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Effects of intensified forestry on the landscape-scale extinction risk of dead-wood dependent species

Short title: Effects of intensified forestry on extinction risks

Thomas Ranius^{1,*}, Jean-Michel Roberge²

¹ Department of Ecology, Swedish University of Agricultural Sciences (SLU), Uppsala, Sweden

² Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences (SLU), S-90183 Umeå, Sweden

* Corresponding author. Dept. of Ecology, SLU, Box 7044, SE-750 07 Uppsala, Sweden, Email: thomas.ranius@ekol.slu.se, Phone: ++46-18-67 23 34, Fax: ++46-18-67 28 90.

1 **Abstract**

2 In the future, a significant proportion of northern forests may become intensively
3 managed through the planting of monospecific stands of native or introduced trees, and
4 the use of multiple silvicultural treatments such as forest fertilization. Such an
5 intensification of management in selected parts of the landscape is suggested by different
6 zoning models, for example the Triad approach, which is under evaluation in some
7 regions of North America. In this study, based on Fennoscandian conditions, we
8 predicted landscape-scale extinction risks of five hypothetical model insect species
9 dependent on fresh dead wood from Norway spruce (*Picea abies*), by simulating
10 colonizations and local extinctions in forest stands. Intensified forestry applied to 50 % of
11 the spruce stands led to strongly increased extinction risks of all species during the
12 following 150 years. For one species – the sun-exposure specialist – there were strong
13 effects already after 50 years. The negative effects of intensive plantation forestry could
14 be compensated for by taking greater biodiversity conservation measures in other
15 managed forests or by setting aside more forests. This is consistent with the Triad model,
16 which is according to our analyses an effective way to decrease extinction risks,
17 especially for the short-dispersing species and the species associated with closed forest. A
18 zoning of forest land into intensive forestry, conventional forestry, and set asides may be
19 better at combining increased timber production and maintenance of biodiversity in
20 comparison to landscapes where all production forests are managed in the same way.

21

22 **Keywords:** CWD, functional zoning, metapopulation, plantation forestry, population
23 viability analysis, saproxylic insects, Triad

24 **Introduction**

25 Forest management includes a range of intensities, from management based on close-to-
26 nature principles (e.g., Madsen and Hahn 2008) to plantation forestry involving non-
27 native tree species and multiple silvicultural treatments. Plantation forestry generally
28 implies that tree species (native or introduced) are sown or planted so that evenly spaced
29 and even-aged monocultures are obtained. In 2006 it was estimated that plantation forests
30 covered 3.5 % of the forest area in the world, and the covered area was increasing with
31 2 % per year (Anonymous 2006).

32 In Sweden, it has been estimated that 4 million ha could be used for intensified
33 forestry, which may be compared with the country's 23 million ha of productive forest.
34 The main part of the land potentially dedicated to intensified forestry is currently
35 supporting conventionally managed forests, and a smaller part is abandoned agricultural
36 land (Larsson et al. 2009). Intensive forestry in Sweden involves multiple silvicultural
37 treatments (including fertilization) in monocultures of introduced tree species such as
38 lodgepole pine (*Pinus contorta*), hybrid aspen (*Populus tremula* × *P. tremuloides*), and
39 hybrid larch (*Larix* × *eurolepsis*), or of native tree species, especially Norway spruce
40 (*Picea abies*) (Larsson et al. 2009). In Sweden, forest plantations are increasing, and in
41 2005 they covered 2.4% of the forest land (Anonymous 2006).

42 Due to negative effects on the abundance of natural forest structures and processes,
43 intensified forestry has been shown to have negative effects on large numbers of naturally
44 occurring species at the scale of forest stands (e.g., Baguette et al. 1994; Chey et al. 1997;
45 Magura et al. 2000). For example, many saproxylic species (i.e. species dependent on
46 dead wood) may be affected because stands managed intensively for the sole aim of
47 maximizing timber production contain virtually no dead wood of larger diameters, except
48 ephemerally in the case of accidental disturbances, where dead trees are typically
49 salvaged shortly after disturbance. When experts were asked about intensified
50 management in Sweden, they estimated that the effect on all evaluated organism groups
51 (vascular plants, lichens, bryophytes, grasses, shrubs, birds, saproxylic species, and red-
52 listed species) would be strongly negative (Gustafsson et al. 2009). Hence, at the scale of
53 individual forest stands, intensive forestry is not compatible with the conservation of
54 native biodiversity. Consequently, implementing intensive forestry over the entire forest

55 land base would clearly not be compatible with society's commitment to sustainable
56 development. However, little is known about the ecological effects of dedicating various
57 proportions of landscapes and regions to intensive forestry.

58 A forest management concept which has gained interest in the past decades is the
59 Triad model (Seymour and Hunter 1992), whereby the forest landscape is divided into
60 three types of uses: (1) intensive forestry, (2) ecological forestry and (3) set-asides. In
61 that zoning system, the negative ecological effects of intensive forestry would be
62 compensated by increased biodiversity conservation measures in the rest of the landscape
63 through ecological forestry and forest protection. Such a zoning model is in place in some
64 regions, e.g. southwestern Australia (Stoneman 2007). The Triad has also been proposed
65 for implementation across Canada's boreal forest (Anonymous 1999) and case studies are
66 ongoing in different regions (e.g. Montigny and MacLean 2006; Messier et al. 2009).
67 However, empirical studies of the consequences of such an approach for biodiversity are
68 difficult, because most species extinctions at the landscape level occur with some delay
69 after the management regime has been changed (Ranius and Kindvall 2006).

70 In this study we use population viability analyses of generalized model species over
71 250 years to isolate the effect of different landscape zoning scenarios in the long term.
72 We predict the landscape-scale extinction risk for five saproxylic model insect species by
73 combining simulations of habitat dynamics with a metapopulation model. The aims were:
74 (1) to analyse how long time it takes before intensified forestry increases the extinction
75 risk at the landscape level for species with different characteristics, (2) to compare the
76 response of species with different habitat affinities and life-history traits, and (3) to test
77 the efficacy of compensation measures whereby greater biodiversity consideration is
78 made in the rest of the landscape to counteract the potential negative effects of intensified
79 forestry.

80

81 **Methods**

82 *The metapopulation model*

83 For a hypothetical forest landscape divided into forest stands, we used computer
84 simulations to predict the availability of dead wood in every forest stand and the
85 colonization-extinction dynamics of the saproxylic model species in these stands. As

86 response variable we used the extinction risk at the landscape level, estimated from 1,000
87 replicates for each scenario–species combination. This number of replicates is sufficient
88 to obtain stable outcomes among simulation runs.

89 We used the incidence function model (IFM) equation to predict colonization-
90 extinction dynamics (Hanski 1994; 2000). Every year each stand could either be occupied
91 or not by a local population. The amount of habitat (denoted by Q) in the forest stand is
92 equal to the volume of dead wood suitable for the species.

