Salvage logging effects on regulating ecosystem services and fuel loads

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Salvage logging, or logging after natural disturbances such as wildfires, insect outbreaks, and windstorms, is carried out to recover some of a forest's natural and/or economic capital. However, trade-offs between management objectives and a lack of consensus on the ecological consequences of salvage logging impair science-based decision making on the management of forests after natural disturbances. We conducted a global meta-analysis of the impacts of salvage logging on regulating ecosystem services and on fuel loads, as a frequent post-disturbance objective is preventing subsequent wildfires that could be fueled by the accumulation of dead trunks and branches. Salvage logging affected ecosystem services in a moderately negative way, regardless of disturbance type and severity, time elapsed since salvage logging, intensity of salvage logging, and the group of regulating ecosystem services being considered. However, prolonging the time between natural disturbance and salvage logging mitigated negative effects on regulating ecosystem services. Salvage logging had no overall effect on surface fuels; rather, different fuel types responded differently depending on the time elapsed since salvage logging. Delaying salvage logging by ~2–4 years may reduce negative ecological impacts without affecting surface fuel loads.

Front Ecol Environ 2020; 18(7):391–400, doi:10.1002/fee.2219

The frequency, severity, and extent of many natural disturbances, including wildfires, insect outbreaks, and storm events, are changing in many parts of the world as a result of land-use modification (Pausas *et al.* 2008; Taylor *et al.* 2014) and climate change (Seidl *et al.* 2017; Sommerfeld *et al.* 2018). Natural disturbances are key drivers of the ecological and evolutionary dynamics of ecosystems (Bond and Keeley 2005; Fernandez-Vega *et al.* 2017), yet there is a lack of consensus on appropriate management of disturbed forests. Ongoing shifts in disturbance characteristics demand increased attention to define post-disturbance management actions that enhance ecological resilience.

In a nutshell:

- The ecological effects of salvage logging and its impacts on subsequent wildfires are the subjects of ongoing policy debates
- Our global meta-analysis reveals that salvage logging has a negative effect on regulating ecosystem services (eg regulation of water conditions and soil quality)
- Salvage logging affected surface fuel loading by increasing small fuels (eg small branches) in the short term and reducing large fuels (eg tree trunks) in the long term
- Despite these general findings, individual studies on salvage logging report variable effects; management can therefore be adjusted to address case-specific ecological conditions and management goals
- Delaying logging after the occurrence of natural disturbances can mitigate ecological impacts without affecting surface fuel loads

Salvage logging – the harvesting of trees affected by disturbances (Figure 1) – is commonly applied worldwide (Lindenmayer *et al.* 2008; Leverkus *et al.* 2018b; Müller *et al.* 2019) in both production forests (eg Radeloff *et al.* 2000) and protected areas (eg Schiermeier 2016; Leverkus *et al.* 2017; Thorn *et al.* 2017). The primary motivations for salvage logging are to recover a forest's economic value and to reduce the risk of other, subsequent disturbances (Lindenmayer *et al.* 2008; Müller *et al.* 2019). Wood decay after disturbance quickly reduces timber quality for industry, prompting rapid intervention to preserve economic capital. Conversely, natural disturbances change the fuel structure of a forest: conifer needles fall during tree die-off due to insect outbreaks, and trees and branches fall during storms or after fires, resulting in accumulations of dead biomass on the ground (Peterson *et al.* 2015). Therefore, another common management objective of salvage logging is fuel reduction to limit catastrophic additional fires following other disturbances (Fraver *et al.* 2011).

Salvage logging often covers larger areas and is more intensive than conventional green-tree harvesting (Leverkus *et al.* 2018a). Salvage logging affects naturally disturbed forests through two key mechanisms (Figure 1): (1) mechanical disturbance caused by logging operations, which directly

