

This is an author produced version of a paper published in Global Ecology and Biogeography.

This paper has been peer-reviewed but may not include the final publisher proof-corrections or pagination.

Citation for the published paper:

Alexandro B. Leverkus David B. Lindenmayer Simon Thorn Lena Gustafsson. (2018) Salvage logging in the world's forests: Interactions between natural disturbance and logging need recognition. *Global Ecology and Biogeography*. Volume: 27, Number: 10, pp 1140-1154. http://dx.doi.org/10.1111/geb.12772.

Access to the published version may require journal subscription. Published with permission from: John Wiley & Sons.

Standard set statement from the publisher:

"This is the peer reviewed version of the above article, which has been published in final form at https://doi.org/10.1111/geb.12772. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving."

Epsilon Open Archive http://epsilon.slu.se

1	Concepts paper
2	
3	Salvage logging in the world's forests: interactions between natural
4	disturbance and logging need recognition
5	
6	Running head: Salvage logging and disturbance interactions
7	
8	
9	Alexandro B. Leverkus ^{1*} , David B. Lindenmayer ² , Simon Thorn ³ , Lena Gustafsson ⁴
10	
11	
12	¹ Departamento de Ciencias de la Vida, Universidad de Alcalá de Henares, Madrid, Spain.
13	alexandro.leverkus@uah.es
14	² Fenner School of Environment and Society, The Australian National University, Canberra
15	ACT 2614, Australia. David.Lindenmayer@anu.edu.au
16	³ Field Station Fabrikschleichach, Department of Animal Ecology and Tropical Biology
17	(Zoology III), Julius-Maximilians-University Würzburg, Glashüttenstraße 5, 96181
18	Rauhenebrach, Germany. <u>simon@thornonline.de</u>
19	⁴ Department of Ecology, Swedish University of Agricultural Sciences (SLU), P.O. Box
20	7044, SE-750 07 Uppsala, Sweden. Lena.Gustafsson@slu.se
21	*Commence to along the longely of Tal. 124 (22(80028
21 22	*Correspondence to <u>alexandro.leverkus@uah.es;</u> Tel.: +34 622689928
22	Acknowledgements
23 24	J. Ruiz Guzmán and E. Stengel assisted in the literature review. ABL acknowledges support
24 25	from grants P12-RNM-2705 from Junta de Andalucía, FJCI-2015-23687 from Spanish
25	MINECO, and CAS17/00374 from Spanish MECD. We thank two anonymous reviewers
20	for thoughtful comments that improved the manuscript.
27	for moughtur comments mat improved the manuscript.
29	Biosketch

30 AL is a postdoctoral fellow whose research focuses on post-fire regeneration and the effects 31 of salvage logging in the Sierra Nevada National Park, Spain. LG has a long career in 32 reconciling forestry practices with biodiversity conservation in Sweden. ST is a postdoc at 33 the University of Würzburg and his work has focused on the effects of salvage logging on 34 biodiversity in the Bavarian Forest National Park, Germany. DBL is a conservation 35 biologist who was among the first scientists to bring attention to and produce research 36 syntheses on the ecological effects of salvage logging; his empirical research focuses on the 37 Mountain Ash forests of Victoria, Australia. The authors are collaborating to synthesise the 38 ecological consequences of salvage logging at a global scale, involving qualitative and 39 quantitative methods.

- 40
- 41

42 Abstract

43

44 Aim. Large disturbances increasingly shape the world's forests. Concomitantly, increasing 45 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 46 47 disturbance and logging disturbance, including interactions so far unnoticed. Here, we use 48 recent advances in disturbance-interaction theory to disentangle and describe the 49 mechanisms through which natural disturbance (e.g. wildfire, insect outbreak or 50 windstorm) can interact with anthropogenic disturbance (logging) to produce unanticipated 51 effects. We also explore to what extent such interactions have been addressed in empirical 52 research globally.

53

54 Insights. First, many ecological responses to salvage logging likely result from interaction 55 modifications-i.e., from non-additive effects between natural disturbance and logging. 56 However, based on a systematic review encompassing 209 relevant papers, we found that 57 interaction modifications have been largely neglected. Second, salvage logging constitutes 58 an interaction chain because natural disturbances increase the likelihood, intensity and 59 extent of subsequent logging disturbance due to complex socio-ecological interactions. 60 Both interaction modifications and interaction chains can be driven by nonlinear responses 61 to the severity of each disturbance. We show that, whereas many of the effects of salvage

62	logging likely arise from the multiple kinds of disturbance interactions between natural
63	disturbance and logging, they have mostly been overlooked in research to date.
64	
65	Conclusions. Interactions between natural disturbance and logging imply that increasing
66	disturbances will produce even more disturbance, and with unknown characteristics and
67	consequences. Disentangling the pathways producing disturbance interactions is thus
68	crucial to guide management and policy regarding naturally disturbed forests.
69	
70	
71	Keywords: multiple disturbances, linked disturbances, compounded disturbances, salvage
72	harvesting, post-disturbance management, clearcutting, synergism, antagonism, cascading
73	effect, disturbance driver
74	

