School of Veterinary and Life Sciences, Murdoch University, 90 South Street, Murdoch, Western Australia 6150, Australia. J.Fontaine@murdoch.edu.au, Tel.: +61893606075.

Sylvie Gauthier. Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 rue du P.E.P.S., Quebec, Canada. sylvie.gauthier2@canada.ca, Tel.: +4186485829.

Christian Hebert. Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 Du P.E.P.S., P.O. Box 10380, Quebec, Canada. christian.hebert@canada.ca, Tel.: +4186485896.

Torsten Hothorn. University of Zürich, Division of Biostatistics, Hirschengraben 84, 8001 Zürich, Switzerland. torsten.hothorn@uzh.ch, Tel.: +41 44 634 48 17

Richard L. Hutto. Division of Biological Sciences, University of Montana, Missoula MT 59812, USA. hutto@mso.umt.edu, Tel.: +14062434292.

Eun-Jae Lee, Urban Planning Research Group, Daejeon Sejong Research Institute, Daejeon 34863, Korea. 2lejae@hanmail.net, Tel.: +82425303521.

Alexandro B. Leverkus. Ecology Unit, Department of Life Sciences, University of Alcalá. Campus Universitario, 28805 Alcalá de Henares, Spain. leverkus@ugr.es, Tel.: +34622689928.

David B. Lindenmayer. Fenner School of Environment and Society, The Australian National University, Canberra ACT 2601, Australia. David.Lindenmayer@anu.edu.au, Tel.: +61261250654.

Martin K. Obrist. WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Biodiversity and Conservation Biology, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland. martin.obrist@wsl.ch, Tel.: +41447392466.

Josep Rost. Department of Environmental Sciences and Food Industries, University of Vic-Central, University of Catalonia. Carrer de la Laura 13, 08500 Vic, Catalonia, Spain. joseprost@gmail.com, Tel.: +34972418269.

Sebastian Seibold. Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany; Chair for Terrestrial Ecology, Department of Ecology and Ecosystem Management, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany. sebastian-seibold@gmx.de, Tel.: +4985529600179.

Rupert Seidl. Institute of Silviculture, Department of Forest- and Soil Sciences, University of Natural Resources and Life Sciences Vienna, Peter Jordan Straße 82, 1190 Vienna, Austria. rupert.seidl@boku.ac.at, Tel.: +4314765491328.

Dominik Thom. Institute of Silviculture, Department of Forest- and Soil Sciences, University of Natural Resources and Life Sciences Vienna, Peter Jordan Straße 82, 1190 Vienna, Austria. dominik.thom@boku.ac.at, Tel.: +4314765491348.

Kaysandra Waldron. Department of Wood and Forest Sciences, Laval University, 2325 Rue de la Terrasse, Québec, Canada, G1V 0A6. kaysandra.waldron.1@ulaval.ca, Tel.: +418656213116293.

Beat Wermelinger. WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Forest Dynamics - Forest Entomology, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland. beat.wermelinger@wsl.ch, Tel.: +447392258.

Maria-Barbara Winter. Forest Research Institute of Baden-Württemberg (FVA), Wonnhaldestraße 4, 79100 Freiburg, Germany. maria-barbara.winter@forst.bwl.de, Tel.: +497614018-331.

Michal Zmihorski. Swedish University of Agricultural Sciences, Department of Ecology, Box 7044, Uppsala, Sweden. zmihorski@miiz.waw.pl, Tel.: +46018672229.

Jörg Müller. Field Station Fabrikschleichach, University of Würzburg, Glashüttenstr. 5, 96181 Rauhenebrach, Germany; Bavarian Forest National Park, Freyunger Str. 2, 94481, Grafenau; Germany. Joerg.Mueller@npv-bw.bayern.de, Tel.: +4985529600179.

Running title: Impacts of salvage logging on biodiversity

Corresponding Author: Simon Thorn. (+49) 931.31.83057 simon@thornonline.de

Summary

1. Logging to 'salvage' economic returns from forests impacted by natural disturbances has become increasingly prevalent globally. Despite potential negative effects on biodiversity, salvage logging is often conducted, even in areas otherwise excluded from logging and reserved for nature conservation, inter alia because strategic priorities for post-disturbance management are widely lacking.
2. A review of the existing literature revealed that most studies investigating the effects of salvage logging on biodiversity have been conducted less than five years following natural disturbances, and focused on non-saproxylic organisms.
3. A meta-analysis across 24 species groups revealed that salvage logging significantly decreases numbers of species of eight broad taxonomic groups. Richness of dead-wood dependent taxa (i.e. saproxylic organisms) decreased more strongly than richness of non-saproxylic taxa. By contrast, taxonomic groups typically associated with open habitats increased in the number of species after salvage logging.
4. By analysing 134 original species abundance matrices, we demonstrate that salvage logging significantly alters community composition in seven of 17 species groups, particularly affecting saproxylic assemblages.
5. *Synthesis and applications.* Our results suggest that salvage logging is not consistent with the management objectives of protected areas. Substantial changes, such as the retention of dead wood in naturally disturbed forests, are needed to support biodiversity. Future

research should investigate the amount and spatio-temporal distribution of retained dead wood needed to maintain all components of biodiversity.

Keywords: bark-beetle, post-disturbance logging, fire, windstorm, climate change, natural disturbances, dead wood, salvage logging, disturbed forests, saproxylic taxa

Introduction

The frequency and extent of stand-replacing natural disturbances, such as wildfires, windstorms and insect-outbreaks, has increased considerably during recent decades, particularly in the Northern Hemisphere (Kurz *et al.* 2008; Seidl *et al.* 2014). Natural disturbances can enhance structural heterogeneity of forests, create habitats for species-rich assemblages of high conservation value, and increase the long-term resilience of forests to future stressors (Swanson *et al.* 2011). However, societal demand for timber and/or pest reduction compels forest managers to 'salvage' timber by logging before it deteriorates, a common practice even in locations otherwise exempt from conventional green-tree harvesting, such as national parks or wilderness areas (Fig.1) (Thorn *et al.* 2014; Chylarecki & Selva 2016). Such salvage logging reduces the amount of dead wood, alters successional trajectories, affects biodiversity, and can influence restoration costs and subsequent fire hazard (Lindenmayer, Burton & Franklin 2008; Waldron, Ruel & Gauthier 2013). Consequently, conflicts often emerge between natural resource managers, policy-makers and conservationists on how to handle naturally disturbed forests (Lindenmayer *et al.* 2004; Schmiegelow *et al.* 2006; González & Veblen 2007; Lindenmayer, Thorn & Banks 2017). This has resulted in intense public debates (Stokstad 2006; Nikiforuk 2011; Lindenmayer, Thorn & Banks 2017).

Different natural disturbance regimes leave distinct types of biological and/or structural legacies (Franklin *et al.* 2000). For instance, forests killed by wildfire or insect-outbreaks are characterized by large numbers of snags, while windstorms create uprooted trees (Swanson *et al.* 2011). Salvage logging typically removes or alters these legacies. The responses of saproxylic and non-saproxylic species groups to salvage logging thus depend on their relation to (dead wood) legacies affected by salvage logging (Lindenmayer, Burton & Franklin 2008). Consequently, different taxonomic groups in different types of natural disturbances may respond differently to salvage logging (Zmihorski & Durska 2011). Numerous studies have focused on the effects of salvage logging after natural disturbances on species richness and the community composition of various taxa such as vascular plants (Stuart *et al.* 1993; Macdonald 2007; Blair *et al.* 2016), carabids (Phillips *et al.* 2006; Koivula & Spence 2006; Cobb, Langor & Spence 2007), birds (Saab, Russell & Dudley 2009; Nappi & Drapeau 2009; Castro, Moreno-Rueda & Hódar 2010; Zmihorski 2010; Choi *et al.* 2014; Thorn *et al.* 2016c), and saproxylic organisms (i.e. those depending on dead wood during some part of their life cycles; Cobb et al. 2011; Norvez et al. 2013).

