



Salvage Logging Strongly Affects Woodpecker Abundance and Reproduction: a Meta-analysis

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Abstract

Purpose of Review Wildfires, wind storms, and pest outbreaks are the main large-scale disturbances of temperate and boreal forests, which often generate large amounts of deadwood in the landscape. Salvage and sanitation loggings (hereafter salvage logging) are usually practiced following such disturbance events and the generated deadwood is then extracted from the forest. Those practices affect a broad array of species, including fungi, lichens, invertebrates, and vertebrates that make use of deadwood either as habitat, food resource, foraging substrate, or as shelter. Woodpeckers, being a key group of forest birds dependent on deadwood, can be affected by salvage logging in two ways: (1) a reduction in the availability of food (i.e. removal of deadwood along with the saproxylic and predatory invertebrates that usually colonize dead or dying trees following forest disturbances) and (2) a decrease in potential nest sites due to the removal of dead trees. Therefore, we assessed the global effects of salvage logging on woodpecker abundance and reproduction by conducting a meta-analysis of published and unpublished data. We focused on comparing woodpeckers' responses to forest disturbance in salvage-logged and unlogged sites. We considered different types of responses found in the literature, including abundance, occurrence, nest density, and breeding success. When analyzing the responses of woodpeckers, we also accounted for the potential effects of tree density, time since logging, elevation, latitude, and the continent.

Recent Findings We found that both numbers and reproduction of woodpeckers were affected by salvage logging following a disturbance event. Apart from salvage logging, woodpecker responses were not significantly related to any other variables. This highlights that salvage logging can pose a substantial threat to woodpecker assemblages as well as secondary cavity-users dependent on them.

Summary Salvage logging and related practices that affect deadwood availability should be carefully planned and preferably avoided entirely in areas important for woodpecker conservation. In managed forests, deadwood should be retained in sufficient quantities to avoid detrimental impacts on woodpeckers and on forest biodiversity in general.

Keywords Biodiversity loss · Birds · Disturbance ecology · Forest management · Holarctic forests · Sanitary felling

Introduction

Wildfires, wind storms, and pest outbreaks are the main disturbances of temperate and boreal forests [1–3]. Such disturbances can generate large amounts of deadwood across a large spatial extent [4, 5]. As a key resource for many species, deadwood is one of the main drivers of

deadwood-dependent species occurrence and diversity [6, 7]. In temperate and boreal forests, the supply of standing and lying deadwood is usually not constant over time and it is heavily affected by forest management [8–11]. Indeed, management for timber production should be carefully planned to preserve the supply of deadwood and to avoid detrimental effects on biodiversity [12, 13, 14]. Nonetheless, forest management practices that reduce deadwood availability, such as salvage logging, are still widely applied in spite of their threat to biodiversity [15]. Salvage logging is practiced when disturbance events generate damaged or dying trees and deadwood, which are extracted from the forest for timber production to prevent or reduce economic

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losses. A particular case of salvage logging is sanitary logging which is compulsory in many countries and is aimed at removing pest-infested trees to prevent the spread of pest outbreaks and to limit tree damage. These practices clearly reduce the amount of deadwood in the forest [16] and may disrupt the deadwood supply for many species. A large body of research has shown the negative effects of salvage logging on numerous species including birds and other vertebrates, various invertebrates, lichens and fungi [17••, 18]. One of the major consequences is that biological communities in salvage-logged forests differ from those in unmanaged forests, in terms of species, functional groups, and evolutionary lineages [19••, 20, 21].

Among the first species to experience detrimental effects following salvage logging are those strictly dependent on deadwood for multiple aspects of their ecology, such as woodpeckers. Dead and decaying wood are fundamental for both nesting and foraging activities of woodpeckers [22•, 23–27]. Some species, for instance, strongly prefer dead over live trees for nesting [28], thus preferring recently disturbed forests [29]. Although deadwood in general is the main feeding substrate of many woodpecker species [30–32], standing deadwood is fundamental for providing nest sites [6, 33]. By providing microhabitats and cavities often exploited by other birds, mammals, and invertebrates, woodpeckers fulfil key functions in forests and their presence affects biological communities [34–38, 39••]. Hence, the occurrence of many species in forest communities depends on the availability of deadwood and the provisioning of cavities by woodpeckers [40, 41].

Despite the importance of woodpeckers for forest communities, their role does not seem to be appropriately recognized in forest management plans. Salvage logging is still intensively practiced, even in protected areas [15, 42•], without retaining enough deadwood to maintain biodiversity [43]. This situation persists even though the negative effects of this practice for many woodpecker species are broadly recognized and can include reductions in occurrence and abundance [19••, 44] and in nest survival [45]. However, some studies detected no negative population or nest survival responses of woodpeckers to salvage logging [46, 47]. Therefore, these effects probably vary depending on the woodpecker species and the specific type of forest disturbances. In order to clarify the effects of salvage logging on entire woodpecker assemblages and on their responses to post-disturbance forest conditions, we conducted a meta-analysis of existing research. In contrast to previous meta-analyses that have assessed effects on multiple higher-level taxa [17••, 48, 49], we carried out an in-depth analysis specifically on woodpeckers with the following objectives:

1. To quantify the overall response of woodpecker assemblages to disturbances (i.e. fire, wind storms, and/or

insect outbreaks) in salvage-logged and unlogged disturbed forests

2. To evaluate if abundance or reproduction of woodpeckers is additionally compromised by salvage logging
3. To understand the responses in relation to environmental covariates including elevation, latitude, tree density, and the number of years since salvage logging occurred

We summarize knowledge that describes and quantifies the response of woodpecker assemblages to salvage logging in disturbed forests and provide suggestions for management.