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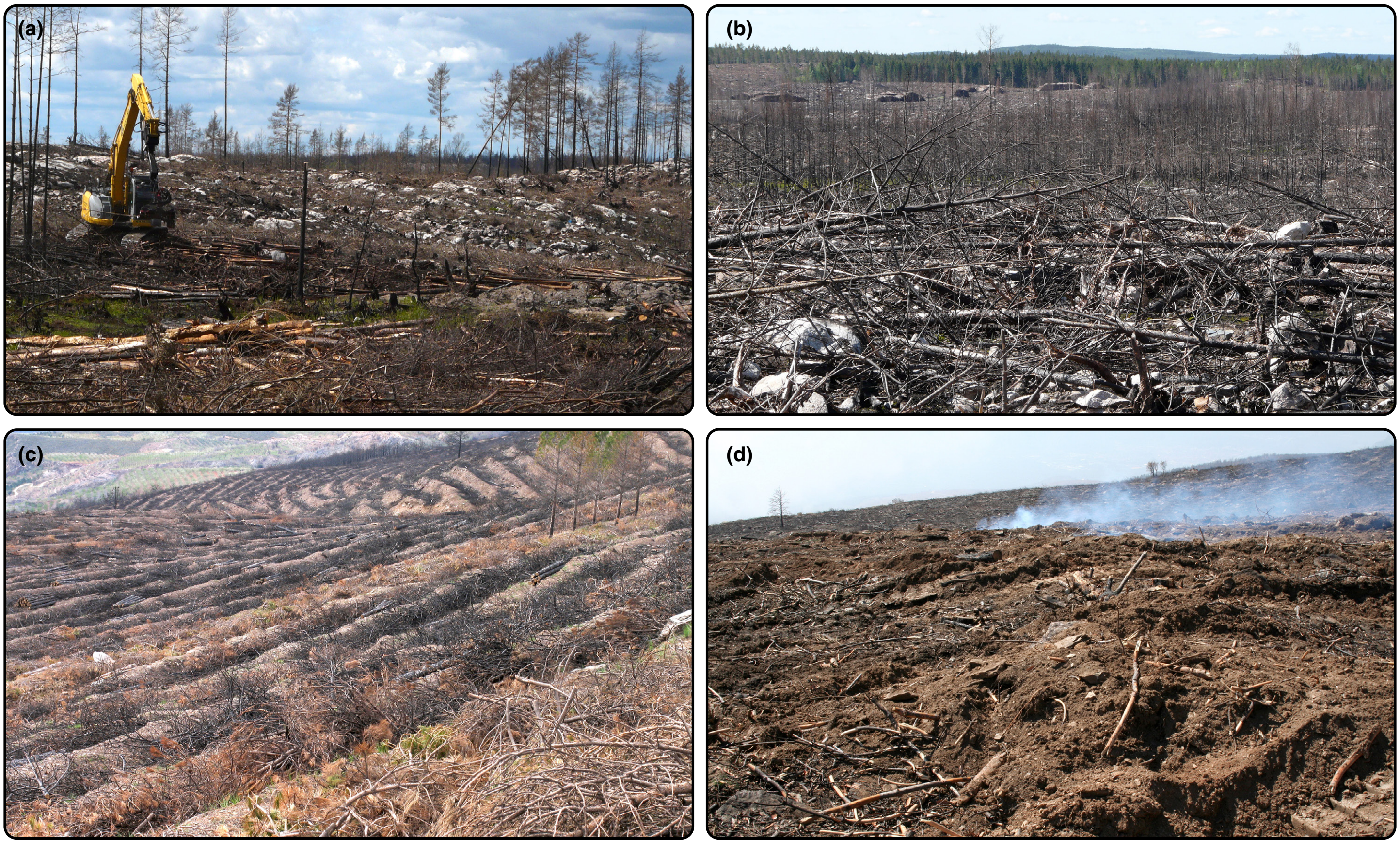

Figure 1. Salvage logging is a common management response to natural disturbances around the world, exemplified here by two specific wildfire events: (a and b) the Västmanland fire in Sweden in 2014, and (c and d) the Lanjarón fire in Spain in 2005. Salvage logging modifies the physical structure of the disturbed ecosystem drastically, as most of the large wood is removed and substantial amounts of woody debris are left on the ground (a–c) unless specific fuel-reduction treatments are undertaken, as in (d). Ecological impacts also occur through the mechanical effects of logging operations, for example through soil disturbance (d).

affects soils and vegetation (eg Bowd *et al.* 2019), and (2) modification and removal of disturbance legacies (the remaining structures of the original forest, including dead wood, seed banks, and remnant vegetation patches; Johnstone *et al.* 2016). The potential negative ecological effects of salvage logging have been highlighted repeatedly (Lindenmayer *et al.* 2004, 2017; Beschta *et al.* 2004). To assess such effects, many empirical studies have examined the ecological impacts of salvage logging on multiple taxonomic groups (reviewed in Thorn *et al.* 2018), while other studies have quantified effects on hydrological flows, microclimate regulation, nutrient cycling, and other ecological processes (Lindenmayer *et al.* 2008; Leverkus *et al.* 2018b). Many of these impacts are related to the provision of ecosystem services that are valuable to human societies (MA 2005). However, individual studies on salvage logging report variable effects on ecosystem services. In an otherwise excellent review of the effects of natural disturbances on ecosystem services, Thom and Seidl (2016) did not provide an in-depth, quantitative analysis of salvage logging effects, which was beyond the scope of that paper. Furthermore, limited case studies to date show that salvage logging can reduce (Johnson *et al.* 2013; Peterson *et al.* 2015) or increase (Donato *et al.* 2006; Thompson *et al.* 2007) fire risk, or produce mixed responses (Fraver *et al.* 2011; Rhoades *et al.* 2018). Regardless, salvage logging can generate trade-offs between ecological and fuel-reduction objectives; for example, reducing the amount of dead wood can help meet fuel-reduction goals but eliminate important habitat features for certain taxa (Thorn *et al.* 2015). However, there are currently no comprehensive, quantitative reviews of the ecological effects of salvage logging on ecosystem services and fire risk.

