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Research Article

Resilience impacts of a secondary disturbance: Meta-analysis of salvage logging effects on tree regeneration

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Abstract

1. Intense controversy surrounds the compounded disturbance of salvage logging, which superimposes an anthropogenic disturbance on already disturbed ecosystems and thereby provides a litmus test of forest regeneration and resilience.
2. We conducted meta-analysis to assess whether salvage logging affects tree regeneration, and whether potential effect moderators (disturbance type and severity, logging intensity, time elapsed between disturbance and logging or since logging, forest type and age, regeneration syndrome and aridity) modify this overall effect. Thirty-seven publications yielded 305 effect sizes for tree density and 135 for height.
3. We found no significant effect of salvage logging on tree density or height. Also, most effect moderators were not significant. The effect size of salvage logging on tree density increased over time after logging, potentially indicating resilience to initial salvage logging impacts. Tree density in old (>100 years) disturbed forests was less negatively affected by salvage logging than in young (<50 years) and intermediate-aged forests. Study site and phylogenetic relatedness improved model fit, indicating modulation by local ecological factors and tree species characteristics.
4. *Synthesis*. Salvage logging does not produce generalised detrimental effects on tree regeneration. Potential impacts and their mitigation should be assessed upon knowledge of local conditions and species.

KEYWORDS
compounded disturbance, forest disturbance, insect outbreak, regeneration, salvage harvest, storm, succession, wildfire

1 | INTRODUCTION

Natural disturbances such as wildfires, storms and insect outbreaks shape the ecological and evolutionary dynamics of terrestrial ecosystems around the world (Pausas & Keeley, 2014). As a result, ecosystems are generally resistant—able to avoid disturbance impacts—and resilient—able to recover after disturbance—under the local disturbance regime (Johnstone et al., 2016; Nimmo et al., 2015). However, disturbance regimes are changing around the world, as disturbances are becoming more frequent, widespread and intense, and occurring at unprecedented times and places (Seidl et al., 2017). Such shifts are sparking concerns about the capacity of ecosystems to recover (Johnstone et al., 2016), thus increasing the need to understand the factors that affect resilience.

One key concern about forest resilience is the impact of compounded disturbances, among which salvage logging is widespread (Kleinman et al., 2019; Leverkus et al., 2018). Salvage logging, which involves felling and extracting disturbance-affected trees, is a globally widespread practice (Müller et al., 2019) and it has become the subject of much controversy due to its potential impact on forest resilience (Lindenmayer et al., 2017). A major focus of the ongoing debate is the potential impact of salvage logging on tree natural regeneration.

Tree species that regenerate through resprouting (i.e. that regenerate above-ground tissues from protected buds by using stored carbohydrates; Pausas et al., 2004) may be affected if young resprouts are harmed during logging operations and are therefore forced to resprout again (Lindenmayer & Noss, 2006). Contrarily, 'seeders' (i.e. species that recruit from the seeds stored in the seed bank; Pausas et al., 2004) may be affected if a natural disturbance triggers widespread germination and subsequent logging operations destroy the seedlings (Lindenmayer & Noss, 2006).

Beyond its direct effects on seedling or sapling survival, salvage logging can also impact tree regeneration by increasing microclimatic stress (Marañón-Jiménez et al., 2013) and reducing mutualistic interactions such as mycorrhization (Beck et al., 2020) and seed dispersal (Leverkus & Castro, 2017). However, salvage logging could also enhance regeneration through mechanisms such as soil scarification, increased irradiance and seed dissemination during logging operations (Peterson et al., 2009; Royo et al., 2016). Ultimately, the effect of salvage logging can depend on the identity, timing and intensity of each of the two disturbances (i.e., the natural one and salvage logging), on plant traits associated with regeneration (Peterson et al., 2009), or on the time-scale over which effects are measured (Macdonald, 2007). In spite of the significance of salvage logging in both forest management and ecology, we are not aware of previous reviews that quantify its effects on tree regeneration. Previous reviews are either qualitative or focused on a particular ecosystem and disturbance type (Rodríguez Martínez et al., 2013; Royo et al., 2016; Taeroe et al., 2019).