76 Introduction

77 Natural disturbances are affecting increasing amounts of forest globally (Pausas *et al.*,

- 78 2008; Seidl et al., 2017). Although forests generally have the capacity to regenerate under
- 79 historical disturbance regimes (Turner, 2010; Fernandez-Vega et al., 2017), there is
- 80 concern that novel disturbance conditions –such as altered disturbance frequencies or
- 81 multiple disturbances close in time- can affect ecosystem function and biodiversity and
- 82 ultimately trigger regime shifts (Peters *et al.*, 2011; Johnstone *et al.*, 2016; Sato &
- Lindenmayer, 2017; Stevens-Rumann *et al.*, 2017). Recent theoretical and empirical
- 84 advances have shown that multiple natural disturbances, such as wildfires, insect outbreaks,
- 85 windstorms, and grazing, can interact by affecting the likelihood of occurrence and
- 86 modulating the effects of one another, so that disturbance effects can often be understood
- 87 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
- 89 disturbances can be expected to result from interactions with other related, natural
- 90 disturbances. Concomitant to increases in natural disturbance, salvage logging –the felling
- 91 and removal of disturbance-affected trees- is a widespread and increasing human response
- 92 to natural disturbance worldwide (Lindenmayer *et al.*, 2004, 2008, 2017). The effects of
- 93 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
- 96 natural disturbance and logging disturbance can be expected.
- 97 Disturbance interactions can arise from two fundamentally-different mechanistic pathways (Didham et al., 2007; Buma, 2015; Foster et al., 2016), and there is increasing 98 99 recognition that a good understanding of these mechanisms is crucial for defining effective 100 management strategies (Foster et al., 2016). Disturbances interact when the legacies left 101 behind by one disturbance are functionally connected to another disturbance -i.e. when 102 they change the resistance and/or the resilience of the ecosystem to another disturbance 103 (James et al., 2007; Buma, 2015). On one hand, ecological responses to two consecutive 104 disturbances may differ from the addition of the response to each kind of disturbance in 105 isolation, which is termed an interaction modification (Table 1; Didham et al., 2007; Foster 106 et al., 2016). Additionally, one form of disturbance can change the likelihood and
- 107 magnitude of subsequent disturbance events via an *interaction chain* (Didham *et al.*, 2007;

108 Foster et al., 2016). Both types of interaction can show nonlinear behaviour relative to the 109 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 110 111 subsequently harvested, as salvage logging generally occurs within the first two years after 112 natural disturbance to avoid the deterioration of the wood (Leverkus et al., 2018). However, 113 despite intense and ongoing public, academic, and political controversy surrounding 114 salvage logging (Beschta et al., 1995; Lindenmayer et al., 2004, 2017; DellaSala et al., 115 2006; Donato et al., 2006a; Schiermeier, 2016; Leverkus et al., 2017a,b; Müller et al., 116 2018; Thorn et al., 2018) and numerous studies aiming to assess its ecological 117 consequences (reviewed in Leverkus et al., 2018 and Thorn et al., 2018), explicit 118 consideration of interactions between salvage logging and the preceding natural disturbance 119 has mostly been neglected in empirical studies. As a result, to be able to understand the 120 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; 121 122 Buma, 2015; Foster et al., 2016), with special focus on disturbance interactions and on the 123 mechanisms through which such interactions may occur.

124 Here, we discuss interactions between natural and anthropogenic disturbances, using 125 recent development of ecological theory (under the framework provided by Foster et al., 126 2016) to characterise salvage logging and its ecological effects. By applying the concepts of 127 interaction modifications, interaction chains, and nonlinear effects (Foster et al., 2016), we 128 aim to disaggregate the mechanisms driving ecological interactions related to salvage 129 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 130 131 paper is organised in four sections, comprising (1) Interaction modifications, (2) Interaction 132 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 133 134 the paper, we provide reasoned arguments on the applicability of disturbance interaction 135 theory to salvage logging, evidence for interactions from the peer-reviewed literature, 136 examples of the mechanisms producing such interactions, ways to distinguish the 137 contribution of each interaction type, and some key implications for conservation and 138 management. We emphasize that empirical research on salvage logging has only 139 superficially addressed disturbance interactions to date, whereas they are fundamental to

- 140 understand the ecological consequences of this increasingly prevalent practice and should
- 141 be carefully considered when designing new studies.
- 142

143 Salvage logging and interaction modifications

144

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).

150

151 Do salvage logging effects result from interaction modifications?

152 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 153 154 effects of the natural disturbance and the logging disturbance ($E_{SL} = E_D + E_L$). However, 155 many ecosystem responses to salvage logging are likely to differ from those of green-tree 156 harvesting due to the different conditions under which each kind of logging occurs (Van 157 Nieuwstadt et al., 2001; Karr et al., 2004; Lindenmayer et al., 2004; DellaSala et al., 2006; 158 Lindenmayer & Noss, 2006). As a result, the ecological effects of salvage logging would 159 result from interaction modifications; i.e., the sum of the effects of the individual 160 disturbances plus the interaction modification effect ($E_{SL} = E_D + E_L + E_{DxL}$). In particular, 161 disturbed forests are characterised by the types, abundances, and spatial distribution of biological legacies (Franklin et al., 2000). Elements such as downed and standing 162 163 deadwood that play key ecological roles (Lindenmayer & Possingham, 1996; Hutto, 2006; 164 Marañón-Jiménez & Castro, 2013; Wagenbrenner et al., 2015; Thorn et al., 2017), soft 165 disturbance edges that constitute appropriate habitat for many species (Hanson & Stuart, 2005), and the temporal dynamics that affect these elements, define such ecosystems and 166 167 set the scene for post-disturbance regeneration. Salvage logging changes the amount, 168 characteristics and spatial arrangement of most biological legacies (Lindenmayer & Ough, 169 2006), and it eliminates much of the spatial heterogeneity produced by a given natural 170 disturbance (Noss et al., 2006). It is thus possible that salvage logging produces interaction 171 modifications through the elimination and alteration of the biological legacies left behind

by the natural disturbance. Theoretically, this could generate mismatches between the