Using a systematic search strategy (CEBC 2010) we conducted a global meta-analysis on the effects of salvage logging on ecosystem services and fuel loads. Our primary research question was: does salvage logging affect the provision of regulating ecosystem services? We expected that individual studies would provide different answers to this question, and that some of the differences could be attributed to the characteristics of studies or response variables, so we also asked the following two secondary research questions: do disturbance type, logging intensity, and other study-related factors moderate the answer to our primary research question? And does the response vary with the group of regulating services considered? We also posed the same questions to assess the effects of salvage logging on fuel loads. In a previous systematic map (Leverkus *et al.* 2018b), we identified the relevant literature addressing these questions, and described the main characteristics (but not the results) of those studies. Our goal here was to answer our research questions through a quantitative assessment of the responses measured in those studies. Overall, we aimed to identify the factors that could mitigate the negative ecological effects of salvage logging and boost the positive ones, while searching for conditions that would facilitate the reconciliation of two key management objectives: namely, enhancing the recovery of regulating ecosystem services while reducing surface fuel loads.

Systematic literature search and meta-analysis

Literature search and data extraction

We conducted a literature search following a systematic review protocol (Leverkus *et al.* 2015) to identify research addressing the ecological effects of salvage logging. To be considered for inclusion within our analysis, individual studies had to: (1) examine forests disturbed by wildfires, windthrows, or insect outbreaks; (2) compare disturbed stands with stands that had undergone subsequent salvage logging; (3) measure a response variable that indicates the provision of a regulating ecosystem service; and (4) contain spatially independent replicates of salvage logging and non-intervention treatments. Our search followed the guidelines and recommendations described in CEBC (2010). In total, 90 relevant publications were identified; the main characteristics of these publications are described in Leverkus *et al.* (2018b), along with additional details about our search methods and study selection criteria.

Here, we have addressed the ecological responses measured in the selected publications (see WebTable 1 for a list of responses). For each response variable and post-disturbance treatment (salvaged/unsalvaged), we extracted the number of independent measurements (eg stands with a given treatment) and the mean and standard deviation of the response variable; these data were obtained from the text, figures, tables, and appendices of the publication, or directly from the authors. We also extracted other study-level variables to test them as effect modifiers (also termed "moderators"): that is, variables that could explain the between-study heterogeneity in results. The effect modifiers that were retrieved consisted of disturbance type (wildfire, windthrow, insect outbreak), disturbance severity, logging intensity, time elapsed between disturbance and logging, and time elapsed between logging and the measurement of the response variable (the latter four modifiers are numerical covariates). These effect modifiers were defined a priori in our systematic review protocol to improve the reliability of results (Higgins and Green 2011). Other predefined variables could not be tested due to lack of reporting consistency. For more details about the effect modifiers, see Leverkus *et al.* (2018b).

Individual studies often reported more than one effect size (eg resulting from the measurement of more than one response variable). When two effect sizes were related to different values of any effect modifier (eg stands logged at different intensity), we included both measurements and modeled their autocorrelation; otherwise, they were merged into a single effect size.

Ecosystem service classification

We classified the response variables into ecosystem service groups following the Common International Classification of Ecosystem Services guidelines (WebTable 1; Haines-Young and Potschin 2018). The ecosystem service groups considered were: "Regulation of baseline flows and extreme events", "Lifecycle maintenance and gene pool protection", "Pest and disease control", "Regulation of soil quality", "Water conditions", and "Atmospheric composition and conditions" (Haines-Young and Potschin 2018). We indicated whether response variables were positive or negative indicators of a given service; for instance, the amount of eroded soil was a negative indicator of the ecosystem service "Control of erosion rates". Several variables were positively related to one ecosystem service while also constituting fuels during potential subsequent wildfire, thereby negatively indicating the ecosystem service "Fire protection"; we therefore additionally placed these effect sizes in an independent response variable called "fuel loads", with five categories consisting of small (<7.6 cm diameter) woody debris, large (>7.6 cm diameter) woody debris, mixed (unspecified) woody debris, litter and duff (organic material in the soil), and live biomass. As wildfires after natural disturbances tend to be surface fires during the time preceding stand recovery (Collins *et al.* 2012), we focused on surface fuels.

Statistical analysis

For each data point, we calculated the effect size of salvage logging with Hedges' g (Hedges and Olkin 1985), which is a standardized mean difference and allows comparisons across different units of measurement (Higgins and Green 2011). Positive values of Hedges' g indicate higher levels of a given ecosystem service in the salvage-logged treatment than in the non-salvaged treatment. Mean effect sizes are considered small when $g < 0.2$, moderate when $g = 0.5$, and large when $g > 0.8$ (Koricheva *et al.* 2013).

We conducted a random-effects meta-analysis, which considers two sources of variance around the mean effect size: the within-study sampling error and the between-study variation in effect-size parameters (Gurevitch and Hedges 1999). This method accounts for the higher precision of studies with greater replication (Higgins and Green 2011). To model the autocorrelation between data points (Nakagawa *et al.* 2017), we specified the following random effects: (1) study (rather than publication, as some studies produced more than one publication; see Leverkus *et al.* [2018b] for details); (2) independent group of stands (if available), nested within study; and

