Concepts paper

Salvage logging in the world's forests: interactions between natural disturbance and logging need recognition

Running head: Salvage logging and disturbance interactions

Alexandro B. Leverkus[1*], David B. Lindenmayer[2], Simon Thorn[3], Lena Gustafsson[4]

[1] Departamento de Ciencias de la Vida, Universidad de Alcalá de Henares, Madrid, Spain. alexandro.leverkus@uah.es

[2] Fenner School of Environment and Society, The Australian National University, Canberra ACT 2614, Australia. David.Lindenmayer@anu.edu.au

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

[4] Department of Ecology, Swedish University of Agricultural Sciences (SLU), P.O. Box 7044, SE-750 07 Uppsala, Sweden. Lena.Gustafsson@slu.se

*Correspondence to alexandro.leverkus@uah.es; Tel.: +34 622689928

Acknowledgements

J. Ruiz Guzmán and E. Stengel assisted in the literature review. ABL acknowledges support from grants P12-RNM-2705 from Junta de Andalucía, FJCI-2015-23687 from Spanish MINECO, and CAS17/00374 from Spanish MECD. We thank two anonymous reviewers for thoughtful comments that improved the manuscript.

Biosketch

AL is a postdoctoral fellow whose research focuses on post-fire regeneration and the effects of salvage logging in the Sierra Nevada National Park, Spain. LG has a long career in reconciling forestry practices with biodiversity conservation in Sweden. ST is a postdoc at the University of Würzburg and his work has focused on the effects of salvage logging on biodiversity in the Bavarian Forest National Park, Germany. DBL is a conservation biologist who was among the first scientists to bring attention to and produce research syntheses on the ecological effects of salvage logging; his empirical research focuses on the Mountain Ash forests of Victoria, Australia. The authors are collaborating to synthesise the ecological consequences of salvage logging at a global scale, involving qualitative and quantitative methods.

Abstract

Aim. Large disturbances increasingly shape the world's forests. Concomitantly, increasing amounts of forest are subject to salvage logging. Understanding and managing the world's forests thus increasingly hinges upon understanding the combined effects of natural disturbance and logging disturbance, including interactions so far unnoticed. Here, we use recent advances in disturbance-interaction theory to disentangle and describe the mechanisms through which natural disturbance (e.g. wildfire, insect outbreak or windstorm) can interact with anthropogenic disturbance (logging) to produce unanticipated effects. We also explore to what extent such interactions have been addressed in empirical research globally.

Insights. First, many ecological responses to salvage logging likely result from interaction modifications–i.e., from non-additive effects between natural disturbance and logging. However, based on a systematic review encompassing 209 relevant papers, we found that interaction modifications have been largely neglected. Second, salvage logging constitutes an interaction chain because natural disturbances increase the likelihood, intensity and extent of subsequent logging disturbance due to complex socio-ecological interactions. Both interaction modifications and interaction chains can be driven by nonlinear responses to the severity of each disturbance. We show that, whereas many of the effects of salvage logging likely arise from the multiple kinds of disturbance interactions between natural disturbance and logging, they have mostly been overlooked in research to date.

Conclusions. Interactions between natural disturbance and logging imply that increasing disturbances will produce even more disturbance, and with unknown characteristics and consequences. Disentangling the pathways producing disturbance interactions is thus crucial to guide management and policy regarding naturally disturbed forests.

Keywords: multiple disturbances, linked disturbances, compounded disturbances, salvage harvesting, post-disturbance management, clearcutting, synergism, antagonism, cascading effect, disturbance driver

Introduction

Natural disturbances are affecting increasing amounts of forest globally (Pausas *et al.*, 2008; Seidl *et al.*, 2017). Although forests generally have the capacity to regenerate under historical disturbance regimes (Turner, 2010; Fernandez-Vega *et al.*, 2017), there is concern that novel disturbance conditions –such as altered disturbance frequencies or multiple disturbances close in time– can affect ecosystem function and biodiversity and ultimately trigger regime shifts (Peters *et al.*, 2011; Johnstone *et al.*, 2016; Sato & Lindenmayer, 2017; Stevens-Rumann *et al.*, 2017). Recent theoretical and empirical advances have shown that multiple natural disturbances, such as wildfires, insect outbreaks, windstorms, and grazing, can interact by affecting the likelihood of occurrence and modulating the effects of one another, so that disturbance effects can often be understood only through the explicit consideration of their interaction (Didham *et al.*, 2007; Buma, 2015; Foster *et al.*, 2016; Gill *et al.*, 2017). Similarly, the outcomes of anthropogenic disturbances can be expected to result from interactions with other related, natural disturbances. Concomitant to increases in natural disturbance, salvage logging –the felling and removal of disturbance-affected trees– is a widespread and increasing human response to natural disturbance worldwide (Lindenmayer *et al.*, 2004, 2008, 2017). The effects of harvesting disturbed forests are generally considered to differ from those of harvesting undisturbed forests (Karr *et al.*, 2004; Lindenmayer *et al.*, 2004; DellaSala *et al.*, 2006; Lindenmayer & Noss, 2006; Thorn *et al.*, 2015), indicating that interactions between the natural disturbance and logging disturbance can be expected.

Disturbance interactions can arise from two fundamentally-different mechanistic pathways (Didham *et al.*, 2007; Buma, 2015; Foster *et al.*, 2016), and there is increasing recognition that a good understanding of these mechanisms is crucial for defining effective management strategies (Foster *et al.*, 2016). Disturbances interact when the legacies left behind by one disturbance are functionally connected to another disturbance –i.e. when they change the resistance and/or the resilience of the ecosystem to another disturbance (James *et al.*, 2007; Buma, 2015). On one hand, ecological responses to two consecutive disturbances may differ from the addition of the response to each kind of disturbance in isolation, which is termed an *interaction modification* (Table 1; Didham *et al.*, 2007; Foster *et al.*, 2016). Additionally, one form of disturbance can change the likelihood and magnitude of subsequent disturbance events via an *interaction chain* (Didham *et al.*, 2007;

Foster *et al.*, 2016). Both types of interaction can show *nonlinear behaviour* relative to the intensity or severity of any of the disturbances (Peters *et al.*, 2004). We argue that all these mechanisms likely operate when natural disturbance leaves behind dead trees that are subsequently harvested, as salvage logging generally occurs within the first two years after natural disturbance to avoid the deterioration of the wood (Leverkus *et al.*, 2018). However, despite intense and ongoing public, academic, and political controversy surrounding salvage logging (Beschta *et al.*, 1995; Lindenmayer *et al.*, 2004, 2017; DellaSala *et al.*, 2006; Donato *et al.*, 2006a; Schiermeier, 2016; Leverkus *et al.*, 2017a,b; Müller *et al.*, 2018; Thorn *et al.*, 2018) and numerous studies aiming to assess its ecological consequences (reviewed in Leverkus *et al.*, 2018 and Thorn *et al.*, 2018), explicit consideration of interactions between salvage logging and the preceding natural disturbance has mostly been neglected in empirical studies. As a result, to be able to understand the outcomes of salvage logging and mitigate its negative effects, there is a need to place its ecological effects within the framework of disturbance theory (e.g., Didham *et al.*, 2007; Buma, 2015; Foster *et al.*, 2016), with special focus on disturbance interactions and on the mechanisms through which such interactions may occur.

Here, we discuss interactions between natural and anthropogenic disturbances, using recent development of ecological theory (under the framework provided by Foster *et al.*, 2016) to characterise salvage logging and its ecological effects. By applying the concepts of interaction modifications, interaction chains, and nonlinear effects (Foster *et al.*, 2016), we aim to disaggregate the mechanisms driving ecological interactions related to salvage logging. We use data from a systematic literature review on salvage logging (Leverkus *et al.*, 2018) to explore the extent to which interactions have been addressed to date. Our paper is organised in four sections, comprising (1) Interaction modifications, (2) Interaction chains, (3) Nonlinear behaviour, and (4) Recommendations for policy and practice. Here we do not address the potential for cross-scale interactions (Peters *et al.*, 2007). Throughout the paper, we provide reasoned arguments on the applicability of disturbance interaction theory to salvage logging, evidence for interactions from the peer-reviewed literature, examples of the mechanisms producing such interactions, ways to distinguish the contribution of each interaction type, and some key implications for conservation and management. We emphasize that empirical research on salvage logging has only superficially addressed disturbance interactions to date, whereas they are fundamental to understand the ecological consequences of this increasingly prevalent practice and should be carefully considered when designing new studies.

Salvage logging and interaction modifications

The biological legacies left behind by one disturbance can affect the resilience of the ecosystem to another disturbance (Buma, 2015). As a result, the effect of both disturbances combined may not be additive, so that outcomes cannot be predicted from understanding the response to each disturbance in isolation. This is called an interaction modification (Didham *et al.*, 2007; Foster *et al.*, 2016).

Do salvage logging effects result from interaction modifications?

