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1 **Cost-efficient strategies to preserve dead wood-dependent species in a**
2 **managed forest landscape**

3

4 Running head: Cost-efficient species preservation

5

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21

22 **Abstract**

23 Negative consequences of intensive forest management on biodiversity are often mitigated
24 by setting aside old forest, but alternative strategies have been suggested. We have
25 compared simulated consequences of two of these alternatives, setting aside young forests
26 or extending rotation periods, to that of current practice in managed boreal forest. In all
27 scenarios we applied a constant conservation budget and predicted forest development and
28 harvesting over 200 years. As a proxy for biodiversity conservation, we projected the
29 extinction risk of a dead wood-dependent beetle, *Diacanthous undulatus*, in a 50 km²
30 landscape in central Sweden, using a colonization-extinction model. During the first
31 century, setting aside young forest stands rather than old stands increased extinction risk
32 because young stands have lower habitat quality. However, habitat quality of young forests
33 increased as they aged and they were much cheaper than old stands. Therefore, the strategy
34 allowed a larger set-aside area (within the budget constraint), resulting in lower extinction
35 risk and harvested timber volumes in the second century. Prolonging rotations also
36 decreased the extinction risk but was less cost-effective. The most cost-effective strategy in
37 the long term (200 years) was to set aside a mixture of old and young forest. However,
38 setting aside young stands rather than prolonging rotations or setting aside old stands
39 delays both the benefits (lower extinction risk) and costs (lost harvest volumes), so the
40 optimal strategy depends on the assumed societal values and hence discount rates.

41

42 **Keywords:** conservation strategy, discounting, forest age, population viability, prolonged
43 rotation, time horizon

44

45 **1. Introduction**

46 Intensive forest production has modified forests worldwide, often with strongly negative
47 effects on biodiversity (Secretariat of the Convention on Biological Diversity 2010). Since
48 maintenance of biodiversity is regarded as an important goal in sustainable forestry, efforts
49 are made to mitigate these effects (Lindenmayer and Franklin 2002). The policy often aims
50 at maintaining species in populations that are viable in the long term (e.g. Anonymous
51 2016 The environmental goals of Sweden). This is often done by establishing set-asides
52 (i.e. conservation areas exempt from timber extraction), typically to protect biodiversity
53 ‘hotspots’ in order to maximize current species richness within budgetary and other socio-
54 economic constraints (e.g. Virolainen et al. 2000). However, especially in landscapes with
55 little remaining unmanaged forest, such a strategy may result in small and isolated
56 protected areas, often providing poor prospects for long-term viability of some species’
57 populations (Öckinger and Nilsson 2010). Thus, to evaluate the consequences of
58 conservation strategies on biodiversity, it is important to adopt a long temporal perspective,
59 including more than one rotation, i.e. typically more than a century (Ranius and Roberge
60 2011). Furthermore, it is often crucial to recognize that habitats are dynamic, and that
61 suitable habitats for forest species may occur not only in protected areas, but also in
62 managed production forest matrices (e.g. Lindenmayer and Franklin 2002, Schroeder et al.
63 2007). Therefore, both species and habitat dynamics as well as both production and set-
64 aside forests should be considered when evaluating effects of conservation strategies on
65 biodiversity in forest landscapes.

66 In the even-aged forest management systems dominating in many parts of the world,
67 forest stands are harvested by clearcutting and then actively regenerated. In such managed

68 forest landscapes, old forest cover smaller areas than in naturally-dynamic forest
69 landscapes (Lindenmayer and Franklin 2002). This impairs biodiversity, because forests in
70 later successional stages contain structures and species that are rare or absent in younger
71 forests (Lassauce et al. 2013). Therefore, older forests have been traditionally prioritized
72 over younger ones when selecting set-asides (Gustafsson and Perhans 2010). However,
73 results from two recent analyses suggest that it may be more cost-efficient, in terms of
74 conservation benefits that can be obtained with a given budget, to set-aside young forests
75 (Lundström et al. 2016; Mazziotta et al. 2016). This is mainly because timber products
76 cannot be extracted from young forests for several decades, so they are much cheaper to set
77 aside than mature stands. However, the cited studies did not address two factors,
78 population persistence and future levels of harvestable timber volumes, which must be
79 considered in comprehensive assessments of the consequences of setting aside young
80 forests for biodiversity and forestry.

81 Rotations are sometimes prolonged in managed forest in order to promote
82 biodiversity (Lassauce et al. 2013). This increases amounts of habitats for species that
83 require structures associated with old trees and large-diameter dead wood (Jonsson et al.
84 2006; Lassauce et al. 2013), especially if the prolonged rotations are not accompanied by
85 extra thinnings (Roberge et al. 2016). Thus, prolonging rotations increases landscape-scale
86 habitat availability for various taxa that might otherwise be threatened (Jonsson et al. 2006;
87 Juutinen et al. 2014; Mönkkönen et al. 2014). Moreover, prolonged rotations increase the
88 length of the temporal window when conditions are suitable for these species, which may
89 strongly improve their persistence by favorably changing the relationship between
90 colonization and extinction rates (Keymer et al. 2000). However, we are not aware of any

91 published analysis of prolonging rotations' effects on colonization-extinction dynamics
92 and hence population persistence.

93 The aims of this study are to elucidate long-term biodiversity consequences of setting
94 aside young forests and prolonging rotations in managed forest landscapes, including
95 hitherto neglected effects on population persistence and levels of harvestable timber
96 volumes. By projecting forest development and population dynamics over 200 years in a
97 managed forest landscape in central Sweden, and comparing outcomes with those of a
98 scenario with no conservation efforts, we evaluate the following four strategies for
99 conserving biodiversity: setting aside old stands, young stands, or mixtures of old and
100 young stands, and prolonging the rotations. We consider three responses: timber
101 production (i.e. the total harvested volume of trees), habitat availability, and population
102 persistence of a focal species. The budget, in terms of net present value of timber (NPV), is
103 kept constant in all scenarios. The focal species is a previously red-listed beetle,
104 *Diacanthous undulatus*, which inhabits dead wood. Its population persistence is projected
105 using a colonization-extinction model that we developed from presence/absence data
106 collected in the considered landscape. *Diacanthous undulatus* occurs both on clear-cuts
107 and in old (managed and unmanaged) forests, but 10-60 year-old managed forests offer
108 little or no habitat for the species. Hence, by using this focal species we acknowledge that
109 both managed and unmanaged forests, and young as well as old forests, may be important
110 for the conservation of forest species. Since the species model used is dynamic, the
111 outcome reflects not only habitat availability but also effects of colonization-extinction
112 dynamics.