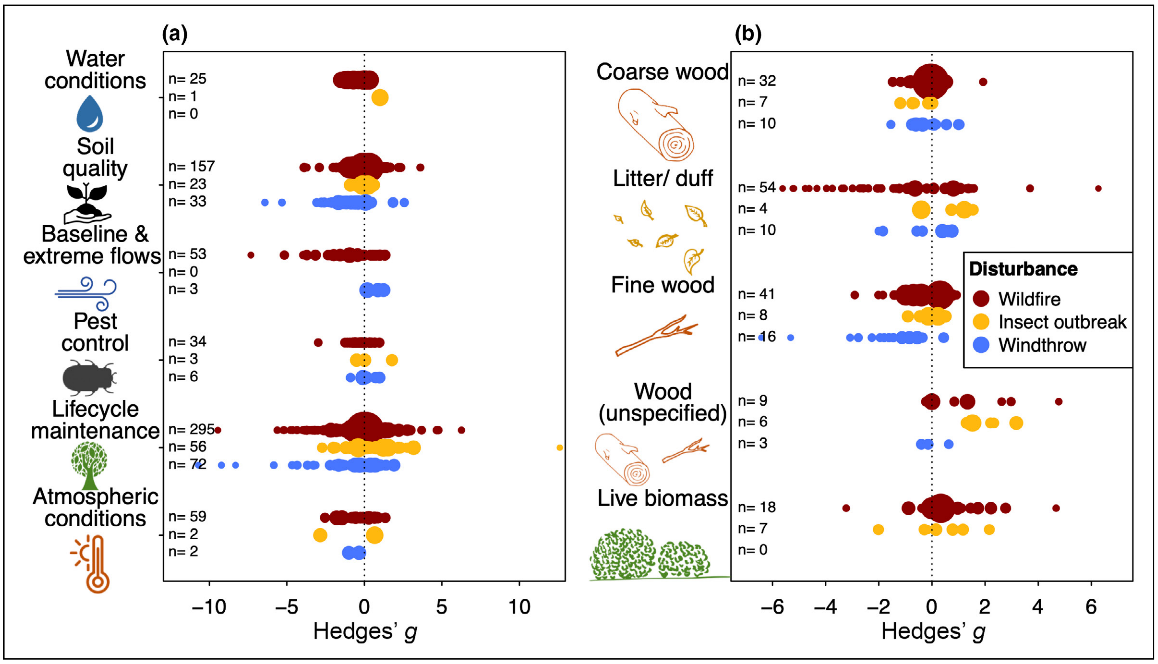

Figure 2. Effect sizes of individual data points categorized by response variable groups and disturbance type. The panels show the values of Hedges' *g* (a) in the whole database, categorized by ecosystem service group, and (b) for the fuel-load data, categorized by fuel type (note that this is a subset of the overall dataset). Values beside the y-axis are the number of data points. Point sizes are proportional to the inverse of the standard errors. Values to the right of the vertical dashed line indicate positive effect sizes. The distribution of data across each of the continuous variables is shown in WebFigure 1.

(3) stands with different interventions compared to one single control group (if available), at the same level of independent groups of stands.

Two types of models were fitted. First, to answer our primary research question, we conducted a random-effects meta-analysis. For this analysis, we fitted only the intercept (ie the overall mean effect size) and the random effects, which permitted us to assess whether the overall effect of salvage logging on ecosystem services differed from zero. To quantify heterogeneity in this model, we used the Q statistic (Viechtbauer 2010). Second, to answer our secondary research questions, we conducted a mixed-effects meta-analysis, in which the causes of heterogeneity were explored by including the above-described effect modifiers as fixed effects. Effect modifiers aim to explain the variation of "true effects" between studies, and represent an interaction between the effect of salvage logging and the modifier (Gurevitch and Hedges 1999). Uneven distribution of the data across covariate levels precluded testing interactions between the modifiers. We obtained the significance of effect modifiers from Q tests covering all the parameters related to a given factor (Viechtbauer 2010). In the final model, we used an omnibus test of moderators (Q_M) to assess the null hypothesis that all coefficients except the intercept were simultaneously zero, and a further test (Q_E) to assess the significance of residual heterogeneity. We considered all effects significant at $P \leq 0.05$.

We performed this modeling procedure for our entire dataset, and then constructed further models following the same procedure but with a subset of the data consisting of "fuel loads". We included all of the above-mentioned covariates as effect moderators, but we substituted the ecosystem service group with the type of fuel (a factor with five levels). Because we were interested in the temporal dynamics of different fuels after salvage logging and there were sufficient data for this model, we included an interaction between fuel type and time after logging. For tests of reporting bias and sensitivity analyses, see WebPanel 1.

All analyses were conducted in R v3.3.1 (R Core Team 2016), with the meta-analysis fitted using the *rma.mv* function of the *metafor* package (Viechtbauer 2010).

Results

Of the 90 publications retrieved from the literature search (Leverkus *et al.* 2018b), 62 contained relevant data. These 62 publications came from 41 study sites and provided 824 data points (WebTable 1). Approximately two-thirds of the individual data points ($n = 518$) generated negative Hedges' g values. The data were unevenly distributed across the combinations of disturbance types and ecosystem service groups (Figure 2a). In total, 225 data points from 37 publications representing 30 individual study sites addressed a response variable that was categorized as a fuel load (Figure 2b). The distribution of the data across each of the continuous variables is shown in WebFigure 1.