Two main effects of salvage logging on biodiversity arise recurrently from the current body of literature. First, salvage logging reduces the richness of taxonomic groups or particular species that depend on dead wood. For instance, salvage logging decreased nesting density of cavity-nesting birds, usually breeding in fire-killed trees (Hutto & Gallo 2006). Similarly, post-storm logging decreased the total number of saproxylic beetle species and the number of threatened species (Thorn *et al.* 2014). Second, studies that investigate a set of different taxonomic groups have demonstrated that salvage logging can alter the community composition of both saproxylic and non-saproxylic organisms, while the effects on the overall number of species can be low (Thorn *et al.* 2016a). For instance, post-storm salvage logging in Minnesota greatly diminished bird communities, while fewer differences in the tree cover were detected (Lain *et al.* 2008). However, previous attempts to summarise knowledge on the effects of salvage logging on biodiversity have focused mainly on salvage logging of burned forests (McIver & Starr 2000; Lindenmayer & Noss 2006; Lindenmayer, Burton & Franklin 2008; Thorn *et al.* 2016b), and a quantitative assessment of salvage logging impacts on biodiversity is still lacking, particularly across different taxonomic groups and in response to different types of disturbances (Fig. 1).

Here, we reviewed the scientific literature and compiled existing data to quantify the effects of salvage logging after wildfire, windstorms and insect-outbreaks on i) species numbers via a meta-analysis of 238 individual comparisons of salvaged/-unsalvaged areas; and ii) community composition based on a subset of 134 original species abundance matrices. We also tested the hypothesis that the impacts of salvage logging are more pronounced for saproxylic species groups than for non-saproxylic groups regarding the number of species and community composition within different types of natural disturbances.

Materials and methods

Literature search

We followed guidelines for systematic literature reviews (Pullin & Stewart 2006) to compile comparisons of species richness between salvaged and unsalvaged fire-, wind- or insect-affected forests. We screened the electronic data bases Web of Science, Scopus and Google Scholar on February 15th 2016 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 (> 2000 articles), we retained only field-based studies after having screened the title and abstract. Modelling studies were excluded. We also added relevant papers from reference lists in published studies. We restricted studies to those providing comparisons between completely salvage logged plots and completely unsalvaged control plots according to the information given in the respective studies. This means that on salvage logged plots, more than 75% of the trees were affected by natural disturbance and then completely salvage logged without further treatment such as tree planting or legacy retention. Lower intensifies of natural disturbances have been rarely targeted by scientific studies. Salvage logging operations thus resembled conventional clear-cutting. Unsalvaged control plots had to be affected by the same natural disturbance event but without any human intervention. Salvage logged plots had to be of similar size, surveyed with the same field methods during the same study period, and with the same sampling effort as unsalvaged control plots.

To examine wheter pseudo-replication (i.e. all plots nested within one area) might bias the results of our meta-analysis (Ramage *et al.* 2013), we carefully selected the studies according to their designs, and we used statistics that account for pseudo-replication (see below). The spatial arrangement of plots in all studies was checked based on method descriptions and/or original geographic coordinates. We contacted authors to provide data or to clarify their study designs where necessary (see Data sources section). Studies without true replicates (e.g., all salvaged plots nested and separated from unsalvaged control plots) were excluded from the analysis to ensure valid effect sizes (Halme *et al.* 2010). Studies using the same set of field plots and/or the same study area (e.g., Samcheok Forest, Korea) were identified and nested in all subsequent statistical analyses to control for pseudo-replication within study areas. We also excluded studies that sampled forests undergoing multiple types of disturbances. Salvage logging had to be conducted immediately (< 12 months) after natural disturbance took place. Mean number of species and standard deviation values per sampling unit were extracted from published text and tables, or from figures using PLOT DIGITIZER 2.6.2. (www.plotdigitizer.sourceforge.net). Last, we compiled data on covariates by extracting information on the disturbance type and the time since disturbance, or the time since subsequent salvage logging, respectively. In addition, we compiled original species abundance matrices that underpinned the published papers, which allowed us to explore the effects of salvage logging on community composition.

Meta-analysis

All analyses were conducted in R 3.3.1 (www.r-project.org). Prior to statistical analysis, species were assigned to one of the following taxonomic groups and associations with dead wood (i.e. saproxylic/non-saproxylic) based on the description in the articles. These where: amphibians, ants, bats, bees and wasps, birds, carabids, epigeal lichens, epigeal mosses, epigeal spiders, epixylic lichens, epixylic mosses, harvestmen, hover flies, land snails, nocturnal moths, non-saproxylic beetles (excluding carabids), reptiles, rodents, saproxylic beetles, scuttle flies, springtails, true bugs, vascular plants, and wood-inhabiting fungi. For the analysis comparing responses of saproxylic and non-saproxylic species groups, we defined saproxylic beetles, wood-inhabiting fungi, and epixylic lichens and mosses as saproxylic and all other species groups as non-saproxylic.

For comparing numbers of species between salvaged and unsalvaged naturally disturbed plots described in the published literature, we used Hedges' d, which accounts for differences in sampling effort across studies and for small sample sizes (Hedges & Olkin 1985). Positive values of Hedges' d indicate higher numbers of species in salvage logged plots, whereas negative values indicate a loss in numbers of species attributed to salvage logging (i.e. higher numbers of species in unsalvaged naturally disturbed plots). Mean absolute effect sizes of $d = 0.2$ indicate a small effect, $d = 0.5$ a moderate effect, and $d = 0.8$ a large effect (Koricheva, Gurevitch & Mengersen 2013).

We used multi-level linear mixed-effects models, provided by the R function 'rma.mv' in the 'metafor' package (Viechtbauer 2010), to test the effect of taxonomic group as categorical predictor and year since disturbance as a numerical covariate on Hedges' d as response variable. Hedge's d values were weighted by the corresponding sampling variance within the statistical model. Furthermore, study site was included as a random effect in the model (i.e. moderator term) to control for unmeasured site specificities and repeated measurements (pseudo-replication) within one study site. This means that multiple data points per study were possible if studies examined multiple taxonomic groups or if studies lasted for more than one year. We subtracted the intercept from the effect sizes (by including '-1' in the model formula) to evaluate if observed Hedges' d differed significantly from zero (for details and model formula see Table S1).

To evaluate the effects of salvage logging on saproxylic versus non-saproxylic groups, we fitted a second model with Hedges' d as response variable. We again included the year after natural disturbance and subsequent logging as a numerical predictor variable and study site as well as taxonomic group as random factors. Furthermore, we added the interaction of dead-wood dependence (i.e. saproxylic / non-saproxylic) with natural disturbance type as predictors to test whether the effect of salvage logging on the number of species in saproxylic and non-saproxylic groups differed within different types of natural disturbances. We implemented a simultaneous inference procedure to compare saproxylic and non-saproxylic species groups within each disturbance type (Hothorn, Bretz & Westfall 2008). This procedure allowed us to test if responses of saproxylic and non-saproxylic taxa vary among fire, wind and insect disturbed forests (for details and model formula see Table S2). Last, we conducted funnel plots by means of the function 'funnel' from the 'metafor' package to assess publication bias (Koricheva et al. 2013; Fig. S1).