Methods

Literature Search

We used a broad definition of ‘salvage logging’, including both typical salvage logging and sanitary logging. Our literature search (see below) also considered the synonyms ‘salvage felling’ and ‘sanitation felling’ in the search string. Most of the literature refers to ‘salvage logging’ (or felling), whereas ‘sanitary logging’ (or felling) is mentioned by far fewer studies. We searched the Web of Science (WoS) database on October 27, 2021, and complemented our search with further articles obtained by examining the literature cited in the articles retrieved by the main WoS search results. The WoS database was searched using the following search strings: (1) TS = (woodpecker* AND salvage* AND logging*); (2) TS = (bird* AND salvage* AND logging*); and (3) TS = (woodpecker* AND ((salvage* AND logging*) OR disturbance)). We then merged the 3 search strings using the operator ‘OR’ to obtain the final article list. In addition, we also searched the Swiss Wildlife Information Service database (<https://www.swisonline.ch/en/home>) for literature in German on October 22, 2021, with the keywords ‘Picidae UND Scolytinae’ (Picidae AND Scolytinae), ‘Picidae UND Feuer’ (Picidae AND fire), ‘Picidae UND Waldbau’ (Picidae AND forestry (or silviculture)), and ‘Picidae UND Wald’ (Picidae AND forest) (please note that this database has a more limited set of potential keywords that can be searched). The search returned 233 articles in total, including both peer-reviewed and grey literature (e.g. technical reports or master/Ph.D. theses). Furthermore, we collected unpublished datasets from several sources (Table 1). Articles that did not report explicit results about woodpeckers or that did not address explicitly the effect of salvage logging were excluded. These concerned, for instance, articles which dealt with the effects of salvage logging on birds from a forecast modelling perspective [18, 50], did not report explicitly on woodpecker responses to salvage logging [51, 52], or focused more on the effects of natural disturbance events

Table 1 Description of the unpublished datasets retrieved and included in this study. Each dataset provided abundance responses

Location	Disturbance	Forest type	Most recent data-year	No. of years	No. of plots	Reference
Sweden	Fire	Scots pine <i>Pinus sylvestris</i> (53%), Norway spruce <i>Picea abies</i> (18%), mixed coniferous (22%), deciduous (7%)	2020	6	110	Mikusiński unpublished data; early results included in [55]
Germany	Wind	European beech <i>Fagus sylvatica</i>	2021	3	18	Thorn unpublished data
Slovakia	Wind	Norway spruce <i>Picea abies</i> (88%), mixed coniferous (10%), mixed (2%)	2020	3	20	Krištín unpublished data; early results included in [56]
Poland	Wind	Scots pine <i>Pinus sylvestris</i> (81%), Norway spruce <i>Picea abies</i> (11%), deciduous (8%)	2021	7	144	Żmihorski unpublished data

rather than on the effects of salvage logging on woodpeckers [53, 54].

We divided the studies according to the natural disturbance events into fire, windthrow, or bark beetle outbreaks. We analyzed the responses of woodpeckers at sites that were salvage-logged following natural disturbance, and considered control sites those affected by natural disturbance but not salvage-logged. We included data from both studies that reported single species or aggregated results for the woodpecker assemblage, whereby we excluded the wryneck *Jynx torquilla* as it does not excavate its own cavities.

Meta-analysis

Data about woodpecker responses were heterogeneous among datasets, including metrics describing numerical responses such as abundance or probability of occurrence, and metrics describing functional responses such as reproductive success. Traditional meta-analysis requires homogeneous metrics to derive effect size measures such as the standardized mean difference [57, 58]. To overcome this limitation, we maximized data integration by opting for a more flexible approach that allowed us to model the different response metrics of woodpeckers included in each dataset [59]. We considered two main types of woodpecker responses to forest disturbance, based on the potential use by woodpeckers of the deadwood resource created by the disturbance event: numerical responses (including metrics such as abundance and density of individuals), assumed as a response to the increase in deadwood-dependent prey items (bark beetles and wood-boring insects); and functional responses (including metrics such as number of nests, nest density, and reproductive success), assumed as a response to the increase in potential nest site substrates. From each dataset, we extracted the mean value reported for each given metric with standard deviation for every ‘treatment-year’, i.e. salvage logging following natural disturbance *versus* no salvage logging following natural disturbance. Most of

the woodpecker species included in the datasets occurred with < 30 records, except for those typical of disturbed forests, such as the black-backed woodpecker *Picoides arcticus*. Moreover, our aim was to measure the global effect of salvage logging on the entire woodpecker assemblage, and therefore, we summed the species mean responses and averaged the species response variances. For articles that presented data and results in visual formats, we used Web-PlotDigitizer 4.5 [60] to extract data. In order to obtain comparable response measures, independent of the response metric and type, we scaled the means and standard deviations of the woodpecker responses within each dataset. Responses were scaled by subtracting from them the individual dataset mean response and dividing the resulting quantity by the dataset standard deviation. Standard deviations were scaled by averaging their variances. We also extracted additional variables associated with each woodpecker dataset when available, including tree density, the number of years after logging, the mean elevation of the study site, latitude, and the continent as a broad geographic location.