113

114 **2. Methods**

115 *2.1. Study landscape*

116 The simulations were based on data collected in the Delsbo area, central Sweden (62° N,
117 16° E). We used *D. undulatus* occurrence data collected in 68 forest stands in a 28 × 28
118 km² block of land including a 4 km wide buffer zone (Schroeder et al. 2007). Our
119 predictions of species persistence and forest production considered a 50 km² square located
120 within that block of land. Most (80%) of the Delsbo area is covered by productive forests
121 (i.e. forests with annual wood volume growth exceeding 1 m³/ha). The landscape is typical
122 for the Swedish boreal region, with Scots pine (*Pinus sylvestris* L.) and Norway spruce
123 (*Picea abies* (L.) Karsten) being the dominant tree species. The height above sea level
124 varies from 140 m to 530 m. Currently, most forest stands in the area are constituents of
125 the first generation of even-aged forest created by clear-cut harvesting. The average
126 volume of dead wood in the managed stands is 13.8 m³ ha⁻¹, about twice as high as the
127 Swedish average (Ekbom et al. 2006).

128 The industrial forest owners (Holmen Skog AB and Bergvik Skog AB) have been
129 FSC-certified since the late 1990s, and thus follow the requirements to set aside 5% of the
130 forest land at the scale of whole stands (Forest Stewardship Council 2010).

131

132 *Study species*

133 *Diacanthous undulatus* is a representative of the species-rich insect community dwelling
134 under bark of dead wood, which is negatively affected by reductions in the amount of dead
135 wood due to forestry (Jonsell et al. 1998). It was previously classified as near threatened
136 (NT) on the Swedish red list (Gärdenfors 2010), but its status has recently been changed to

137 least concern (LC) (Swedish Species Information Centre 2015). The species is a predator,
138 and occurs in dead wood from both coniferous and deciduous trees (Nilsson and
139 Baranowski 1996) in unmanaged forest, old managed forest, and clear-cuts, but not young
140 managed forest stands because they only have small amounts of dead wood with bark
141 (Schroeder et al. 2007). In a managed forest landscape, this species seems to occur as a
142 habitat-tracking metapopulations, since (i) local populations can go extinct both due to
143 stochastic events in small populations (average number of larvae per 1m² of bark is
144 estimated to 1.5 in occupied patches) and habitat patches becoming unsuitable (during the
145 rotation, managed forest stands have periods when being suitable and unsuitable for the
146 species), (ii) the probability of occurrence increases with the time since the stand became
147 suitable, which suggests a dispersal limitation, and (iii) predictions from a habitat-tracking
148 metapopulation model were significantly correlated with the current occurrence patterns
149 (Schroeder et al. 2007).

150 The information about current populations of *D. undulatus* used in this study was
151 drawn from a presence/absence dataset obtained from a field study carried out during
152 2001-2003, described in detail by Schroeder et al. (2007). A stratified sampling design was
153 applied, which means that we collected data from randomly selected forest stands of the
154 following categories: clearcuts (20 stands), old managed forest (28 stands), set asides (10
155 stands) and nature reserves (10 stands), while beetle data were impossible to collect from
156 young managed forests simply because there was too little dead wood to sample. Briefly,
157 the presence/absence of *D. undulatus* larvae was assessed by peeling bark from dead wood
158 objects (diameter > 10 cm, both downed and standing and of different tree species), sieving
159 the material, and extracting larvae (if present) in Tullgren funnels. Use of this method

160 ensures that any detected members of the species must have originated from reproduction
161 in the stand. If available, 1 m² of bark from 10 dead wood objects were sampled per stand,
162 otherwise as many as possible. We assessed presence/absence at one time for each stand;
163 the species was present in 15 stands out of 68.

164

165

166 *2.2 Modelling forest development and optimizing forest management*

167 We modelled forest development and management using tree growth, regeneration and
168 mortality functions implemented in the forest planning tool Heureka PlanWise (Wikström
169 et al. 2011). Starting from current forest conditions in the study landscape (modelled using
170 average values for tree age, basal area, stem density, site index, and tree species
171 distributions obtained from stand-level databases maintained by the industrial landowners),
172 we predicted developments in the following 200 years.

173 For each stand, a number of management programs were simulated, each consisting
174 of a sequence of treatments (planting, pre-commercial thinning, thinning and clearcutting,
175 or no treatment) applied over 200 years divided into five-year time periods. In all cases
176 even-aged management was simulated, as this is the prevailing management practice in the
177 area. The regeneration settings for the current and subsequent generations of a stand were
178 the same, since the dominating tree species generally depends on the soil characteristics.

179 The harvest revenues from timber and pulpwood were calculated using theoretical
180 bucking of trees (Näsberg 1985) and stumpage prices drawn from the prevailing industry
181 price list for the region (Mellanskog 2013). The NPV for a given management program
182 was computed as the sum of discounted net revenues for an infinite time horizon

183 (approximated by assuming that the same management regime would be repeated in
184 perpetuity after two rotations), with a discount rate of 3%, which is the commonly used
185 rate in the region.

186 Thinning guides were used to determine timing and intensity of thinning for a
187 baseline management program, and the timing was subsequently varied by the Heureka
188 system when generating management program alternatives. The minimum clear-cut age
189 allowed is set by the Swedish Forest Act as a function of site index and main tree species
190 (Anon. 1994), and varies for most stands addressed in this study between 60 and 90 years.
191 The system also generated a number of programs with longer rotation lengths for each
192 stand. Optimization algorithms were used to choose the management program that
193 maximized the NPV of each stand.

194 We assumed in all scenarios, including the scenario with no conservation efforts, that
195 5% of each stand would be left for free development at clearcutting to meet FSC
196 certification requirements (Forest Stewardship Council 2010). We assumed that with no
197 conservation efforts, NPV from forest management would be maximized for each stand.
198 We used mixed integer programming (MIP) to maximize the NPV under each scenario,
199 and let the system calculate a clear-cutting age for each stand that maximized the NPV.
200 This was, on average, 19.9 years after the minimum allowed clear-cutting age. Therefore,
201 we calculated the optimal harvest age for each stand as the minimum legal clear-cutting
202 age plus 20 years. The mean rotation period in the simulations was 88 years (range: 70 to
203 145 years). To obtain scenarios with prolonged rotations, we added extra years but did not
204 change anything else in the management regime. For instance, to obtain a prologation of 40
205 years, 60 years were added to the minimum legal clear-cutting age.