- 173 legacies that remain after the second disturbance and the evolutionary adaptations of
- 174 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.*,
- 176 2018), whereas green-tree operations generally impact other sets of taxa that are associated
- 177 with living trees (Berg *et al.*, 1994).
- 178

179 *Evidence for interaction modifications –systematic literature review*

180 Empirically detecting interaction modifications requires measuring a given response 181 variable in factorial combinations of two factors -natural disturbance and logging- as well 182 as explicit consideration of the interaction term in statistical analyses (Foster et al., 2016). 183 Such a design encompasses four kinds of forest states (or treatments): undisturbed, logged, 184 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 185 186 of the global scientific literature on salvage logging effects (Leverkus et al., 2018). 187 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 188 189 empirical studies published anytime until 31/12/2016 that fulfilled the conditions of a) 190 being field based, b) including one treatment where forest was disturbed (by wind, fire, or 191 insect outbreaks) but not logged, and c) including a treatment where the forest was affected 192 by the same disturbance and subsequently salvage logged. In contrast with the systematic 193 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 194 195 of the four forest states outlined above were included. We found that, out of 209 retrieved 196 papers (Figure 1), nearly two thirds compared the salvage logging treatment only with 197 disturbed forest, with nearly the remaining third additionally including undisturbed forest 198 as a reference (Table 2). Only eight papers (4% of all papers; Cobb et al., 2007, 2010, 199 2011; Smith et al., 2008; Whicker et al., 2008; Kishchuk et al., 2015, 2016; Blair et al., 200 2016), belonging to four studies -in Alberta and Ontario, Canada; New Mexico, USA; and 201 Victoria, Australia-included a factorial disturbance by logging design (Table 2), although 202 only one paper explicitly considered the interaction between natural disturbance and 203 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 ecologicalresponses that can occur.

206

207 Implications of interaction modifications

208 The four studies we identified revealed that the responses to natural disturbance and 209 logging can range from antagonistic to synergistic depending on the variable being 210 considered, passing through all kinds of ecological interaction categories, including additive effects (Piggott et al., 2015). Interaction modifications from salvage logging would 211 212 imply that the anthropogenic disturbance occurs under conditions of altered resilience 213 generated by the previous, natural disturbance (Buma, 2015). Ultimately, interaction 214 modifications could create conditions beyond the capacity of ecosystems to recover (Buma, 215 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 216 appropriate and efficient kind of study design and conservation efforts to the most relevant 217 218 targets.

219

220 Salvage logging and interaction chains

221 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

223 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).

225 For example, blowdown events can modify fuel structure and consequently the extent and

severity of wildfires (Cannon *et al.*, 2017).

227

228 Does salvage logging constitute an interaction chain?

Assessing disturbance interaction chains requires exploring whether the mechanisms that

230 produce forest resistance to disturbance change following a prior disturbance (Buma,

231 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

233 given area of forest, as well as how these may change following natural disturbance –i.e. it

234 requires addressing complex social-ecological interactions. Therefore, are forests more

prone to being logged after natural disturbance than in the absence of disturbance, orlogged at greater intensity or spatial extent?

In production forests, where management practices are driven primarily by 237 238 economic considerations, what limits logging in the absence of disturbance is chiefly the 239 expectation that the increase in value from not logging at a particular time –i.e. from 240 waiting to complete rotational cycles- is greater than if the wood is harvested (Wagner, 241 2012). Natural disturbance represents a tipping point in this regard: the economic value of a 242 stand stops increasing and starts decreasing due to factors like the decomposition of wood 243 and the expansion of insect galleries. There are additional considerations for salvage 244 logging, such as the market for salvaged timber, the available infrastructure (e.g., roads), 245 the need and cost of subsequent reforestation, and the policy and regulation framework. 246 Therefore, natural disturbance generates a shift in the main motivation that drives (or 247 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., 248 249 2008).

250 In protected forests, logging is primarily limited to meet nature conservation and 251 human recreation objectives. Following disturbance, protection may weaken, partly because 252 disturbed forests are often perceived as of lower ecological value than undisturbed forests 253 (Noss & Lindenmayer, 2006) and partly because salvage logging is sometimes perceived to 254 constitute the best-available method for ecological restoration (Müller et al., 2018). In 255 addition, following disturbance, conservation objectives are often overtaken by other 256 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 257 258 other infrastructure. Salvage logging also aims to reduce some negative consequences of 259 disturbance, such as limited access across the disturbed area (Leverkus et al., 2012). From 260 aesthetical and emotional points of view, disturbed forests are frequently regarded as "ugly 261 tree cemeteries" or disorganised stands needing to be "cleaned-up" (Noss & Lindenmayer, 262 2006). Such triggers and motivations are generally absent in undisturbed forests, and they 263 imply that the aims and values that limited logging in the absence of disturbance are 264 substituted by others more favourable to logging once disturbance occurs -thus inducing 265 the interaction chain.