93 The probability of colonization of an unoccupied stand is a function of its
94 connectivity to existing local populations. The connectivity, S , of stand i is defined as:

95

$$96 S_i = \sum e^{-\alpha d_{ij}} p_j Q_j \quad \text{eq (1)}$$

97

98 where $p = 0$ for unoccupied and $p = 1$ for occupied stands, Q is the amount of habitat, d is
99 the distance between stands i and j , and $1/\alpha$ is the mean dispersal distance. The yearly
100 colonization probability C of an unoccupied stand is assumed to be a function of
101 connectivity and the constant y :

102

$$103 C_i = S_i^2 / (S_i^2 + y^2) \quad \text{eq (2)}$$

104

105 A higher value of y implies that a higher connectivity (i.e. larger populations nearby) is
106 required to obtain a given colonization probability, which may be due to a stronger Allee
107 effect. The yearly extinction probability for an occupied stand is given by

108

$$109 E_i = \min\{1, (u / Q_i^x)(1 - C_i)\} \quad \text{eq (3)}$$

110

111 where u and x are species-specific parameters and $(1 - C_i)$ represents the rescue effect.
112 The risk of extinction of a local population is assumed to be inversely related to Q ,
113 because population size tends to be smaller when the habitat amount is lower, which
114 generates a higher risk of local extinction. u reflects the level of the local extinction risk
115 and x the difference in extinction risk between stands holding large vs. small dead wood
116 amounts.

117

118 *Model species*

119 We modeled the metapopulation dynamics of five generalized model species of insects
120 having different characteristics regarding mean dispersal distance and substrate
121 requirements: a “normal” (i.e. average) species, a long-distance disperser, a short-
122 distance disperser, a closed-forest specialist and a sun-exposure specialist (Table 1).
123 Furthermore, due to poor empirical knowledge about local extinction risks and turnover
124 rates, we modeled four additional species to explore the sensitivity to the local extinction
125 risk parameters. All species were dependent on dead wood of Norway spruce being
126 younger than 10 years and having a diameter >10 cm. Young dead wood is an important
127 substrate, especially for saproxylic insects living under bark, because almost a half of
128 Norway spruce dead wood is without bark after 10 years (calculated from data presented
129 in Ranius et al. 2003). The inner bark and subcortical space of dead trees is an important
130 microhabitat; among 542 saproxylic red-listed invertebrates in Sweden, 168 (31 %) are
131 directly dependent on bark as a microhabitat (Jonsell et al. 1998). We assumed that 50 %
132 of the volume of dead wood less than 10 years old and having a diameter > 10 cm was
133 suitable as habitat for the model species. The remaining 50 % was unsuitable, for
134 instance, because of unfavorable microclimate or absence of appropriate rot types. We
135 adjusted the value of γ after setting the values for the other parameters in such a way that
136 the extinction risk during the following 250 years became about 50 % for all model
137 species if the current management regime (95% conventionally managed and 5% set-
138 asides) would prevail during the whole period. Hence, all model species represent species
139 which would run a significant risk of extinction given today’s management regime.

140 There are only a few studies of the spatial occurrence patterns of saproxylic insects
141 in boreal forests that indicate at which spatial scale colonizations take place. For the
142 saproxylic beetle *Hadreule elongatula* there was a positive relationship between
143 occupancy and the amount of habitat (clear-cuts with high stumps) within a radius of 1
144 km (Schroeder et al. 2006), and for *Bellamira scalaris* between larval abundance and the
145 non-coniferous forest cover within a radius of 1.2 km (Saint-Germain and Drapeau 2011).
146 For another saproxylic beetle, *Harminius undulatus*, the strongest relationship between
147 observed occurrence patterns and stand-scale probability of occurrence was predicted by

148 a metapopulation model in which $1/\alpha$ (using eq. 1) was set to 1500 – 2500 m (Schroeder
149 et al. 2007). Furthermore, in a study of beetles (Coleoptera) and bugs (Hemiptera)
150 specialized on fresh aspen (*Populus tremula*) wood, the strongest relationship between
151 species richness and amount of aspen wood in the surrounding was obtained with $1/\alpha =$
152 93 m (Ranius et al., subm ms). Consequently, we assumed mean dispersal distances
153 varying between 100 m and 2 km for the model species.

154 For u and x , which regulates the local extinction risk, no relevant empirical data are
155 available. We believe that the extinction risk within a smaller area (with the rescue effect
156 excluded) is high for many saproxylic insect species, because their abundance may be
157 very low (for many species, on average a few individuals per managed forest stand;
158 Schroeder et al. 2006) However, in forest landscapes local extinctions may still be rare
159 because they are counteracted by a rescue effect (i.e by immigration from surrounding
160 forest stands). For the normal species, we adjusted the values of x and u to obtain a yearly
161 extinction risk of 10 % in an average future unmanaged stand, and 50 % at the stand age
162 with the lowest amount of dead wood in a future conventionally managed forest and with
163 the rescue effect excluded. As a sensitivity analysis, we also tested “normal” species with
164 other combinations of local extinction risks (2 % and 50 %; 25 % and 50 %; 10 % and 20
165 %; and 10% and 80 %, in unmanaged stands and in stands with the lowest amount of
166 dead wood in managed forest, respectively).

167 For the sun-exposure and closed forest species, we used the same x -value as for
168 normal species and adjusted u to obtain a local extinction risk of 10 % under the best
169 conditions also for these species. We assumed that in stands with high amounts of dead
170 wood ($Q > 1.15\text{m}^3/\text{ha}$, which is the case for all unmanaged forest and some managed
171 forest; Fig. 1) the species with long-distance dispersal had a higher extinction risk than
172 the normal species; x and u were set so the local extinction risk in a future unmanaged
173 stand was 25 % per year. On the contrary, the species with short-distance dispersal was
174 given values of x and u that generated a local extinction risk in a future unmanaged stand
175 of only 2 %. This is based on knowledge that strong dispersers may be poorer
176 competitors than weak dispersers (Tilman et al. 1994) and that populations with higher
177 dispersal rates and ranges tend to suffer to a larger extent from dispersal mortality (Fahrig

178 2007). We believe this makes a difference especially when the density of dead wood is
179 high. Hence, we adjusted x and u so the extinction risk remains the same as for the
180 normal species (50 %) when $Q = 1.15 \text{ m}^3/\text{ha}$. Higher levels of dispersal may also lower
181 the actual local extinction risk due to a rescue effect. However, this effect is not included
182 in the x and u parameters but is a separate factor (eq. 3).

183 For all species except two (the closed forest and sun-exposure species) the dead
184 wood was of equal quality independent on forest age. We assumed that for the sun-
185 exposure specialist, dead wood was only suitable in managed forests with an age < 20
186 years, and to some extent (only $0.5 \text{ m}^3/\text{ha}$) in unmanaged forest, while the other dead
187 wood (in managed forests > 20 years + all dead wood in unmanaged forest except 0.5
188 m^3/ha which is assumed to be sun-exposed) was suitable for the closed forest specialist.
189 This is because in unmanaged forest, gaps are created due to small-scale disturbances,
190 while gaps are generally avoided in even-aged forest management (Caron et al. 2009). A
191 large proportion of the saproxylic beetles has indeed a preference either for sun-exposed
192 or shaded conditions (Lindhe et al. 2005), but the preferences are rarely so strong as in
193 the cases of the closed forest and sun-exposure specialists. Thus, we analyzed species at
194 two extremes (closed forest and sun-exposure specialists) and a midpoint (normal
195 species) of the scale, acknowledging that real species are more or less continuously
196 distributed along that scale.