206

207 *2.3 Modelling species persistence*

208 Based on snapshot data alone, Schroeder et al. (2007) concluded that in a managed forest
209 landscape, *D. undulatus* occurs in a habitat-tracking metapopulation, with each forest stand
210 constituting a habitat patch. Studies of other saproxylic beetles based on repeated surveys
211 have confirmed that saproxylic beetles are indeed colonising and going extinct from forest
212 stands, where successional habitat changes is an important factor (Ranius et al. 2014;
213 Rubene et al. 2014). Thus, we based our modelling based on the assumption that in each
214 year, colonizations may occur in suitable forest stands where the species is absent and
215 extinctions from stands where the species is present. Here, local colonizations and
216 extinctions of the focal species (i.e. the metapopulation dynamics) were predicted using
217 equations and parameters obtained from Monte Carlo simulations using presence/absence
218 data from the study area described in the Appendix A. The equations are based on
219 metapopulation theory, assuming that the patch-level rate of colonisation is related with the
220 connectivity to dispersal sources and the rate of local extinction with the amount of habitat
221 (Hanski 1994). Our equations otherwise follow the incidence function model (Hanski
222 1994), but we assumed that our system is not in an equilibrium (see Schroeder et al. 2007).
223 The parameterized model predicted current presence/absence better than a null model (with
224 50 replicates, presence was predicted for 39% of those occupied, and for 21% of those
225 unoccupied, while randomly 25% would have been predicted as occupied in both
226 categories; $p < 0.001$, χ^2 test).

227 We obtained information about the future habitat quality of forest stands from the
228 predicted future forest conditions. The productive forest stands in the study landscape were

229 divided into three types: *i*) unmanaged forests, which are assumed to be always suitable for
230 *D. undulatus*; *ii*) stands managed with clearcutting, which are suitable for *D. undulatus*
231 when they are < 10 years and ≥ 60 years old and unsuitable at all other ages; and *iii*) stands
232 planted with the exotic tree species lodgepole pine (*Pinus contorta*), which are never
233 suitable for *D. undulatus*. We modelled habitat quality in suitable stands as described in the
234 Appendix B, assuming that it increases with increases in abundance of the species'
235 substrate (dead wood with bark) and reductions in altitude (Schroeder et al. 2007).

236 The size of the simulated area was adjusted to 50 km² to obtain extinction risks
237 allowing comparisons between scenarios; in considerably smaller or larger areas the
238 extinction risks over 200 years are always close to 100% and 0%, respectively, so between-
239 scenario differences are masked. We assumed that rates of immigration of individuals from
240 adjacent landscapes were equal to the emigration rates. To ensure this equivalence in the
241 simulations we wrapped around the edges of the landscape so stands situated at the left and
242 upper margins were bounded to those at the right and lower margins, respectively, as if
243 they were located on a donut-shaped surface.

244

245 *2.4 Scenarios for setting aside stands and prolonging rotations*

246 First, we applied a “No conservation effort” scenario, where no forest land was set aside at
247 the scale of whole stands and the rotations were not prolonged. Second, we tested a
248 scenario close to the current management regime. In this scenario, 5% of the forest land
249 was set aside, the oldest stands being selected as set-asides. The cost of this scenario, in
250 terms of the loss of NVP relative to the NPV in the “No conservation efforts” scenario was
251 used to set the budget for conservation. This cost equals the sum of the NPV of the set-

252 asides, which in our analyzed 50 km² area was 9.14 million SEK. We compared this with
253 other scenarios where conservation efforts were conducted with the same budget
254 constraint. Initially, we tested scenarios where a varying proportion of the budget was
255 allocated for setting aside the youngest stands. In these scenarios, 100, 80, 60, 40, 20 and
256 0% of the budget was assigned to setting aside old stands and the rest to setting aside
257 young stands. Finally, we tested scenarios with rotations prolonged by 20 and 40, while we
258 found it impossible to use the whole budget if they were prolonged by only 5 or 10 years.
259 In each case the prolongation was applied to as many randomly selected stands as possible
260 under the budget constraint. Below, we only present the outcome from the prolongation
261 that resulted in the lowest extinction risk (i.e. 20 years).

262 All scenarios implicitly assumed that for each stand a management regime (counting
263 “No management” as one regime) is defined at the beginning and maintained during the
264 whole simulation period (200 years). When selecting the youngest and oldest stands for
265 setting aside, stands with the lowest and highest initial ages, respectively, were selected
266 until the maximum cost allowed by the budget was reached. The stands with prolonged
267 rotations were selected randomly, regardless of their initial age.

268

269 **3. Results**

270 All tested conservation efforts – setting aside young or old forest, or prolonging rotations –
271 had clearly positive effects on species persistence in comparison to conducting no
272 conservation efforts (Fig. 1). During the first century, setting aside mainly old stands was
273 the most efficient strategy to decrease the extinction risk. However, during the second
274 century, the extinction risk was much lower when at least some young forest was set aside

275 (Fig. 1), because habitat availability was considerably higher during that period when
276 setting aside young forest instead of old ones (Fig. 2a). Over the whole period, the
277 extinction risk was lowest when about 80% of the budget was spent on setting aside the
278 oldest stands and the remaining 20% on setting aside the youngest ones (Fig. 1).

279 When the rotation period was prolonged by 20 years throughout the 200-year period,
280 it included 79% of the forest area. During the first century this resulted in similar
281 extinction risks to those obtained in the best set-aside scenarios, but during the second
282 century the extinction risk was higher than for any scenario involving set-asides (Fig. 1).

283 Because the youngest stands were much cheaper to set aside than the oldest, with a
284 constant conservation budget the total set-aside area increased with the proportion of
285 young forest (Fig. 3). Thus, the harvested volume decreased more when young forest was
286 set aside than when old forest was set aside. This difference was slightly more pronounced
287 during the second century (Fig. 4). Prolonged rotations had a clearly negative effect on the
288 harvested volume only during the first century (Fig. 4).