We modelled woodpeckers’ responses to forest disturbance in salvage-logged and unlogged forests with a Bayesian hierarchical linear mixed-effect model [59]. We assumed that the unbiased response of the woodpecker assemblage to disturbance, covering all response metrics and types, differs between salvage-logged and unlogged sites. Our aim was to estimate such differences by modelling that difference as an additive component of the woodpecker response in salvage-logged forests. For each salvage-logged site, we considered the sub-model:

$$y_i \sim \text{Normal}\left(Y_i, \sigma_y^2\right) \quad (1)$$

where y_i is the woodpeckers’ observed mean response to disturbance at the site i , which is assumed to follow a normal distribution centred around the latent mean Y_i , and σ_y^2 is the observed variance of y_i . The variable Y_i was also assumed to follow a normal distribution:

$$Y_i \sim \text{Normal}(\mu_i, \sigma_y^2) \quad (2)$$

where μ_i represents the latent unbiased response of the woodpecker assemblage to disturbance. Variability between studies was modelled as a random effect. Therefore, if we consider the random effect γ_{ki} of the k^{th} dataset at site i , and the salvage logging effect θ , we can describe our model for salvage-logged sites as:

$$\log(\mu_i) = \theta + y_{ki} + \text{cov}_i \quad (3)$$

where ‘cov’ indicates a generic variable included as fixed effect. Simultaneously, we modelled the response in control sites j as the sub-model:

$$x_j \sim \text{Normal}(X_j, \sigma_x^2) \quad (4)$$

$$X_j \sim \text{Normal}(v_j, \sigma_x^2) \quad (5)$$

$$\log(v_j) = y_{kj} + \text{cov}_j \quad (6)$$

Considering that the random effects γ_{ki} and γ_{kj} were drawn from the same normal distribution (as they identify the same dataset), the main difference between the two models is the presence of the salvage logging effect θ . The parameters μ_i and ν_j are the unbiased response of woodpeckers to disturbance at each salvage-logged and unlogged site-year, respectively. The parameters μ_i and ν_j represent the standardized responses, independent of the metric or type of response (e.g. abundance or nest success) and can range from 0 to ∞ . The parameter θ indicates a significant effect of salvage logging on woodpeckers’ responses, if it is significantly different from 0.

In addition to the basic random-effect model, we included several variables as covariates of the fixed effects in the model. We tested whether woodpeckers’ responses differed according to the response types (i.e. numerical and functional) by modelling the response type as a binary covariate where 0 = numerical and 1 = functional. We also tested the effect of the continent (North America vs Europe) as a binary covariate. Continuous covariates, instead, comprised tree density (n/ha), elevation (m a.s.l.), latitude, and the number of years since salvage logging occurred, and were scaled prior to the analysis. We did not consider other potential covariates, such as natural disturbance type or the proportion of salvage logged wood, because either the variability in the response was too low or the number of datasets reporting the variable was too small. The variable ‘tree density’ was available for a limited number of datasets for 58 sites (41 salvage logged and 17 unlogged), whereas the full dataset included 141 sites (89 salvage logged and 52 unlogged). Hence, we performed a separate model selection for models with and

without tree density. The two sets of models included 32 models each. The first model set included the null model (i.e. the model without fixed effect) for comparison. Model selection was performed using the Watanabe-AIC (WAIC), which measures the fitness of a model, with lower values indicating a better fit [61]. As for the AIC [62], models scoring WAIC close to the lowest scoring model are considered similarly supported [63]. We considered that a Bayesian credible estimate (equivalent to ‘significant’ in frequentist inference) would be drawn from a posterior distribution that did not cross 0 for $\geq 95\%$ of the posterior samples, meaning that we used the f value (a mirror of the p value), which ranges from 0 to 1, and indicates the overlap of a parameter estimate with 0. We employed the Bayesian R^2 to measure the proportion of explained variance of the two sub-models [64]. We used uninformative priors for modelling our parameters: for response variables and random effects, we used $\text{Normal}[\text{mean} = 0, \text{tau} = 1/\sqrt{\text{Uniform}(0, 10)}]$; and for fixed effects, $\text{Normal}(0, \text{sd} = 4)$. We ran one chain of 220,000 iterations, of which the first 20,000 were discarded, and the remaining iterations were thinned by 10. The convergence of chains was visually assessed and the null model chains are provided in the supplementary information (Fig. S1, S2). We conducted the meta-analysis using Bayesian hierarchical models [59], built with the package ‘nimble’ (model code available in the supplementary information) [65, 66] in R 4.1.0 [67].

Results

Literature Search

The meta-analysis made use of 25 datasets from the period 1982–2020, of which 21 were retrieved from published articles obtained after screening the literature search results. Four were added from unpublished datasets. Eight datasets investigated woodpecker functional responses, while the remaining focused on numerical responses. Studies were carried out in North America and Europe (Fig. 1). No article from other continents where salvage logging is practiced could be included, although the literature search before the screening returned some articles from Asia (e.g. [68]). The woodpecker assemblages in the retrieved datasets included twelve out of 23 woodpecker species from North American assemblages, and seven out of ten species from European assemblages (Table 2). Five datasets included data from boreal forests where tree species composition was reported as dominated by coniferous species or mixed conifer-broadleaf (Fig. 1). The remaining datasets included only conifer-dominated forests and one broadleaf-dominated forest. The main natural disturbance investigated was fire, whereas windthrow was included in six datasets and bark beetle