If natural disturbance and logging effects were additive, it would be unnecessary to study salvage logging effects, as these could be predicted by the addition of the known individual effects of the natural disturbance and the logging disturbance ($E_{SL} = E_D + E_L$). However, many ecosystem responses to salvage logging are likely to differ from those of green-tree harvesting due to the different conditions under which each kind of logging occurs (Van Nieuwstadt *et al.*, 2001; Karr *et al.*, 2004; Lindenmayer *et al.*, 2004; DellaSala *et al.*, 2006; Lindenmayer & Noss, 2006). As a result, the ecological effects of salvage logging would result from interaction modifications; i.e., the sum of the effects of the individual disturbances plus the interaction modification effect ($E_{SL} = E_D + E_L + E_{DxL}$). In particular, disturbed forests are characterised by the types, abundances, and spatial distribution of biological legacies (Franklin *et al.*, 2000). Elements such as downed and standing deadwood that play key ecological roles (Lindenmayer & Possingham, 1996; Hutto, 2006; Marañón-Jiménez & Castro, 2013; Wagenbrenner *et al.*, 2015; Thorn *et al.*, 2017), soft disturbance edges that constitute appropriate habitat for many species (Hanson & Stuart, 2005), and the temporal dynamics that affect these elements, define such ecosystems and set the scene for post-disturbance regeneration. Salvage logging changes the amount, characteristics and spatial arrangement of most biological legacies (Lindenmayer & Ough, 2006), and it eliminates much of the spatial heterogeneity produced by a given natural disturbance (Noss *et al.*, 2006). It is thus possible that salvage logging produces interaction modifications through the elimination and alteration of the biological legacies left behind by the natural disturbance. Theoretically, this could generate mismatches between the legacies that remain after the second disturbance and the evolutionary adaptations of organisms to cope with disturbance (Johnstone *et al.*, 2016). Further, as salvage logging targets the extraction of dead wood, it mostly affects saproxylic organisms (Thorn *et al.*, 2018), whereas green-tree operations generally impact other sets of taxa that are associated with living trees (Berg *et al.*, 1994).

Evidence for interaction modifications –systematic literature review

Empirically detecting interaction modifications requires measuring a given response variable in factorial combinations of two factors –natural disturbance and logging– as well as explicit consideration of the interaction term in statistical analyses (Foster *et al.*, 2016). Such a design encompasses four kinds of forest states (or treatments): undisturbed, logged, naturally disturbed, and disturbed + logged (salvage logged) forest. To assess the extent to which these interaction modifications have been tested, we made use of a systematic review of the global scientific literature on salvage logging effects (Leverkus *et al.*, 2018). Following the review protocol for that study (Leverkus *et al.*, 2015), we searched in the Web of Science, Scopus, and several other websites and search engines to retrieve all the empirical studies published anytime until 31/12/2016 that fulfilled the conditions of a) being field based, b) including one treatment where forest was disturbed (by wind, fire, or insect outbreaks) but not logged, and c) including a treatment where the forest was affected by the same disturbance and subsequently salvage logged. In contrast with the systematic review, for this paper we did not impose limits regarding the response variables being studied or the quality of the study. For each of the retrieved studies, we noted whether each of the four forest states outlined above were included. We found that, out of 209 retrieved papers (Figure 1), nearly two thirds compared the salvage logging treatment only with disturbed forest, with nearly the remaining third additionally including undisturbed forest as a reference (Table 2). Only eight papers (4% of all papers; Cobb *et al.*, 2007, 2010, 2011; Smith *et al.*, 2008; Whicker *et al.*, 2008; Kishchuk *et al.*, 2015, 2016; Blair *et al.*, 2016), belonging to four studies –in Alberta and Ontario, Canada; New Mexico, USA; and Victoria, Australia– included a factorial disturbance by logging design (Table 2), although only one paper explicitly considered the interaction between natural disturbance and logging (thinning) in statistical analyses (Whicker *et al.*, 2008). In Figure 2, we provide some examples of the results of these studies, highlighting some of the kinds of ecological responses that can occur.

Implications of interaction modifications

The four studies we identified revealed that the responses to natural disturbance and logging can range from antagonistic to synergistic depending on the variable being considered, passing through all kinds of ecological interaction categories, including additive effects (Piggott *et al.*, 2015). Interaction modifications from salvage logging would imply that the anthropogenic disturbance occurs under conditions of altered resilience generated by the previous, natural disturbance (Buma, 2015). Ultimately, interaction modifications could create conditions beyond the capacity of ecosystems to recover (Buma, 2015; Johnstone *et al.*, 2016). Understanding what kinds of variables show each kind of response, and over what time frames, could help direct future research efforts to the most appropriate and efficient kind of study design and conservation efforts to the most relevant targets.

Salvage logging and interaction chains

The biological legacies left behind by a disturbance can affect the factors governing ecosystem resistance to subsequent disturbance (Buma, 2015). As a result, one disturbance can modify the probability of occurrence, spatial extent, intensity or severity of another disturbance – this is called an interaction chain (Didham *et al.*, 2007; Foster *et al.*, 2016). For example, blowdown events can modify fuel structure and consequently the extent and severity of wildfires (Cannon *et al.*, 2017).

Does salvage logging constitute an interaction chain?

Assessing disturbance interaction chains requires exploring whether the mechanisms that produce forest resistance to disturbance change following a prior disturbance (Buma, 2015). In the context of salvage logging, assessing changes in resistance involves evaluating the human motivations, perceptions and values behind the decision to harvest a given area of forest, as well as how these may change following natural disturbance –i.e. it requires addressing complex social-ecological interactions. Therefore, are forests more prone to being logged after natural disturbance than in the absence of disturbance, or logged at greater intensity or spatial extent?

In production forests, where management practices are driven primarily by economic considerations, what limits logging in the absence of disturbance is chiefly the expectation that the increase in value from not logging at a particular time –i.e. from waiting to complete rotational cycles– is greater than if the wood is harvested (Wagner, 2012). Natural disturbance represents a tipping point in this regard: the economic value of a stand stops increasing and starts decreasing due to factors like the decomposition of wood and the expansion of insect galleries. There are additional considerations for salvage logging, such as the market for salvaged timber, the available infrastructure (e.g., roads), the need and cost of subsequent reforestation, and the policy and regulation framework. Therefore, natural disturbance generates a shift in the main motivation that drives (or limits) logging in production forests, which often triggers the impulse to harvest “now or never” to secure some of the remaining economic value of the wood (Lindenmayer *et al.*, 2008).

In protected forests, logging is primarily limited to meet nature conservation and human recreation objectives. Following disturbance, protection may weaken, partly because disturbed forests are often perceived as of lower ecological value than undisturbed forests (Noss & Lindenmayer, 2006) and partly because salvage logging is sometimes perceived to constitute the best-available method for ecological restoration (Müller *et al.*, 2018). In addition, following disturbance, conservation objectives are often overtaken by other arguments. Initially, the rapid collapse of dead trees (e.g., Molinas-González *et al.*, 2017) constitutes a public safety hazard that demands logging of affected trees near roads and other infrastructure. Salvage logging also aims to reduce some negative consequences of disturbance, such as limited access across the disturbed area (Leverkus *et al.*, 2012). From aesthetical and emotional points of view, disturbed forests are frequently regarded as “ugly tree cemeteries” or disorganised stands needing to be “cleaned-up” (Noss & Lindenmayer, 2006). Such triggers and motivations are generally absent in undisturbed forests, and they imply that the aims and values that limited logging in the absence of disturbance are substituted by others more favourable to logging once disturbance occurs –thus inducing the interaction chain.

Another mechanism triggering the interaction chain lies within the context of interaction chains itself. The accumulation of dead wood after windthrow and/or insect outbreaks can increase the extent and intensity of subsequent wildfires (Kulakowski & Veblen, 2007; Collins *et al.*, 2012; Johnson *et al.*, 2013). Windthrow events leave a landscape characterised by weakened trees that may constitute the breeding ground for pest insects that can also invade neighbouring forest (Schroeder, 2007; Stadelmann *et al.*, 2013). Such interaction chains between natural disturbances are widely recognised and feared, and their avoidance constitutes a major motivation for salvage logging (Fraver *et al.*, 2011; Thorn *et al.*, 2017; Müller *et al.*, 2018). For example, Swedish legislation obliges salvage logging after storms to leave a maximum of 5m^3 ha^{-1} of deadwood to prevent bark beetle outbreaks (Swedish Forest Agency, 2011). Salvage logging may succeed in preventing such interaction chains (Schroeder & Lindelöw, 2002; Buma & Wessman, 2012; Stadelmann *et al.*, 2013) or it may not (Donato *et al.*, 2006b; Kulakowski & Veblen, 2007; Fraver *et al.*, 2011; Pasztor *et al.*, 2014). However, from an ecosystem perspective, the aim of preventing one interaction chain paradoxically represents a major driving mechanism of yet another interaction chain: that of disturbance followed by logging. Subsequently, other interaction chains can be initiated, as post-disturbance logging can reduce ecosystem resistance to disturbances such as browsing by large ungulates (Leverkus *et al.*, 2013; Kramer *et al.*, 2014) or invasion by alien plant species (Moreira *et al.*, 2013).

Another feature of interaction chains is that salvage operations are often more intense than during green-tree harvesting, particularly as a result of a lack, or at least relaxation, of environmental prescriptions to logging after natural disturbance (Lindenmayer & Noss, 2006; Lewis *et al.*, 2008). This also results from salvage logging operations being more difficult and time-consuming in cases where the trees are broken and bent (e.g., after storms), thus producing a larger impact on the soil and vegetation (Lindenmayer *et al.*, 2008).