266 Another mechanism triggering the interaction chain lies within the context of 267 interaction chains itself. The accumulation of dead wood after windthrow and/or insect outbreaks can increase the extent and intensity of subsequent wildfires (Kulakowski & 268 269 Veblen, 2007; Collins et al., 2012; Johnson et al., 2013). Windthrow events leave a 270 landscape characterised by weakened trees that may constitute the breeding ground for pest 271 insects that can also invade neighbouring forest (Schroeder, 2007; Stadelmann et al., 2013). 272 Such interaction chains between natural disturbances are widely recognised and feared, and 273 their avoidance constitutes a major motivation for salvage logging (Fraver *et al.*, 2011; 274 Thorn et al., 2017; Müller et al., 2018). For example, Swedish legislation obliges salvage logging after storms to leave a maximum of 5m³ ha⁻¹ of deadwood to prevent bark beetle 275 276 outbreaks (Swedish Forest Agency, 2011). Salvage logging may succeed in preventing such 277 interaction chains (Schroeder & Lindelöw, 2002; Buma & Wessman, 2012; Stadelmann et 278 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 279 280 one interaction chain paradoxically represents a major driving mechanism of yet another 281 interaction chain: that of disturbance followed by logging. Subsequently, other interaction 282 chains can be initiated, as post-disturbance logging can reduce ecosystem resistance to 283 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). 284

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).

292

293 *Evidence for the interaction chain*

A good example of disturbance-induced increases in the likelihood of logging is in

295 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,

298 2016), and windthrows in the Monarch Butterfly Reserve in Mexico, where logging aims to 299 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 300 301 Wisconsin, Radeloff et al. (2000) found that forests were 3 to 6 times more likely to be 302 logged than before the outbreak. In fact, immediate, large-scale salvage logging after major 303 disturbances is so common that reductions in the price of wood due to the flooding of the 304 market are a well-known sequel of disturbance (Peter & Bogdanski, 2010). Salvage 305 clearcuts are also often much larger than traditional, green-tree clearcuts (Radeloff et al., 306 2000; Hebblewhite et al., 2009; Sullivan et al., 2010). For example, mean clearcut size 307 increased fourfold after a mountain pine beetle outbreak in the southern Rocky Mountains 308 of Colorado (Collins et al., 2010). Referring to an extremely widespread beetle outbreak in 309 British Columbia, Sullivan et al. (2010, p.750) describe that "salvage logging is essentially 310 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 311 312 Uppsala, Sweden, which burnt ca. 14,000 ha of production forest. After the fire, forest 313 owners sought to sell the affected timber and improve regeneration conditions, which 314 resulted 1) in trees being cut at ages that would otherwise be considered unsuitably young 315 for harvesting (Figure 3-a), 2) logging at higher intensity than usual (Figure 3-b), and 3) the 316 creation of a continuous clearcut much larger than usual (Figure 3-c; however, some of the 317 burnt forest was acquired by the Swedish Government to create a nature reserve).

318

319 Implications of the interaction chain

320 Interaction chains constitute a major mechanism driving the ecological effects of salvage 321 logging. The first is that, once a natural disturbance occurs, logging can occur in places 322 where it would otherwise not, including protected areas and old-growth or very young 323 forests (Müller et al., 2018). In such a way, land-use policies that do not anticipate the risk 324 of disturbances may fail in defining where logging should or should not occur (Müller et 325 al., 2018). Furthermore, natural disturbance can be used as a justification to harvest forests, 326 stands or individual trees that were not affected by the natural disturbance under the 327 umbrella of salvage logging operations (e.g., Wang et al., 2006; Peter & Bogdanski, 2010), 328 a process termed "by-catch" (Lindenmayer et al., 2008). By-catch can be hard to avoid in 329 salvage operations where healthy and disturbance-affected trees are intermingled within

330 single stands (Peter & Bogdanski, 2010), and it is sometimes thought to be necessary to 331 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 332 333 disturbance (Wang et al., 2006; Lindenmayer et al., 2008). In addition, logging being more 334 intense and occurring at larger scales after disturbance than in its absence undermines the 335 essential role of biological legacies in post-disturbance ecosystem regeneration (Franklin et 336 al., 2000; Johnstone et al., 2016). For example, the large size of salvage clearcuts can affect 337 plant natural regeneration via seed dispersal due to increasing distances from seed sources 338 (Ritchie & Knapp, 2014; Leverkus et al., 2016).

339 Due to interaction chains, the climatic drivers of a given disturbance can indirectly 340 increase the magnitude of subsequent, connected disturbances (Seidl et al., 2017). As a 341 result, the consequences of the initial disturbance driver are carried over to another 342 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 343 344 climatic conditions associated with major natural disturbances (Lindenmayer *et al.*, 2008). 345 For example, drought typically precedes wildfire and beetle infestations, and windthrow 346 events are often associated with high rainfall, producing wet ground. Logging after such 347 disturbances thus occurs at a time of reduced ecosystem resilience due to drought (Harvey 348 et al., 2016), or it can amplify soil disturbance by ground-based machinery if the soil is wet 349 (Lindenmayer & Noss, 2006). Within an average of less than two years (Leverkus et al., 350 2018), the ecosystem passes from an undisturbed state to being subject to the combined 351 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 352 353 (Seidl *et al.*, 2017), the frequency and magnitude of cascading effects related to salvage 354 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 362 seed bank due to the salvage logged stand being too young or the large distance from seed 363 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 364 365 after logging; or d) cascading effects, such as when disturbance and salvage logging follow 366 severe drought and resprouting plant species are too weak to resprout twice (after fire and 367 again after logging). Effective management to tackle the interaction and avoid regeneration 368 failure requires knowledge of the mechanism driving each response -management 369 decisions made under wrong assumptions of the mechanism underlying the interaction can 370 fail to produce the desired outcomes and even produce the opposite effects (Foster et al., 371 2016).