Effects of salvage logging on ecosystem services

The random-effects meta-analysis revealed a significant effect of salvage logging on regulating ecosystem services ($z = -3.70$;

Table 1. Results of mixed-effects meta-analysis for salvage logging effects on ecosystem services

Tested moderators*	Q	df	P
Disturbance type	1.08	2	0.58
Ecosystem service group	20.36	5	<0.01
Time disturbance – salvage	4.13	1	0.04
Time salvage – measurement	0.96	1	0.33
Salvage intensity	0.07	1	0.79
Disturbance severity	1.50	1	0.22
Whole model			
Q_M	142.42	12	<0.001
Q_E	1946.78	811	<0.001

Notes: moderators in bold are significant. Q_M = omnibus test for all the parameters in the model; Q_E = test for residual heterogeneity. *The variance of individual estimates was also included in the model (results not shown). df = degrees of freedom.

$P < 0.001$), with a small-to-moderate negative effect size (estimate = –0.26; 95% confidence interval [CI] = –0.39, –0.12). There was high heterogeneity across studies in this model (Q = 2209.20, degrees of freedom [df] = 823, $P < 0.001$).

The mixed-effects meta-analysis indicated that only two of the tested moderators – ecosystem service group, and time between disturbance and salvage logging – significantly modified the overall effect of salvage logging (Table 1; Figure 3a). The positive slope for the effect of time indicated that the effect of salvage logging became less negative with increasing time elapsed between the natural disturbance and salvage logging, and eventually did not significantly differ from zero, at around 4 years after the natural disturbance (Figure 4a; note that uncertainty increased with time due to the smaller number of studies where logging occurred in later years). Conversely, although the factor "ecosystem service group" was significant (Table 1), none of the intercepts for a particular ecosystem service group differed significantly from zero (Figure 3a), indicating that some groups were affected by salvage logging in ways that differed significantly from one another but that none of the individual groups was affected in a significantly positive or negative way.

Effects of salvage logging on fuel loads

The random-effects meta-analysis revealed no significant effect of salvage logging on fuel loads (estimate = –0.10; 95% CI: –0.35, 0.15; z = –0.81; P = 0.42). Heterogeneity across the data was also very high for this analysis (Q = 798.50, df = 224, $P < 0.001$).

The mixed-effects meta-analysis indicated that different fuel types responded differently to salvage logging (Table 2; Figure 3b). However, there was a significant interaction between fuel type and time (Table 2; Figure 4b), meaning that the effect of salvage logging on different fuel types depended on the time elapsed since logging. Fine wood (<7.6 cm diameter; mainly twigs and branches) increased significantly immediately after salvage logging, but this effect had largely disappeared after ~5 years. There was no initial effect of salvage logging on downed

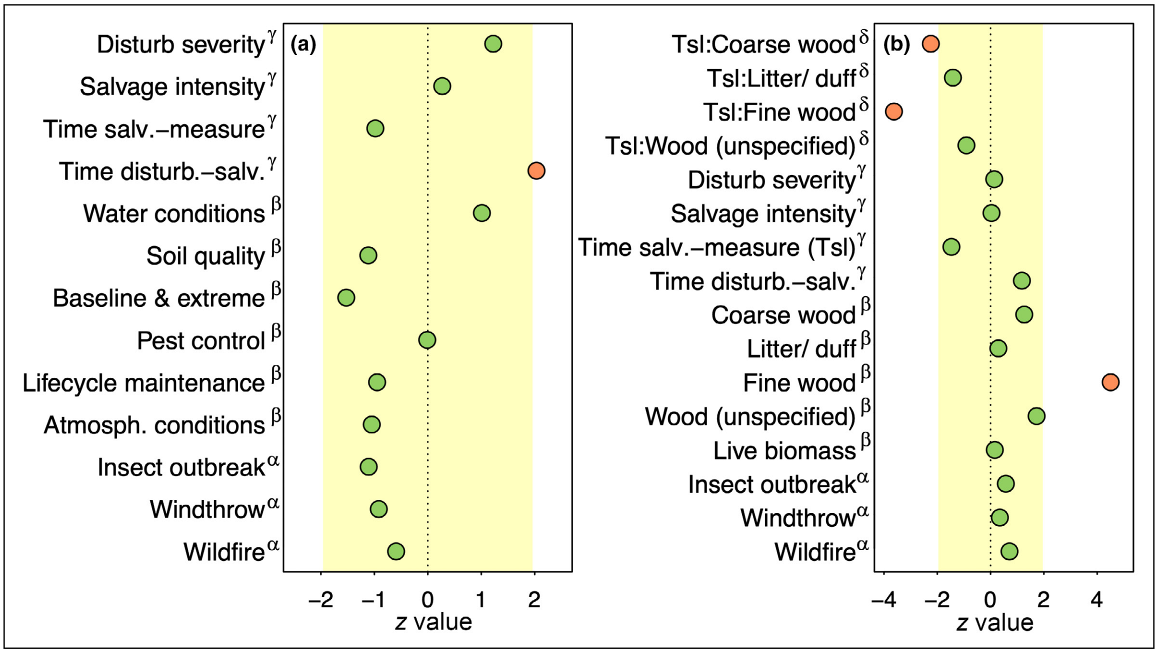

Figure 3. z values for individual coefficients from mixed-effects meta-analyses for (a) the whole dataset and (b) the fuel-load data. Yellow shading indicates the space between z = –1.96 and z = 1.96; orange circles outside of this shaded region indicate significance. The values for the levels of the two factors (α = disturbance type, β = ecosystem service or fuel type) indicate whether the intercept of the model differed significantly from zero. Values for the continuous variables (γ) indicate whether the slope for the effect of each variable differed significantly from zero. Interaction terms (δ) indicate whether the slope of the time effect for a given fuel type differed significantly from the slope for the reference level (live biomass). The effects of significant variables are shown in Figure 4.