Evidence for the interaction chain

A good example of disturbance-induced increases in the likelihood of logging is in protected areas where conventional logging is prohibited (Müller *et al.*, 2018). Cases include the Sierra Nevada National Park in Spain after a wildfire in 2005 (Leverkus *et al.*, 2016), bark-beetle affected areas in the Białowieża National Park in Poland (Schiermeier, 2016), and windthrows in the Monarch Butterfly Reserve in Mexico, where logging aims to reduce fire risk (Leverkus *et al.*, 2017b). However, disturbance also increases the likelihood of logging in production forests. For instance, after a jack pine budworm outbreak in Wisconsin, Radeloff *et al.* (2000) found that forests were 3 to 6 times more likely to be logged than before the outbreak. In fact, immediate, large-scale salvage logging after major disturbances is so common that reductions in the price of wood due to the flooding of the market are a well-known sequel of disturbance (Peter & Bogdanski, 2010). Salvage clearcuts are also often much larger than traditional, green-tree clearcuts (Radeloff *et al.*, 2000; Hebblewhite *et al.*, 2009; Sullivan *et al.*, 2010). For example, mean clearcut size increased fourfold after a mountain pine beetle outbreak in the southern Rocky Mountains of Colorado (Collins *et al.*, 2010). Referring to an extremely widespread beetle outbreak in British Columbia, Sullivan *et al.* (2010, p.750) describe that "salvage logging is essentially very large-scale clearcutting and may result in openings covering 1000s of ha". Another illustration of salvage logging as an interaction chain comes from the 2014 fire near Uppsala, Sweden, which burnt ca. 14,000 ha of production forest. After the fire, forest owners sought to sell the affected timber and improve regeneration conditions, which resulted 1) in trees being cut at ages that would otherwise be considered unsuitably young for harvesting (Figure 3-a), 2) logging at higher intensity than usual (Figure 3-b), and 3) the creation of a continuous clearcut much larger than usual (Figure 3-c; however, some of the burnt forest was acquired by the Swedish Government to create a nature reserve).

Implications of the interaction chain

Interaction chains constitute a major mechanism driving the ecological effects of salvage logging. The first is that, once a natural disturbance occurs, logging can occur in places where it would otherwise not, including protected areas and old-growth or very young forests (Müller *et al.*, 2018). In such a way, land-use policies that do not anticipate the risk of disturbances may fail in defining where logging should or should not occur (Müller *et al.*, 2018). Furthermore, natural disturbance can be used as a justification to harvest forests, stands or individual trees that were not affected by the natural disturbance under the umbrella of salvage logging operations (e.g., Wang *et al.*, 2006; Peter & Bogdanski, 2010), a process termed "by-catch" (Lindenmayer *et al.*, 2008). By-catch can be hard to avoid in salvage operations where healthy and disturbance-affected trees are intermingled within single stands (Peter & Bogdanski, 2010), and it is sometimes thought to be necessary to partially compensate for the higher cost of salvage operations and the reduced value of the wood. A major risk in this regard is that logging is conducted beyond the boundaries of the disturbance (Wang *et al.*, 2006; Lindenmayer *et al.*, 2008). In addition, logging being more intense and occurring at larger scales after disturbance than in its absence undermines the essential role of biological legacies in post-disturbance ecosystem regeneration (Franklin *et al.*, 2000; Johnstone *et al.*, 2016). For example, the large size of salvage clearcuts can affect plant natural regeneration via seed dispersal due to increasing distances from seed sources (Ritchie & Knapp, 2014; Leverkus *et al.*, 2016).

Due to interaction chains, the climatic drivers of a given disturbance can indirectly increase the magnitude of subsequent, connected disturbances (Seidl *et al.*, 2017). As a result, the consequences of the initial disturbance driver are carried over to another disturbance type –these are called cascading effects (Buma, 2015). Salvage logging can bring about cascading effects, as the impacts of harvesting can be amplified due to the climatic conditions associated with major natural disturbances (Lindenmayer *et al.*, 2008). For example, drought typically precedes wildfire and beetle infestations, and windthrow events are often associated with high rainfall, producing wet ground. Logging after such disturbances thus occurs at a time of reduced ecosystem resilience due to drought (Harvey *et al.*, 2016), or it can amplify soil disturbance by ground-based machinery if the soil is wet (Lindenmayer & Noss, 2006). Within an average of less than two years (Leverkus *et al.*, 2018), the ecosystem passes from an undisturbed state to being subject to the combined impacts of climatic stress, natural disturbance, and logging (Lindenmayer *et al.*, 2008). Because the climatic drivers of disturbances are increasing as a result of climate change (Seidl *et al.*, 2017), the frequency and magnitude of cascading effects related to salvage logging also should be expected to increase.

Another implication of interaction chains is that they can become the driving mechanism producing interaction modifications (Buma, 2015). As a result, an effect of fire and subsequent logging on tree regeneration may arise from several non-mutually exclusive mechanisms related to: a) interaction modifications, such as the triggering of seedling emergence by the initial disturbance and their subsequent destruction by machinery, or high mortality due to the lack of suitable conditions for growth caused by changes in the abiotic environment; b) consequences of the interaction chain, such as the lack of an appropriate seed bank due to the salvage logged stand being too young or the large distance from seed sources resulting from huge salvage clearcuts; c) interaction chains initiated by salvage logging, such as stronger herbivory by ungulates or intense competition by invasive species after logging; or d) cascading effects, such as when disturbance and salvage logging follow severe drought and resprouting plant species are too weak to resprout twice (after fire and again after logging). Effective management to tackle the interaction and avoid regeneration failure requires knowledge of the mechanism driving each response –management decisions made under wrong assumptions of the mechanism underlying the interaction can fail to produce the desired outcomes and even produce the opposite effects (Foster *et al.*, 2016).

Distinguishing the contribution of interaction modification and chain effects

An experimental test for disturbance interaction modifications requires explicit consideration of the interaction chain. If salvage logging affects forest stands of a broader age range than green-tree harvesting, a design controlling for stand age would fail to address the full array of effects of the interacting disturbances (Figure 4). Conversely, if the interaction chain is not controlled –for example if salvage study plots are located on larger clearcuts than green-tree logging plots–, the effects of the interaction modification would be confounded with those of the interaction chain (Figure 4). Although some of the aspects of interaction chains (such as cascading effects) are extremely difficult to isolate in individual studies, other aspects can be addressed through careful study design. First, to address interaction modifications, these are best tested under the factorial combination of disturbance and logging treatments, with logging applied with the same machinery, intensity, extent, and in similar forest as green-tree harvesting. Second, individual aspects of the interaction chain could be assessed by comparing salvage logged stands of different dimensions (to test the effects of salvage clearcuts being larger), salvaged stands with different degrees of dead-tree retention (effects of salvage operations being more intense), salvaged stands of a range of pre-disturbance ages (effects of salvage clearcuts being less selective), etc. And third, it may be of interest to establish herbivore exclosures and, where applicable, careful removal of invasive species, to assess the extent to which salvage logging effects are modulated by interaction chains with subsequent disturbances. Although such designs are very hard to implement due to the unpredictability of natural disturbances and political, legal, and economic constraints (e.g., Slesak *et al.*, 2015), even partial designs should clearly address the specific mechanisms driving interactions. Finally, given issues such as climate change, cascading effects, and shifting disturbance regimes (Seidl *et al.*, 2017), it is essential that individual studies thoroughly report on stand conditions and the characteristics of disturbance events to allow future quantitative reviews on the topic.

Nonlinear behaviour in natural disturbance x logging interactions

The response of ecosystems to disturbance, and the magnitude of disturbance interaction chains and interaction modifications, can show nonlinear behaviour relative to the intensity or severity of the individual disturbances (Peterson, 2002; Peters *et al.*, 2004; Foster *et al.*, 2016). Nonlinearities mean that small differences in the severity of one of the disturbances can generate disproportionally large differences in effects. For example, a study in Colorado found that high-severity windthrow increased the severity of subsequent fire due to the accumulation of large amounts of coarse woody debris and hence reduced tree regeneration, whereas patches of low-severity windthrow –particularly below the threshold of 64 downed trees ha^{-1}– mitigated the impact of subsequent wildfire on seedling regeneration (Buma & Wessman, 2011). Identifying such thresholds can be critical for defining appropriate management strategies (Peters *et al.*, 2004), for example by providing better assessments of post-disturbance tree regeneration capacity. The potential for nonlinear responses precludes the extrapolation of disturbance effects beyond and between the particular disturbance intensities assessed in a study (Foster *et al.*, 2016). Further, due to nonlinear effects, the kinds of responses detected in a given study (antagonism, synergism, additive effects) can be a function of the intensity levels selected in the study and do not necessarily reflect a finding that is generalizable to other disturbance intensity levels (see Foster *et al.*, 2016 for examples).

Nonlinear behaviour in interaction modifications

To assess nonlinearities in interactive responses to two consecutive disturbances, at least one of them must be sampled over a range of intensities, preferably as a continuous variable (Foster *et al.*, 2016). Of the 209 articles retrieved in our systematic literature search described above, we found that 14% (n = 30) sampled over different levels of severity of the natural disturbance or at least used some proxy of disturbance severity as a covariate (although not many studies specifically addressed nonlinear effects). An example of a nonlinear interaction comes from (Royo *et al.*, 2016), who found that salvage logging after a tornado in Pennsylvania, USA, reduced tree sapling basal area and density, but only at high windthrow severity and only 1-2 years after logging. In that study, the interactive effects of a tornado and logging caused a change in successional trajectory, yet only at high wind-disturbance severity.