Analysis of community composition

Based on the reviewed literature, we compiled original species abundance matrices to quantify changes in community composition induced by salvage logging. Quantifying changes in community composition among large heterogeneous datasets is challenging and requires statistical methods able to deal with issues such as unbalanced sampling effort and which generate a standardized effect size that is comparable among different species groups and survey techniques. Thus, we used permutational multivariate analysis of variance using distance matrices (Legendre & Anderson 1999), performed by means of the function 'adonis' in the package 'vegan' (Oksanen *et al.* 2016). This analysis provides a pseudo F-value, based on 999 permutations, that quantifies the deviance from the null-hypothesis, while simultaneously accounting for imbalanced study designs (McArdle & Anderson 2001). Consequently, large values of F correspond to large changes in community composition induced by salvage logging. This F-value represents the standardized difference between communities in salvage logged and unsalvaged naturally disturbed plots within one species abundance matrix (e.g. differences in bird communities six years after wildfire and salvage logging in Oregon). We rigorously restricted this analysis to those abundance matrices that yielded valid pseudo F-values over the course of permutations; i.e. those matrices which generated less than 99 real permutations were excluded. These restrictions resulted in a total number of 134 matrices, which supplied F-values for the following analysis outlined below.

To test if salvage logging changed community composition in different taxonomic groups, we modelled pseudo F-values in linear mixed models provided by the function 'lmer' in the 'lme4' package assuming a Gaussian error distribution (Bolker *et al.* 2009). We included taxonomic group as categorical predictor and the year since disturbance as a numerical covariate. Furthermore, we included study site as a random effect to control for possible differences among study sites and repeated measurements within one study site. We omitted the intercept from the model formula to determine if F-values differed significantly from zero. Thus, significant changes in community composition of a taxonomic group due to salvage logging were indicated by F-values significantly larger than zero (for details and model formula see Table S3).

As for the analysis of Hedges' d, a second model was fitted to test whether the effects of salvage logging on community composition differed between saproxylic and non-saproxylic species groups in different types of disturbances. Therefore, we included the year after disturbance and the interaction of saproxylic/ non-saproxylic with disturbance type as predictors. Taxonomic group and study site were included as random factors in this model. We implemented a simultaneous inference procedure to compare saproxylic and non-saproxylic species groups within each disturbance type (for details and model formula see Table S4).

Results

Our meta-analysis showed that the effects of salvage logging have been studied primarily for birds, vascular plants and carabids, particularly in burned forests. Studies were conducted primarily in North America and Europe, but lacking in tropical regions (Fig. 1). Furthermore, there was a clear lack of studies investigating saproxylic taxa. Out of 238 compiled data points, 170 covered a period of five years or less after disturbance, with studies addressing the long-term effects of salvage logging being rare (Fig. 2). Only one study (Hutto & Gallo 2006) was available that provided data on the effects of salvage logging for more than 20 years after disturbances (Fig. 2).

Half of individual comparisons produced values of Hedges' d lower than zero, indicating higher numbers of species in non-salvage logged areas than salvage logged areas (Fig. 3). We found significantly lower species numbers of epigeal and epixylic mosses, birds, wood-inhabiting fungi, saproxylic beetles, springtails and epixylic as well as epigeal lichens in salvage logged areas compared to non-salvage logged areas (Fig. 3a). By contrast, numbers of species of land snails, epigeal spiders and carabids were higher in salvage logged areas than in unsalvaged areas (Fig. 3a). Thirteen of 24 taxonomic groups, including vascular plants, exhibited no significant response in numbers of species to salvage logging (Fig. 3a).

Numbers of species of saproxylic taxa significantly decreased compared to non-saproxylic taxa in storm-felled and burned forests (Fig. 4a). The negative effect of salvage logging on number of species increased with time elapsed since disturbance and subsequent salvage logging, although long-term data on salvage logging are scarce.

Salvage logging was associated with significant changes in community composition in seven of 17 taxonomic groups (Fig. 3b). These seven groups were epigeal spiders, carabids, vascular plants, birds, wood-inhabiting fungi, saproxylic beetles, and epixylic lichens (Fig. 3b). Time elapsed since disturbance had no effect on the strength of logging-induced changes to community composition (Table S3). Furthermore, logging-induced changes in community composition were stronger for saproxylic taxa than for non-saproxylic taxa in storm-disturbed forests. However, data availability was scarce in insect-affected forest and lacking in burned forests (Fig. 4b).

Discussion

Our study revealed that salvage logging can result in significant changes in species numbers and/or in altered community composition. Negative effects were particularly strong for taxa that depend on dead wood. By contrast, numbers of species of taxa that are commonly characterized by species-rich assemblages in open habitats, such as carabids and epigeal spiders, responded positively to salvage logging. Despite positive effects of salvage logging on taxa associated with open habitats, strong negative effects on saproxylic groups call for substantial changes in how disturbed forests are routinely managed.

Naturally disturbed forests are characterised by large volumes of dead wood with high structural diversity (Swanson *et al.* 2011). By contrast, salvage logging typically reduces the amount and heterogeneity of dead wood by removing tree trunks (Keyser, Smith & Shepperd 2009; Priewasser *et al.* 2013). Not surprisingly, salvage logging reduced the numbers of species of saproxylic groups (Fig. 2 & 3). However, not only a decreasing dead wood amount but likewise a logging-induced shift in dead wood quality may have additional impacts on saproxylic taxa. Salvage logging not only reduces the amount of large tree trunks, but also alters characteristic conditions, such as decay stages or diameter distributions, of the remaining dead wood (Waldron, Ruel & Gauthier 2013). For instance, branches cut during post-storm logging remain on the ground but are overgrown by ground vegetation. The resulting shift in microclimatic conditions then modifies resource quality, leading to a loss of saproxylic beetles that depend on sun-exposed, dry branches (Thorn *et al.* 2014).

It is important to note that losses of dead-wood dependent species can be present also within taxonomic groups that displayed no response in their overall species numbers (Fig. 3a). For instance, birds (the most studied vertebrate group) were slightly negatively affected by salvage logging (Fig. 3a), despite few species being directly dependent on dead wood. Nevertheless, several forest-dwelling bird species depend on snags, cavities or natural regeneration in post-disturbance forest stands. The removal of such legacies by salvage logging can cause a loss of associated bird species and consequently an overall lower number of bird species in logged areas (Hutto & Gallo 2006; Werner *et al.* 2015). Although the overall number of bird species decreased less strongly than, for instance, the number of saproxylic beetle species (Fig. 3a), bird species that depend on post-disturbance habitat characteristics are often of high conservation interest. For instance, salvage logging after high severity wildfires can lead to lower site occupancies of Northern Spotted Owls (*Strix occidentalis caurina*) on logged than on unlogged sites in Oregon (Clark, Anthony & Andrews 2013).

Our study revealed that salvage logging caused significant changes in community composition for seven species groups (Fig. 3b), with saproxylic species groups being affected most strongly (Fig 4b). Such alterations in community composition might reflect the establishment of open-habitat species or/and a simultaneous loss of forest specialists. For instance, salvage logging can increase the abundance of open-habitat carabid beetles (Koivula & Spence 2006) or promote the establishment of non-forest vegetation (Stuart *et al.* 1993; Van Nieuwstadt, Sheil & Kartawinata 2001). Hence, species groups that are commonly characterized by species-rich assemblages in open habitats, such as carabids or epigeal spiders, can display an overall increase in numbers of species in response to salvage logging (Fig. 3a). Likewise, salvage logging can cause an increase in herb- and grass-feeding moths but a decrease of saproxylic and detritus-feeding moth species (Thorn *et al.* 2015). Such contrasting responses within and between species groups can mask the overall impact of salvage logging on biodiversity in coarse-scale analyses (i.e. Thom & Seidl 2016). Numerous species of high conservation interest, such as the Red-cockaded woodpecker (*Leuconotopicus borealis*), depend on dead wood in burned forests (Conner, Rudolph & Walters 2001). The results of our study therefore indicate that the biodiversity of saproxylic taxa could be enhanced by a modified management of naturally disturbed forests. By contrast, populations of species associated with open habitats, such as the Sharp-tailed Grouse (*Tympanuchus phasianellus*) in North America, may persist or even increase in the larger remaining area subject to unmodified management, i.e. salvage logging (Radeloff, Mladenoff & Boyce 2000).