372

373 Distinguishing the contribution of interaction modification and chain effects

374 An experimental test for disturbance interaction modifications requires explicit consideration of the interaction chain. If salvage logging affects forest stands of a broader 375 376 age range than green-tree harvesting, a design controlling for stand age would fail to 377 address the full array of effects of the interacting disturbances (Figure 4). Conversely, if the 378 interaction chain is not controlled -for example if salvage study plots are located on larger 379 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 380 381 of interaction chains (such as cascading effects) are extremely difficult to isolate in 382 individual studies, other aspects can be addressed through careful study design. First, to 383 address interaction modifications, these are best tested under the factorial combination of disturbance and logging treatments, with logging applied with the same machinery, 384 385 intensity, extent, and in similar forest as green-tree harvesting. Second, individual aspects 386 of the interaction chain could be assessed by comparing salvage logged stands of different 387 dimensions (to test the effects of salvage clearcuts being larger), salvaged stands with 388 different degrees of dead-tree retention (effects of salvage operations being more intense), 389 salvaged stands of a range of pre-disturbance ages (effects of salvage clearcuts being less 390 selective), etc. And third, it may be of interest to establish herbivore exclosures and, where 391 applicable, careful removal of invasive species, to assess the extent to which salvage 392 logging effects are modulated by interaction chains with subsequent disturbances. Although 393 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
- 395 should clearly address the specific mechanisms driving interactions. Finally, given issues
- such as climate change, cascading effects, and shifting disturbance regimes (Seidl *et al.*,
- 397 2017), it is essential that individual studies thoroughly report on stand conditions and the
- 398 characteristics of disturbance events to allow future quantitative reviews on the topic.
- 399

400 Nonlinear behaviour in natural disturbance x logging interactions

- 401 The response of ecosystems to disturbance, and the magnitude of disturbance interaction 402 chains and interaction modifications, can show nonlinear behaviour relative to the intensity 403 or severity of the individual disturbances (Peterson, 2002; Peters et al., 2004; Foster et al., 404 2016). Nonlinearities mean that small differences in the severity of one of the disturbances 405 can generate disproportionally large differences in effects. For example, a study in 406 Colorado found that high-severity windthrow increased the severity of subsequent fire due 407 to the accumulation of large amounts of coarse woody debris and hence reduced tree 408 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 409 regeneration (Buma & Wessman, 2011). Identifying such thresholds can be critical for 410 411 defining appropriate management strategies (Peters et al., 2004), for example by providing 412 better assessments of post-disturbance tree regeneration capacity. The potential for 413 nonlinear responses precludes the extrapolation of disturbance effects beyond and between 414 the particular disturbance intensities assessed in a study (Foster et al., 2016). Further, due 415 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 416 417 and do not necessarily reflect a finding that is generalizable to other disturbance intensity 418 levels (see Foster et al., 2016 for examples).
- 419
- 420 Nonlinear behaviour in interaction modifications
- 421 To assess nonlinearities in interactive responses to two consecutive disturbances, at least
- 422 one of them must be sampled over a range of intensities, preferably as a continuous variable
- 423 (Foster *et al.*, 2016). Of the 209 articles retrieved in our systematic literature search
- 424 described above, we found that 14% (n = 30) sampled over different levels of severity of
- 425 the natural disturbance or at least used some proxy of disturbance severity as a covariate

426 (although not many studies specifically addressed nonlinear effects). An example of a

427 nonlinear interaction comes from (Royo *et al.*, 2016), who found that salvage logging after

428 a tornado in Pennsylvania, USA, reduced tree sapling basal area and density, but only at

429 high windthrow severity and only 1-2 years after logging. In that study, the interactive

430 effects of a tornado and logging caused a change in successional trajectory, yet only at high

431 wind-disturbance severity.

432 Some studies also tested the effects of variable salvage logging intensities. Of the 433 209 papers, 24% (n = 50) included some measure of salvage logging intensity or 434 encompassed different salvage logging treatments that differed in the intensity of the 435 intervention. A study with five experimental salvage logging intensities (with 0, 25, 50, 75, 436 and 100% retention) was established after the 2002 Cone Fire in California. Although 437 nonlinear behaviour was not specifically addressed, the results of that study suggest that 438 some response variables –such as shrub cover– may show nonlinear effects of salvage 439 logging intensity, and that some others -fine woody debris in this case- can show nonlinear 440 interactions between salvage intensity and time (Knapp & Ritchie, 2016). Conversely, the 441 sampling of 255 stands across Oregon and Washington showed that the response of woody 442 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.

449

450 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).

465

466 *Implications of nonlinear behaviour*

467 A major implication of possible nonlinearities is that the effects of salvage logging could be 468 modulated by where and how it is conducted. Can the negative consequences of salvage 469 logging be mitigated if operations target stands below a certain severity level of the 470 preceding natural disturbance? Do threshold values in snag retention govern the response of 471 organisms to salvage logging? Are such thresholds similar to those seen for green-tree 472 harvesting? Such questions remain largely unanswered. It is noteworthy that, in contrast to 473 salvage logging, research on green-tree harvesting has already produced valuable 474 information on the benefits of single- and group-tree retention (Fedrowitz et al., 2014; Mori 475 & Kitagawa, 2014). As a result, the concept of retention forestry was created, targeting the 476 long-term retention of key structural elements and organisms to promote the "continuity in 477 forest structure, composition, and complexity that promotes maintenance of biodiversity 478 and ecological functions at different spatial scales" (Lindenmayer et al., 2012). Such an 479 approach currently lacks a counterpart in disturbed forests (Lindenmayer et al., 2018), 480 while it is precisely in such forests that biological legacies are crucial for regeneration 481 (Franklin *et al.*, 2000). Paradoxically, whereas green-tree retention aims to emulate natural 482 disturbance dynamics (Lindenmayer et al., 2012), once a natural disturbance occurs, the 483 most common response is salvage logging. Important unresolved questions to guide the 484 applicability of the retention approach to disturbed forests include: To what extent does 485 dead tree retention in salvage logged areas have similar effects to snag retention in areas 486 subject to green-tree retention harvesting? And, do potential differences result from 487 nonlinear effects of disturbance or logging intensity?