197

198 *The landscape model*

199 We simulated habitat development in a model landscape of $13.4 \text{ km} \times 13.4 \text{ km}$, which is
200 similar to the scale suggested to be used in landscape planning of Swedish forests
201 (Larsson and Danell 2001). The landscape consisted of 3,600 squares, corresponding to
202 forest stands. Each square was 5 ha, which is near the average size of harvested forest
203 stands in Sweden (Anonymous 2010). Because we assumed this landscape to be adjacent
204 to similar landscapes, the edges of the landscape were wrapped around. Thus, stands
205 situated at the left and upper margin were bounded to those at the right and lower margin,
206 respectively, as if they were located on a donut-shaped surface. Tree species composition
207 of each stand was determined stochastically for each stand, with a 40 % probability of
208 being a Norway spruce stand (in Sweden, 41 % of the growing stock is Norway spruce;

209 Anonymous 2010). We assumed that the rest of the landscape was entirely unsuitable for
210 the model species.

211 The extinction risk may be dependent on present occurrence patterns. To obtain
212 realistic occurrence patterns, we started the simulations 100 years before present. We
213 assumed that the landscape had been unaffected by commercial forestry based on clear-
214 cutting until 100 years ago, and that the species were present in every spruce stand at that
215 time. During the following 100 years, 0.95 % of the forest was clear-cut annually. We
216 assumed that today 95 % of the forest has been managed, and that the age distribution is
217 even among managed forest stands. The simulated scenarios we compared all started with
218 the same current landscape situation and covered a period of 250 years from now. The
219 extinction risk was estimated as the proportion of all replicates in which the species had
220 gone extinct at the landscape level every 50 years for 250 years into the future.

221 We assumed that the unmanaged forest stands are currently unevenly distributed in
222 the landscape. We did this by dividing the landscape into 36 equally large (500 ha)
223 squares. Each square was randomly assigned a value, representing the probability for
224 each forest stand (5 ha) within the square to have been left unmanaged until today. These
225 probability values were distributed between 5×10^{-9} % and 50 %, by using the equation P
226 $= 5 \times 10^x$, in which P is the probability value for each square, and x is a stochastic
227 variable, randomly given a value between -9 and 1 according to an even distribution.
228 Each stand was randomly determined as having been managed or not, based on the
229 probability value for the square where it was situated. When the number of set asides was
230 increased from now into the future, we assumed that stands of ages with the highest
231 amount of dead wood were selected.

232 The habitat amount changed over time, as determined by the management regime
233 of the forest (Fig. 1). We predicted the amount of dead wood in managed forest in
234 relation with stand age as in Ranius et al. (2003), i.e. by simulating dead wood dynamics
235 taking into consideration forest growth, tree mortality, dead wood decay, and destruction
236 of dead wood during forestry operations. We assumed a site index (i.e. tree height at an
237 age of 100 years) of 24 m and a rotation period of 100 years. Furthermore, we assumed
238 that since about 10 years ago the forestry is biodiversity-oriented, following FSC's
239 certification regulations (Anonymous 2000), but that no concerns were taken to preserve

240 dead wood before that. In unmanaged forest, we assumed that the average amount of
241 dead wood was constant over time. This is close to reality if forests are dominated by
242 fine-scale disturbances (Jonsson 2000), which at least sometimes is the case in
243 Fennoscandian spruce forests (e.g., Hörnberg et al. 2005; Steijlen and Zackrisson 1987).
244 For both managed and unmanaged forests we used two measures of stochastic variability
245 in the predictions: one between stands and one between years within each stand. We
246 estimated the variability from 500 replicate simulation runs.

247 We emulated the effect of weather by including regional stochasticity, which
248 affected the extinction risk and colonization rate by generating a temporal change in
249 habitat amount, Q . This factor was equal for the entire landscape but varied stochastically
250 between years according to a normal distribution. Arbitrarily, we set the coefficient of
251 variation of this factor to 0.25.

252

253 *Scenarios*

254 In the simulations, forest stands were managed in three different ways from today and
255 250 years into the future:

- 256 i) free development (i.e. no management)
- 257 ii) conventional forestry (following certification standards)
- 258 iii) intensive plantation forestry based on Norway spruce or another (native or
259 introduced) tree species

260 We assumed that at the beginning of the simulations (i.e., 100 years before today), the
261 amount of suitable dead wood corresponds to 50 % of what is found in old-growth
262 forests. Indeed, the amount of dead wood at that time was often considerably lower than
263 in old-growth forest because there was a lower density of living trees due to cattle
264 grazing and selective logging (e.g., Lindbladh 1999; Sippola et al. 2001; Groven et al.
265 2002). We assumed that the amount of dead wood has further decreased because of
266 increased management during the past 100 years, so forests that have been left for free
267 development until today were assumed to contain 30 % of the dead wood volume that
268 occurs in old-growth forests. This is consistent with survey data of Swedish key habitats
269 with Norway spruce (Jönsson and Jonsson 2007). Setting aside these forests will increase
270 the amount of dead wood in the future; we assumed that after 40 years the volume of

271 suitable dead wood will have increased from the current 30 % to 80 %. However, it will
272 never reach 100 %, because some dead wood is removed also from unmanaged forests,
273 especially in the event of extensive storm felling in order to decrease the risk of damage
274 by the spruce bark beetle *Ips typographus* to nearby managed forest (Schroeder 2007).
275 This means that the amount of suitable dead wood (i.e. younger than 10 years old, with
276 diameter > 10 cm) in forests with free development is first 4.16 m³/ha today and 11.10
277 m³/ha after 40 years. In future conventionally managed forest, the amount of suitable
278 dead wood varies with stand age, with an average of 2.08 m³/ha. We assumed that
279 intensively managed plantations are totally unsuitable for the model species (i.e. there is
280 no suitable dead wood). This is likely to be the case if intensive forestry is based on the
281 plantation of non-native tree species which are unsuitable for the Norway spruce
282 specialists. As regards Norway spruce plantations, this assumption implies that intensive
283 multiple-entry silviculture minimizes natural tree death and allows salvaging dying trees
284 which may occur accidentally after disturbance.

285 In all scenarios simulating future conditions, conventional forest management
286 initially takes place in 95 % of the forest stands. Intensive forestry can become
287 implemented only when forest stands are harvested. Furthermore, we assumed that each
288 year only 50 % of the clear-cuts were suitable for implementing intensive forestry, due to
289 e.g. variations in landowners' interests, transport infrastructure or terrain characteristics.
290 Consequently, the higher the proportion of intensive forestry, the longer time it will take
291 until the new distribution of management types is reached; because about 1 % of the
292 forest is cut annually it takes, for instance, ten years until the new level is reached for the
293 scenario with 5 % intensive forestry, while it takes 100 years to reach 50 % intensive
294 forestry.

295 In Scenario 1, the proportions of forest subject to intensive forestry and
296 conventional management varied, and no measures were implemented to compensate the
297 landscape-scale loss of dead wood resulting from an intensification of management
298 (Table 2). In the other two sets of scenarios, compensations were implemented to
299 maintain the amount of dead wood constant at the landscape level. Scenario 2 involved
300 compensation by increasing the amount of dead wood in managed forest through changed
301 management (more green tree retention at final logging; Table 3). Scenario 3 involved

302 compensation by setting aside more forest (Table 4). Hence, in sets 2 and 3, the total
303 amount of dead wood in the landscape was the same for all scenarios.