The two major incentives for salvage logging are to reduce economic losses caused by a natural disturbance and to omit mass reproduction and spread of insect pests that develop in trees killed or weakened by a preceding natural disturbance. For instance, salvage logging of storm-felled Norway spruce (*Picea abies*) decreased new infestations of nearby trees by the European spruce bark beetle (*Ips typographus*) at a landscape scale (Stadelmann *et al.* 2013). Salvage logging is therefore the predominant response to natural disturbances in wood production forests, but pest control is regularly used to justify salvage logging in protected areas. For instance, the Białowieża Forest National Park on the border between Poland and Belarus, which is the last primeval lowland forest in Europe, is currently obliged to salvage logging of areas affected by *I. typographus* on attempt to avoid further infestations (Chylarecki & Selva 2016). Such an approach to disturbed forests neglects that regional factors, such as summer drought, can promote outbreaks of *I. typographus* more strongly than local stand variables (Seidl *et al.* 2015). Furthermore, salvage logged timber is usually of substantially lower economic value than normally harvested timber due to a rapid colonization by wood-inhabiting fungi and to the fact that disturbances affect forests of any age, so that generalised salvage logging operations necessarily include younger stands that otherwise would not be harvested (Leverkus *et al.* 2012). Our results demonstrate that salvage logging has strong and negative effects on many taxonomic groups, particularly those associated with dead wood, and that it is thus not consistent with biodiversity conservation goals. Along with questionable economic outputs and pest reducing effects, we argue that salvage logging should be excluded from protected areas such as national parks.

The incidence of stand-replacing natural disturbances remains spatially and temporally unpredictable (Berry *et al.* 2015), creating inherent uncertainty about appropriate management of naturally disturbed forests. Hence, management plans need to be jointly developed with (and confirmed by) stakeholders, scientists and natural resource managers before the next disturbance occurs (Lindenmayer, Likens & Franklin 2010). Such management plans could, for instance, encompass an a priori identification of salvage logging exclusion zones based on ecological data (e.g. Nappi *et al.* 2011). Forest managers also may target the preservation of structural key attributes in naturally disturbed forests, including snags or tipped uproot plates of windthrown trees (Hutto 2006). Retention of trees during green-tree harvests has become an increasingly common tool around the globe to help conserve forest biodiversity (Gustafsson *et al.* 2012; Mori & Kitagawa 2014; Fedrowitz *et al.* 2014). To obtain some economic return while retaining dead-wood dependent taxa, we recommend a simple expansion of the green-tree retention approach to include naturally disturbed forests.

Retention approaches in naturally disturbed forests could be expected to be less costly than in green-tree harvest due to the lower opportunity cost of not harvesting disturbance-killed trees.

Approximately 70% of the studies we compiled spanned less than five years; studies addressing the long-term effects of salvage logging are rare (Fig. 2). However, dead wood, and particularly snags, are long-lasting key biological legacies, and their loss can have long-lasting effects on biodiversity (Hutto 2006). Hence, future research should target the long-term effects of salvage logging after natural disturbances. There are also taxonomic biases in existing studies investigating the effects of salvage logging after natural disturbances. In particular, saproxylic groups such as wood-inhabiting fungi have been underrepresented in empirical studies despite their high diversity and importance for ecosystem functioning. Future research should therefore target particularly saproxylic species groups. By contrast, other groups have been relatively well studied in one disturbance type (e.g. birds in burned forests), but less in others, and studies were conducted primarily in North America, Europe, and Asia, but lacking in tropical regions (Fig. 1). However, different types of natural disturbances in different parts of the world can act at very different spatial scales and may require different retention approaches (Kulakowski *et al.* 2016). Furthermore, coniferous forests of the Northern Hemisphere - in contrast to tropical forests - are naturally prone to large-scale natural disturbances (Lindenmayer, Burton & Franklin 2008), whereas disturbances in tropical forests mostly have anthropogenic causes associated with long-term land-use change (e.g. fire to open space for livestock grazing and agriculture; Peres, Barlow & Laurance 2006). Nevertheless, natural disturbances such as for example windstorms, affect tropical forests as well as temperate forests, and salvage logging effects on tropical forests should be targeted in future research (e.g. Lawton & Putz 1988).

In conclusion, these data from a wide range of studies demonstrates that salvage logging has a range of effects on species numbers and community composition of various taxonomic groups, with important negative consequences for several groups, especially saproxylic ones. While current policies for enhancing biodiversity and ecosystem services, such as green-tree retention (e.g., Gustafsson et al. 2012), focus mainly on forests subjected to traditional logging operations, such policies are largely absent from naturally disturbed forests. We therefore call for an expansion of the green-tree retention approaches to include naturally disturbed forests by leaving substantial amounts of deadwood on site to reduce the impact of salvage logging on biodiversity.

Authors' contributions

S.T. and J.M initiated the study. S.T. analysed and interpreted the data and wrote the first draft of the paper. The authors named from S.T. to J.M. are listed alphabetically, as they contributed equally in gathering field data, providing corrections to subsequent manuscript drafts and discussing ideas.

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Data accessibility

All data are from previously published articles, see 'Data sources'. Date from these articles can be made available upon reasonable request from original data owners. A list of data sources used in the study are provided in the Data sources section.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1: Funnel plot.

Table S1: Statistical results corresponding to Fig 2a.

Table S2: Statistical results corresponding to Fig 3a.

Table S3: Statistical results corresponding to Fig 2b.

Table S4: Statistical results corresponding to Fig 3b.

References

Berry, L.E., Driscoll, D.A., Stein, J.A., Blanchard, W., Banks, S.C., Bradstock, R.A. & Lindenmayer, D.B. (2015) Identifying the location of fire refuges in wet forest ecosystems. *Ecological Applications*, **25**, 2337–2348.

Blair, D.P., McBurney, L.M., Blanchard, W., Banks, S.C. & Lindenmayer, D.B. (2016) Disturbance gradient shows logging affects plant functional groups more than fire. *Ecological Applications*, **26**, n/a-n/a.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.-S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, **24**, 127–135.

Castro, J., Moreno-Rueda, G. & Hódar, J. (2010) Experimental test of postfire management in pine forests: impact of salvage logging versus partial cutting and nonintervention on bird-species assemblages. *Conservation Biology*, **24**, 810–819.

Choi, C.-Y., Lee, E.-J., Nam, H.-Y., Lee, W.-S. & Lim, J.-H. (2014) Temporal changes in the breeding bird community caused by post-fire treatments after the Samcheok forest fire in Korea. *Landscape and Ecological Engineering*, **10**, 203–214.

Chylarecki, P. & Selva, N. (2016) Ancient forest: spare it from clearance. *Nature*, **530**, 419.

Clark, D.A., Anthony, R.G. & Andrews, L.S. (2013) Relationship between wildfire, salvage logging, and occupancy of nesting territories by northern spotted owls. *The Journal of Wildlife Management*, **77**, 672–688.

Cobb, T.P., Langor, D.W. & Spence, J.R. (2007) Biodiversity and multiple disturbances: boreal forest ground beetle (Coleoptera: Carabidae) responses to wildfire, harvesting, and herbicide. *Canadian Journal of Forest Research*, **37**, 1310–1323.

Cobb, T.P., Morissette, J.L., Jacobs, J.M., Koivula, M.J., Spence, J.R. & Langor, D.W. (2011) Effects of postfire salvage logging on deadwood-associated beetles. *Conservation Biology*, **25**, 94–104.

Conner, R., Rudolph, D.C. & Walters, J.R. (2001) *The Red-Cockated Woodpecker Surviving in a Fire-Maintained Ecosystem*. The University of

Texas Press, Austin.