Some studies also tested the effects of variable salvage logging intensities. Of the 209 papers, 24% (n = 50) included some measure of salvage logging intensity or encompassed different salvage logging treatments that differed in the intensity of the intervention. A study with five experimental salvage logging intensities (with 0, 25, 50, 75, and 100% retention) was established after the 2002 Cone Fire in California. Although nonlinear behaviour was not specifically addressed, the results of that study suggest that some response variables –such as shrub cover– may show nonlinear effects of salvage logging intensity, and that some others –fine woody debris in this case– can show nonlinear interactions between salvage intensity and time (Knapp & Ritchie, 2016). Conversely, the sampling of 255 stands across Oregon and Washington showed that the response of woody fuels to post-fire salvage logging was a nonlinear function of time (Peterson *et al.*, 2015).

Very few studies (3.3%; 7 articles) considered the effects of disturbance severity and logging intensity simultaneously. McIver and McNeil (2006) used measurements of the number of stems removed during harvest after the Summit Fire in Oregon, as well as proxies of fire severity, as covariates in their analyses, and they found that logging intensity explained more variation in post-fire soil losses than fire severity. These results are important for understanding the mechanisms driving salvage logging impacts.

Nonlinear behaviour in the interaction chain

The severity of natural disturbance can affect the extent of the interaction chain in nonlinear ways. For example, as trees surviving wildfire are susceptible to hosting pest beetles (Amman & Ryan, 1991), low-severity wildfire can promote high-intensity logging to remove such trees, whereas high-severity wildfire –above the threshold of producing widespread tree mortality– can reduce the perceived need for tree removal and thus lead to low-intensity logging or no logging at all. Another threshold may exist at a degree of damage severity beyond the capacity to recover sufficient economic value from the timber, especially in cases where salvaging timber, and not subsequent stand development, is the main priority. As a third example, a stand affected by low-severity wind damage may still be more valuable if the surviving trees are allowed to continue growing, yet above a certain damage severity, a decision to salvage the stand would be made. Understanding the nonlinear character of natural disturbance severity in defining the decision to salvage log should also be regarded as a relevant issue in defining regional-scale policy on the management of disturbed forests and logging set-asides (Müller *et al.*, 2018).

Implications of nonlinear behaviour

A major implication of possible nonlinearities is that the effects of salvage logging could be modulated by where and how it is conducted. Can the negative consequences of salvage logging be mitigated if operations target stands below a certain severity level of the preceding natural disturbance? Do threshold values in snag retention govern the response of organisms to salvage logging? Are such thresholds similar to those seen for green-tree harvesting? Such questions remain largely unanswered. It is noteworthy that, in contrast to salvage logging, research on green-tree harvesting has already produced valuable information on the benefits of single- and group-tree retention (Fedrowitz *et al.*, 2014; Mori & Kitagawa, 2014). As a result, the concept of retention forestry was created, targeting the long-term retention of key structural elements and organisms to promote the "continuity in forest structure, composition, and complexity that promotes maintenance of biodiversity and ecological functions at different spatial scales" (Lindenmayer *et al.*, 2012). Such an approach currently lacks a counterpart in disturbed forests (Lindenmayer *et al.*, 2018), while it is precisely in such forests that biological legacies are crucial for regeneration (Franklin *et al.*, 2000). Paradoxically, whereas green-tree retention aims to emulate natural disturbance dynamics (Lindenmayer *et al.*, 2012), once a natural disturbance occurs, the most common response is salvage logging. Important unresolved questions to guide the applicability of the retention approach to disturbed forests include: To what extent does dead tree retention in salvage logged areas have similar effects to snag retention in areas subject to green-tree retention harvesting? And, do potential differences result from nonlinear effects of disturbance or logging intensity?

Using knowledge on interactions to improve policy and practice

Some of the interactions between natural disturbance and logging are driven by the generalised lack, or weakening, of logging prescriptions once natural disturbance has taken place (Lindenmayer *et al.*, 2008). This often includes rapid, crisis-style decision-making due to the lack of planning and fear of the quick loss of economic value of the wood (Lindenmayer *et al.*, 2008). As many of the interactions described above occur within the context of specific policy and regulatory contexts, they can also be modulated through changes in policy, law, and education. Logging is an anthropogenic disturbance and hence there are opportunities to control where, how, and how much salvage logging should occur after disturbance (Müller *et al.*, 2018). Enhanced policies and practices should be based on our understanding of interaction effects, such as the existence of synergistic effects of disturbance and logging (interaction modifications), the effect that salvage logging produces on the risk of subsequent disturbance (interaction chains), the thresholds of salvage intensity at which important habitat features are lost (nonlinear behaviour) and the capacity for natural regeneration when logging follows fire preceded by severe drought (cascading effects). For example, cascading effects can be reduced by controlling the timing of salvage logging. On the other hand, great challenges remain in the face of uncertainty, as salvage logging can have unforeseeable effects related to interactions with subsequent disturbances. For instance, whereas post-storm salvage logging can negatively impact tree regeneration (Rumbaitis del Rio, 2006), this effect can turn out positive if it mitigates the severity of subsequent fire (Buma & Wessman, 2011).

Conclusions

Paine and colleagues (1998) argued that understanding the ecological interactions arising from multiple disturbances would be essential for environmental management in the 21st century. As revealed by our systematic review, two decades later we are still some way from understanding the interactive nature of a key sequence of natural and anthropogenic disturbances. In fact, the majority of studies on salvage logging lack the necessary design to test for interactions between natural disturbance and logging, despite many mentioning interactions as likely explanations of their results. To avoid unexpected responses of ecosystem functions and services, as well as losses in forest resilience and biodiversity worldwide, policies regarding disturbed forests need to account for the problems arising from interacting disturbances, recognising that salvage logging, by definition, constitutes a sequence of disturbances. To guide such policies, the design of studies on salvage logging requires explicit assessment of the multiple pathways through which natural disturbance and logging interact, including interaction modifications, interaction chains, nonlinear behaviour in the interactions, cascading effects, and potential subsequent disturbances. This requires not only addressing the ecological effects of disturbance at the scale of stands, but also disentangling the socio-ecological interactions leading to the concatenation of natural and anthropogenic disturbances and assessing the effects of such interactions at broader spatial and temporal scales. In a world of shifting disturbance regimes, where forests are increasingly susceptible to the effects of individual and multiple natural disturbances, and where salvage logging typically follows, we require better understanding of the role that our response to natural disturbances is playing in defining the future of the world's forests.

References

Amman, G.D. & Ryan, K.C. (1991) Insect infestation of fire-injured trees in the Greater Yellowstone Area. *Department of Agriculture, Forest Service, Intermountain Research Station*, **Res. Note**, 1–9.

Berg, A., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M. & Weslien, J. (1994) Threatened plant, animal, and fungus species in Swedish forests: Distribution and habitat associations. *Conservation Biology*, **8**, 718–731.

Beschta, R.L., Frissell, C. a, Gresswell, R.E., Hauer, R., Karr, J.R., Minshall, G.W., Perry, D. a & Rhodes, J.J. (1995) Wildfire and salvage logging. 16 pp.

Blair, D.P., McBurney, L.M., Blanchard, W., Banks, S.C. & Lindenmayer, D.B. (2016) Disturbance gradient shows logging affects plant functional groups more than fire. *Ecological Applications*, **26**, 2280–2301.

Buma, B. (2015) Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere*, **6**, Art70.

Buma, B. & Wessman, C.A. (2012) Differential species responses to compounded perturbations and implications for landscape heterogeneity and resilience. *Forest Ecology and Management*, **266**, 25–33.

Buma, B. & Wessman, C.A. (2011) Disturbance interactions can impact resilience mechanisms of forests. *Ecosphere*, **2**, art64.

Cannon, J.B., Peterson, C.J., O'Brien, J.J. & Brewer, J.S. (2017) A classification of interactions between forest disturbance from wind and fire. *Journal of Ecology*, **406**, 381–390.

Cobb, T.P., Hannam, K.D., Kishchuk, B.E., Langor, D.W., Quideau, S.A. & Spence, J.R. (2010) Wood-feeding beetles and soil nutrient cycling in burned forests: Implications of post-fire salvage logging. *Agricultural and Forest Entomology*, **12**, 9–18.

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

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

Collins, B.J., Rhoades, C.C., Battaglia, M.A. & Hubbard, R.M. (2012) The effects of bark beetle outbreaks on forest development, fuel loads and potential fire behavior in salvage logged and untreated lodgepole pine forests. *Forest Ecology and Management*, **284**, 260–268.

Collins, B.J., Rhoades, C.C., Underhill, J. & Hubbard, R.M. (2010) Post-harvest seedling recruitment following mountain pine beetle infestation of Colorado lodgepole pine stands: a comparison using historic survey records. *Canadian Journal of Forest Research*, **40**, 2452–2456.

DellaSala, D.A., Karr, J.R., Schoennagel, T., Perry, D., Noss, R.F., Lindenmayer, D., Beschta, R., Hutto, R.L., Swanson, M.E. & Evans, J. (2006) Post-fire logging debate ignores many issues. *Science*, **314**, 51–52.