289

290 **4. Discussion**

291 *4.1 Young vs. old set asides*

292 Traditionally, old stands have been prioritized when selecting set-asides for biodiversity
293 conservation (Gustafsson and Perhans 2010), mainly because they harbor structures and
294 species that are rare in forest landscapes dominated by managed forest. The present study
295 shows, in accordance with previous findings (Lundström et al. 2016; Mazziotta et al. 2016)
296 that it may be favorable to set aside young stands too. This is due to the fact that they are
297 cheaper to protect, meaning that larger areas can be set aside with a given conservation

298 budget. However, for species dependent on structures that mainly occur in old forest, there
299 will be a long delay before setting aside young forest results in increased habitat amounts.
300 This is especially problematic in managed landscapes with bottlenecks in habitat
301 availability. Such bottlenecks occurred in the prediction for our study area (i.e. the habitat
302 availability was lower at 0-50 years than both earlier and later; Fig. 2a), and have been
303 observed in other managed forest landscapes in Sweden (Roberge et al. 2015). We found
304 that extinction risk was most strongly reduced when about 20% of the budget was spent on
305 young set-asides and the rest on old ones. These proportions combine the advantages of
306 including very young forests that are cheapest to set aside and old forests which limit
307 bottleneck effects. The optimal proportions probably depend on the target species and
308 landscapes (cf. Mazziotta et al. 2016). However, we conclude that with a long planning
309 horizon, allocating a proportion of conservation resources for setting aside young stands
310 may be highly advantageous, as long as old stands are also set aside.

311 Given a certain conservation budget, setting aside a larger area of young forest rather
312 than old forest implies a decrease in the total production forest area and hence future
313 amounts of timber potentially harvested in the forest landscape (Fig. 4). The estimated cost
314 of setting aside young forest is comparatively low, despite the consequent reductions in
315 future timber harvest, because the income loss is discounted and in the far future. The
316 higher the assumed discount rate, the more favorable is the net income in the near future
317 relative to later incomes. Therefore, the discount rate may have a large influence when
318 comparing the cost-effectiveness of conservation scenarios (Mazziotta et al. 2016). This
319 rate is highly dependent on the decision-maker's preferences and may vary over time. Thus
320 there is no consensus regarding its correct value (e.g. Hepburn and Kondouri 2007).

321 However, the 3% interest rate used in this study is typical for forest management
322 calculations in Sweden, reflecting moderate risk and profit expectations (e.g. Brealey et al.
323 2012).

324 Both young and old forest may harbor structures that are important for biodiversity.
325 Our study species occurs in old forest and also in dead wood on clear-cuts for a few years
326 following cutting (Schroeder et al. 2007). Other species may strongly prefer either old
327 forest or clear-cuts, since these habitats offer strongly diverging environmental conditions
328 (Kaila et al. 1997). For species living in old forests, setting aside such forests is an
329 adequate conservation measure, but the present study suggests that setting aside young
330 forest could also be an efficient measure in the long term. However, at least some forest
331 species (although not our study species) seem to require habitat continuity (Siitonen and
332 Saaristo 2000) and for them it may be necessary to retain older forests which have never
333 been clear-cut. Habitats of high conservation value that occur after clearcutting and forest
334 fires may be legacies from the previous stand, such as dead wood (Kaila et al. 1997;
335 Rubene et al. 2014) or created by the disturbances, such as flower-rich sites (Rubene et al.
336 2015) and artificially created high stumps (Djupström et al. 2012). Many of these
337 structures and associated species will be lost during the succession, regardless of whether
338 the stand is set aside or not. Therefore, measures other than setting aside stands may be
339 needed to sustain these species, such as applying more conservation-promoting practices
340 during forestry operations, maintaining more gaps, and delaying the densification of young
341 forest (Rubene et al. 2014). In conclusion, the main value of setting aside old forests is that
342 it maintains current conservation values, while the main rationale of permanently setting

343 aside young forests is to secure high conservation values in the future, rather than to
344 maintain present values.

345

346 *4.2. Prolongation of the rotation periods*

347 Landscape-level extinction risks were lower when rotations were prolonged by 20 years
348 than in the scenario with no conservation efforts. This was at least partly due to increases
349 in total habitat availability at the landscape scale (cf. Mönkkönen et al. 2014), but
350 prolonging rotations may also extend the period when stands provide suitable habitats, and
351 thus increase probabilities of their colonization (cf. Keymer et al. 2000). However, the
352 optimal scenario for prolonging rotations still resulted in a higher extinction risk than the
353 optimal scenario of set-asides. Thus, our results suggest that prolonging rotations is a less
354 efficient measure than setting aside stands. This is a likely outcome especially for species
355 with low colonization ability (such as some epiphytes; Löbel et al. 2006), because such
356 species are favored by the occurrence of sites where they can persist over long periods but
357 cannot readily recolonize managed forest stands, which change over time (Ranius and
358 Roberge 2011). However, for stronger dispersers site persistence has weaker effects, since
359 they are better at tracking the changing habitat in managed forests. Prolonging the rotation
360 had a clear negative effect on the landscape-level harvested volumes only during the first
361 century, mainly because the harvest occasions become delayed. Thus, the main cost of
362 prolonging the rotation is delaying income from forest harvesting, which decreases the
363 value of income due to discounting. Thus, prolonged rotations caused quite moderate costs
364 per unit forest area (on average 9 % decrease in net present value). For that reason,
365 prolonging rotations may still be an attractive option for forest owners. For instance, some

366 may prefer to postpone harvesting, to keep possibilities open and decide later whether to
367 set aside a stand or cut it. This feature has been utilized in forest conservation programs
368 based on temporal contracts agreed between private landowners and the government (e.g.
369 Juutinen et al. 2008). There are also other advantages associated with prolonged rotations,
370 such as generally positive effects on e.g. aesthetics, water quality, soil nutrients, and berry-
371 picking (Roberge et al. 2016). Nevertheless, given the low long-term effect of prolonged
372 rotations observed in this study, and its limited value for species with low dispersal ability,
373 prolongation of rotations should be combined with setting aside forests in the same
374 landscape if the aim is to conserve wider biodiversity.