Fedrowitz, K., Koricheva, J., Baker, S.C., Lindenmayer, D.B., Palik, B., Rosenvald, R., Beese, W., Franklin, J.F., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygeson, A. & Gustafsson, L. (2014) Can retention forestry help conserve biodiversity? A meta-analysis. *Journal of Applied Ecology*, **51**, 1669–1679.

Franklin, J.F., Lindenmayer, D., Macmahon, J.A., Mckee, A., Perry, D.A., Waide, R. & Foster, D. (2000) Threads of continuity: Ecosystem disturbances, biological legacies and ecosystem recovery. *Conservation Biology in Practice*, **1**, 8–16.

González, M.E. & Veblen, T.T. (2007) Wildfire in Araucaria araucana forests and ecological considerations about salvage logging in areas recently burned. *Revista Chilena de Historia Natural*, **80**, 243–253.

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D.B., Lõhmus, A., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-thygeson, A., Volney, W.J.A., Wayne, A. & Franklin, J.F. (2012) Retention forestry to maintain multifunctional forests: a world perspective. *Bioscience*, **62**, 633–645.

Halme, P., Toivanen, T., Honkanen, M., Kotiaho, J.S., Mönkkönen, M. & Timonen, J. (2010) Flawed meta-analysis of biodiversity effects of forest management. *Conservation Biology*, **24**, 1154–1156.

Hedges, L. V. & Olkin, I. (1985) *Statistical Methods for Meta-Analysis.* CA: Academic Press, San Diego.

Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometrical Journal*, **50**, 346–363.

Hutto, R.L. (2006) Toward meaningful snag-management guidelines for postfire salvage logging in North American conifer forests. *Conservation Biology*, **20**, 984–993.

Hutto, R.L. & Gallo, S.M. (2006) The effects of postfire salvage logging on cavity-nesting birds. *Condor*, **108**, 817–831.

Keyser, T.L., Smith, F.W. & Shepperd, W.D. (2009) Short-term impact of post-fire salvage logging on regeneration, hazardous fuel accumulation, and understorey development in ponderosa pine forests of the Black Hills, SD, USA. *International Journal of Wildland Fire*, **18**, 451–458.

Koivula, M. & Spence, J.R. (2006) Effects of post-fire salvage logging on boreal mixed-wood ground beetle assemblages (Coleoptera, Carabidae). *Forest Ecology and Management*, **236**, 102–112.

Koricheva, J., Gurevitch, J. & Mengersen, K. (2013) *Handbook of Meta-Analysis in Ecology and Evolution* (eds J. Koricheva, J. Gurevitch, & K. Mengersen). Princeton University Press, Princeton.

Kulakowski, D., Seidl, R., Holeksa, J., Kuuluvainen, T., Nagel, T.A., Panayotov, M., Svoboda, M., Thorn, S., Vacchiano, G., Whitlock, C., Wohlgemuth, T. & Bebi, P. (2016) A walk on the wild side: Disturbance dynamics and the conservation and management of European mountain forest ecosystems. *Forest Ecology and Management*, **388**, 120–131.

Kurz, W., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T. & Safranyik, L. (2008) Mountain pine beetle and forest carbon feedback to climate change. *Nature*, **452**, 987–990.

Lain, E.J., Haney, A., Burris, J.M. & Burton, J. (2008) Response of vegetation and birds to severe wind disturbance and salvage logging in a southern boreal forest. *Forest Ecology and Management*, **256**, 863–871.

Lawton, R. & Putz, F.E. (1988) Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. *Ecology*, **69**, 764–777.

Legendre, P. & Anderson, M.J. (1999) Distance-based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs*, **69**, 1–24.

Leverkus, A.B., Puerta-Pinero, C., Álvarez, J.R.G., Navarro, J. & Castro, J. (2012) Post-fire salvage logging increases restoration costs in a Mediterranean mountain ecosystem. *New Forests*, **43**, 601–613.

Lindenmayer, D., Burton, P.J. & Franklin, J.F. (2008) *Salvage Logging and Its*

Ecological Consequences. Island Press, Washington.

Lindenmayer, D.B., Foster, D.R., Franklin, J.F., Hunter, M.L., Noss, R.F., Schmiegelow, F.A. & Perry, D. (2004) Salvage harvesting policies after natural disturbance. *Science*, **303**, 1303.

Lindenmayer, D.B., Likens, G.E. & Franklin, J.F. (2010) Rapid responses to facilitate ecological discoveries from major disturbances. *Frontiers in Ecology and the Environment*, **8**, 527–532.

Lindenmayer, D.B. & Noss, R.F. (2006) Salvage logging, ecosystem processes, and biodiversity conservation. *Conservation Biology*, **20**, 946–948.

Lindenmayer, D., Thorn, S. & Banks, S. (2017) Please do not disturb ecosystems further. *Nature Ecology and Evolution*, **1**, 1–8.

Macdonald, S.E. (2007) Effects of partial post-fire salvage harvesting on vegetation communities in the boreal mixedwood forest region of northeastern Alberta, Canada. *Forest Ecology and Management*, **239**, 21–31.

McArdle, B.H. & Anderson, M.J. (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology*, **82**, 290–297.

McIver, J.D. & Starr, L. (2000) *Environmental Effects of Postfire Logging: Literatur Review and Annotated Bibliography*. U.S. Department of

Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Mori, A.S. & Kitagawa, R. (2014) Retention forestry as a major paradigm for safeguarding forest biodiversity in productive landscapes: A global meta-analysis. *Biological Conservation*, **175**, 65–73.

Nappi, A. & Drapeau, P. (2009) Reproductive success of the black-backed woodpecker (Picoides arcticus) in burned boreal forests: Are burns source habitats? *Biological Conservation*, **142**, 1381–1391.

Nappi, A., Stéphane, D., Bujold, F., Chabot, M., Dumont, M.-C., Duval, J., Drapeau, P., Gauthier, S., Brais, S., Peltier, J. & Bergeron, I. (2011) *Harvesting in Burned Forests - Issues and Orientations for Ecosystem-Based Management*. Ministère des Ressources naturelles et de la Faune, Direction de l'environnement et de la protection des forêts, Québec.

Van Nieuwstadt, M.G.L., Sheil, D. & Kartawinata, K. (2001) The ecological consequences of logging in the burned forests of East Kalimantan , Indonesia. *Conservation Biology*, **15**, 1183–1186.

Nikiforuk, A. (2011) *Empire of the Beetle: How Human Folly and a Tiny Bug Are Killing North America's Great Forests*, First Edit. Greystone Books.

Norvez, O., Hébert, C., Bélanger, L., Hebert, C. & Belanger, L. (2013) Impact of salvage logging on stand structure and beetle diversity in boreal balsam fir forest, 20 years after a spruce budworm outbreak. *Forest Ecology and Management*, **302**, 122–132.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2016) vegan: Community Ecology Package, https://cran.r-project.org/package=vegan

Peres, C.A., Barlow, J. & Laurance, W.F. (2006) Detecting anthropogenic disturbance in tropical forests. *Trends in Ecology and Evolution*, **21**, 227–229.

Phillips, I.D., Cobb, T.P., Spence, J.R. & Brigham, R.M. (2006) Salvage logging, edge effects, and carabid beetles: Connections to conservation and sustainable forest management. *Environmental Entomology*, **35**, 950–957.

Priewasser, K., Brang, P., Bachofen, H., Bugmann, H. & Wohlgemuth, T. (2013) Impacts of salvage-logging on the status of deadwood after windthrow in Swiss forests. *European Journal of Forest Research*, **132**, 231–240.

Pullin, A.S. & Stewart, G.B. (2006) Guidelines for systematic review in conservation and environmental management. *Conservation Biology*, **20**, 1647–1656.