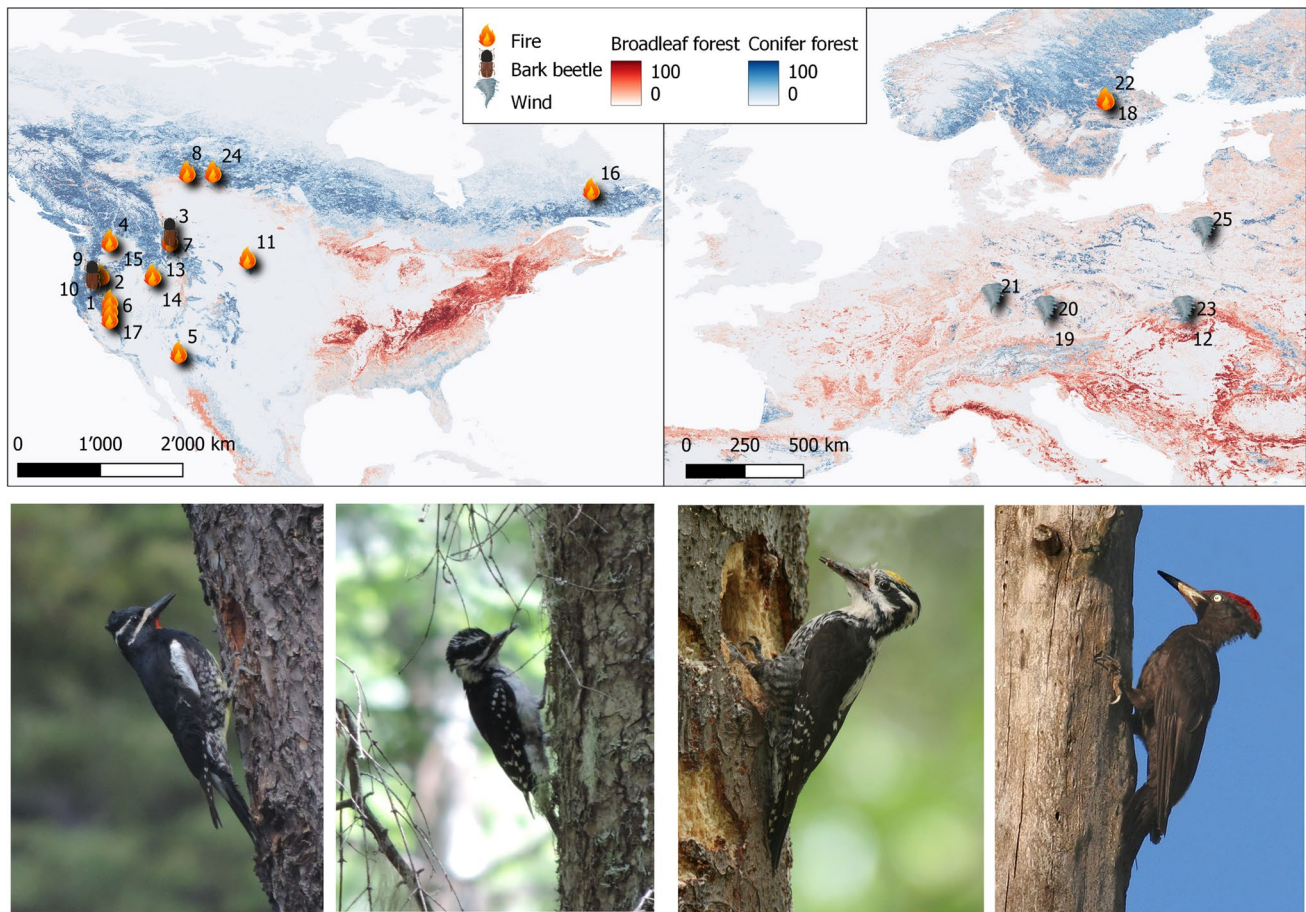


Fig. 1 Study locations of the datasets and examples of woodpecker species included in the meta-analysis. Species depicted from the left: *Sphyrapicus thyroideus*, *Leuconotopicus villosus*, (photo credits: Marco Basile); *Picooides tridactylus*, *Dryocopus martius* (photo credits: Stano Harvančík). Numbers in maps correspond to references: 1. Cahall and Hayes, (2009) [69], 2. Campos et al. (2019) [70], 3. Caton (1996) [71], 4. Haggard and Gaines (2001) [72], 5. Blake (1982) [73], 6. Hanson and North (2008) [74], 7. Hutto and Gallo (2006) [75], 8. Koivula and Schmiegelow (2007) [76], 9. Kroll et al. (2010) [47],

10. Kroll et al. (2012) [77] 11. Kronland and Restani (2011) [78], 12. Repel et al. (2020) [79], 13–14. Saab and Vierling (2001) [80], 15. Saab et al. (2007) [81], 16. Schwab et al. (2006) [82], 17. Tarbill et al. (2018) [44], 18. Žmihorski et al. (2019) [55], 19. Werner et al. (2015) [83], 20. Georgiev et al. (2021) [84], 21. Thorn unpublished, 22. Mikusiński unpublished, 23. Krištín unpublished, 24. Van Wilgenburg and Hobson (2008) [85], 25. Žmihorski unpublished. Forest cover layers from Tuanmu and Jetz (2014) [86]

outbreaks in four datasets (Fig. 1). However, in two cases, bark beetle outbreaks were triggered by windthrows or were following wildfires, so that it was not possible to separate the causes. Regarding the sampling design, two studies did not have control sites as they compared the effects of different salvage logging applications.

Meta-analysis Results

The meta-analysis included several metrics describing the numerical and functional responses of woodpeckers to forest disturbances (Table 2). The North American species were reported to respond negatively to salvage logging in 69.8% of the cases, positively in 22.6%, and neutrally in 7.6% (Table 2). In contrast, the European species responded

negatively in 50% of the cases, positively in 33.3%, and neutrally in 25% (Table 2, note that some datasets reported multiple metrics, hence the total is greater than 100%). The two model sets showed similar empirical support for all models, as the maximum Δ WAIC was 0.8 (Tables S1, S2). However, only few models returned a credible estimate for the salvage logging effect. Since the null model was one of those, we selected it as the best model for inference, given that it is more parsimonious in the number of parameters.