304

305 *Estimations of changes in annual harvestable volume at the landscape level*

306 For each scenario, we conducted a rough estimation of how the annual harvestable
307 volume differed compared to the scenario with no intensive plantation forestry. The
308 estimations were based on the following assumptions:

309 *i)* In intensively managed forests, the volume production over 100 years is expected to be
310 95 % higher than in conventionally managed forests at the stand scale. This is based on
311 predictions made for 15% of all forest land in Sweden which would be dedicated to
312 intensive production involving fertilization, clone forestry based on Norway spruce and
313 plantation of lodgepole pine (Fahlvik et al. 2009; Larsson et al. 2009).

314 *ii)* In set asides, the harvestable volume is equal to 0 m³/ha.

315 *iii)* For conventionally managed forest, we made calculations from the data presented in
316 Jonsson et al. (2006). We assumed a forest situated in central Sweden. All compensation
317 was assumed to be made by green tree retention at final harvest, and it was assumed to
318 result in a decrease in volume production equal to 0.75 times the proportion of area that is
319 retained, which is consistent with assumptions made in Jonsson et al. (2006).

320

321 **Results**

322 Intensified plantation forestry applied to 50% of the spruce stands had increased the
323 extinction risk relatively strongly compared to the *status quo* scenario (i.e. no intensive
324 plantation forestry) for all species after 150 years (Fig. 2). For four of the five species,
325 most of the expected extinctions took place 50–150 years from the intensification of
326 forestry. The sun-exposure specialist was an exception, as most extinctions took place
327 already during the first 50 years.

328 The extinction risk increased rather gradually with an increasing proportion of
329 intensive plantation forestry for all species under Scenario 1 (no compensation), but the
330 degree of increase varied much among species (Fig. 3). For the short-dispersing species
331 and the closed-forest specialist, extinction risk increased more slowly with increasing

332 proportion of intensive plantation forestry than for the long-dispersing species and the
333 sun-exposure specialist.

334 Given that compensations were made to maintain mean dead wood volumes
335 constant at the landscape level, the extinction risk decreased with an increasing area of
336 intensified forestry in many cases (Fig. 3). Compensation by setting aside forest was a
337 very effective way of decreasing the extinction risk for the normal species, the short-
338 distance disperser and the closed-forest species. Compensation through changed
339 management was generally less effective; in most cases it resulted in more similar
340 extinction risks compared to the scenario with no intensive plantation forestry. Moreover,
341 the sensitivity analysis showed that the four additional variants based on different ranges
342 of local extinction risk yielded outcomes which were qualitatively similar to those for the
343 normal species, suggesting that the general pattern is robust to variation in the local
344 extinction parameters (Appendix).

345 The response of the sun-exposure specialist differed clearly from that of most
346 other model species: its extinction risk increased with the area of intensified forestry,
347 even with compensation efforts made (Fig. 3). Compensation through set-asides was
348 clearly ineffective for that species, whereas compensation through adapted management
349 resulted only in a slightly lower extinction risk than without compensations made, except
350 at 50% intensive plantation forestry, where compensation through management was
351 better at mitigating the negative effects of intensive forestry. Also for the long-distance
352 disperser the compensation measures were less effective than in other species:
353 compensation kept extinction risk at a level rather close to that of *status quo* scenario, no
354 matter the proportion of intensive plantation forestry, i.e. it did not result in strongly
355 decreased extinction risk.

356 Implementing intensive plantation forestry increased the harvestable timber
357 volume production at the landscape scale in the long term (Tables 2, 3 & 4). This was
358 clearly the case even if the negative effects of intensified forestry on dead wood were
359 compensated for by increased conservation efforts elsewhere in the landscape. The
360 scenarios involving compensation through set-asides (Table 3) yielded smaller increases
361 in harvestable volume compared to those assuming compensation through changed
362 management (Table 2).

363

364 **Discussion**

365 This study suggests that intensified forestry has negative effects on biodiversity at the
366 landscape level if no compensations are made for nature conservation. Still, negative
367 effects on population persistence were limited when intensive forestry was applied to
368 only 5 – 10 % of the spruce stands. However, it should be emphasized that the amount of
369 suitable habitat required for population persistence differs widely among species (e.g.,
370 Baguette et al. 2000; Vance et al. 2003; Holland et al. 2005). Some very demanding
371 forest species are most likely unable to persist in a managed forest landscape independent
372 on whether the forests are managed intensively or conventionally (Ranius and Fahrig
373 2006), while other species with lesser requirements can be expected to persist even at
374 high proportions of intensive plantation forestry. In this study, we parameterized the
375 models to represent species which are already sensitive to forestry given today's
376 management regime. Hence, the effects observed on the model species are probably
377 stronger than we should expect for forest species in general. Rather, they reflect the
378 effects expected for species which are currently red-listed. We studied specialized
379 saproxylic insects, but we believe that our results also apply to a much wider range of
380 species, because the mechanisms behind the outcome (specialized species are strongly
381 negatively affected by intensified forestry, and are able to use the habitat more efficiently
382 if it occurs more aggregated in the landscape) are likely to be common to many, if not
383 most, other groups of forest organisms.

384 In this study we assumed that intensive forestry was applied on forest land of
385 average productivity and conservation value. In Sweden, it has been suggested that
386 intensive forestry will be applied only on land of low conservation value (Larsson et al.
387 2009). On the contrary, intensive forestry is probably more profitable on the most
388 productive land, which often also is land of high conservation value. Therefore, the
389 negative impacts may become both larger or smaller than suggested by this study,
390 depending on where intensive forestry is being implemented.

391 The simulation outcome indicates that it takes a long time before species richness
392 at the landscape level is affected. When intensive plantation forestry was applied to 50%
393 of the stands, the extinction risk of the model species did not increase strongly over the

394 first 50 years except for the sun-exposure specialist. However, extinction risks of all
395 species had increased strongly after 150 years compared to the *status quo* scenario (Fig.
396 2). It has been suggested that intensification of forestry in Sweden should be
397 implemented within an adaptive management framework over a time period of 20 years
398 (Larsson et al. 2009). To some extent it is possible to study effects on biodiversity at the
399 stand level over a 20-year period. However, according to the present study we should not
400 expect any significant effects on biodiversity at the landscape level over such a short
401 period. To gain knowledge about the effects of intensive plantation forestry at the
402 landscape scale without having to wait so long, we must rely on modeling studies like
403 this one, or retrospective studies in landscapes which already have characteristics
404 comparable with future landscapes containing intensively managed forests.

405 The effects of intensive plantation forestry differed among species with different
406 habitat affinities and life-history traits. In biodiversity conservation, focus has often been
407 on species associated with forests in late successional stages (e.g., Bauhus et al. 2009;
408 Fritz et al. 2008; Siitonen and Saaristo 2000) and species with a limited dispersal
409 (Baguette et al. 2000; Kotiaho et al. 2005). Populations of such species are typically
410 conserved by setting aside forests. Our results show that for such species, an
411 intensification of forestry is more advantageous than the current management regime if
412 intensification in parts of the landscape is compensated by setting aside more forests (Fig.
413 3). However, this compensation measure was ineffective for the sun-exposure specialist,
414 which was highly sensitive to intensive plantation forestry at the landscape scale, even
415 already after 50 years. Clear-cuts may potentially host a species-rich insect fauna
416 (Sippola et al. 2002), because they harbor species associated with sun-exposed habitat
417 that originally occurred after forest fires. In the light of the trend for an intensification of
418 forestry in northern forests, our results call for an increased interest in species associated
419 with early successional stages.