Radeloff, V.C., Mladenoff, D.J. & Boyce, M.S. (2000) Effects of interacting disturbances on landscape patterns: Budworm defoliation and salvage logging. *Ecological Applications*, **10**, 233–247.

Ramage, B.S., Sheil, D., Salim, H.M.W., Fletcher, C., Mustafa, N.Z.A., Luruthusamay, J.C., Harrison, R.D., Butod, E., Dzulkiply, A.D., Kassim, A.R. & Potts, M.D. (2013) Pseudoreplication in Tropical Forests and the Resulting Effects on Biodiversity Conservation. *Conservation Biology*, **27**, 364–372.

Saab, V., Russell, R.E. & Dudley, J.G. (2009) Nest-site selection by cavity-nesting birds in relation to postfire salvage logging. *Forest Ecology and Management*, **257**, 151–159.

Schmiegelow, F.K.A., Stepnisky, D.P., Stambaugh, C.A. & Koivula, M. (2006) Reconciling salvage logging of boreal forests with a natural-disturbance management model. *Conservation Biology*, **20**, 971–983.

Seidl, R., Müller, J., Hothorn, T., Bässler, C., Heurich, M. & Kautz, M. (2015) Small beetle, large-scale drivers: How regional and landscape factors affect outbreaks of the European spruce bark beetle. *Journal of Applied Ecology*, **53**, 530–540.

Seidl, R., Schelhaas, M.-J., Rammer, W. & Verkerk, P.J. (2014) Increasing forest disturbances in Europe and their impact on carbon storage. *Nature Clim. Change*, **4**, 806–810.

Stadelmann, G., Bugmann, H., Meier, F., Wermelinger, B. & Bigler, C. (2013) Effects of salvage logging and sanitation felling on bark beetle (Ips typographus L.) infestations. *Forest Ecology and Management*, **305**, 273–281.

Stokstad, E. (2006) Salvage logging research continues to generate sparks. *Science*, **311**, 761.

Stuart, J.D., Grifantini, M.C., Fox III, L. & Fox, L. (1993) Early successional pathways following wildfire and subsequent silvicultural treatment in Douglas-fir/hardwood forests, NW California. *Forest Science*, **39**, 561–572.

Swanson, M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L., Lindenmayer, D.B. & Swanson, F.J. (2011) The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment*, **9**, 117–125.

Thom, D. & Seidl, R. (2016) Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biological Reviews*, **91**, 760–781.

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

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

Thorn, S., Bässler, C., Svoboda, M. & Müller, J. (2016b) Effects of natural disturbances and salvage logging on biodiversity - Lessons from the Bohemian Forest. *Forest Ecology and Management*, **388**, 113–119.

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

Viechtbauer, W. (2010) Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, **36**, 1–48.

Waldron, K., Ruel, J. & Gauthier, S. (2013) Forest structural attributes after windthrow and consequences of salvage logging. *Forest Ecology and Management*, **289**, 28–37.

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

Zmihorski, M. (2010) The effect of windthrow and its management on breeding bird communities in a managed forest. *Biodiversity and Conservation*, **19**, 1871–1882.

Zmihorski, M. & Durska, E. (2011) The effect of contrasting management types on two distinct taxonomic groups in a large-scaled windthrow. *European Journal of Forest Research*, **130**, 589–600.

Data sources

Barnouin, T. (2005) *Évaluation de L ' Importance Des Forêts Affectées Par La Tordeuse Des Bourgeons de L â ™ Épinette , Choristoneura Fumiferana (Clem .), Dans Le Maintien de La Diversité Des Coléoptères Saproxyliques*. Université Laval Quebec.

Blair, D.P., McBurney, L.M., Blanchard, W., Banks, S.C. & Lindenmayer, D.B. (2016) Disturbance gradient shows logging affects plant functional groups more than fire. *Ecological Applications*, **26**, n/a-n/a.

Boucher, D., Gauthier, S., Noël, J., Greene, D.F. & Bergeron, Y. (2014) Salvage logging affects early post-fire tree composition in Canadian boreal forest. *Forest Ecology and Management*, **325**, 118–127.

Bradbury, S.M. (2006) Response of the post-fire bryophyte community to salvage logging in boreal mixedwood forests of northeastern Alberta, Canada. *Forest Ecology and Management*, **234**, 313–

322.

Cahall, R.E. & Hayes, J.P. (2009) Influences of postfire salvage logging on forest birds in the Eastern Cascades, Oregon, USA. *Forest Ecology and Management*, **257**, 1119–1128.

Castro, J., Moreno-Rueda, G. & Hódar, J. (2010) Experimental test of postfire management in pine forests: impact of salvage logging versus partial cutting and nonintervention on bird-species assemblages. *Conservation Biology*, **24**, 810–819.

Choi, C. (2007) Effects of Postfire Logging on bird populations and communities in burned forests. *Journal of the Korean forest society*, **96**, 115–123.

Choi, C.-Y., Lee, E.-J., Nam, H.-Y., Lee, W.-S. & Lim, J.-H. (2014) Temporal changes in the breeding bird community caused by post-fire treatments after the Samcheok forest fire in Korea. *Landscape and Ecological Engineering*, **10**, 203–214.

Cobb, T.P., Langor, D.W. & Spence, J.R. (2007) Biodiversity and multiple disturbances: boreal forest ground beetle (Coleoptera: Carabidae) responses to wildfire, harvesting, and herbicide. *Canadian Journal of Forest Research*, **37**, 1310–1323.

Cobb, T.P., Morissette, J.L., Jacobs, J.M., Koivula, M.J., Spence, J.R. & Langor, D.W. (2011) Effects of postfire salvage logging on deadwood-associated beetles. *Conservation Biology*, **25**, 94–104.

Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B. & Law, B.E. (2009) Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the Klamath–Siskiyou Mountains. *Canadian Journal of Forest Research*, **39**, 823–838.

Donato, D.C., Fontaine, J.B., Kauffman, J.B., Robinson, D. & Law, B.E. (2013) Fuel mass and forest structure following stand-replacement fire and post-fire logging in a mixed-evergreen forest. *International Journal of Wildland Fire*, **22**, 652–666.

Duelli, P., Obrist, M.K. & Wermelinger, B. (2002) Windthrow-induced changes in faunistic biodiversity in alpine spruce forests. *Forest Snow and Landscape Research*, **131**, 117–131.

Durska, E. (2013) Effects of disturbances on scuttle flies (Diptera: Phoridae) in Pine Forests. *Biodiversity and Conservation*, **22**, 1991–2021.

Fontaine, J.B. (2007) *Influences of High Severity Fire and Postfire Logging on Avian and Small Mammal Communities of the Siskiyou Mountains, Oregon, USA*. Oregon State University.

Fontaine, J.B., Donato, D.C., Robinson, W.D., Law, B.E. & Kauffman, J.B. (2009) Bird communities following high-severity fire: Response to single and repeat fires in a mixed-evergreen forest, Oregon, USA. *Forest Ecology and Management*, **257**, 1496–1504.

Hebert et al. unpub., for methods and study design see: Norvez *et al.* (2013)

Hutto, R.L. & Gallo, S.M. (2006) The effects of postfire salvage logging on cavity-nesting birds. *Condor*, **108**, 817–831.

Jeffrey, O. (2013) *Effets Des Coupes de Récupération Sur Les Successions Naturelles de Coléoptères Saproxyliques Le Long D'une Chronoséquence de 15 Ans Après Feu En Forêt Boréale Commerciale*. Univer.

Jonasova, M. & Prach, K. (2008) The influence of bark beetles outbreak vs. salvage logging on ground layer vegetation in Central European mountain spruce forests. *Biological Conservation*, **141**, 1525–1535.

Koivula, M. & Spence, J.R. (2006) Effects of post-fire salvage logging on boreal mixed-wood ground beetle assemblages (Coleoptera, Carabidae). *Forest Ecology and Management*, **236**, 102–112.