375

376 *4.3 Spatial and temporal scales*

377 The outcome from this kind of analyses is highly scale-dependent, in terms of both
378 economic returns and species persistence. If the scenarios are applied at the spatial scale
379 considered in our analyses (50 km²), they will not have market-level effects (cf. Nalle et al.
380 2014). Thus we assumed that prices would be the same in all scenarios. However, if they
381 were applied over larger regions the scenarios would have different effects on future
382 industrial timber supplies (Fig. 4). Economic theory suggests that reductions in timber
383 supply will result in higher prices, which will benefit forest owners but impair profitability
384 of the forest industry (Johansson and Löfgren 1985). Predicted levels of extinction risks are
385 also inversely dependent on the size of the simulated landscape. Therefore, although useful
386 for comparing relative effects of various scenarios, our analyses provide no indications of
387 extinction risks of *D. undulatus* at national or other larger scales.

388 The outcome is also highly dependent on the considered time horizon. A time
389 horizon of up to 100 years is commonly used for long-term forest planning (e.g. Öhman
390 and Eriksson 2010). However, we found that the outcome, in terms of relative extinction
391 risks, may be substantially different if it is extended with another 100 years. Two reasons
392 for the differences in risks between the first and second centuries are that habitat amounts
393 vary over time (Fig. 2), and populations of the focal organisms were larger at the starting
394 point than after 100 years. In this study, reductions in extinction risks were not discounted,
395 i.e. we assumed that the society's values of ecological benefits would remain constant
396 throughout the study period. There is no consensus regarding methodology for defining
397 likely interest rates regarding environmental benefits that may accrue far in the future (e.g.
398 Nordhaus 2007; Weitzman 2010). However, it is widely assumed that discount rates for
399 environmental benefits from nature conservation should be well below rates applied for
400 economic benefits (Gollier 2010; Kula and Evans 2011). This is because ecological and
401 biodiversity values are at least partially non-substitutable by economic growth or
402 consumption. Nature conservation is intended to ensure intergenerational equity and
403 provide an adequate basis for long-term persistence of biodiversity, which suggests that
404 biodiversity will be equally or even more valuable in the future than at present.

405

406 **5. Conclusions**

407 Since old stands are generally expensive to protect, given the financial resources
408 commonly available for conservation, set-aside areas will remain small. Thus losses of
409 timber harvest will also remain small. Much more extensive areas of younger stands can be
410 set aside within given budgetary constraints, because they are cheaper. In the long run this

411 would increase amounts of habitats that are scarce in production forests, and decrease
412 potential future timber harvests. Prolonging rotations reduced extinction risks of our focal
413 organism, but was less cost-efficient than setting aside forest. Thus, the most cost-efficient
414 strategy to preserve the study species over 200 years was to set aside a mixture of old and
415 young forest. However, setting aside young stands rather than prolonging rotations or
416 setting aside old stands delays both landscape-level costs (losses of harvested volumes) and
417 benefits (reductions in extinction risks), so the optimal strategy depends on the assumed
418 societal values and hence discount rates.

419 Because model parameters are based on scant data, and we only studied a single
420 species in a certain landscape, the outcome should not be generalized incautiously, but
421 considered an example of a possible outcome. However, our results may well apply to
422 numerous forest species associated with large-diameter dead wood. This habitat harbors a
423 species-rich community of conservation concern, since the amount of large-diameter dead
424 wood has severely declined in regions with intensive forest management (Jonsson et al.
425 2005). Moreover, our study area is largely representative of managed boreal landscapes of
426 northern Europe, where management has been intensive in recent decades. Hence, our
427 results are likely relevant to numerous landscapes facing similar conservation challenges.

428

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435

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439

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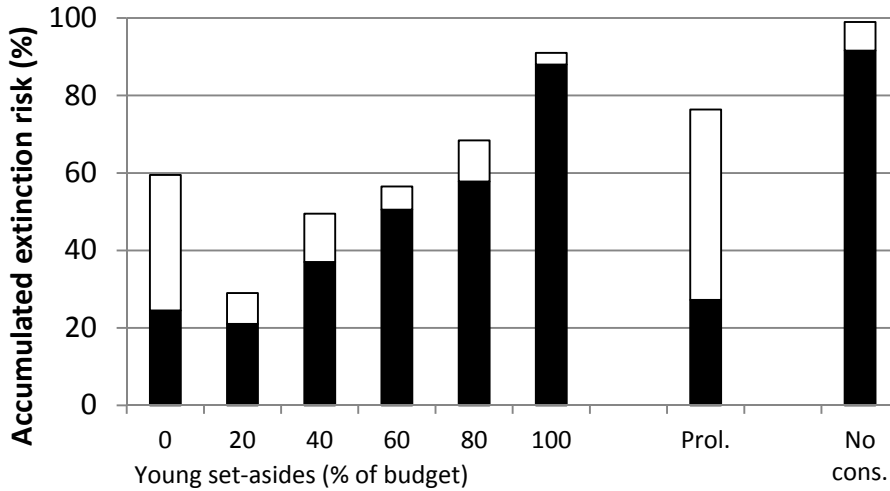
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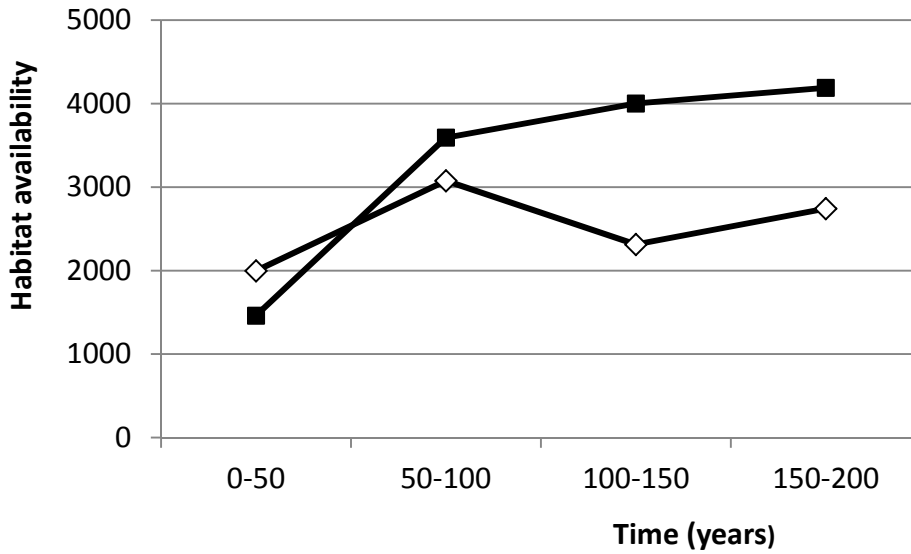
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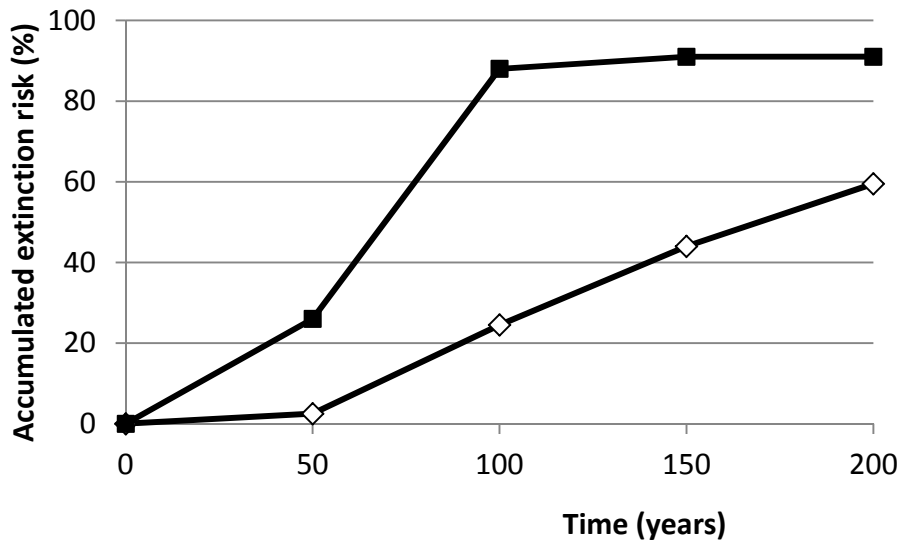
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569 Fig. 1. Predicted accumulated extinction risk for a beetle, *Diacanthous undulatus*, in a 50
570 km² managed forest landscape during a 200-year period, under seven scenarios with the
571 same conservation budget and one scenario with no conservation efforts. Black = during
572 the first century from now (0-100 yrs), white = during the second century (100-200 yrs). In
573 the first six scenarios, forest stands are selected for setting aside based on their age; the
574 numbers (0, 20, ..., 100) indicate the percentage of the budget allocated to setting aside the
575 youngest stands, while the rest is spent on the oldest stands. "Prol" is a scenario with the
576 same conservation budget in which the rotation period of randomly chosen stands is
577 prolonged by 20 years. In all scenarios, some trees were retained in stands at clearcutting
578 in accordance with FSC rules.