420 We found that for three of the five model species (including the “normal” species
421 assumed to represent an average red-listed species), extinction risk actually decreased
422 with an increasing proportion of intensive plantation forestry compared to the *status quo*
423 scenario (i.e. 0 % intensive forestry), given that appropriate compensations were made
424 elsewhere to keep the mean dead wood volumes constant over the whole landscape. This

425 is due to the fact that the compensation measures resulted in a better spatial aggregation
426 of dead wood and hence positive effects on species persistence in stands subjected to
427 these compensation measures, which were stronger than the negative effects of a
428 decreased total area of suitable stands in the landscape. We assumed that all set asides
429 had an area of 5 ha, but in many real landscapes there may be much larger areas of high
430 conservation value that may be set aside. That will generally tend to decrease the
431 extinction risk in comparison to have only 5-ha set asides (Ranius and Kindvall 2006),
432 and consequently the present study probably tends to underestimate the usefulness of
433 setting aside forests as a compensation measure.

434 Hence, our results provide support to zoning approaches such as the Triad,
435 whereby intensive forestry is implemented on part of the land base and protected area
436 networks are expanded to compensate for negative effects of intensified management.
437 Such an approach would decrease biodiversity locally in intensively managed forest
438 stands, but more species would be likely to persist at the landscape level. In a simulation
439 study based on a boreal landscape in Quebec, Canada, Côté et al. (2010) showed that
440 Triad scenarios resulted in larger areas of forest with old-growth properties than current
441 land use, which suggests that many species sensitive to forest management would benefit.
442 In our analyses, we found that timber volume production would increase with an
443 increasing proportion of intensive plantation management, even when dead wood
444 compensation measures were implemented. In a case study in New Brunswick, Canada,
445 Montigny and MacLean (2006) also found that intensive management resulted in
446 increased timber yields in a Triad zoning context. In Quebec, Côté et al. (2010) found
447 that Triad scenarios with 12 % set-asides yielded higher timber volumes in the long term
448 than both a *status quo* scenario and scenarios involving 20 % set-asides.

449 To conclude, a combination of intensive plantation forestry, ecological forestry, and
450 set asides seems to allow for a combination of different goals, such as increased timber
451 production and carbon sequestration, and maintenance of biodiversity. However, we
452 stress that species with different life-history traits may respond differently, and hence the
453 implementation of such a system should be accompanied by continuous biodiversity
454 monitoring allowing for early warning and adaptive management. To implement such a
455 zoning approach in Fennoscandia, some changes in forestry laws and certification

456 standards (e.g. Anonymous 2000) would be required. Also, it should be kept in mind that
457 landscape zoning is easier to implement in regions where forests are publicly owned (e.g.
458 Messier et al. 2009) or where one actor owns most of the land base, and may not be a
459 socially viable option in landscape with highly fragmented ownership.

460

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466 Sciences (SLU), Umeå University, and the Forestry Research Institute of Sweden.

467

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596

597 Table 1. Parameter values for the five different model species. For parameter
598 designations, see *Methods*.

599

Species	u	x	y	$1/\alpha$ (km)	Dead wood exposition
Normal	0.53	0.5	96.5	0.5	All
Long-distance	0.51	0.21	850	2	All
Short-distance	0.56	1	6.8	0.1	All
Sun-exposure	0.39	0.5	6.3	0.5	Sun-exposed
Closed forest	0.51	0.5	88	0.5	Shaded

600

601 Table 2. Mean volume of suitable Norway spruce dead wood (diameter > 10 cm, age <
 602 10 years) across the landscape and change in annual growth of harvestable volume
 603 compared to the *status quo* (0 % intensive forestry) for scenarios assuming varying
 604 proportions of intensive plantation forestry over a period of 100 years. No compensation
 605 is made to counterbalance the loss of dead wood due to intensive plantation forestry
 606 (Scenario 1).

607

Plantation forestry (%)	Conventionally managed (%)	Set aside (%)	Dead wood in managed forest (m ³ ha ⁻¹)	Dead wood (m ³ ha ⁻¹)	Change in harvestable volume (%)
0	95	5	2.08	2.32	0
5	90	5	2.08	2.22	+5
10	85	5	2.08	2.12	+10
25	70	5	2.08	1.80	+25
50	45	5	2.08	1.28	+50

608

609

610 Table 3. Mean volume of suitable Norway spruce dead wood (diameter > 10 cm, age <
611 10 years) across the landscape and change in annual growth of harvestable volume
612 compared to the *status quo* (0 % intensive forestry) for scenarios assuming varying
613 proportions of intensive plantation forestry over a period of 100 years. More dead wood
614 is created in conventionally managed forest to keep mean dead wood volumes constant at
615 the landscape scale with an increasing proportion of intensive plantation forestry
616 (Scenario 2).

617

Plantation forestry (%)	Conventionally managed (%)	Set aside (%)	Dead wood in managed forest (m ³ ha ⁻¹)	Dead wood (m ³ ha ⁻¹)	Change in harvestable volume (%)
0	95	5	2.08	2.32	-
5	90	5	2.20	2.32	+4.7
10	85	5	2.32	2.32	+9.5
25	70	5	2.82	2.32	+23.7
50	45	5	4.40	2.32	+47.3

618

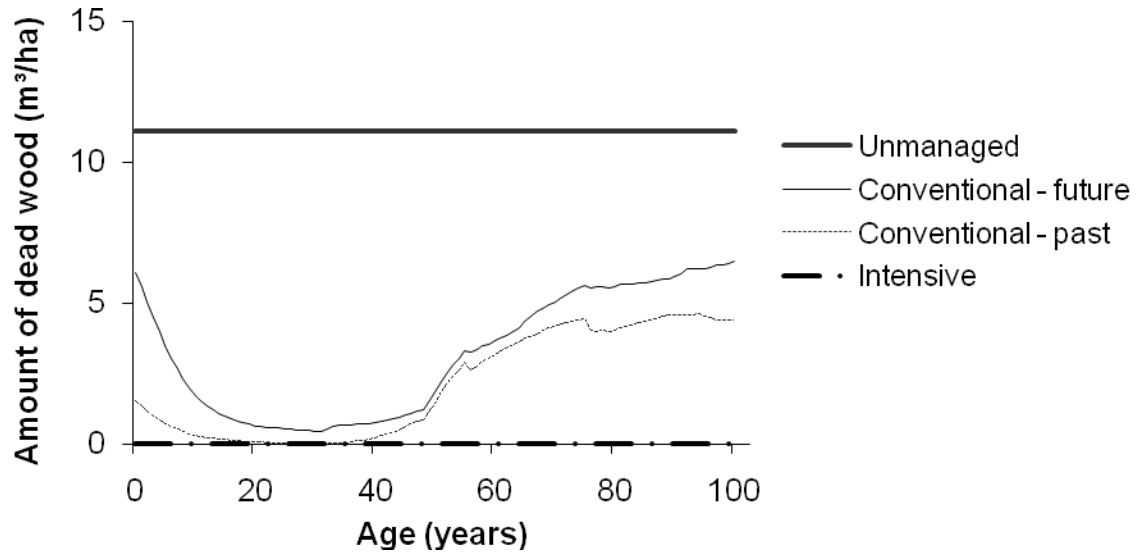
619 Table 4. Mean volume of suitable Norway spruce dead wood (diameter > 10 cm, age <
 620 10 years) across the landscape and change in annual growth of harvestable volume
 621 compared to the *status quo* (0% intensive forestry) for scenarios assuming varying
 622 proportions of intensive plantation forestry over a period of 100 years. More forest is set
 623 aside to keep mean dead wood volumes constant at the landscape scale with an increasing
 624 proportion of intensive plantation forestry (Scenario 3).