488

489 Using knowledge on interactions to improve policy and practice

490 Some of the interactions between natural disturbance and logging are driven by the 491 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 492 493 due to the lack of planning and fear of the quick loss of economic value of the wood 494 (Lindenmayer et al., 2008). As many of the interactions described above occur within the 495 context of specific policy and regulatory contexts, they can also be modulated through 496 changes in policy, law, and education. Logging is an anthropogenic disturbance and hence 497 there are opportunities to control where, how, and how much salvage logging should occur 498 after disturbance (Müller et al., 2018). Enhanced policies and practices should be based on 499 our understanding of interaction effects, such as the existence of synergistic effects of 500 disturbance and logging (interaction modifications), the effect that salvage logging 501 produces on the risk of subsequent disturbance (interaction chains), the thresholds of 502 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 503 504 (cascading effects). For example, cascading effects can be reduced by controlling the 505 timing of salvage logging. On the other hand, great challenges remain in the face of 506 uncertainty, as salvage logging can have unforeseeable effects related to interactions with 507 subsequent disturbances. For instance, whereas post-storm salvage logging can negatively 508 impact tree regeneration (Rumbaitis del Rio, 2006), this effect can turn out positive if it 509 mitigates the severity of subsequent fire (Buma & Wessman, 2011).

510

511 Conclusions

Paine and colleagues (1998) argued that understanding the ecological interactions arising 512 from multiple disturbances would be essential for environmental management in the 21st 513 514 century. As revealed by our systematic review, two decades later we are still some way 515 from understanding the interactive nature of a key sequence of natural and anthropogenic 516 disturbances. In fact, the majority of studies on salvage logging lack the necessary design to 517 test for interactions between natural disturbance and logging, despite many mentioning 518 interactions as likely explanations of their results. To avoid unexpected responses of 519 ecosystem functions and services, as well as losses in forest resilience and biodiversity 520 worldwide, policies regarding disturbed forests need to account for the problems arising 521 from interacting disturbances, recognising that salvage logging, by definition, constitutes a

522 sequence of disturbances. To guide such policies, the design of studies on salvage logging 523 requires explicit assessment of the multiple pathways through which natural disturbance and logging interact, including interaction modifications, interaction chains, nonlinear 524 behaviour in the interactions, cascading effects, and potential subsequent disturbances. This 525 526 requires not only addressing the ecological effects of disturbance at the scale of stands, but 527 also disentangling the socio-ecological interactions leading to the concatenation of natural 528 and anthropogenic disturbances and assessing the effects of such interactions at broader 529 spatial and temporal scales. In a world of shifting disturbance regimes, where forests are 530 increasingly susceptible to the effects of individual and multiple natural disturbances, and 531 where salvage logging typically follows, we require better understanding of the role that 532 our response to natural disturbances is playing in defining the future of the world's forests. 533 534 References

- 535
- 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.
- 542 Beschta, R.L., Frissell, C. a, Gresswell, R.E., Hauer, R., Karr, J.R., Minshall, G.W., Perry,
 543 D. a & Rhodes, J.J. (1995) Wildfire and salvage logging. 16 pp.
- 544 Blair, D.P., McBurney, L.M., Blanchard, W., Banks, S.C. & Lindenmayer, D.B. (2016)
 545 Disturbance gradient shows logging affects plant functional groups more than fire.
- 546 *Ecological Applications*, **26**, 2280–2301.
- 547 Buma, B. (2015) Disturbance interactions: characterization, prediction, and the potential for
 548 cascading effects. *Ecosphere*, 6, Art70.
- 549 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.
- 560 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.
- 563 Cobb, T.P., Morissette, J.L., Jacobs, J.M., Koivula, M.J., Spence, J.R. & Langor, D.W.
- 564 (2011) Effects of postfire salvage logging on deadwood-associated beetles.
 565 *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.
- 570 Collins, B.J., Rhoades, C.C., Underhill, J. & Hubbard, R.M. (2010) Post-harvest seedling
 571 recruitment following mountain pine beetle infestation of Colorado lodgepole pine
 572 stands: a comparison using historic survey records. *Canadian Journal of Forest*573 *Research*, 40, 2452–2456.
- 574 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.
- 577 Didham, R.K., Tylianakis, J.M., Gemmell, N.J., Rand, T.A. & Ewers, R.M. (2007)
- 578 Interactive effects of habitat modification and species invasion on native species
 579 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
- 582 Increases Fire Risk." *Science*, **313**, 4–6.
- 583 Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B. & Law, B.E.
- 584 (2006b) Post-wildfire logging hinders regeneration and increases fire risk. *Science*,
- **311**, 352.

- 586 Fedrowitz, K., Koricheva, J., Baker, S.C., Lindenmayer, D.B., Palik, B., Rosenvald, R.,
- 587 Beese, W., Franklin, J.F., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygeson,
- A. & Gustafsson, L. (2014) Can retention forestry help conserve biodiversity? A metaanalysis. *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
- 592 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.
- 599 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.
- 608 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., SverdrupThygeson, A., Volney, W.J.A., Wayne, A. & Franklin, J.F. (2012) Retention forestry
- 611 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 standreplacing burn patches. *Global Ecology and Biogeography*, 25, 655–669.