579 a)



580 b)
581



582

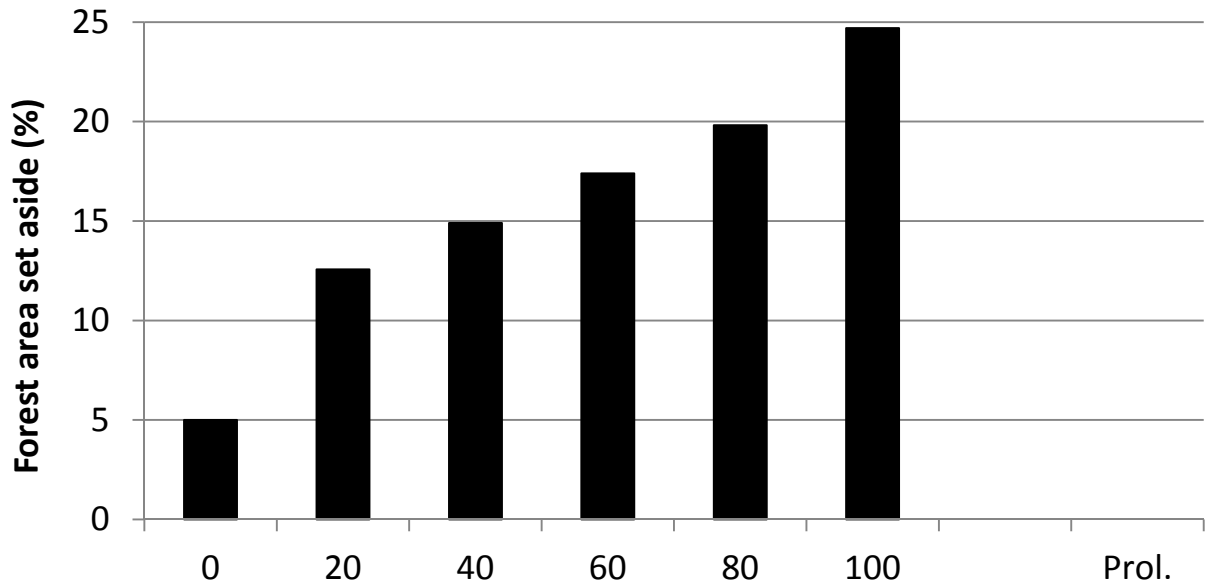
583 Fig. 2. Predicted habitat availability (a) and accumulated extinction risk (b) for the beetle

584 *Diacanthous undulatus* in a 50 km² managed forest landscape, in scenarios where the

585 youngest (black squares) or oldest (open diamonds) stands are set aside, with the same

586 conservation constraints. Predicted habitat availability refers to mean amounts, over 50-

587 year periods, measured as described in the Appendix A.