625

Plantation forestry (%)	Conventionally managed (%)	Set aside (%)	Dead wood in managed forest (m ³ ha ⁻¹)	Dead wood (m ³ ha ⁻¹)	Change in harvestable volume (%)
0	95	5	2.08	2.32	0
5	87.86	7.14	2.08	2.32	+2.9
10	80.72	9.28	2.08	2.32	+5.7
25	59.3	15.7	2.08	2.32	+14.3
50	23.6	26.4	2.08	2.32	+28.6

626

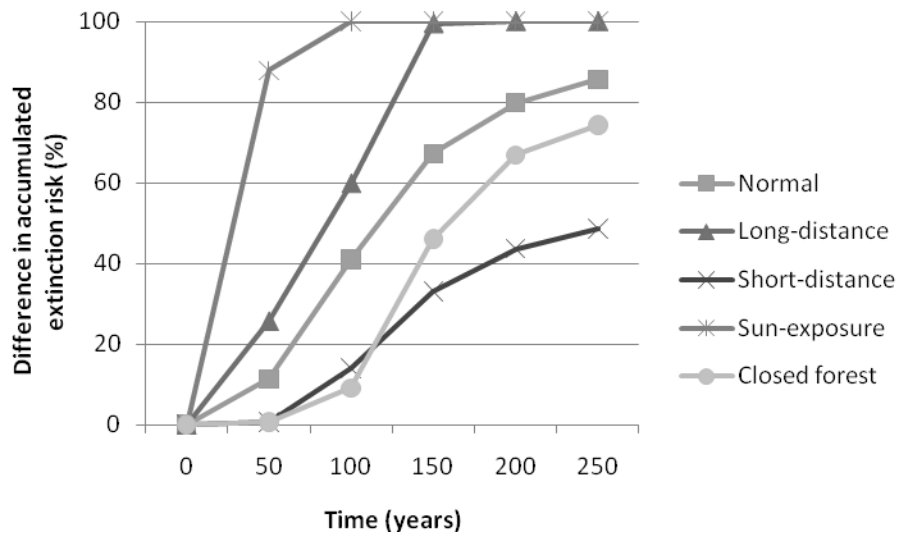
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629

630 Fig. 1. Amount of dead wood of Norway spruce suitable for the model species (diameter > 10 cm,
 631 age < 10 years) over a 100-year rotation. Output from simulations of dead wood dynamics (taking
 632 into account forest growth, tree mortality, dead wood decay, and destruction of dead wood by
 633 forestry operations) of unmanaged forest in the future, conventionally managed forest in the past
 634 (until ten years ago) and future (started ten years ago), and intensively managed Norway spruce
 635 forests.

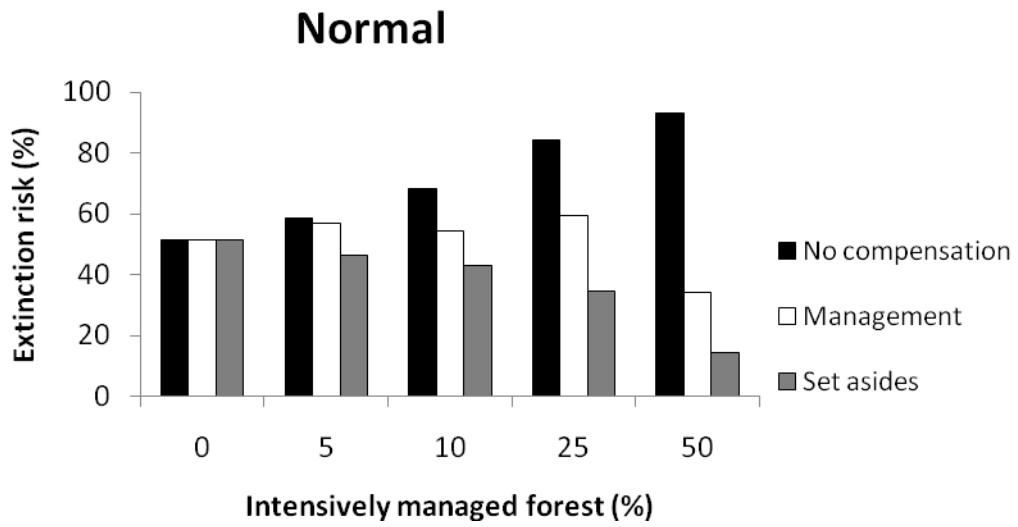
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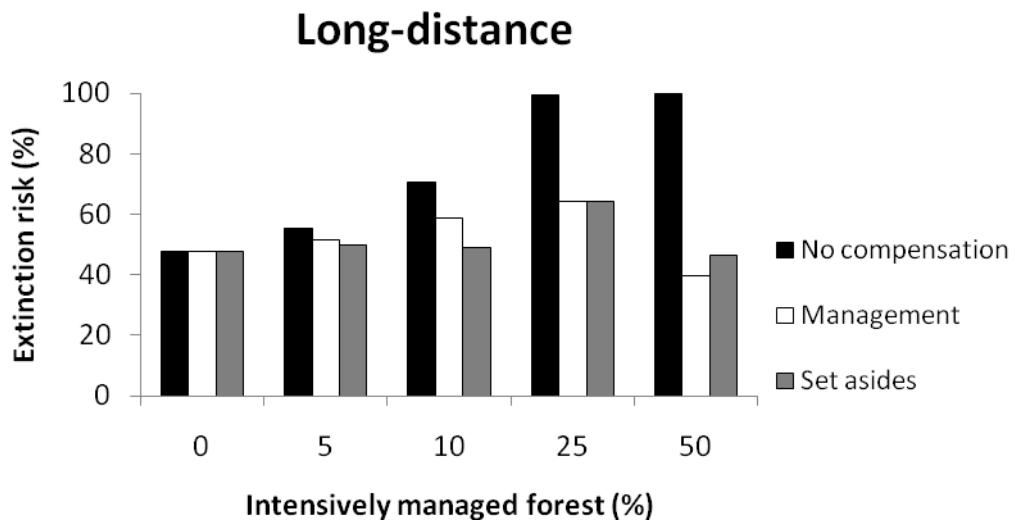
637

638 Fig. 2. Difference in accumulated extinction risk if 50% of the current spruce stands are
639 dedicated to intensive plantation management and no compensation measures are taken.
640 The difference is calculated as $(\text{Extinction risk with 50\% intensive forestry} - \text{Extinction risk without intensive forestry}) / (1 - \text{Extinction risk without intensive forestry})$. For
641 risk without intensive forestry) / (1 - Extinction risk without intensive forestry). For
642 species characteristics, see Table 1.