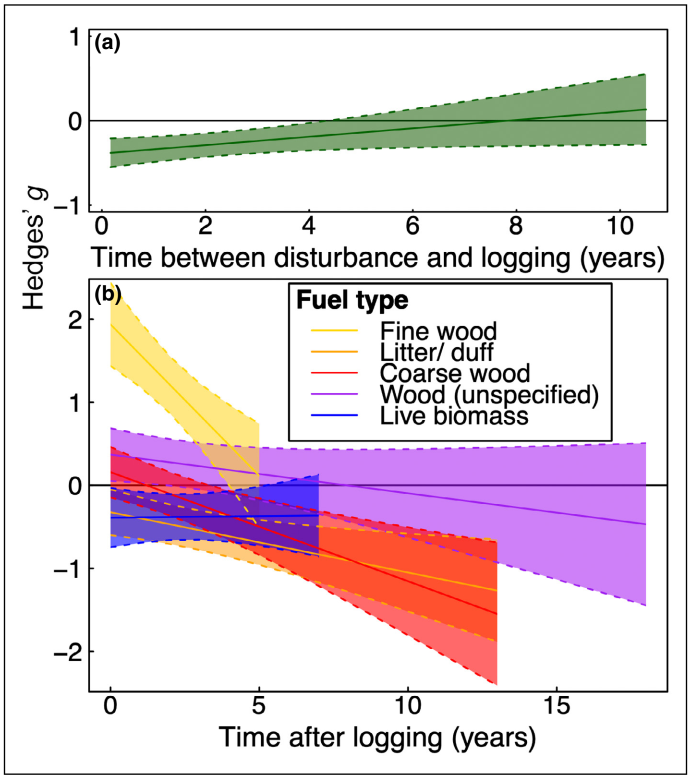

Figure 4. Model predictions for (a) how time elapsed between disturbance and logging modifies the effect size of salvage logging on regulating ecosystem services, and (b) the interaction between fuel type and time elapsed since logging on the effect size of salvage logging on fuel loads. Descending slopes indicate that the effect of salvage logging becomes more negative as time increases. Solid lines are mean estimates, and shaded areas between dashed lines are the 95% confidence intervals. The values are predictions from a model pooling disturbance type and with all continuous covariates set to their median value. The temporal predictions are constrained to the range of data available for each response variable.

Table 2. Results of mixed-effects meta-analysis for salvage logging effects on surface fuels

Tested moderators*	*Q*	df	*P*
Disturbance type	0.62	2	0.73
Fuel type	98.20	4	<0.001
Time disturbance – salvage	1.38	1	0.24
Time salvage – measurement	2.16	1	0.14
Salvage intensity	0.00	1	0.97
Disturbance severity	0.02	1	0.89
Fuel type × time salvage – measurement	38.12	4	<0.001
Whole model			
Q_M	218.69	15	<0.001
Q_E	499.38	209	<0.001

Notes: moderators in bold are significant. Q_M = omnibus test for all the parameters in the model; Q_E = test for residual heterogeneity. *The variance of individual estimates was also included in the model (results not shown). df = degrees of freedom.

coarse wood (>7.6 cm diameter; mainly tree trunks), but the effect size followed a negative trend and became significantly negative ~4 years after logging. The amount of litter and duff was slightly negatively affected by salvage logging, an effect that was amplified over time. Live biomass exhibited a small negative response to salvage logging and no change in effect size over time.

Implications for management

Our meta-analysis revealed that salvage logging produces negative impacts on regulating ecosystem services. As one of the first – if not the first – global quantitative accounts of the ecological effects of salvage logging beyond biodiversity effects, we demonstrate the overall consequences of this controversial practice, thereby contributing to a long-lasting debate that to date has relied largely on deductions, case studies, and management traditions.

We found that the longer the time between a natural disturbance and logging, the less negative the effect of salvage logging; this is – to the best of our knowledge – the first time that this trend has been identified. Previous studies have lacked the capacity to test for such effects, which highlights one of the advantages of conducting meta-analyses (Koricheva *et al.* 2013). Our finding could have arisen from forest ecological functions being more vulnerable to logging immediately after natural disturbance than if logging occurs in the absence of a previous disturbance (Lindenmayer *et al.* 2008). As natural disturbances remove the canopy trees – which otherwise exert strong competition – such perturbations are often followed by strong regeneration of vegetation, coupled with recovery of soil functions. This gradual recovery possibly enhances the resilience of ecosystem services and functions to mitigate the impact of subsequent disturbance by logging. However, our dataset included only a limited number of studies involving long time lags between natural disturbance and subsequent logging (WebFigure 1), and most of these studies were conducted in beetle-infested stands, where not all trees die immediately at the time of the disturbance and salvage logging can be postponed to allow for partial stand recovery. Finally, logging after the emergence of new tree seedlings can damage stand regeneration (Blair *et al.* 2016), and this risk must be evaluated in the context of logging methods and stand characteristics.