Didham, R.K., Tylianakis, J.M., Gemmell, N.J., Rand, T.A. & Ewers, R.M. (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology and Evolution*, **22**, 489–496.

Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B. & Law, B.. (2006a) Response to Comments on "Post Wildfire Logging Hinders Regeneration and Increases Fire Risk." *Science*, **313**, 4–6.

Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B. & Law, B.E. (2006b) Post-wildfire logging hinders regeneration and increases fire risk. *Science*, **311**, 352.

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

Fernandez-Vega, J., Covey, K.R. & Ashton, M.S. (2017) Tamm Review: Large-scale infrequent disturbances and their role in regenerating shade-intolerant tree species in Mesoamerican rainforests: Implications for sustainable forest management. *Forest Ecology and Management*, **395**, 48–68.

Foster, C.N., Sato, C.F., Lindenmayer, D.B. & Barton, P.S. (2016) Integrating theory into disturbance interaction experiments to better inform ecosystem management. *Global Change Biology*, **22**, 1325–1335.

Franklin, J.F., Lindenmayer, D., Macmahon, J.A., Mckee, A., Perry, D.A., Waide, R. & Foster, D. (2000) Threads of continuity. *Conservation in Practice*, **1**, 8–17.

Fraver, S., Jain, T., Bradford, J.B., D'Amato, A.W., Kastendick, D., Palik, B., Shinneman, D. & Stanovick, J. (2011) The efficacy of salvage logging in reducing subsequent fire severity in conifer-dominated forests of Minnesota, USA. *Ecological Applications*, **21**, 1895–1901.

Gill, N.S., Jarvis, D., Veblen, T.T., Pickett, S.T.A. & Kulakowski, D. (2017) Is initial post-disturbance regeneration indicative of longer-term trajectories? *Ecosphere*, **8**, e01924.

Grimm, V. & Wissel, C. (1997) Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia*, **109**, 323–334.

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

Hanson, J.J. & Stuart, J.D. (2005) Vegetation responses to natural and salvage logged fire edges in Douglas-fir/hardwood forests. *Forest Ecology and Management*, **214**, 266–278.

Harvey, B.J., Donato, D.C. & Turner, M.G. (2016) High and dry: Post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. *Global Ecology and Biogeography*, **25**, 655–669.

Hebblewhite, M., Munro, R.H. & Merrill, E.H. (2009) Trophic consequences of postfire logging in a wolf-ungulate system. *Forest Ecology and Management*, **257**, 1053–1062.

Hutto, R.L. (2006) Toward meaningful snag-management guidelines for postfire Salvage Logging in North American Conifer Forests. *Conservation Biology*, **20**, 984–993.

James, P.M.A., Fortin, M.J., Fall, A., Kneeshaw, D. & Messier, C. (2007) The effects of spatial legacies following shifting management practices and fire on boreal forest age structure. *Ecosystems*, **10**, 1261–1277.

Johnson, M.C., Halofsky, J.E. & Peterson, D.L. (2013) Effects of salvage logging and pile-and-burn on fuel loading, potential fire behaviour, fuel consumption and emissions. *International Journal of Wildland Fire*, **22**, 757–769.

Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E., Mack, M.C., Meentemeyer, R.K., Metz, M.R., Perry, G.L.W., Schoennagel, T. & Turner, M.G. (2016) Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment*, **14**, 369–378.

Karr, J.R., Rhodes, J.J., Minshall, G.W., Hauer, F.R., Beschta, R.L., Frissell, C. a. & Perry, D. a. (2004) The effects of postfire salvage logging on aquatic ecosystems in the American West. *BioScience*, **54**, 1029.

Kishchuk, B.E., Morris, D.M., Lorente, M., Keddy, T., Sidders, D., Quideau, S., Thiffault, E., Kwiaton, M. & Maynard, D. (2016) Disturbance intensity and dominant cover type influence rate of boreal soil carbon change: a Canadian multi-regional analysis. *Forest Ecology and Management*, **381**, 48–62.

Kishchuk, B.E., Thiffault, E., Lorente, M., Quideau, S., Keddy, T. & Sidders, D. (2015) Decadal soil and stand response to fire, harvest, and salvage-logging disturbances in the western boreal mixedwood forest of Alberta, Canada. *Canadian Journal of Forest Research*, **45**, 141–152.

Knapp, E.E. & Ritchie, M.W. (2016) Response of understory vegetation to salvage logging following a high-severity wildfire. *Ecosphere*, **7**, Art.e01550.

Kramer, K., Brang, P., Bachofen, H., Bugmann, H. & Wohlgemuth, T. (2014) Site factors are more important than salvage logging for tree regeneration after wind disturbance in Central European forests. *Forest Ecology and Management*, **331**, 116–128.

Kulakowski, D. & Veblen, T.T. (2007) Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. *Ecology*, **88**, 759–769.

Leverkus, A.B., Castro, J., Puerta-Piñero, C. & Rey Benayas, J.M. (2013) Suitability of the management of habitat complexity, acorn burial depth, and a chemical repellent for post-fire reforestation of oaks. *Ecological Engineering*, **53**, 15–22.

Leverkus, A.B., Gustafsson, L., Rey Benayas, J.M. & Castro, J. (2015) Does post-disturbance salvage logging affect the provision of ecosystem services? A systematic review protocol. *Environmental Evidence*, **4**, art16.

Leverkus, A.B., Jaramillo-López, P.F., Brower, L.P., Lindenmayer, D.B. & Williams, E.H. (2017a) Mexico's logging threatens butterflies. *Science*, **358**, 1008.

Leverkus, A.B., Jaramillo-López, P.F., Brower, L.P., Lindenmayer, D.B. & Williams, E.H. (2017b) Mexico's logging threatens butterflies. *Science*, **358**, 1008.

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

Leverkus, A.B., Rey Benayas, J.M. & Castro, J. (2016) Shifting demographic conflicts across recruitment cohorts in a dynamic post-disturbance landscape. *Ecology*, **97**, 2628–2639.

Leverkus, A.B., Rey Benayas, J.M., Castro, J., Boucher, D., Brewer, S., Collins, B.M., Donato, D., Fraver, S., Kishchuk, B.E., Lee, E.-J., Lindenmayer, D., Lingua, E., Macdonald, E., Marzano, R., Rhoades, C.C., Thorn, S., Royo, A., Wagenbrenner, J.W., Waldron, K., Wohlgemuth, T. & Gustafsson, L. (2018) Salvage logging effects on regulating and supporting ecosystem services – A systematic map. *Canadian Journal of Forest Research (In press)*.

Lewis, D., St Pierre, C. & McCrone, A. (2008) Trends in salvage-logging practices in mountain pine beetle-affected landscapes: implications to biodiversity conservation. *BC Journal of Ecosystems and Management*, **9**, 115–119.

Lindenmayer, D., Thorn, S. & Banks, S. (2017) Please do not disturb ecosystems further. *Nature Ecology and Evolution*, **1**, art31.

Lindenmayer, D.B., Burton, P.J. & Franklin, J.F. (2008) *Salvage logging and its ecological consequences*, Island Press, Washington, D.C.

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

Lindenmayer, D.B., Franklin, J.F., Lõhmus, a., Baker, S.C., Bauhus, J., Beese, W., Brodie, a., Kiehl, B., Kouki, J., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, a., Volney, J., Wayne, a. & Gustafsson, L. (2012) A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. *Conservation Letters*, **5**, 421–431.

Lindenmayer, D.B., McBurney, L., Blair, D., Wood, J. & Banks, S.C. (2018) From unburnt to salvage logged: quantifying bird responses to different levels of disturbance severity. *Journal of Applied Ecology*, **In press**.

Lindenmayer, D.B. & Noss, R.F. (2006) Salvage logging, ecosystem processes, and biodiversity conservation. *Conservation Biology*, **20**, 949–958.

Lindenmayer, D.B. & Ough, K. (2006) Salvage logging in the montane ash eucalypt forests of the Central Highlands of Victoria and its potential impacts on biodiversity. *Conservation Biology*, **20**, 1005–1015.

Lindenmayer, D.B. & Possingham, H.P. (1996) Ranking Conservation and Timber Management Options for Leadbeater ' s Possum in Southeastern Australia Using Population Viability Analysis. *Conservation Biology*, **10**, 235–251.

Marañón-Jiménez, S. & Castro, J. (2013) Effect of decomposing post-fire coarse woody debris on soil fertility and nutrient availability in a Mediterranean ecosystem. *Biogeochemistry*, **112**, 519–535.

McIver, J.D. & McNeil, R. (2006) Soil disturbance and hill-slope sediment transport after logging of a severly burned site in Northeastern Oregon. *Western Journal of Applied Forestry*, **21**, 123–133.

Molinas-González, C.R., Leverkus, A.B., Marañón-Jiménez, S. & Castro, J. (2017) Fall rate of burt pines acroos an elevational gradient in a mediterranean mountain. *European Journal of Forest Research*, **136**, 401–409.

Moreira, F., Ferreira, a., Abrantes, N., Catry, F., Fernandes, P., Roxo, L., Keizer, J.J. & Silva, J. (2013) Occurrence of native and exotic invasive trees in burned pine and eucalypt plantations: Implications for post-fire forest conversion. *Ecological Engineering*, **58**, 296–302.