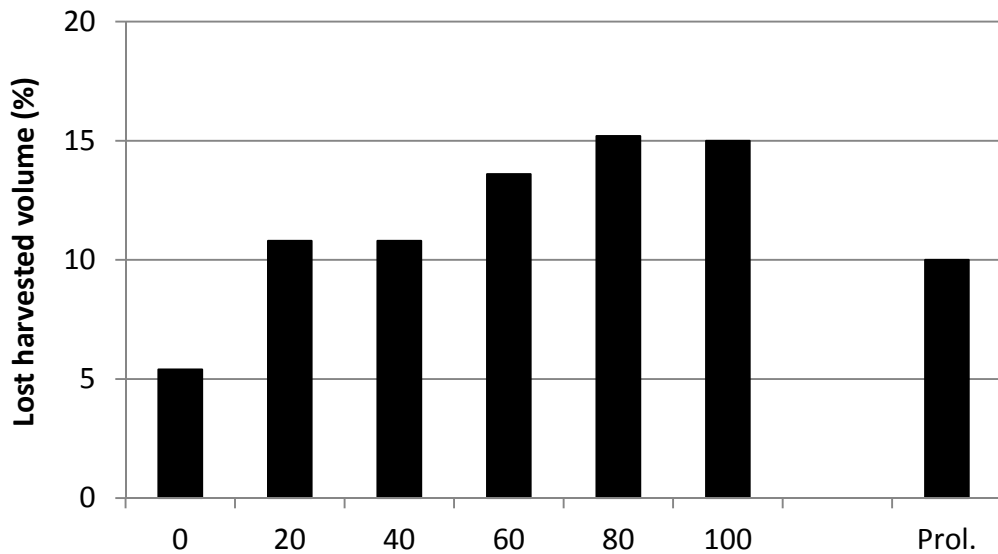
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590 Fig. 3. Areas (%) of forest set aside when percentages of a given conservation budget from
 591 0 to 100 (x axis) are allocated to setting aside the youngest stands and the rest to setting
 592 aside the oldest stands. No forest is set aside if the same budget is used to prolong rotations
 593 (Prol.). In the Prol. scenario the rotation period of randomly chosen stands covering 79%
 594 of the forest area is prolonged by 20 years. In all scenarios, some trees are retained in
 595 stands at clearcutting in accordance with FSC rules.

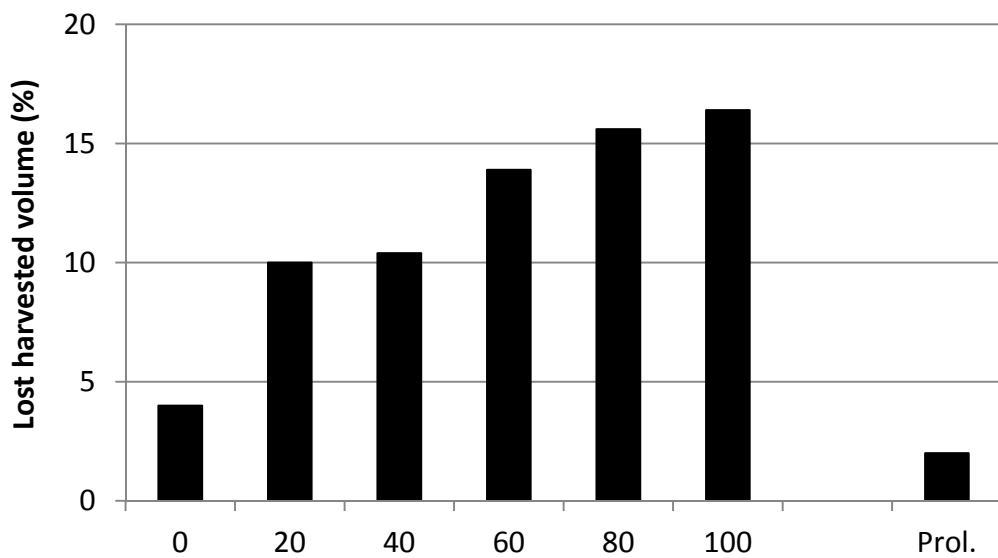
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597

598 a)



599 b)
600



601

602 Fig. 4. Percentage of the harvest volume lost, relative to the volume in a scenario with no

603 retained stands and no prolonged rotations. a) during the first century from now, and b)

604 during the second century. In the first six scenarios forest stands are selected for setting

605 aside based on their age; the numbers (0, 20, ..., 100) indicate the percentage of the budget

606 allocated to setting aside the youngest stands, while the rest is spent on the oldest stands.

607 "Prol" is a scenario with the same conservation budget in which the rotation period of

608 randomly chosen stands is prolonged by 20 years. In all scenarios, some trees are retained
609 in stands at clearcutting in accordance with FSC rules.

610 **Appendix A**

611 *Fitting a metapopulation model*

612 We fitted a metapopulation model using stand-level presence/absence data and Monte
613 Carlo simulations. We assumed a dynamic landscape, as described in the *Methods* section
614 and Appendix B, and that colonizations and extinctions are not currently in equilibrium in
615 the study landscape, because the landscape-level amount of habitat has decreased in recent
616 decades. In the Monte Carlo simulations, we started with a wide range of values for each of
617 the seven unknown parameters in the model (Table A.1). These ranges are collectively
618 referred to as a parameter space. By repeated simulations, the parameter space was
619 successively narrowed in the following way. In each simulation, we ran a set of 1000
620 replicates with parameter values randomly chosen within the parameter space. Each
621 replicate resulted in a prediction of presence/absence for every forest stand in the study
622 landscape, which was compared with field data. When a replicate resulted in an occupancy
623 of 12–32% (field data: 22%) and a significantly ($p < 0.05$, χ^2) positive correlation between
624 predicted and observed presence/absence, the combination of parameter values was
625 identified as a “probable combination”. However, for the first 10 simulations, we only
626 considered the occupancy, since significant correlations in presence/absence data were
627 very rare. For each set of 1,000 replicates, we analyzed the effect of one parameter at a
628 time by dividing the parameter value interval into four equally large sections. We
629 identified one or two parameters that had the biggest difference in proportion of probable
630 combinations between sections. Then we decreased the parameter space by 50%, by
631 delimiting the interval for the parameters with the biggest difference so only the sections
632 with the highest proportion of probable combinations remained. When this had been done

633 50 times, there were only small differences between the parameter value interval sections.
634 The mean value in each parameter interval in the final parameter space was used as a
635 parameter value in the simulation of future development (Table A.1). Two variables, α and
636 u , had strong effects on the occupancy in opposite directions. To increase the probability of
637 obtaining “probable combinations”, we substituted the u parameter by a function with two
638 parameters, a and b :

639

$$640 \quad u = a - b \alpha \quad \text{eq. (A.1)}$$

641

642 The a and b parameters were treated in the same manner as the other parameters, as
643 described above. With this approach, we obtained a parameter combination consistent with
644 field data.