Here, we present a meta-analysis on the effects of salvage logging on the post-disturbance regeneration of trees. We focus on trees that regenerated after disturbance as seedlings or young resprouts and exclude advance regeneration. We consider such effects as impacts on one key aspect of forest resilience, as they imply a change in regeneration after one natural disturbance (Xu et al., 2017). We aim to assess whether there is an overall impact of salvage logging on the density, height and survival of tree regeneration and whether factors related to the natural and the logging disturbances, the species involved, and the time elapsed, modify this overall effect. Our study should thus provide timely input to a long-lasting debate about the impacts of increasingly common, compounded natural and anthropogenic disturbances on forest resilience.

2 | MATERIALS AND METHODS

2.1 | Study selection and inclusion

For the present meta-analysis, we used the scientific literature on the ecological effects of salvage logging that was identified in a global systematic map (Leverkus, Rey Benayas, et al., 2018). To be included in the systematic map, the studies had to provide comparisons of forest plots exposed to two different treatments, namely plots affected by natural disturbance (wildfire, insect outbreak or windthrow; prescribed burning was excluded) and plots within the same forest that were additionally salvage-logged after the disturbance. We included 'Control-Intervention' and 'Before-After Control-Intervention' designs yet excluded Before-After designs. Also, studies had to be replicated at the scale of the management intervention. To identify the publications, we followed a systematic review protocol (Leverkus et al., 2015). We conducted primary searches in English in Web of Science and Scopus, secondary searches in specialised websites and databases (Directory of Open Access Journals, CABI database of forest science, Canadian Forest Service, USDA Forest Service and Google Scholar), and supplementary searches in the reference lists of relevant articles. We then assessed the relevance of the publications in a three-step elimination procedure, in which we contrasted each publication with the inclusion criteria indicated above at the level of (a) titles, (b) abstracts and (c) the whole publication.

To identify the studies with relevant data for the present meta-analysis, we updated the literature searches of our systematic map (more extensively described in Leverkus, Rey Benayas, et al., 2018) to incorporate all studies published until 31 December 2018. Among all the retrieved studies, we then selected those that addressed a relevant response variable, namely the density, height or survival of regenerating trees (including the height or survival of artificial regeneration with local species). We included studies that used different methods and units of measurement as long as they addressed one of the aforementioned response variables and the measurements and plot-level sampling effort were the same for both treatments within the study (Koricheva et al., 2013). Each comparison between salvaged and unsalvaged plots produced one effect size, for which we obtained the mean, standard deviation and number of replicates per treatment. To avoid within-study spatial autocorrelation, the obtained responses were aggregated at the level of replicates (e.g. mean and SD of tree height at the plot level, rather than the height of individual trees) and we used random effects for multiple effect sizes from the same study (see *Statistical analyses* below).

For each effect size—represented by one row in the data—we also obtained the following meta-data:

- Disturbance type. One of: wildfire, insect outbreak or windthrow.
- Forest leaf habit. One of: broadleaf, conifer or mixed.
- Forest age before disturbance. This was generally provided as a number of years since previous stand-replacing disturbance. We classified this into three broad categories: (a) young forest (<50 years old); (b) mature forest (50–99 years); and (c) old forest (≥100 years).
- Disturbance severity. This was obtained through indications of percent tree mortality, percent basal area dead or qualitative indications. Where a severity range was provided, we recorded its median. Some studies only provided a qualitative estimation of severity, to which we attributed the following severity percentages: Low severity, 30%; Low to moderate, 45%; Moderate, 60%;

Moderate to High or Mixed or Variable, 75%; High, 90%; and Severe, 100%.

- Salvage intensity. We obtained an approximation of logging intensity through quantitative or qualitative indicators available in the publications. The quantitative indicators referred to the percent basal area or percent trees that were removed. We attributed percentages to qualitative indicators as follows: Moderate to low intensity, 50%; Moderate or Variable, 75%; High, 90%; and Clearcut, 100%.
- Time (in years) elapsed between the natural disturbance and logging. We recorded median values if a range of values was provided (e.g. if logging occurred over a period of time).
- Time (in years) elapsed between salvage logging and the measurement of the response variable.
- Tree species' regeneration syndrome (resprouter, seeder or both). To obtain this, we searched each tree species in specialised books (Carreras Egaña et al., 1996; López González, 2007; Ruiz de la Torre, 1979) and the US Forest Service website (https://www.fs.usda.gov).
- Global Aridity Index. We obtained the value for each study site from the Global Aridity Index and Potential Evapotranspiration Climate Database (Trabucco & Zomer, 2019).