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

Müller, J., Noss, R., Thorn, S., Bässler, C., Leverkus, A.B. & Lindenmayer, D. (2018) Increasing disturbance demands new policies to conserve intact forest. *Conservation Letters*, e12449.

Van Nieuwstadt, M.G.. L., Sheil, D. & Kartawinata, K. (2001) The Ecological Consequences of Logging in the Burned Forests of East Kalimantan, Indonesia. *Conservation Biology*, **15**, 1183–1186.

Noss, R.F., Franklin, J.F., Baker, W.L., Schoennagel, T. & Moyle, P.B. (2006) Managing fire-prone forests in the western United States. *Frontiers in Ecology and the Environment*, **4**, 481–487.

Noss, R.F. & Lindenmayer, D.B. (2006) The ecological effects of salvage logging after natural disturbance. *Conservation Biology*, **20**, 946–948.

Paine, R.T., Tegner, M.J. & Johnson, E.A. (1998) Compounded perturbations yield ecological surprises. *Ecosystems*, **1**, 535–545.

Pasztor, F., Matulla, C., Zuvela-Aloise, M., Rammer, W. & Lexer, M.J. (2014) Developing predictive models of wind damage in Austrian forests. *Annals of Forest Science*, **72**, 289–301.

Pausas, J.G., Llovet, J., Anselm, R. & Vallejo, R. (2008) Are wildfires a disaster in the Mediterranean basin? – A review. *International Journal of Wildland Fire*, **17**, 713–723.

Peter, B. & Bogdanski, B. (2010) *The economics of salvage harvesting and reforestation in British Columbia's mountain pine beetle-affected forests*, Natural Resources Canada, Canada.

Peters, D.P.C., Bestelmeyer, B.T. & Turner, M.G. (2007) Cross-scale interactions and changing pattern-process relationships: Consequences for system dynamics. *Ecosystems*, **10**, 790–796.

Peters, D.P.C., Lugo, A.E., Chapin, F.S., Pickett, S.T.A., Duniway, M., Rocha, A. V., Swanson, F.J., Laney, C. & Jones, J. (2011) Cross-system comparisons elucidate disturbance complexities and generalities. *Ecosphere*, **2**, art81.

Peters, D.P.C., Pielke, R.A., Bestelmeyer, B.T., Allen, C.D., Munson-McGee, S. & Havstad, K.M. (2004) Cross-scale interactions, nonlinearities, and forecasting catastrophic events. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 15130–15135.

Peterson, D.W., Dodson, E.K. & Harrod, R.J. (2015) Post-fire logging reduces surface woody fuels up to four decades following wildfire. *Forest Ecology and Management*, **338**, 84–91.

Peterson, G.D. (2002) Contagious disturbance, ecological memory, and the emergence of landscape pattern. *Ecosystems*, **5**, 329–338.

Piggott, J.J., Townsend, C.R. & Matthaei, C.D. (2015) Reconceptualizing synergism and antagonism among multiple stressors. *Ecology and Evolution*, **5**, 1538–1547.

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

Ritchie, M.W. & Knapp, E.E. (2014) Establishment of a long-term fire salvage study in an interior Ponderosa pine forest. *Journal of Forestry*, **112**, 395–400.

Royo, A.A., Peterson, C.J., Stanovick, J.S. & Carson, W.P. (2016) Evaluating the ecological impacts of salvage logging: Can natural and anthropogenic disturbances promote coexistence? *Ecology*, **97**, 1566–1582.

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

Sato, C.F. & Lindenmayer, D.B. (2017) Meeting the global ecosystem collapse challenge. *Conservation Letters*, **11**, e12348.

Schiermeier, Q. (2016) Pristine forest at risk. *Nature*, **530**, 393.

Schroeder, L.M. (2007) Retention or salvage logging of standing trees killed by the spruce bark beetle Ips typographus: Consequences for dead wood dynamics and biodiversity. *Scandinavian Journal of Forest Research*, **22**, 524–530.

Schroeder, L.M. & Lindelöw, A. (2002) Attacks on living spruce trees by the bark beetle Ips typographus (Col. Scolytidae) following a storm-felling: a comparison between stands with and without removal of wind-felled trees. *Agricultural and*, **4**, 47–56.

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T.A. & Reyer, C.P.O. (2017) Forest disturbances under climate change. *Nature Climate Change*, **7**, 395–402.

Slesak, R.A., Schoenholtz, S.H. & Evans, D. (2015) Hillslope erosion two and three years after wildfire, skyline salvage logging, and site preparation in southern Oregon, USA. *Forest Ecology and Management*, **342**, 1–7.

Smith, N.R., Kishchuk, B.E. & Mohn, W.W. (2008) Effects of wildfire and harvest disturbances on forest soil bacterial communities. *Applied and Environmental Microbiology*, **74**, 216–224.

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

Stevens-Rumann, C.S., Kemp, K.B., Higuera, P.E., Harvey, B.J., Rother, M.T., Donato, D.C., Morgan, P. & Veblen, T.T. (2017) Evidence for declining forest resilience to wildfires under climate change. *Ecology Letters*, **21**, 243–252.

Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F. & Ransome, D.B. (2010) Green-tree retention and life after the beetle: Stand structure and small mammals 30 years after salvage harvesting. *Silva Fennica*, **44**, 749–774.

Swedish Forest Agency (2011) *Skogsstyrelsens allmänna råd och föreskrifter till Skogsvårdslagen*, SKSFS, Jönköping.

Thorn, S., Bässler, C., Bernhardt-Römermann, M., Cadotte, M., Heibl, C., Schäfer, H., Seibold, S. & Müller, J. (2015) Changes in the dominant assembly mechanism drives species loss caused by declining resources. *Ecology Letters*, **19**, 109–215.

Thorn, S., Bässler, C., Brandl, R., Burton, P., Cahall, R., Campbell, J.L., Castro, J., Choi, C.-Y., Cobb, T., Donato, D., Durska, E., Fontaine, J., Gauthier, S., Hebert, C., Hothorn, T., Hutto, R., Lee, E.-J., Leverkus, A., Lindenmayer, D., Obrist, M., Rost, J., Seibold, S., Seidl, R., Thom, D., Waldron, K; Wermelinger, B., Winter, M.-B., Zmihorski, M. & Müller, J. (2018) Impacts of salvage logging on biodiversity – a meta-analysis. *Journal of Applied Ecology*, **55**, 279–289.

Thorn, S., Bässler, C., Svoboda, M. & Müller, J. (2017) Effects of natural disturbances and salvage logging on biodiversity - Lessons from the Bohemian Forest. *Forest Ecology and Management*, **388**, 113–119.

Turner, M.G. (2010) Disturbance and landscape dynamics in a changing world. *Ecology*, **91**, 2833–2849.

U.S. Environmental Protection Agency Terms of Environment: Glossary, Abbreviations and Acronyms, Revised December 1997.

Wagenbrenner, J.W., MacDonald, L.H., Coats, R.N., Robichaud, P.R. & Brown, R.E. (2015) Effects of post-fire salvage logging and a skid trail treatment on ground cover, soils, and sediment production in the interior western United States. *Forest Ecology and Management*, **335**, 176–193.

Wagner, J. (2012) *Forestry economics: A managerial approach*, Routledge, New York NY.

Wang, X., He, H.S., Li, X. & Hu, Y. (2006) Assessing the cumulative effects of postfire management on forest landscape dynamics in northeastern China. *Canadian Journal of Forest Research*, **36**, 1992–2002.

Whicker, J.J., Pinder, J.E. & Breshears, D.D. (2008) Thinning semiarid forests amplifies wind erosion comparably to wildfire: Implications for restoration and soil stability. *Journal of Arid Environments*, **72**, 494–508.

White, P.S. & Pickett, S.T.A. (1985) *Natural Disturbance and Patch Dynamics: An Introduction*, Academic Press, INC., Orlando, Florida.

Data accessibility

The data used for this manuscript are freely available as a tab-delimited text file at the University of Alcala institutional data repository at https://edatos.consorciomadrono.es/dataset.xhtml? persistentId=doi:10.21950/MF3TH1.