643

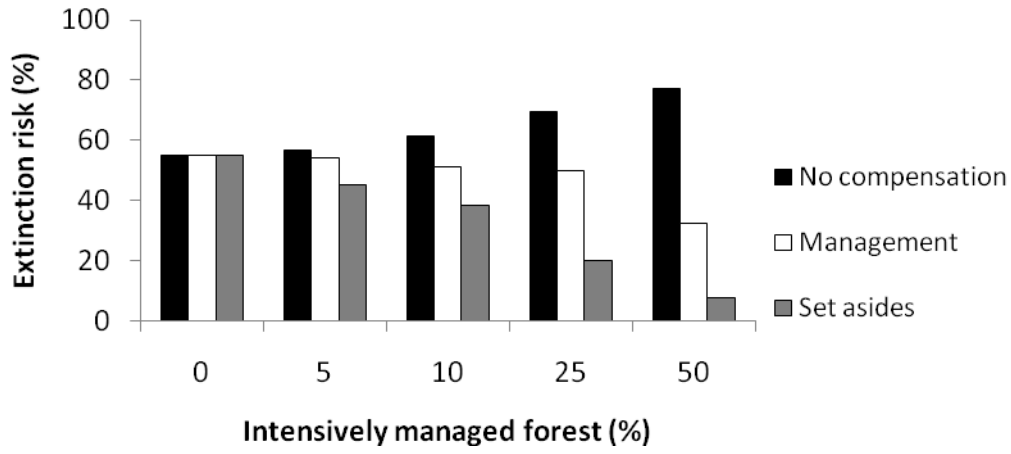


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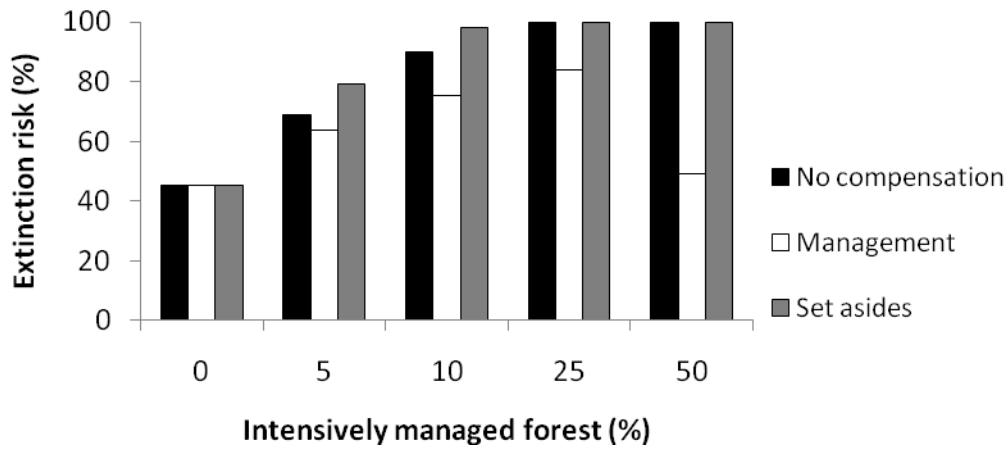
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Short-distance



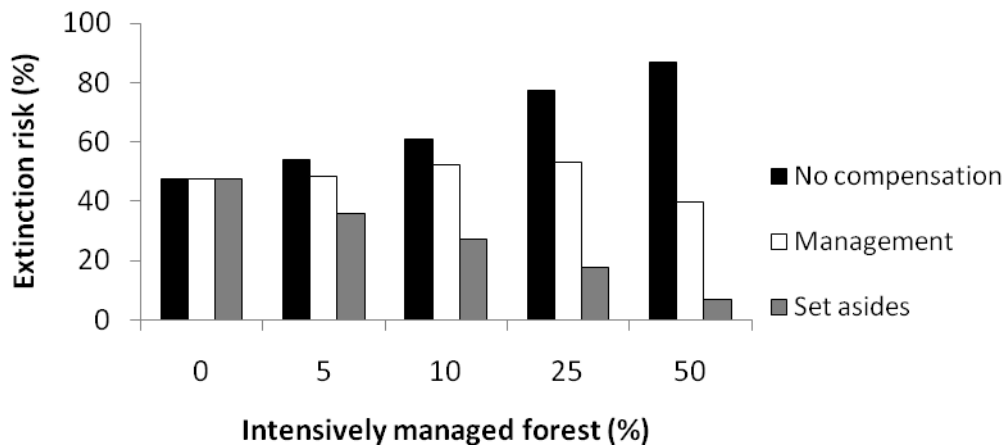
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Sun-exposure



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Closed forest

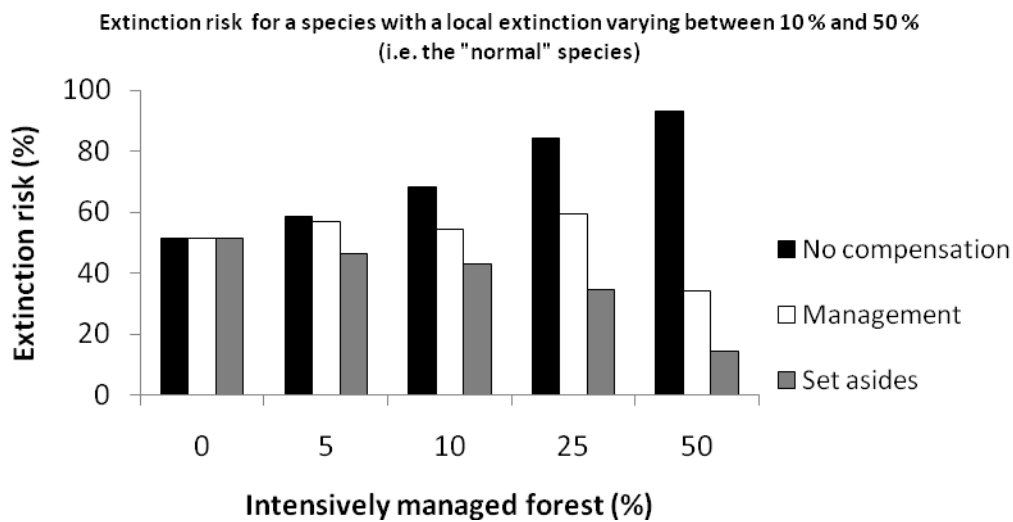


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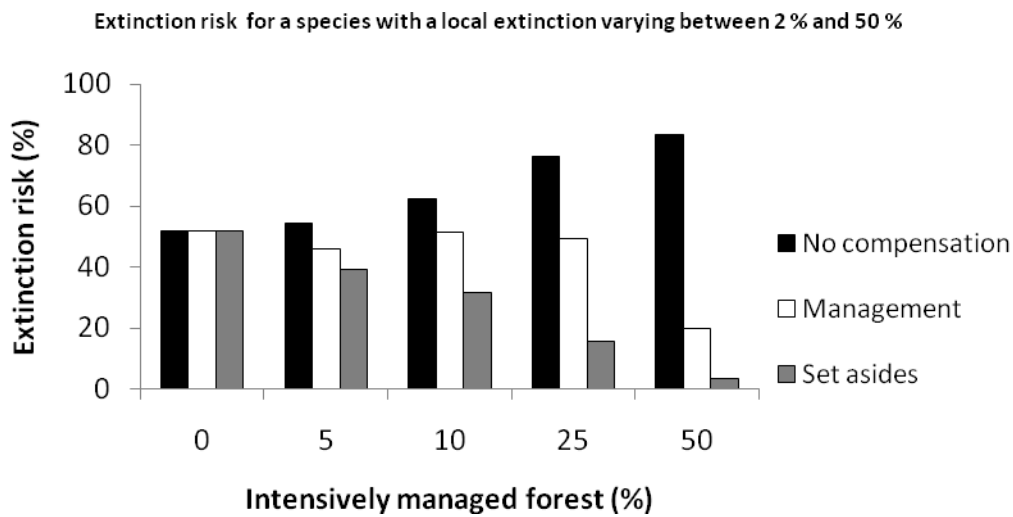
649