To adequately test hypotheses on organismal responses to the environment, it is important to take into account that evolutionary relatedness is expected to influence biological functions and trait values (Cadotte et al., 2013). For this reason, we quantified the evolutionary co-ancestry of the tree species in our database by inferring a phylogeny with the R package V.PhyloMaker (Jin & Qian, 2019; Figure S1). We then used the distances within the resulting correlation matrix to control for non-independence among species.

2.2 | Statistical analysis

We converted the response variables to effect sizes using Hedges' g (Hedges & Olkin, 1985). We then conducted meta-regressions in two steps to assess our study questions.

First, we conducted random-effects meta-analyses to assess whether there was an overall effect of salvage logging on tree regeneration. Here, we fitted only an intercept (overall effect), controlling for the autocorrelation structure of the data (with study location and phylogenetic correlation as random effects). We assessed the contribution of these random effects to model fit by comparing the AIC of models including and excluding the corresponding v. In the second step of modelling described below we always included both sources of autocorrelation (Nakagawa et al., 2017). We assessed the residual heterogeneity of the model with the Q statistic (Viechtbauer, 2010).

Second, to assess the causes underlying the between-study heterogeneity in effect sizes, we conducted mixed-effects meta-analyses, introducing the moderators in the model. These included four categorical and five continuous variables, which are described in the section above and the range or levels of which are indicated in Table 2. We performed a model simplification procedure to assess the effect of moderators (Crawley, 2013). Initially, we included all the moderators in a full model and sequentially simplified it by removing non-significant terms; significance was based on likelihood ratio tests. The minimal adequate model contains only effects with $p \leq 0.05$. We interpret the effects of moderators as significant at $p \leq 0.01$ and as marginally significant at $p \leq 0.05$. To control for potential reporting bias, all reported models include the variance of the effect size as a covariate, which is an extension of Egger's test for mixed-effects meta-regression (Higgins & Green, 2011). This whole procedure was conducted for tree density and then repeated for tree height; there were insufficient data to analyse tree survival. Analyses were run with the metafor package (Viechtbauer, 2010) in R version 3.6.1 (R Core Team, 2016).

3 | RESULTS

We identified 37 relevant studies that provided data for this meta-analysis. They came from 35 study locations in Mediterranean, temperate and boreal forests (Figure 1) and, altogether, produced 305

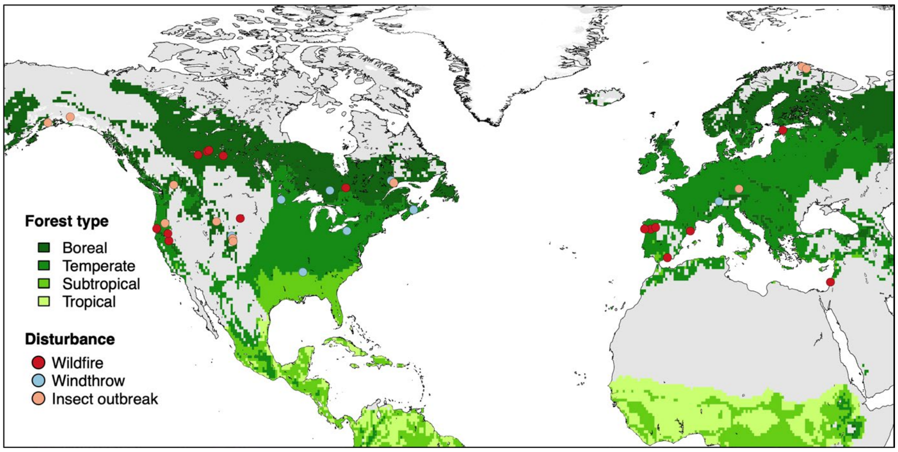

FIGURE 1 Location of the studies included in this meta-analysis

effect sizes for tree density, 135 effect sizes for tree height, and 21 for survival (which were insufficient for analysis). For the distribution of the data across the assessed moderators, see Supporting Information S2.