The Bayesian R^2 for the salvage logging and control sub-models was 0.69 (range = 0.51–0.92) and 0.79 (0.61–0.98), respectively. The salvage logging effect θ was consistently negative in all models (Tables S1, S2), with the best model estimating an effect of -1.34 (± 0.74 SD, 95% CI = -2.83 to 0.07 , $f = 0.04$). The difference between the response of

Table 2 Woodpecker species included in the published studies considered in the meta-analysis, with response metrics and the observed direction of the response in the salvage logged sites of the referenced studies. *SL*, salvage logging; ↓ = decrease; ↑ = increase; ↔ = neutral. Multiple arrows indicate different effects were found in the referenced studies

Species	Location	Response	SL effect	References
<i>Dryocopus pileatus</i>	N America	Abundance	↓↑	[76]
		Nest numbers	↓	[71]
<i>Colaptes auratus</i>	N America	Abundance	↓	[73]
			↑	[76]
			↔	[77]
			↔	[78]
		Nest density	↓	[75]
		↓	[78]	
		↓	[81]	
		Nest numbers	↓	[71]
<i>Sphyrapicus nuchalis</i>	N America	Nest density	↓	[75]
		Nest numbers	↓	[71]
<i>Sphyrapicus thyroideus</i>	N America	Abundance	↑	[77]
		Nest density	↓	[75]
		Nest numbers	↑	[47]
<i>Sphyrapicus varius</i>	N America	Abundance	↑	[76]
<i>Melanerpes lewis</i>	N America	Nest density	↓	[75]
			↑	[81]
		Nest success	↓↓	[80]
<i>Melanerpes erythrocephalus</i>	N America	Abundance	↔	[78]
		Nest density	↑	[78]
<i>Picoides dorsalis</i>	N America	Abundance	↓↑	[76]
		Nest density	↓	[75]
		Nest numbers	↓	[71]
<i>Picoides arcticus</i>	N America	Abundance	↓	[69]
			↓↑	[76]
			↓	[77]
			↓	[82]
		Occurrence	↓	[74]
		Nest density	↓	[75]
			↓	[81]
			↓	[44]
		Nest numbers	↓	[71]
			↓	[47]
	↓↔	[76]		
<i>Dryobates pubescens</i>	N America	Nest density	↓	[75]
		Nest numbers	↓	[71]
		Abundance	↓	[73]
<i>Leuconotopicus villosus</i>	N America		↓↑	[76]
			↑	[77]
			↓	[78]
		Density	↓	[69]
		Occurrence	↓	[74]
		Nest numbers	↓	[71]
			↑	[47]
		Nest density	↓	[78]
			↓	[81]
<i>Leuconotopicus albolarvatus</i>	N America	Occurrence	↓	[74]
<i>Picus viridis</i>	Europe	Abundance	↑	[55]
			↑	[84]
<i>Picus canus</i>	Europe	Abundance	↑	[55]

Table 2 (continued)

Species	Location	Response	SL effect	References
<i>Dryocopus martius</i>	Europe	Abundance	↓	[55]
			↓	Žmihorski unpublished
			↔	Mikusiński unpublished
			↑	[83]
			↔	[84]
<i>Picoides tridactylus</i>	Europe	Density	↓	[79]
		Abundance	↓	[55]
			↔	Mikusiński unpublished
			↓	Krištín unpublished
<i>Dendrocopos major</i>	Europe	Density	↓↑	[79]
		Abundance	↑	[55]
			↓	Žmihorski unpublished
			↔	Mikusiński unpublished
			↓	Krištín unpublished
			↓	Thorn unpublished
			↓	[83]
			↑	[84]
Density	↓↑	[79]		
<i>Dendrocopos leucotos</i>	Europe	Abundance	↔	[55]
<i>Dryobates minor</i>	Europe	Abundance	↓	[55]

woodpecker assemblages in salvage-logged and unlogged forests was always negative (Fig. 2). While in unlogged sites woodpecker responses to natural disturbance were

very variable with a mean response of 0.13 ± 0.05 , in salvage logged sites, the model estimated much smaller responses with a mean of 0.04 ± 0.01 (Fig. 3). The raw

Fig. 2 Effect of salvage logging on woodpeckers' responses to forest disturbance for the datasets included in this meta-analysis. Dots indicate the difference in the response between salvage-logged and unlogged sites. *Saab and Vierling (2001) [80] provide two metrics of woodpecker response and it is included twice. Lines indicate 95% credible intervals