- 618 Hebblewhite, M., Munro, R.H. & Merrill, E.H. (2009) Trophic consequences of postfire
- 619 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 pileand-burn on fuel loading, potential fire behaviour, fuel consumption and emissions. *International Journal of Wildland Fire*, 22, 757–769.
- 628 Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E.,
- 629 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.
- 635 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
- 637 influence rate of boreal soil carbon change: a Canadian multi-regional analysis. *Forest*638 *Ecology and Management*, **381**, 48–62.
- 639 Kishchuk, B.E., Thiffault, E., Lorente, M., Quideau, S., Keddy, T. & Sidders, D. (2015)
- 640 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
- 647 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.

- 650 Leverkus, A.B., Castro, J., Puerta-Piñero, C. & Rey Benayas, J.M. (2013) Suitability of the
- 651 management of habitat complexity, acorn burial depth, and a chemical repellent for
- post-fire reforestation of oaks. *Ecological Engineering*, **53**, 15–22.
- 653 Leverkus, A.B., Gustafsson, L., Rey Benayas, J.M. & Castro, J. (2015) Does
- 654 post-disturbance salvage logging affect the provision of ecosystem services? A

655 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.,
- 668 Macdonald, E., Marzano, R., Rhoades, C.C., Thorn, S., Royo, A., Wagenbrenner,
- 569 J.W., Waldron, K., Wohlgemuth, T. & Gustafsson, L. (2018) Salvage logging effects
- 670 on regulating and supporting ecosystem services A systematic map. *Canadian*671 *Journal of Forest Research (In press).*
- 672 Lewis, D., St Pierre, C. & McCrone, A. (2008) Trends in salvage-logging practices in
- 673 mountain pine beetle-affected landscapes: implications to biodiversity conservation.
- 674 *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.
- 679 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.

- 682 Lindenmayer, D.B., Franklin, J.F., Lõhmus, a., Baker, S.C., Bauhus, J., Beese, W., Brodie,
- 683 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
- 686 issues. *Conservation Letters*, **5**, 421–431.
- 687 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.
- 692 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.
- 701 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.
- 707 Moreira, F., Ferreira, a., Abrantes, N., Catry, F., Fernandes, P., Roxo, L., Keizer, J.J. &
- 708 Silva, J. (2013) Occurrence of native and exotic invasive trees in burned pine and
- eucalypt plantations: Implications for post-fire forest conversion. *Ecological*
- 710 *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.
- 717 Van Nieuwstadt, M.G., L., Sheil, D. & Kartawinata, K. (2001) The Ecological
- 718 Consequences of Logging in the Burned Forests of East Kalimantan, Indonesia.
- 719 *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.
- 739 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.
- 742 Peters, D.P.C., Pielke, R.A., Bestelmeyer, B.T., Allen, C.D., Munson-McGee, S. &
- 743 Havstad, K.M. (2004) Cross-scale interactions, nonlinearities, and forecasting
- 744 catastrophic events. Proceedings of the National Academy of Sciences of the United
- 745 *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.
- 766 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.
- 770 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,
- 775 M., Fabrika, M., Nagel, T.A. & Reyer, C.P.O. (2017) Forest disturbances under
- climate change. *Nature Climate Change*, 7, 395–402.
- 777 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.
- 783 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.
- 789 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.
- 792 Swedish Forest Agency (2011) *Skogsstyrelsens allmänna råd och föreskrifter till* 793 *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.
- 797 Thorn, S., Bässler, C., Brandl, R., Burton, P., Cahall, R., Campbell, J.L., Castro, J., Choi,
- 798 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.,
- 800 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.
- 806 Turner, M.G. (2010) Disturbance and landscape dynamics in a changing world. *Ecology*,
 807 91, 2833–2849.
- 808 U.S. Environmental Protection Agency Terms of Environment: Glossary, Abbreviations
 809 and Acronyms, Revised December 1997.

810	Wagenbrenner, J.W., MacDonald, L.H., Coats, R.N., Robichaud, P.R. & Brown, R.E.
811	(2015) Effects of post-fire salvage logging and a skid trail treatment on ground cover,
812	soils, and sediment production in the interior western United States. Forest Ecology
813	and Management, 335 , 176–193.
814	Wagner, J. (2012) Forestry economics: A managerial approach, Routledge, New York NY.
815	Wang, X., He, H.S., Li, X. & Hu, Y. (2006) Assessing the cumulative effects of postfire
816	management on forest landscape dynamics in northeastern China. Canadian Journal
817	of Forest Research, 36 , 1992–2002.
818	Whicker, J.J., Pinder, J.E. & Breshears, D.D. (2008) Thinning semiarid forests amplifies
819	wind erosion comparably to wildfire: Implications for restoration and soil stability.
820	Journal of Arid Environments, 72, 494–508.
821	White, P.S. & Pickett, S.T.A. (1985) Natural Disturbance and Patch Dynamics: An
822	Introduction, Academic Press, INC., Orlando, Florida.
823	
824	
825	Data accessibility
826	The data used for this manuscript are freely available as a tab-delimited text file at the
827	University of Alcala institutional data repository at
828	https://edatos.consorciomadrono.es/dataset.xhtml? persistentId=doi:10.21950/MF3TH1.
829	
830	