The random-effects meta-analysis for tree density with both tree phylogeny and study location as random effects outperformed those with one random effect or none (Table 1). Our models did not detect an overall effect of salvage logging on tree density (mean effect size = −0.18, $SE = 0.30$; $Q = 0.36$, $df = 1$, $p = 0.55$) but residual heterogeneity was very high ($Q = 460.78$, $df = 304$, $p < 0.001$), indicating that it was justified to assess the effects of potential effect moderators. When including all moderators, the mixed-effects model had lower, non-significant residual heterogeneity ($Q = 321.88$, $df = 290$, $p = 0.10$) although it increased after model simplification ($Q = 373.16$, $df = 297$, $p < 0.01$). The simplified model with the best fit to the data included four moderators, two of which had a significant effect (time elapsed since salvage logging and forest age) and two with only marginally significant effects (logging intensity and disturbance type); the other moderators were non-significant (Table 2). Elapsed time produced a positive slope, which indicates that the effect of salvage logging on tree density became significantly less negative—or more positive—with time after logging (Figure 2a). The effect of forest age was caused by a difference in the response of intermediate-aged forests (50–100 years) to that of young (<50 years) and old forests (>100 years): in intermediate-aged forests, salvage logging produced the lowest intercept (Figure 2a). There was a marginally significant trend of effect sizes becoming more negative at higher salvage intensity and of effect sizes being most positive when logging took place after fire, intermediate when salvage logging followed storm damage, and most negative when logging occurred after insect infestation (Figure 2b).

TABLE 1 AIC of models with different random effects

	Tree density		Tree height	
Random effect	**AIC**	**ΔAIC**[a]	**AIC**	**ΔAIC**[a]
None	731.8		393.6	
Phylogeny	674.7	−57.1	392.4	−1.2
Site	638.7	−93.2	351.6	−42.0
Site + phylogeny	622.3	−109.5	353.6	−40.0

[a] Difference in AIC with the model lacking random effects.

The fit of the models to the tree height data improved most with one random effect (study site; Table 1). We did not detect an overall effect of salvage logging on tree height (mean effect size = −0.19, $SE = 0.17$; $Q = 1.14$, $df = 1$, $p = 0.29$), although residual heterogeneity was again high ($Q = 252.3$, $df = 134$, $p < 0.001$). Including all moderators in the analysis reduced residual heterogeneity, although it remained highly significant ($Q = 191.2$, $df = 120$, $p < 0.001$) and again increased after model simplification ($Q = 210.6$, $df = 132$, $p < 0.001$). Only one of the tested moderators, namely time elapsed between disturbance and logging, was marginally significant (Table 2): the effect size of logging increased (i.e. became more positive) with time elapsed between the natural disturbance and logging (Figure 2c).

TABLE 2 Effect of moderators on the effect size of salvage logging, based on likelihood ratio tests during simplification of mixed-effects meta-analysis

			Tree density ($n = 305$)‡		Tree height ($n = 135$)‡	
Fixed effects	**Levels or range**	***df***	**LRT**	***p***	**LRT**	***p***
Disturbance severity	10–100%	1	0.01[a]	0.92	0.92[h]	0.34
Regeneration syndrome	Resprouter, seeder, both	2	1.10[b]	0.58	2.94[e]	0.23
Time disturbance-logging	0–10.5 year	1	0.68[c]	0.41	5.78*	<0.05
Global aridity index	2,731–22,195	1	1.21[d]	0.27	0.01[a]	0.91
Forest leaf habit	Conifer, broadleaved, mixed	2	2.95[e]	0.23	2.44[d]	0.29
Logging intensity	25–100%	1	4.28*	<0.05	0.68[g]	0.41
Disturbance type	Wildfire, windstorm, insect outbreak	2	8.48*	<0.05	0.92[c]	0.63
Time since logging	0–20 year	1	7.62*	<0.01	0.96[f]	0.33
Forest age	Young, intermediate, old	2	13.45*	<0.01	0.20[b]	0.91

[a–h] The letters indicate the order of removal of terms from the model.

*Terms kept in the simplified model ($p \le 0.05$).

‡Number of data points for analysis.