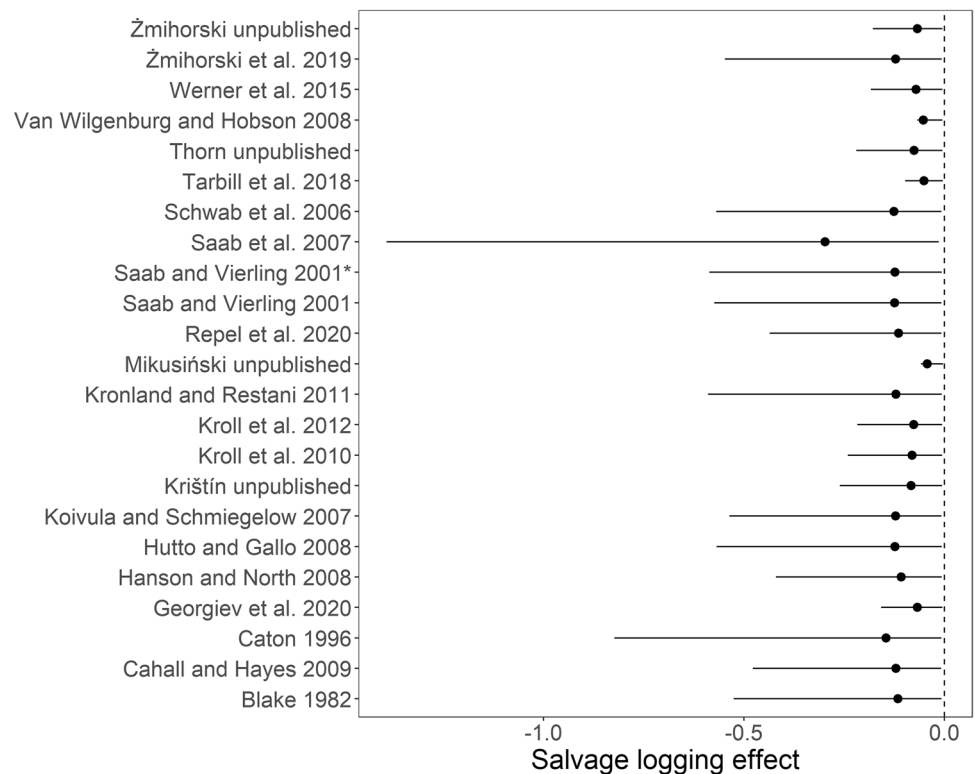
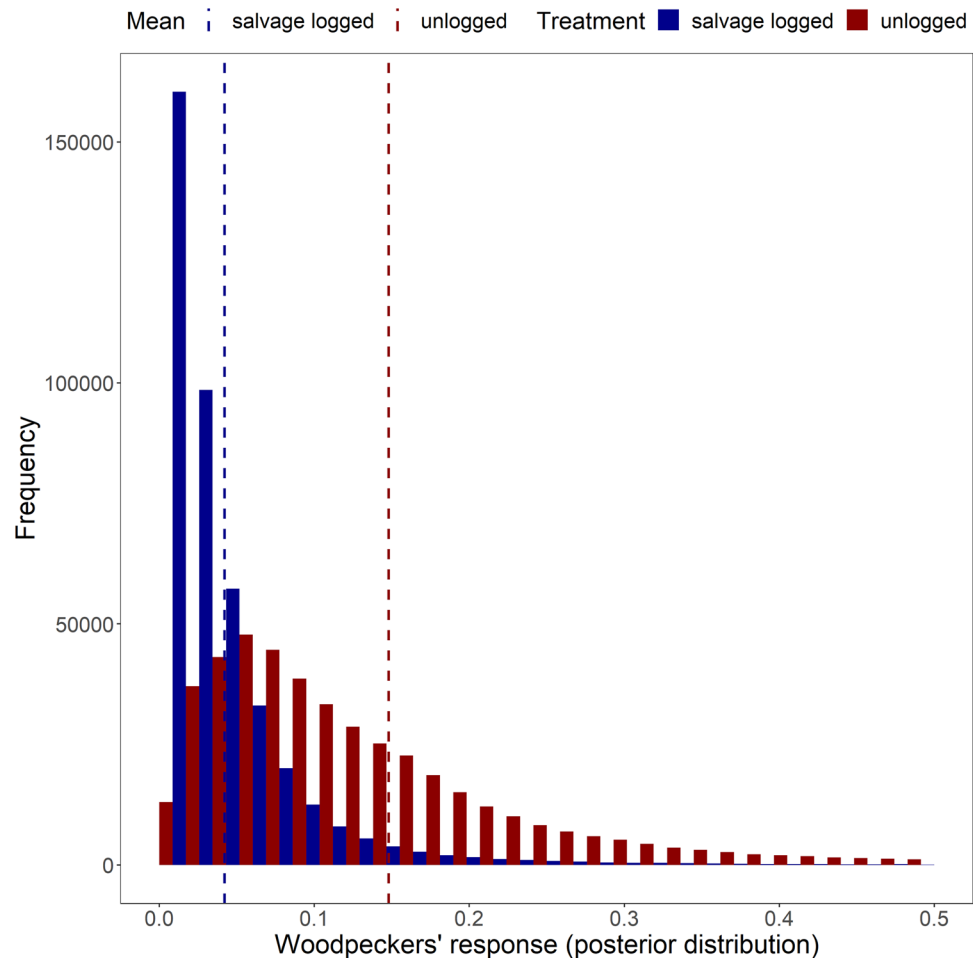


Fig. 3 Posterior distributions of the woodpeckers' response to natural disturbance in salvage-logged and unlogged forests. Bars represent the frequency of values in the posterior estimates. Values closer to 0 indicate smaller responses



data on the natural scale showed differences in woodpecker responses to disturbance in salvage-logged and unlogged forests that varied according to the response metric considered. For instance, abundance decreased by 22.6%, from a global average of 4.92 in unlogged forests to 3.81 in salvage-logged forests; reproductive success went from 0.81 in unlogged forests to 0.72 in salvage-logged forests, down by 11.4%. The model, however, by accounting for the variability among datasets due to differences in species composition and in response size (especially in metrics from unlogged sites, often skewed towards larger values), provided an unbiased assessment of the global effect of salvage logging across all datasets, which was equivalent to a global average decrease by 72.7% (95% CI, 63.2–78.8%) in salvage logged sites compared with disturbed sites without salvage logging.

No difference was found between response types, indicating that salvage logging affected numerical and functional responses of woodpecker assemblages to forest disturbance similarly. No other modelled covariate returned credible estimates, i.e. $\geq 95\%$ of the posterior distribution crossed zero (Fig. 4).