Table 1

Term	Definition
Salvage logging	The harvesting of trees after natural disturbances (Lindenmayer & Noss, 2006)
Green-tree harvesting	The harvesting of trees in the absence of recent natural disturbance
Clearcutting	Harvesting all the trees in one area at one time (U.S. Environmental Protection Agency)
Retention forestry	Management approach alternative to clearcutting where a portion of the original stand is left unlogged to maintain the continuity of structural and compositional diversity (Gustafsson *et al.*, 2012)
Natural disturbance	Any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment (White & Pickett, 1985)
Anthropogenic disturbance	Disturbance of human origin and characteristics that are distinctive from those of natural disturbances
Undisturbed forest	Forest that has not been affected by disturbance
Disturbance intensity	Physical magnitude of the disturbance event per area and time (White & Pickett, 1985)
Disturbance severity	Impact of disturbance on organisms, communities, or ecosystems (White & Pickett, 1985)
Ecosystem resistance	Capacity of an ecosystem to remain essentially unchanged despite the occurrence of disturbances (Grimm & Wissel, 1997)
Ecosystem resilience	Capacity to return to the reference state (or dynamic) after a temporary disturbance (Grimm & Wissel, 1997)
Biological legacies	The organisms, organic materials, and organically-generated environmental patterns that persist through a disturbance and are incorporated into the recovering ecosystem (Franklin *et al.*, 2000)
Driver	A variable that is causally linked, through direct or indirect pathways, to a measured change in a response variable (Didham *et al.*, 2007)

Interaction chain	One disturbance modifies the probability of occurrence, intensity, or extent of another driver and both affect the response variable directly (Foster *et al.*, 2016). Also termed linked disturbances (Buma, 2015)
Cascading effect	Emergent phenomena where a disturbance interaction can extend the impacts of a driver of one disturbance into another disturbance type (Buma, 2015)
Interaction modification	Phenomenon where the per capita effect of one disturbance depends on the effect of a second disturbance (Foster *et al.*, 2016). Also termed compounded disturbances (Buma, 2015)
Non-additive effect	Emergent property of the addition of two factors, whose combined effect differs from the addition of the two individual effects (Piggott *et al.*, 2015)
Synergistic	The effect of two factors applied in combination is greater than the sum of the effects of both factors applied in isolation
Antagonistic	The effect of two factors applied in combination is smaller than the sum of the effects of both factors applied in isolation
Non-linear effect	The change produced in a response variable per unit of an independent variable depends on the magnitude of the independent variable

Table 2

Treatment combinations	Papers* % (N)	Sample Questions and Implications (for any given response variable)
U, L D, SL	3.8 (8)	**Q**: Can the effect of salvage logging be predicted by adding the individual effects of logging and disturbance? Is the effect of salvage logging different from that of green-tree harvesting? **I**: Allows testing each component of the equation: $E_{SL} = E_D + E_L + E_{DxL}$ where E refers to the effect of SL= salvage logging, D= natural disturbance, L= logging, and DxL= disturbance by logging interaction. In cases where $E_{DxL}= 0$, one could predict salvage logging effects from the addition of the known effects of disturbance and logging
U D, SL	32.1 (67)	**Q**: What is the effect of natural disturbance and of subsequent salvage logging? Does salvage logging mitigate or amplify the consequences of natural disturbance? **I**: Allows measuring E_D and comparing its magnitude with that of the subsequent intervention, but E_L and E_{DxL} cannot be distinguished. Excludes testing the predictability of salvage logging effects from the individual effects of natural disturbance and logging or whether the effects of salvage logging and those of green-tree harvesting differ.
L D, SL	2.4 (5)	**Q**: What is the effect of the salvage logging intervention on a disturbed forest? How similar is a salvaged forest to a forest logged without previous disturbance? **I**: Allows measuring the effect of the salvage logging intervention, but there is no clear baseline condition for testing the elements in the above equation. Neither E_D or E_L can be distinguished from E_{DxL}; the selection of treatments rather suggests a 3-level categorical factor.
D, SL	61.7 (129)	**Q**: What is the effect of the salvage logging intervention on a disturbed forest? **I**: Allows measuring the effect of the salvage logging intervention, but not distinguishing whether the measured effect is due to logging *per se* or to logging forest that is disturbed –i.e., E_L confounded with E_{DxL}.

Combinations of forest states (treatments) that were employed in empirical studies on salvage logging and implications of treatment selection for testing interaction effects between the natural disturbance and the logging disturbance. Each treatment combination enables a certain set of questions to be answered, but for a comprehensive understanding of disturbance interaction modifications, factorial treatment combinations are needed.
* Numbers indicate the percentage (and total number) of publications with each kind of study design that were retrieved in a systematic review on the effects of salvage logging on ecosystem services (Leverkus *et al.*, 2018); total number of publications assessed = 209.

Q= example of question that can be asked. I= implications of the design.
= Undisturbed; = Naturally disturbed; = Logged; = Salvage logged; = Not included in the design.

Figure captions

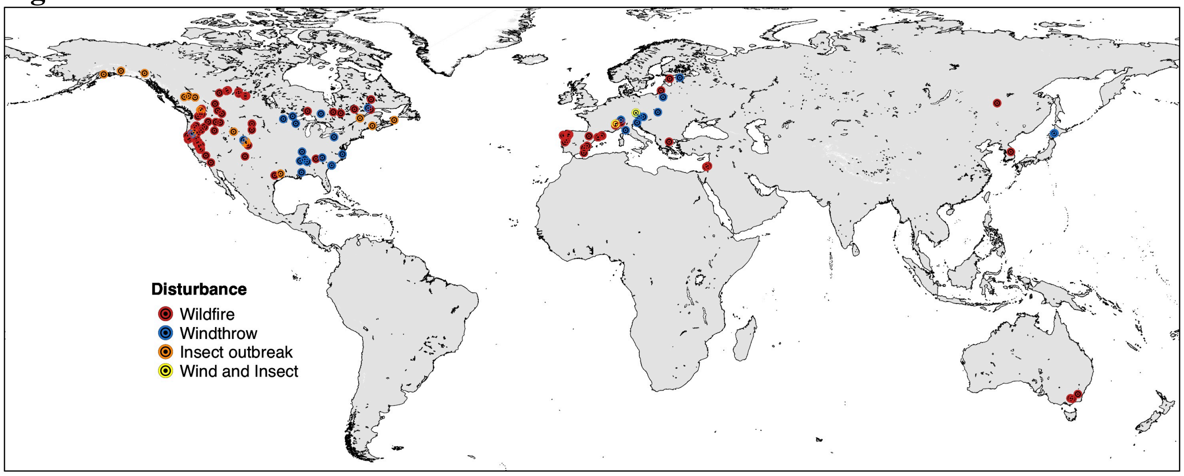
Figure 1. Locations of the studies that produced the 209 publications. One point is shown per study site (see associated data).

Figure 2. Examples of ecological responses to factorial combinations of natural disturbance and logging. A) Additive increases in wind erosion (Whicker *et al.*, 2008), B) additive decreases in bird species richness 7 years after wildfire (Lindenmayer *et al.*, 2018), C) Synergistic decline in tree-fern survival (Blair *et al.*, 2016), D) antagonistic effect on microbial soil carbon (Kishchuk *et al.*, 2015), E) white-spotted sawyer beetles (*Monochamus scutellatus*) only present under individual disturbances (Cobb *et al.*, 2010), F) Combined effect of wildfire and salvage logging on forest floor carbon showing up as a reduction in the speed of recovery (Kishchuk *et al.*, 2015). Panels C to F show cases of interaction modifications. UD= undisturbed; B= burnt; L= logged; SL= burnt and salvage logged.

Figure 3. Interaction chain between natural disturbance and logging. Three of the most pervasive differences between green-tree and salvage harvesting are: (a) that the latter affects stands that would otherwise be deemed unsuitable for logging, for example due to their young age; (b) that salvage logging operations tend to be more intense; and (c) that salvage clearcuts are generally much larger than green-tree clearcuts. These are characteristics of the interaction chain involving fire and subsequent logging. In (c), the huge post-fire clearcut (out of the 14000 ha burned, about 5500 ha were salvage logged) contrasts with the smaller green-tree clearcuts around the burnt area, signalled with white arrows. Photos from the 2014 fire near Uppsala, Sweden.

Figure 4. Potential confounding between interaction modification and interaction chain effects. The figure shows factorial combinations of natural disturbance x logging leading to four forest states: a) undisturbed, b) logged, c) disturbed, and d) salvage logged. Trees (or stands) of various ages are depicted, distributed within a site (or landscape). To empirically test for interaction modification effects from salvage logging (i.e., whether the effects of natural disturbance and logging are additive when the latter follows the first), treatment combinations a-d are required. The trees (or stands) in circles represent a mature pre-disturbance condition that would generally be the target of research across the four treatments. Note, however, that the interaction chain between disturbance and logging implies that salvage logging also targets stands that would be deemed too young for harvest in the absence of disturbance, and that salvage clearcuts are often larger (Figure 3). The design here shown would thus a) fail in showing the range of effects of salvage logging, as younger salvaged stands are not considered, and b) confound the interaction modification effect with potential effects of the interaction chain, as the study plots in d are located on a larger clearcut than in b. Also, potential nonlinear behaviour in the response to one or both disturbances would reduce the capacity to predict outcomes at levels of disturbance severity that differ from those tested in the experiment.