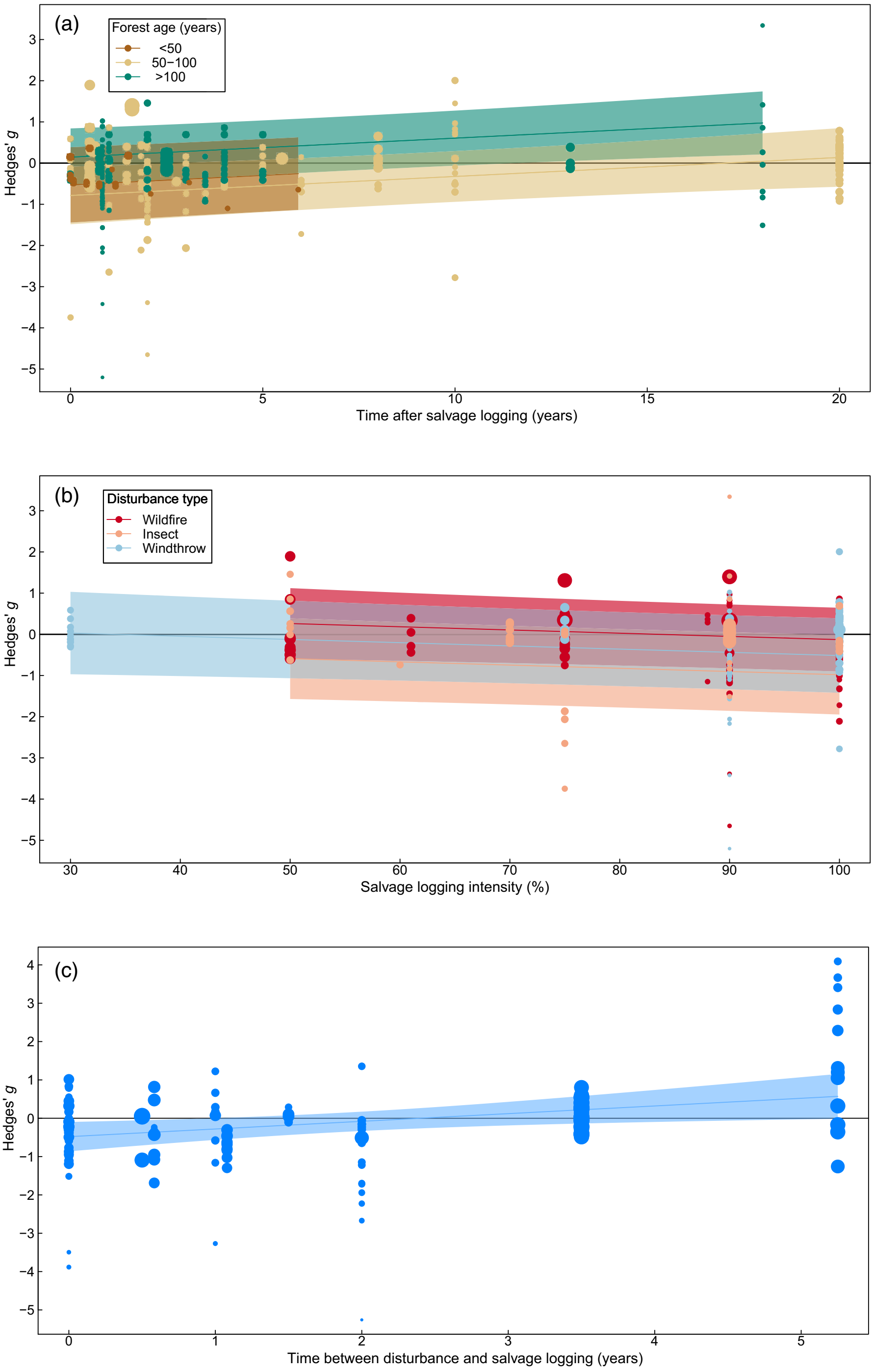

FIGURE 2 Model predictions for the effect of moderators on the effect size of salvage logging on tree density (a, b) and height (c). (a) Effect sizes of salvage logging on tree density increased with time after logging, and were greater in old forests than in young and intermediate-aged forests. (b) Effect sizes on tree density showed a marginally significant decrease with intensity of salvage logging and were lower after insect outbreaks than after windthrow or wildfire. (c) The effect size of salvage logging on tree height increased with time between disturbance and logging. The pointsin all graphs indicate the effect sizes of individual studies, with their size inversely proportional to the effect size variance (and thus proportional to their contribution to the model). For simplification, disturbance is set to windthrow and logging intensity to its median value in (a), while forest age is set to <50 and time after logging to its median in (b). Solid lines = mean prediction; shaded polygons = 95% confidence bounds