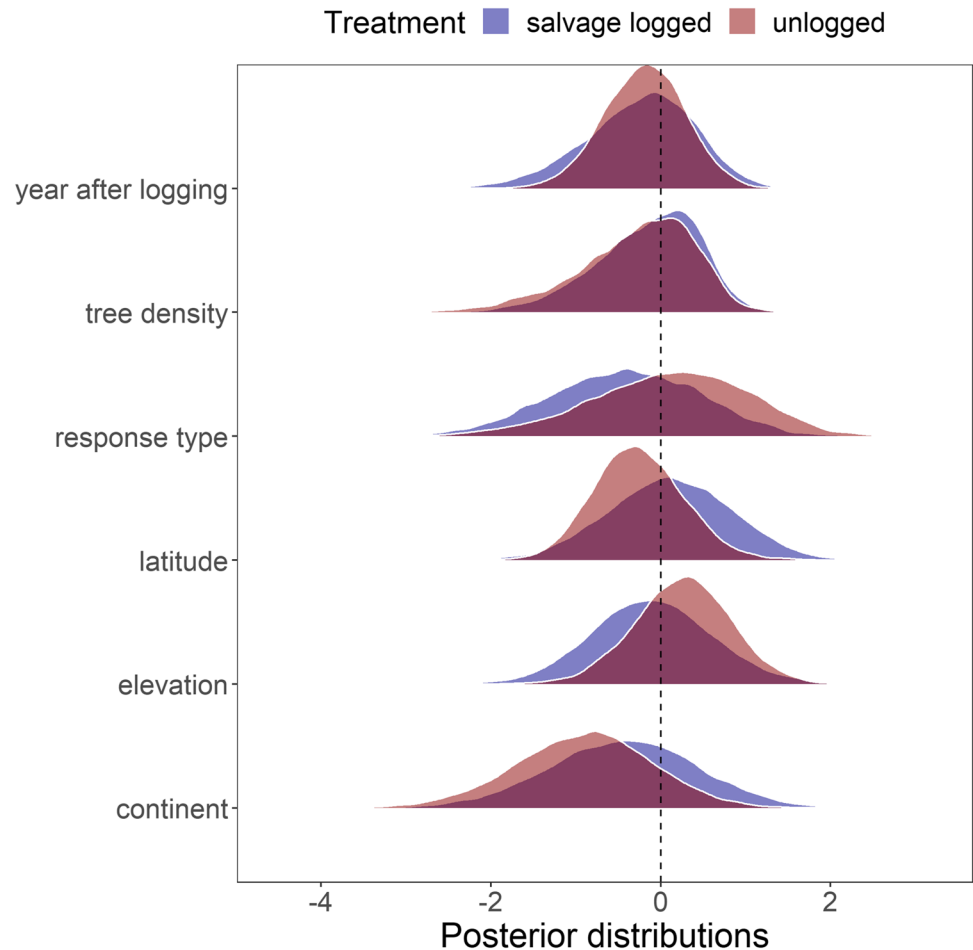
Discussion

Woodpeckers' Responses in Salvage-Logged Forests

Our meta-analysis of data from 21 published and four unpublished datasets quantified the detrimental effects of salvage logging on woodpeckers' assemblages. Specifically, woodpeckers' abundance or reproduction decreased on average by 72.7% in the presence of salvage logging, compared to unlogged disturbed sites. In addition, no difference emerged between numerical and functional responses, indicating that salvage-logging can similarly affect both woodpeckers' abundance and reproduction. In other words, whatever the response of woodpeckers to forest disturbance is, considering either their abundance or reproduction, we estimated an average 72.7% decrease when salvage logging is practiced.

The dependence of woodpeckers on standing deadwood, and especially recently dead trees, makes them particularly susceptible to the removal of this resource from forests [26, 32]. The black-backed woodpecker, for instance, is almost exclusively found in recently disturbed forests of North

Fig. 4 Posterior estimates of the covariates included in the analysis of woodpeckers' responses to natural disturbance in salvage-logged and unlogged forests. 95% credible intervals of all covariates cross 0. Year after logging, tree density, latitude, and elevation were continuous covariates, whereas response type (numerical vs functional) and continent (N America vs Europe) were binary



America, as it feeds mainly on the larvae of wood-boring insects found in recently burned trees or trees that are killed by beetles [74, 87]. In Europe, the occurrence of specialists feeding on bark beetles and wood-boring insects such as the three-toed woodpecker *Picoides tridactylus* is also tightly linked to the availability of freshly killed trees and snags [23, 27, 33]. Moreover, in recently burned areas, this species utilizes a broader spectrum of foraging substrates which leads to particularly high attractiveness of such places, causing high population densities [88, 89]. Salvage logging, due to economic reasons, focuses on dead and surviving trees with larger diameter (e.g. [90]), meaning that potential feeding substrates and trees suitable as nest sites are largely or completely removed, limiting local feeding and breeding opportunities for woodpeckers, and this impact is long-lasting. Furthermore, a strong reduction in tree density caused by salvage logging may cause increased predation pressure on woodpeckers nesting in more open forests [45].

When considering multiple assemblages, our study showed that their responses to disturbance after salvage logging are smaller (e.g. resulting in lower species abundance or breeding success) than the responses to disturbance in the absence of salvage logging. Some woodpecker species can

actually benefit from the open-habitat condition created by salvage logging as they mainly feed on ground or bark-surface arthropods [46, 77]. However, those benefits are probably less influential for the entire woodpecker assemblage than the detriments linked to the reduction in deadwood availability and permanence in the forest. Hence, salvage logging may also affect those open-habitat species, by limiting the opportunities for nesting.