Kurulok, S.E. & Macdonald, S.E. (2007) Impacts of postfire salvage logging on understory plant communities of the boreal mixedwood forest 2 and 34 years after disturbance. *Canadian Journal of Forest Research*, **37**, 2637–2651.

Lee, E.L.W., Hun, S., Rhim, S.-J., Lee, W.-S. & Son, S.H. (2010) Differences in bird communities in postfire silvicultural practices stands within pine forest of South Korea. *Landscape and Ecological Engineering*, **7**, 137–143.

Lee, E., Lee, W. & Rhim, S.-J. (2008) Characteristics of small rodent populations in post-fire silvicultural management stands within pine forest. *Forest Ecology and Management*, **255**, 1418–1422.

Lee, E.-J., Rhim, S., Son, S. & Lee, W. (2012) Differences in small-mammal and stand structures between unburned and burned pine stands subjected to two different post-fire silvicultural management practices. *Annales Zoologici Fennici*, **2450**, 129–138.

Leverkus, A.B., Lorite, J., Navarro, F.B., Sánchez-Cañete, E.P. & Castro, J. (2014) Post-fire salvage logging alters species composition and reduces cover, richness, and diversity in Mediterranean plant communities. *Journal of environmental management*, **133**, 323–31.

Liepold K. (2004) *Vergleichende Untersuchungen Zur Faunistischen Und Genetischen Diversität von Käferzönosen in Genutzten Und Ungenutzten Bergmischwäldern Des Bayerischen Waldes*. TUM München.

Mehr, M., Brandl, R., Kneib, T. & Müller, J. (2012) The effect of bark beetle infestation and salvage logging on bat activity in a national park. *Biodiversity and Conservation*, **21**, 2775–2786.

Norvez, O., Hébert, C., Bélanger, L., Hebert, C. & Belanger, L. (2013) Impact of salvage logging on stand structure and beetle diversity in boreal balsam fir forest, 20 years after a spruce budworm outbreak. *Forest Ecology and Management*, **302**, 122–132.

Park, C. (2012) *Differences in Characteristics of Amphibian and Reptile Communities due to Different Forest Environment at Forest Fired Area in Samcheok, Gangwon Province*. Seoul National University.

Peterson, C.J. & Leach, A.D. (2008) Salvage logging after windthrow alters microsite diversity, abundance and environment, but not vegetation. *Forestry*, **81**, 361–376.

Rost, J., Clavero, M., Brotons, L. & Pons, P. (2012) The effect of postfire salvage logging on bird communities in Mediterranean pine forests: the benefits for declining species. *Journal of Applied*

Ecology, **49**, 644–651.

Rumbaitis, C.M. & Rumbaitis del Rio, C.M. (2006) Changes in understory composition following catastrophic windthrow and salvage logging in a subalpine forest ecosystem. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **36**, 2943–2954.

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

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

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

Waldron, K., Ruel, J.-C., Gauthier, S., De Grandpré, L. & Peterson, C.J. (2014) Effects of post-windthrow salvage logging on microsites, plant composition and regeneration ed J. Ewald. *Applied Vegetation Science*, **17**, 323–337.

Wermelinger, B., Moretti, M., Duelli, P., Lachat, T., Pezzatti, G.B. & Obrist, M.K. (2017) Impact of windthrow and salvage-logging on taxonomic and functional diversity of forest arthropods. *Forest Ecology and Management*, **391**, 9–18.

Winter, M.-B., Ammer, C., Baier, R., Donato, D.C., Seibold, S. & Müller, J. (2015) Multi-taxon alpha diversity following bark beetle disturbance : Evaluating multi-decade persistence of a diverse early-seral phase. *Forest Ecology and Management*, **338**, 32–45.

Zmihorski, M. (2010) The effect of windthrow and its management on breeding bird communities in a managed forest. *Biodiversity and Conservation*, **19**, 1871–1882.

Figures and figure legends

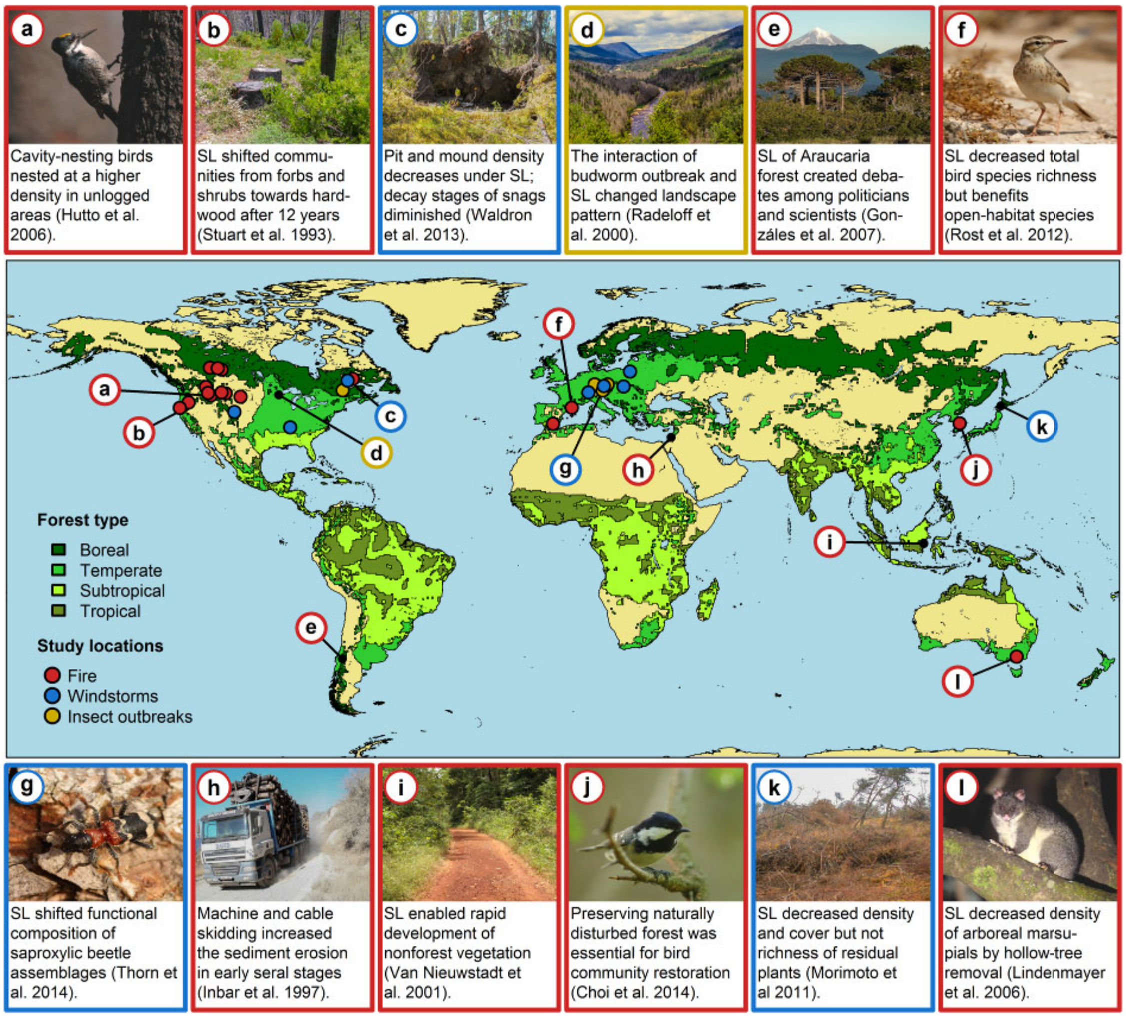

Figure 1: Salvage logging (SL) is commonly applied after wildfires, windstorms or insect-outbreaks, and leads to changes in habitats and community composition in various forest ecosystems around the world (as highlighted by the studies illustrated in panels a-l). Study locations (coloured circles) represent study sites that contributed data to our meta-analysis. Photographs by authors.