4 | DISCUSSION

Our results show that tree regeneration after natural disturbances is not consistently affected by salvage logging, as our meta-analysis found no overall effect of logging on tree density or height. Salvage logging effect sizes on regeneration density became more positive with time elapsed after the logging disturbance. This suggests that forest resilience in terms of species-averaged tree regeneration after natural disturbances is not universally affected by subsequent salvage logging, and that negative impacts tend to diminish over time. However, we found that both the study site and the phylogenetic relatedness of the tree species had a strong influence on results, suggesting that site- and species-related factors modulated salvage logging impacts. Our meta-analysis thus challenges the notion that the coupled impacts of natural and anthropogenic disturbances on forest resilience are generalisable across different locations and tree species.

The lack of a consistent effect of salvage logging on tree height or density in our study contrasts with the recent review by Taeroe et al. (2019), who found that in several studies salvage logging slowed down the recovery of wind-felled forests, and with the results of a meta-analysis that found negative impacts on tree regeneration in burnt Mediterranean forests (Rodríguez Martínez et al., 2013). The apparent contradictions between those and the present study could arise from differences in scope. Our review was not geographically restricted, we included the effect of salvage logging after multiple types of disturbance, and we restricted the analyses only to properly replicated studies. Also, our results indicate the mean response across all tree species. The lack of overall salvage logging effects in our meta-analysis could be related to the mutual cancellation of its effect on different mechanisms related to regeneration. For instance, after windthrow in temperate forests, salvage operations may destroy some seedlings but stimulate the growth of the remaining ones in an environment of reduced competition (Royo et al., 2016). After fire in Mediterranean pine stands, salvage logging can increase tree seedling mortality due to greater abiotic stress but simultaneously increase seedling densities through the dissemination of seeds through the dragging of tree remnants (Marañón-Jiménez et al., 2013). Also, different species may respond in different ways (Buma & Wessman, 2012), thereby masking each other's response to salvage logging in a broad-scope analysis such as ours.

Our results do coincide with the qualitative literature review by Royo et al. (2016), who found that early negative impacts of salvage logging on tree regeneration tend to lessen over time. Whereas the lack of overall salvage logging effects in our meta-analysis suggests that this secondary disturbance does not generally impact resilience to the first, the positive effect of time on effect sizes also suggests resilience of tree regeneration to potential negative early impacts of salvage logging (Peterson & Dodson, 2016; Royo et al., 2016). This could indicate that the mechanisms through which salvage logging negatively affects tree regeneration operate mostly during early developmental stages (e.g. machinery damaging emerging seedlings, or drought stress through the loss of shade-providing deadwood killing young seedlings), whereas they are gradually compensated by mechanisms producing positive effects (such as enhanced sapling survival through lower competition, or the gradual wind-driven colonisation of scarified soil far from the disturbance perimeter) in later years (Taylor et al., 2017).

We also found that regeneration density was less affected by salvage logging in forests that were disturbed at a young (<50 years) or old age (>100 years) than at an intermediate age (50–100 years). The regeneration of young forests might benefit from propagule abundance due to the persistence of early-seral species, which would be the primary colonisers after salvage logging (Taeroe et al., 2019). Also, due to the smaller size of trees, the light environment—a driver of tree responses to disturbance (Taylor et al., 2017)—would be most similar across salvaged and unsalvaged areas in young forests. Contrarily, tree species in old-growth forests may have accumulated propagules over longer timeframes. The finding could also be related to an U-shaped curve indicating that young and old forests tend to be more species-rich than at intermediate stages (Hilmers et al., 2018). However, the pattern of intermediate-aged forests showing less tree regeneration after combinations of disturbances than their younger and older counterparts requires further empirical testing.