Variability in Woodpeckers' Responses

Prior to our meta-analysis, the literature suggested the occurrence of differences in susceptibility to salvage logging between the North American and European woodpecker assemblages as different species show different degrees of dependence on deadwood [32, 91]. The North American deadwood specialists, such as the black-backed, the hairy (*Leuconotopicus villosus*) and the pileated woodpecker (*Dryocopus pileatus*), have a higher relative incidence within North American woodpecker assemblages in comparison with European assemblages, where deadwood specialists such as the three-toed woodpecker and the white-backed woodpecker (*Dendrocopos leucotos*) are much less

common [92–94]. Hence, we expected smaller contrasts in the post-disturbance responses of European woodpeckers between salvage-logged and unlogged forests than in North American woodpeckers. However, no differences emerged in the responses of woodpecker assemblages between the two continents. While this finding may be a consequence of the smaller sample size from Europe, it still highlights the detrimental effects of salvage logging on woodpecker assemblages on both continents.

Similarly, the absence of a significant effect of some covariates known to influence woodpeckers' responses might have been overcome if the sample size had been larger than that available in this study. For instance, the year after logging can be a significant variable explaining changes in species composition and diversity of birds to forest management in general [95]. Indeed, the model including year after logging as a covariate received similar empirical support as the model without this covariate. This pointed towards a negative effect in both salvage-logged and unlogged forests which, however, was more notable in the former.

Our literature search revealed some research gaps, mainly regarding the geographic extent of the topic, and the species and type of disturbance covered. All datasets included in the meta-analysis came from either North America or Europe. Although some articles from eastern Asia were found, they did not meet some of the criteria that are required for inclusion in the analysis, or the necessary information was not provided on request. Some species were over-represented in the datasets whereas others were under-represented. Part of this potential bias is a natural consequence of disturbance specialists being more abundant in their most suitable habitat. Therefore, we suggest that future studies focus on the entire woodpecker assemblage and not only disturbance-specialist species. Finally, fire disturbance was over-represented in North American literature and wind storms dominated studies in Europe. Thus, there is a particular need for more post-fire research in Europe, especially in the Mediterranean basin where fire is a common cause of forest disturbance. In addition, given the considerable increase in the incidence of bark beetle outbreaks in recent years [96], the dynamics of forests impacted by large-scale bark beetle outbreaks should gain more attention from ecologists and ornithologists worldwide.

Management Implications

Salvage logging can effectively decrease the amount of deadwood in the forest even decades after disturbance occurred [16, 97]. In fact, deadwood removal during salvage logging can lead to a decrease or losses of woodpecker populations and, consequently, the loss of associated ecosystem functions [98]. Many species that use woodpecker cavities for nesting, shelter, or storage of food can be negatively impacted

by a decline in woodpeckers or their range fragmentation [38, 39••, 40, 99, 100]. Especially where woodpeckers are the main providers of cavities, such as in North America or boreal Europe, cavity supply should be favoured by forest management policies [25]. For instance, standing dead or decaying trees should be retained as they are preferred by woodpeckers [22•, 101]. Early decay deadwood is associated with increased saproxylic beetle activity [102] since fresh deadwood offers large amounts of nutrient-rich resources in both phloem and sapwood which are suitable for xylophagous and saproxylic species [103]. Therefore, delayed salvaging can also represent an option to allow at least the first phases of deadwood-related processes. This approach can mitigate the effects of salvage logging on woodpeckers [44], although it may not be feasible when the disturbance concerns a pest outbreak that necessitates sanitation felling to prevent or reduce the spread of infestations to other trees [104, 105]. Another option could be selective salvaging that retains trees or stands being most suitable in terms of valuable deadwood provision.

We note that, in light of the evidence of generally negative impacts of salvage logging on woodpeckers, a group of keystone, ecosystem engineer species in forest ecosystems, this widespread practice should be more carefully planned at every spatial and temporal scale to ensure the continuity of the deadwood resources and the supply of wood-boring insects. The diversification of management strategies, including different levels of harvest, an increase in tree species richness, and allowing natural regeneration, represents at the moment the best options to preserve the naturalness of temperate and boreal forests [106–108]. Such multiscale planning could be adapted to consider the regional woodpecker assemblages and the ecological requirements of specific species [109]. In particular, constant monitoring of the bird assemblage can provide timely and important information about the species present at disturbed sites and, consequently, provide reliable information to reduce the intensity of salvage logging interventions with the aim of reducing short- and long-term impacts on woodpeckers. This information is often already collected through bird monitoring schemes in many parts of Europe and North America. Moreover, since different tree species differ in their value as foraging substrate and varying potential for cavity excavation by woodpeckers [37, 109], the retention of trees after natural disturbances could be guided by these characteristics.

Conclusions

In the unlogged forests considered in this meta-analysis, woodpeckers' response to disturbance showed higher variability than in salvage-logged forests, suggesting that the benefits of forest disturbance (new habitat patches, increase

in standing and lying deadwood, increase in wood-boring and saproxylic insects) for the woodpecker assemblage were strongly limited by salvage logging. Indeed, where salvage logging was practiced, woodpecker responses to disturbance consistently led to reductions in abundance or reproduction, compared with areas without salvage logging, across the analyzed datasets. At the same time, our meta-analysis did not identify other significant potential drivers of variability in woodpeckers' responses, such as elevation or tree density, highlighting salvage logging as the single most influential factor altering the natural dynamics of woodpecker assemblages in post-disturbance forests. However, different woodpecker species, due to their ecologies, are expected to have their own trajectories of response to disturbances and post-disturbance management, and there is still insufficient information on the thresholds of how much deadwood should realistically be preserved to avoid detrimental effects on biodiversity and species such as woodpeckers. Therefore, we advise further studies on those responses should be carried out particularly in Europe, South America, Africa, and Asia where such information is still scarce.

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Declarations

Conflict of Interest The authors do not have existing conflict of interest.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

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