831 Table 1

Term	Definition
Salvage	The harvesting of trees after natural disturbances (Lindenmayer & Noss,
logging	2006)
Green-tree	The harvesting of trees in the absence of recent natural disturbance
harvesting	
Clearcutting	Harvesting all the trees in one area at one time (U.S. Environmental Protection
	Agency)
Retention	Management approach alternative to clearcutting where a portion of the
forestry	original stand is left unlogged to maintain the continuity of structural and
	compositional diversity (Gustafsson et al., 2012)
Natural	Any relatively discrete event in time that disrupts ecosystem, community, or
disturbance	population structure and changes resources, substrate availability, or the
	physical environment (White & Pickett, 1985)
Anthropogenic	Disturbance of human origin and characteristics that are distinctive from those
disturbance	of natural disturbances
Undisturbed	Forest that has not been affected by disturbance
forest	
Disturbance	Physical magnitude of the disturbance event per area and time (White &
intensity	Pickett, 1985)
Disturbance	Impact of disturbance on organisms, communities, or ecosystems (White &
severity	Pickett, 1985)
Ecosystem	Capacity of an ecosystem to remain essentially unchanged despite the
resistance	occurrence of disturbances (Grimm & Wissel, 1997)
Ecosystem	Capacity to return to the reference state (or dynamic) after a temporary
resilience	disturbance (Grimm & Wissel, 1997)
Biological	The organisms, organic materials, and organically-generated environmental
legacies	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	One disturbance modifies the probability of occurrence, intensity, or extent of		
chain	another driver and both affect the response variable directly (Foster et al.,		
	2016). Also termed linked disturbances (Buma, 2015)		
Cascading	Emergent phenomena where a disturbance interaction can extend the impacts		
effect	of a driver of one disturbance into another disturbance type (Buma, 2015)		
Interaction	Phenomenon where the per capita effect of one disturbance depends on the		
modification	effect of a second disturbance (Foster et al., 2016). Also termed compounded		
	disturbances (Buma, 2015)		
Non-additive	Emergent property of the addition of two factors, whose combined effect		
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	The change produced in a response variable per unit of an independent		
effect	variable depends on the magnitude of the independent variable		

Table 2

Treatment		Papers*	Sample Questions and Implications
combinations		% (N)	(for any given response variable)
U	L	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= $(L = L)^{-2}$
			logging, and DxL= disturbance by logging interaction.
D	SL		In cases where $E_{DxL}= 0$, one could predict salvage logging effects from the
			addition of the known effects of disturbance and logging
			Q : What is the effect of natural disturbance and of subsequent salvage logging?
U		32.1 (67)	Does salvage logging mitigate or amplify the consequences of natural disturbance?I: Allows measuring E_D and comparing its magnitude with that of the
	SL 3:		subsequent intervention, but E_L and E_{DxL} cannot be distinguished. Excludes
			testing the predictability of salvage logging effects from the individual effects
D			of natural disturbance and logging or whether the effects of salvage logging
			and those of green-tree harvesting differ.
			Q : What is the effect of the salvage logging intervention on a disturbed forest?
	L		How similar is a salvaged forest to a forest logged without previous
			disturbance?
		2.4 (5)	I: Allows measuring the effect of the salvage logging intervention, but there is
		2.4 (3)	no clear baseline condition for testing the elements in the above equation.
D	SL		Neither E_D or E_L can be distinguished from E_{DxL} ; the selection of treatments
Ð	JL		rather suggests a 3-level categorical factor.
			Q : What is the effect of the salvage logging intervention on a disturbed forest?
		61.7	I: Allows measuring the effect of the salvage logging intervention, but not
	ar	(129)	distinguishing whether the measured effect is due to logging per se or to
D	SL		logging forest that is disturbed –i.e., E _L confounded with E _{DxL} .

- 835 Combinations of forest states (treatments) that were employed in empirical studies on
- 836 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.
- 840 * Numbers indicate the percentage (and total number) of publications with each kind of
 841 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.
- 842 ecosystem services (Leverkus *et al.*, 2018); t 843
- 844 Q = example of question that can be asked. I= implications of the design.
- 845 \Box = Undisturbed; = Naturally disturbed; \Box = Logged; = Salvage logged;
- 846 Not included in the design.
- 847
- 848

- 849 Figure captions
- 850

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

853

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

863 logged. 864

865 Figure 3. Interaction chain between natural disturbance and logging. Three of the most 866 pervasive differences between green-tree and salvage harvesting are: (a) that the latter 867 affects stands that would otherwise be deemed unsuitable for logging, for example due to 868 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 869 870 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) 871 872 contrasts with the smaller green-tree clearcuts around the burnt area, signalled with white 873 arrows. Photos from the 2014 fire near Uppsala, Sweden.

874

875 Figure 4. Potential confounding between interaction modification and interaction chain 876 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 877 stands) of various ages are depicted, distributed within a site (or landscape). To empirically 878 879 test for interaction modification effects from salvage logging (i.e., whether the effects of 880 natural disturbance and logging are additive when the latter follows the first), treatment 881 combinations a-d are required. The trees (or stands) in circles represent a mature pre-882 disturbance condition that would generally be the target of research across the four 883 treatments. Note, however, that the interaction chain between disturbance and logging 884 implies that salvage logging also targets stands that would be deemed too young for harvest 885 in the absence of disturbance, and that salvage clearcuts are often larger (Figure 3). The 886 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 887 888 effect with potential effects of the interaction chain, as the study plots in d are located on a 889 larger clearcut than in b. Also, potential nonlinear behaviour in the response to one or both 890 disturbances would reduce the capacity to predict outcomes at levels of disturbance severity 891 that differ from those tested in the experiment.