There were two additional, marginally significant trends in the effect of salvage logging on regeneration density, and one trend for regeneration size. First, tree density was more negatively affected by salvage logging the higher the intensity of logging. This highlights that tree retention may help mitigate the potential impacts of logging even in naturally disturbed ecosystems (Gustafsson et al., 2012; Thorn et al., 2020). Second, salvage logging effects on regeneration density were most negative after beetle outbreaks, intermediate after windthrow, and highest after fire. This result was surprising, given the general conception of logging impacts being particularly strong after fire (DellaSala et al., 2006; Donato et al., 2006). However, fire constitutes a particularly strong evolutionary driver of plant adaptations to disturbance (Pausas & Keeley, 2014); hence, those tree species that inhabit fire-prone ecosystems might be more likely to display mechanisms that also enhance regeneration after subsequent salvage logging. Finally, salvage logging produced more negative effects on tree height if conducted shortly after the natural disturbance and more positive effects if conducted later. This result is again surprising, given that the height differences of regeneration would be expected to be greatest if older seedlings are destroyed by logging. In any case, these trends should be interpreted with caution due to the lack of consistent reporting of salvage intensity across studies and the weak significance of the effects.

Finally, we found a paucity of significant effects of the other analysed moderators. Disturbance severity did not significantly modify the effect size of salvage logging despite it being a key driver of post-disturbance dynamics (Royo et al., 2016). This could result from the logging disturbance homogenising the conditions produced by the previous natural disturbance, as posited by other authors (McIver & Ottmar, 2018; Taboada et al., 2018). Neither forest leaf habit nor regeneration strategy produced differences in the response to salvage logging. The strong phylogenetic signal in our models suggests that closely related species responded in more similar ways than less related species (Cadotte et al., 2013), yet for reasons other than the leaf habit and regeneration syndrome categories tested here. Finer analyses of community functional composition could provide further insights into the drivers of this phylogenetic signal. Similarly, global aridity index did not help explain the strong site effect, which was surprising given that salvage logging effects on microclimatic stress suffered by regeneration have mostly been observed in semi-arid environments (Leverkus et al., 2021). Finally, the response of tree density to salvage logging was not affected by the time elapsed between disturbance and logging, unlike a positive trend on the provision of multiple ecosystem services (Leverkus et al., 2020). However, while not significant in our models, many of these variables could still be important, given both their relevance in defining local responses to salvage logging and the potential interactions with other moderators, which we were unable to test due to the scarcity of data. Future meta-analyses with datasets accumulated over larger timeframes could reveal further insights on interactions between moderators.

5 | CONCLUSIONS AND RESEARCH DIRECTIONS

Our study contributes to a long-lasting debate on the resilience of forests to the compounded effects of natural and salvage logging disturbances (Buma & Wessman, 2012; Donato et al., 2006; Leverkus, Rey Benayas, et al., 2018; Lindenmayer et al., 2017). It highlights that salvage logging impacts on tree regeneration cannot be generalised across species and locations, are most negative at intermediate forest ages, and decline over time. Our results also show that local and species-related factors should be accounted for when forecasting forest resilience to the combination of natural disturbance and salvage logging.

Additionally, we detected some important areas that require further investigation. For instance, the magnitude of salvage logging effects compared to those of the initial disturbance need to be quantified more carefully. Furthermore, we detected trends in the magnitude of salvage logging impacts on tree regeneration produced by disturbance type and logging intensity that warrant further empirical testing. Finally, repeated disturbances might impact resilience in ways beyond tree height and density. More research is needed on the effects of salvage logging on community composition to produce a clearer picture of how resilience in the world's forests may be affected by an increasingly common chain of disturbance events.

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AUTHORS' CONTRIBUTIONS

A.B.L. conceived and designed the study and drafted the manuscript; A.B.L., S.T. and L.G. produced the review protocol and made the initial literature searches; I.P. and C.B. updated the searches; A.B.L., I.P. and R.R.d.C. analysed the data; A.B.L. wrote the first draft which was then improved with input from all authors.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data underlying this meta-analysis are available at https://doi.org/10.30827/Digibug.65078 (Leverkus et al., 2021). The data sources for the meta-analysis are listed in the respective section, below.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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