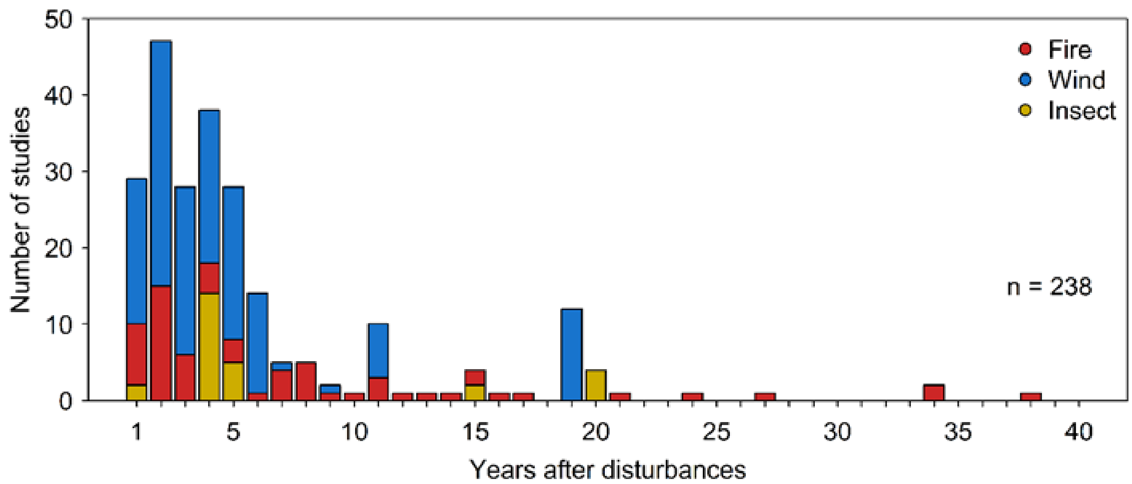

Figure 2: Distribution of studies investigating the effects of salvage logging on biodiversity after wildfire, windstorms and insect-outbreaks according to the years after disturbance.

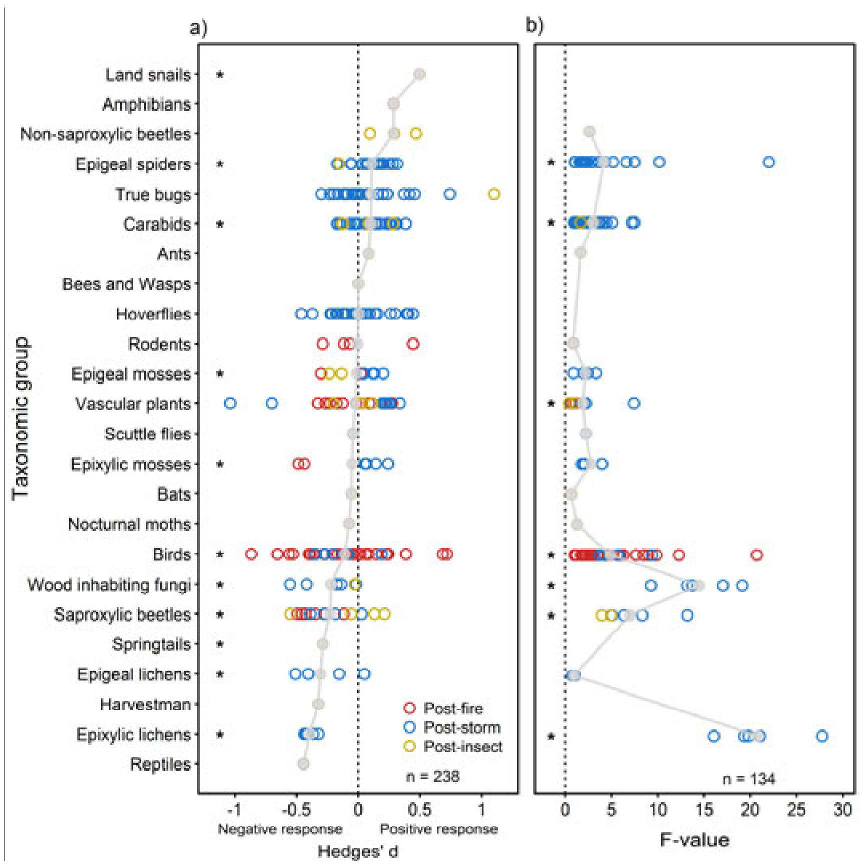

Figure 3: a) Estimated response of Hedges' d based on 238 individual comparisons of species numbers in salvage logged and unsalvaged forests affected by natural disturbances. Higher species numbers in salvage logged areas correspond to positive Hedges' d, whereas negative

values indicate lower species numbers in salvage logged areas. b) Pseudo F-values of permutational multivariate analysis of variance based on 134 individual species abundance matrices. Larger pseudo F-values correspond to larger changes in community composition induced by salvage logging. Asterisks indicate significant responses (see Table S1 and S2 for statistical details). For illustrative purposes, grey dots (and the grey line joining them for emphasis) represent the mean effect size in each taxonomic group.

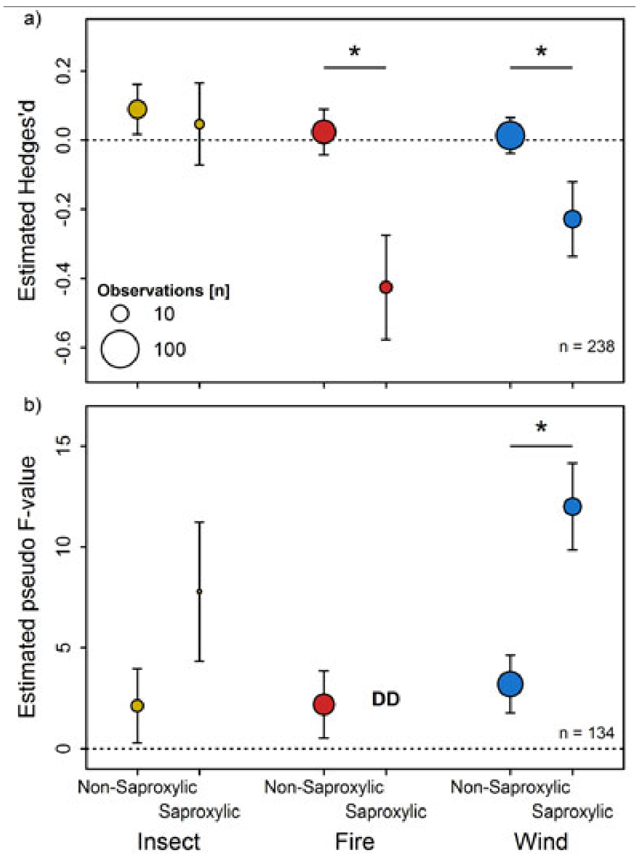

Figure 4: a) Estimated response and corresponding standard error of saproxylic and non-saproxylic taxa to salvage logging based on 238 individual comparisons (based on Hedges' d) of numbers of species in burned, storm- and insect-affected forests. Negative estimates correspond to a decrease in numbers of species by salvage logging (Table S3). b) Estimated response and corresponding standard error in community composition of saproxylic and non-saproxylic taxa based on pseudo F-values of permutational multivariate analysis of variance retained from 134 individual species abundance matrices. Increasing F-values correspond to

larger changes in community composition induced by salvage logging (Table S4). Note, insufficient data (DD) were available for saproxylic taxa in burned forests. Asterisks above dots indicate significant differences in the responses between saproxylic and non-saproxylic taxa within each disturbance type. Number of underlying data points is indicated by the size of the circles, with 10 and 100 size shown for reference.