The reduction of negative effects over time (Figure 4a) has a straightforward management implication: delaying logging after natural disturbances could mitigate some of the negative consequences on regulating ecosystem services. There may even be equilibrium between negative and positive impacts if logging occurs 4 years or more after the natural disturbance. Unfortunately, this recommendation conflicts with several of the most common objectives of salvage logging (Müller *et al.* 2019). The declining quality of timber and the risk of expansion of insect populations that could affect neighboring stands often make salvage logging a short-term priority for forest managers; global recommendations to reconcile the recouping of economic value – which is greatest after prompt salvage logging – with the conservation of other ecosystem services – which is most effective after delayed salvage logging – therefore seem implausible. Instead, achieving multiple objectives requires the generation of guidelines and prescriptions for logging that can be adapted to meet local or regional management objectives, forest characteristics, and available logging methods. For instance, postponing salvage logging may be most viable where forests are salvaged for products that are relatively unaffected by timber quality, such as biomass pellets (Pons and Rost 2016). The conflict between ecological and economic objectives may also change if the value of non-provisioning ecosystem services and its modification by different management interventions is properly quantified (eg Leverkus and Castro 2017).

The need for case-specific considerations

The paucity of significant moderator effects (Tables 1 and 2) suggests that salvage logging impacts are unlikely to vary with these factors in a globally consistent way. However, such factors may still be important. For example, higher logging intensity may produce stronger responses of some stand characteristics, such as surface biomass and average height of standing dead trees (Ritchie and Knapp 2014), yet the high heterogeneity of responses in our data may have precluded identifying significant effects of logging intensity and other carefully selected moderators. This suggests that further research is needed to expand the body of evidence and then to enhance the power of future meta-analyses to identify general trends. In particular, more research is required to evaluate the consequences of salvage logging in the medium to long term, given that the majority of existing studies were relatively short term (less than 5 years after logging; WebFigure 1) and ecological responses can vary non-linearly over time (eg Ritchie and Knapp 2014). More data could also facilitate quantitative assessments of interactions between moderators, which we were unable to perform in the present study due to the absence of combinations between factor levels (eg we found no studies of water conditions after storms; Figure 2a).

Some of the heterogeneity in our models could be related to variables that we were unable to test due to their case-specific importance. For example, some studies reported that salvage logging was conducted during winter snow cover in an effort to lessen impacts on soils (McIver and Ottmar 2007) and that logging equipment influences salvage impacts (Wagenbrenner *et al.* 2016). Other studies reported differences in salvage logging effects due to changes in aspect (Monsanto and Agee 2008), distance from the disturbance boundary (Ritchie and Knapp 2014), elevation (Leverkus *et al.* 2014), and the presence of log piles (Rost *et al.* 2012). These and other examples highlight the importance of evaluating the potential ecological effects of salvage logging on a case-specific basis in addition to following the overall recommendations derived from our meta-analyses. For instance, post-disturbance management often strives to achieve targets related to particular ecosystem services, such as erosion control (Wagenbrenner *et al.* 2016), water quality (Beudert *et al.* 2015), or pest control (Schroeder and Lindelöw 2002), all of which were poorly represented in our dataset.

Salvage logging and fuel loads

One common rationale for salvage logging is that it decreases future fire risk through fuel reduction (Müller *et al.* 2019). However, our results show that the effectiveness of this practice not only varies for different surface fuel types but also changes over time. The prevalence of logs is initially unaffected by salvage logging, because these are similarly rare in both salvaged areas (where they have been removed) and non-salvaged areas (where dead trees are still standing). This result is applicable to logging after wildfires and insect outbreaks (immediately after which dead trees generally remain standing) but not after windthrow events (which create large volumes of fallen trees). Without salvage logging, the fall of standing dead trees gradually increases the amount of coarse surface fuel (Molinas-González *et al.* 2017), which can increase the severity of subsequent wildfires (Cannon *et al.* 2017). However, coarse fuels generally do not increase fire spread due to high moisture content and slow burn speed. Conversely, our results indicated that salvage logging – as compared to non-intervention – increases the amount of fine wood on the ground, a result consistent with previous, albeit local, findings (Donato *et al.* 2006; Peterson *et al.* 2015). This increase in fine wood due to salvage logging was expected, considering the large amounts of small wood residues produced by logging. This finding represents an overall result across the different fuel treatments. As fine fuels burn relatively easily due to their greater surface-to-volume ratio, their greater abundance constitutes a short-term increase in the risk of fire spread after salvage logging. However, this effect disappeared after 5 years, likely due to the combination of decomposition in salvaged areas and the gradual addition of fallen branches from dead standing trees in non-intervention areas. Slash mastication and burning, and the extraction of forest residues for biofuel following salvage logging, may lead to a rapid reduction in the fine woody debris pool and reduce fire risk. However, such activities likely also increase the impact of salvage logging on other ecosystem services (Ranius *et al.* 2018).