650 Fig. 3. Predicted extinction risk for the model species at a landscape level 250 years into the
651 future in relation to the proportion of intensively managed stands. “No compensation” implies that
652 no compensation efforts were conducted, and consequently the mean volume of dead wood at
653 the landscape level varies among the scenarios. “Management” implies that a constant dead
654 wood volume was obtained through increased conservation concern in all conventionally
655 managed forest, and “Set asides” implies that a constant landscape-scale dead wood volume
656 was obtained by setting aside a larger proportion of forest for free development.
657

658 Appendix. Outcome from the sensitivity analyses. Four variants of the normal species (see main
 659 text) are modeled, representing different ranges of variation of the local extinction risk according
 660 to the local amount of dead wood. The bar diagrams show the predicted extinction risk for
 661 species at a landscape level 250 years into the future in relation to the proportion of intensively
 662 managed stands. “No compensation” implies that no compensation efforts were conducted, and
 663 consequently the mean volume of dead wood at the landscape level varies among the scenarios.
 664 “Management” implies that a constant dead wood volume was maintained through increased
 665 conservation concern in all conventionally managed forest, and “Set asides” implies that a
 666 constant landscape-scale dead wood volume was maintained by setting aside a larger proportion
 667 of forest for free development.



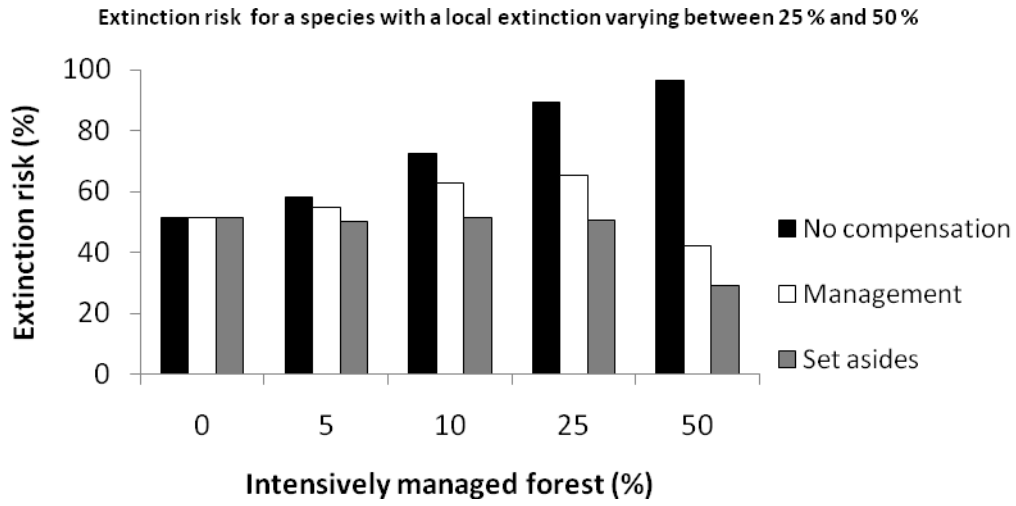
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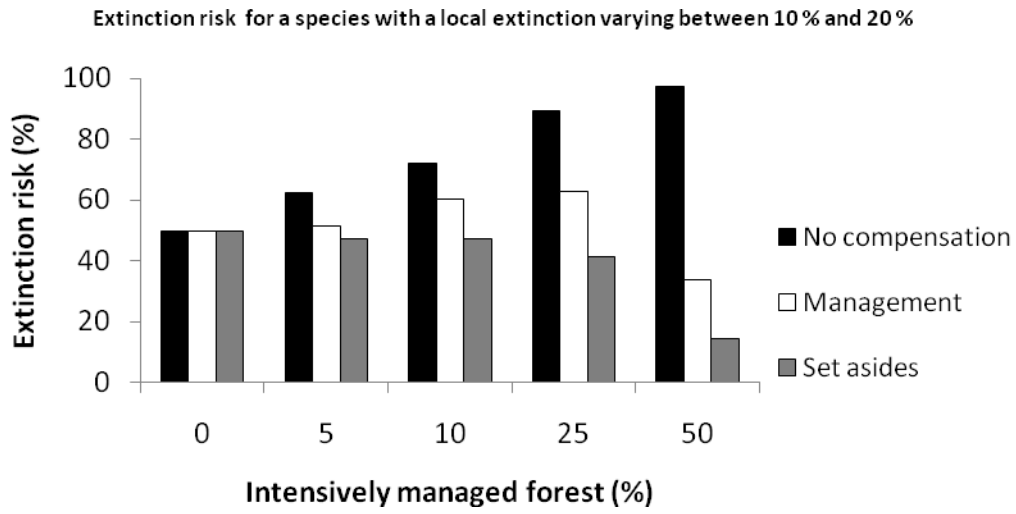
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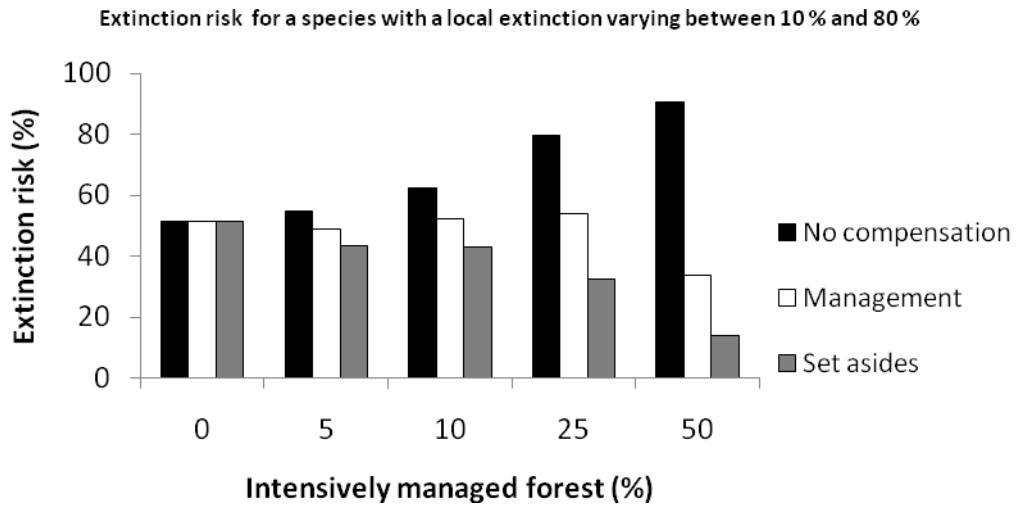


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