Figure 1



Disturbance
Wildfire
Windthrow
Insect outbreak
Wind and Insect

Figure 2

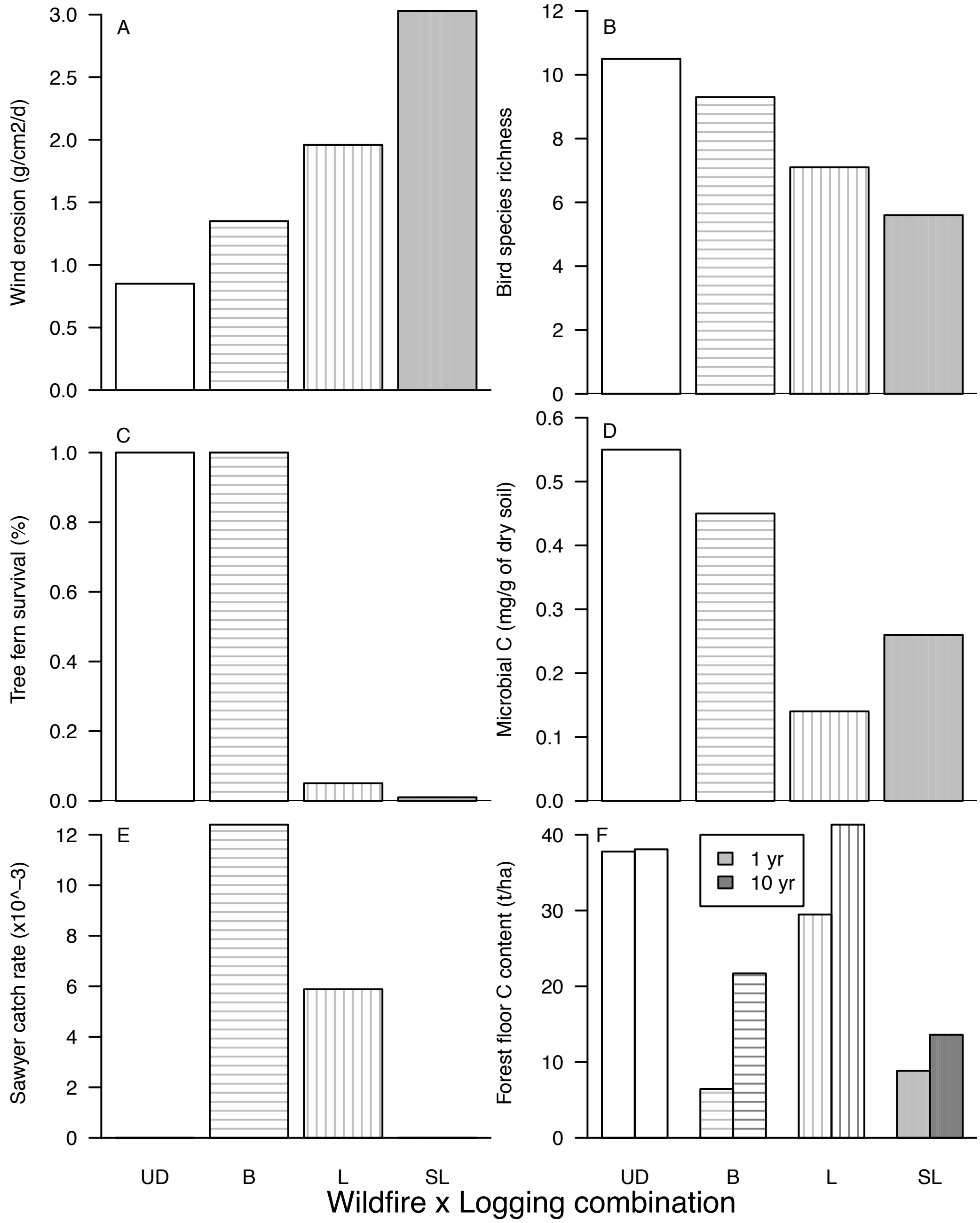

A
Wind erosion (g/cm2/d)
B
Bird species richness
C
Tree fern survival (%)
D
Microbial C (mg/g of dry soil)
E
Sawyer catch rate (x10^-3)
F
Forest floor C content (t/ha)
1 yr
10 yr
UD
B
L
SL
Wildfire x Logging combination

Figure 3

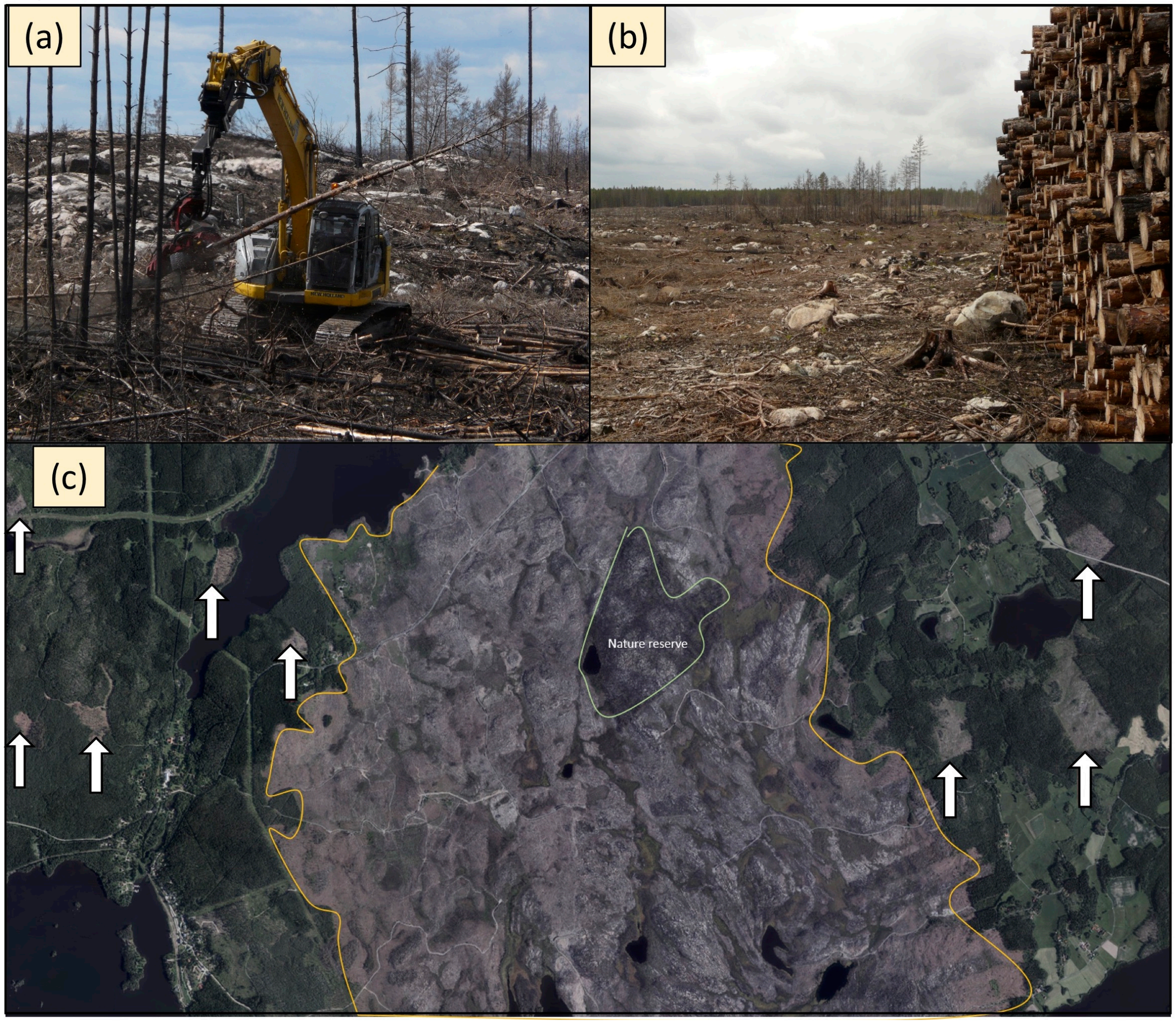
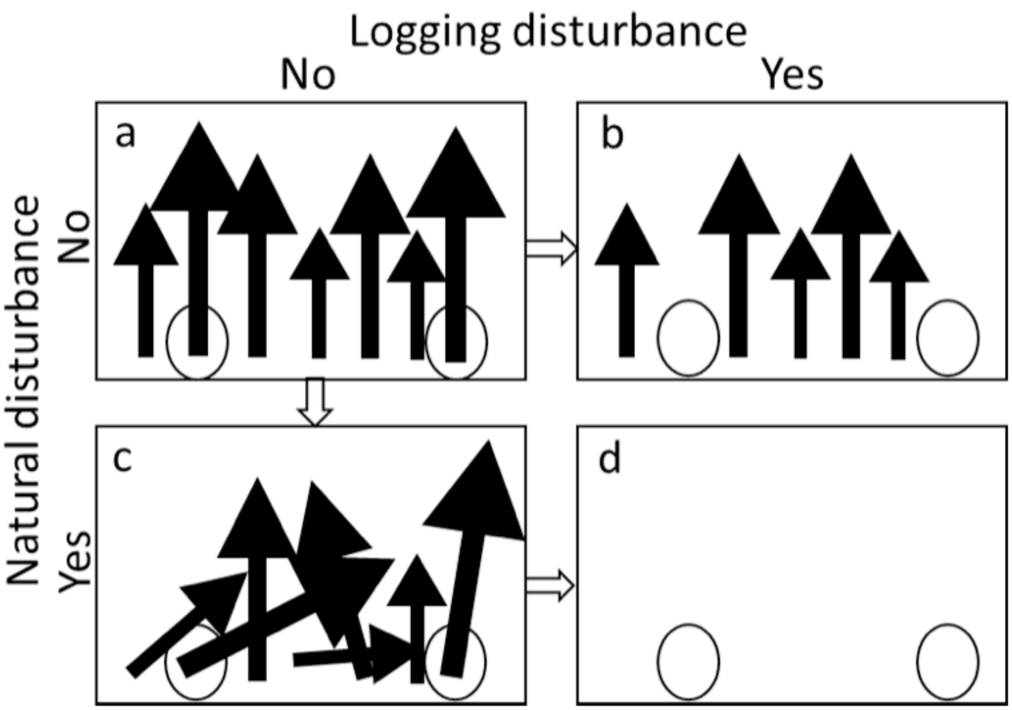


Figure 4


Logging disturbance
No
Yes
Natural disturbance
No
Yes
a
b
c
d