Salvage logging reduced the amount of litter and duff, with such effects amplified over time. A slight reduction of live fuels due to salvage logging remained constant over time. Whether these modifications constitute an actual reduction in fire risk must be evaluated on a case-specific basis, as flammability may vary strongly across vegetation types (Bond and Keeley 2005) and may change throughout plant successional stages (Collins *et al.* 2012). Indeed, the opposite result is also possible; for example, salvage logging can increase fire risk when associated with common actions like extensive reforestation with conifers

(Thompson *et al.* 2007). The behavior of subsequent fires is therefore affected by the temporal trajectories of different fuel types. Modeling studies to project future fuel profiles under different management scenarios for particular ecosystems (Collins *et al.* 2012; Donato *et al.* 2013) provide useful insights to define fuel-reduction treatments over different time frames (eg stand thinning and prescribed burning).

Finally, the effect of salvage logging on fuel loads was not moderated by the time elapsed between a natural disturbance and salvage logging, unlike the effects on ecosystem services as a whole. Because dry fuels accumulate gradually, postponing salvage logging to reduce fuels should be similarly effective throughout the period preceding the collapse of dead trees. This period can last several years after wildfires and insect outbreaks, but the length of time depends on numerous factors, such as soil type and tree species (Molinas-González *et al.* 2017), and is therefore case-specific. In summary, postponing salvage logging can help mitigate its negative impact on regulating ecosystem services while having little effect on its efficacy in changing fuel loads.

Conclusions

The overall negative impact of salvage logging on the provision of regulating ecosystem services calls for careful consideration of alternative management strategies, at least in areas dedicated to nature conservation. This in turn requires explicit consideration of natural disturbances in natural resource management policies to avoid hasty and unplanned decision making. The high residual variability in our models suggests that decisions concerning post-disturbance management should define the amount of salvage logging at large-scale levels (eg regional policy and management plans) but that local variations in climate, geology, topography, and species composition must also be considered. Recovery of ecosystem services in the wake of natural disturbances could be maximized by targeting particular management goals rather than the recovery of all ecosystem services simultaneously, which in many cases may be achieved by applying different management approaches to different parts of the landscape. One potential solution to balance wood supply, fuel loads, and other ecosystem services would be to extract wood from stands judged to be most susceptible to future wildfires while retaining dead wood in more ecologically sensitive places, such as riparian areas.

The time between a natural disturbance and subsequent wildfires can determine the types of interactions between them (Buma 2015; Cannon *et al.* 2017), and it may also regulate whether, and how strongly, salvage logging buffers or amplifies subsequent wildfires. Our results show that management for fuel reduction requires consideration of the temporal dynamics of prevalent fuel types after both disturbances and logging. Because salvage harvesting reduces the gradual accumulation of coarse surface fuels, slightly lessens live biomass, and increasingly reduces the amount of litter and duff compared to untreated areas, it could have a mitigating effect on the intensity of potential future wildfires. However, salvage logging also produces a strong and immediate increase in small fuels, which can enhance fire hazard in the short term unless appropriate fuel-reduction treatments are implemented. Salvage logging can therefore amplify or buffer the interaction between natural disturbances and subsequent fires, although its own role as an ecological disturbance should not be overlooked. If such logging is to occur, prolonging the time between the natural disturbance and the intervention represents a compromise between mitigating the negative ecological effects of salvage logging and its potential effect in buffering the sequence of a natural disturbance followed by a wildfire.

Acknowledgements

We thank several authors who generously provided data for this meta-analysis (WebPanel 2). ABL acknowledges the support of mobility grants from Universidad de Alcalá and Spanish Ministry of Education, postdoctoral fellowships from the Spanish Ministry of Economy and the Alexander von Humboldt Foundation, and Project AS2013/MAE-2719 "REMEDINAL-3" from the Government of Madrid. The data underlying this paper are available through an institutional repository (http://hdl.handle.net/10481/62260).

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Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2219/suppinfo

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FrontiersEcoPics

Too big to fit

Passerine birds disperse the seeds of many fruiting plants, but are limited in the size of the fruits and seeds they can swallow. In these pictures, taken in Tapiraí, Brazil, we see a rufous-bellied thrush (*Turdus rufiventris*) and a yellow-legged thrush (*Turdus flavipes*) attempting to swallow a berry of the palm *Euterpe edulis*, a keystone plant species in the Atlantic Forest. The fruits of *E edulis* are consumed by dozens of frugivore species, from medium-sized passerine birds, such as thrushes, to toucans and guans, which have wider gape sizes and can swallow and disperse seeds with a broad range of sizes. Gape limitation imposes a selective pressure on the size of seeds that is only counteracted in areas where larger-sized frugivores occur. The ongoing extirpation of large-sized frugivores due to hunting and habitat loss has generated a size-selective change in frugivore assemblages, creating an evolutionary trend of decreasing seed sizes in *E edulis* (*Science* 2013; doi.org/10.1126/science.1233774). Smaller seeds have fewer nutrient supplies in the endosperm and are more vulnerable to desiccation, so the evolution toward smaller seeds may affect long-term persistence of populations. Also, because small fruits have less pulp than large ones, they are less rewarding for large-bodied frugivores, which could result in feedbacks between plant and bird fitness. The generality of these evolutionary consequences of defaunation on plant traits is still an open question.

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doi:10.1002/fee.2248