645 The starting point for each Monte Carlo simulation was 1950 and the output was
646 compared with field data from 50 years later. In the simulations, species occurrences in
647 1950 were placed randomly among the forest stands. The initial incidence per patch, I , was
648 varied between 22% (= the current occupancy) and 100%. The probabilities of local
649 colonizations and extinctions were estimated in every stand and every year using eqs. A2-
650 A4, similar to those in Hanski (1994). Based on an assumed Allee effect, the colonization
651 probability, C , was a sigmoid function of connectivity, S :

652

$$653 \quad C_i = S_i^2 / (S_i^2 + y^2) \quad \text{eq. (A.2)}$$

654

655 The connectivity of stand i was defined as:

656
$$S_i = \sqrt{E_i} \sum_{j=1}^n \exp(-\alpha d_{ij}) p_j A_j$$
 eq. (A.3)

657 where $p = 0$ for empty and $p = 1$ for occupied stands, A is the patch size according to eq.
 658 (B.1), n is the total number of stands in the study, d_{ij} is the distance between stands i and j ,
 659 and $1/\alpha$ is the average migration distance. The patch area E_i was included in the equation,
 660 as the probability of reaching a habitat patch is likely to be proportional to the square root
 661 of its area (Hambäck and Englund 2005). For each year, the probability of extinction (U) in
 662 an unsuitable patch is 1, and the probability of extinction in a suitable patch is

663

664
$$U_i = \min \{1, u(1 - C_i) / A_i^x \}$$
 eq. (A.4)

665

666 where u is a parameter governing the extinction risk, x is a parameter governing the effect
 667 of patch size, A is the patch size according to eq. (1), and $(1 - C)$ represents the rescue
 668 effect. When no suitable habitat is available, the larvae of *D. undulatus* do not survive, so
 669 we assumed that the local population immediately goes extinct when a habitat patch
 670 becomes unsuitable.

671 Table A.1. Parameters in the colonization-extinction modelling. When the parameter
 672 values were estimated, we initially tested the whole range of values within the “Interval”.
 673 “Used value” is the parameter estimate used in the simulations.

674

Name	Variable	Interval	Used value
I	Initial incidence	0.22 - 1	0.25
y	Constant reflecting the probability of a population establishing in a focal empty patch, given a certain connectivity with source populations	1 – 1000	1.16
α	Dispersal decay (reflecting inverted mean dispersal distance)	0.0002 – 0.01 ¹	0.00915
u	Local extinction risk	0 – 1	0.0535
x	Constant reflecting how extinction risk varies with patch area	0.1 – 1	0.1
	Regional stochasticity	0 – 1	0.303
	Spatial scale of regional stochasticity	1, all scales; 2, only largest scale; 3, only smallest scale	2

675

676 ¹ the limits were based on the spatial scale of the study landscape.

677

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684 **Appendix B**

685 *Modelling habitat dynamics*

686 For each forest stand, we predicted the temporal development of habitat quality. Habitat
687 quality, A , was assumed to be proportional to the size of inhabiting *D. undulatus*
688 populations and estimated with the following function:

689

690
$$A = E \times H \times D$$
 eq. (B.1)

691

692 where E is the size of the stand (in ha), H an index related to altitude, and D an index
693 reflecting the amount of dead wood (in m³/ha). The value of H was obtained using a
694 logistic regression model, fitted with data on the presence/absence per sieved dead wood
695 item against altitude, L :

696

697
$$H = \exp(6.413 - 0.026L) / (1 + \exp(6.413 - 0.026L))$$
 eq. (B.2)

698

699 The dead wood index, D , was estimated by the following equation:

700

701
$$D = F \times T \times P$$
 eq. (B.3)

702

703 where F is a forestry factor, T is a tree species factor, and P is a stand productivity
704 factor. We assumed that before 1950, $F = 1$ for all stands. Large-scale clearcutting forestry
705 started in 1950, and we assumed after that $F = 0$ for all forests < 60 years old, while for
706 older forests $F = 1$. Since the late 1990s, the forestry has been FSC-certified, so more dead

707 wood has been retained during forestry operations. Thus, we assume that after 1998, $F = 1$
708 during the first 10 years after clearcutting. These assumptions are consistent with observed
709 amounts of dead wood in the study landscape (Ekbom et al. 2006) and results from
710 simulations of dead wood dynamics (Ranius et al. 2003). After a stand is set aside, F
711 increases at a constant rate during the first 100 years from 1 to 3, and remains 3 thereafter.
712 In the study landscape, the amount of dead wood with bark is currently about twice as high
713 in set-asides as in managed forests (Schroeder et al. 2007). The tree species factor, T , was
714 set to 1, 1.2 and 0.75 for stands dominated by Norway spruce, deciduous trees and Scots
715 pine, respectively. This reflects differences in tree mortality observed in mature managed
716 forests in Sweden (Jonsson et al. 2010), and if everything else is equal the amount of dead
717 wood is proportional to the tree mortality rate. The productivity factor, P , was included in
718 the function because the volume of dead wood is approximately proportional to the site
719 index (Ranius et al. 2003). The stand productivity was estimated as a site index
720 corresponding to the tree height when the forest stand is 100 years old. Since the site index
721 was on average 22, we obtained a mean value of 1 for P , by defining it as the site index
722 divided by 22.

723 In forest stands that are close to each other, habitat quality is likely to fluctuate over
724 time in a correlated manner. We considered this by constructing a spatially explicit
725 correlation structure in a similar manner to Gu et al. (2002), with modification of their
726 algorithm because we used forest stands as spatial units, while Gu et al. (2002) used grids.
727 The spatial correlation was represented hierarchically as follows. The study area was
728 divided into four rectangles by randomly placing two lines. Each rectangle was further
729 divided into four parts. This subdivision was done seven times. Each rectangle was given a

730 random factor, R_{ijk} , taken from a normal distribution with mean zero and variance δ^2 . The
731 effective quality $A_{ij}^*(t)$, of forest stands with their midpoints within the grid cell (i,j) at time
732 t was given by:

$$733 \quad A_{ij}^*(t) = A \exp\left(\sum_{k=1}^7 c_k R_{ijk}\right) \quad \text{eq. (B.4)}$$

734 where c_k is a weight chosen to represent the strength of regional stochasticity at scale k
735 (from small to large scales). As input in the Monte Carlo simulations, we used three
736 different sets of weights: *i*) regional stochasticity at all spatial scales, $\{1,1,1,1,1,1,1\}$; *ii*) at
737 the largest scale only, $\{0,0,0,0,0,0,1\}$; and *iii*) at the smallest scale only, $\{1,0,0,0,0,0,0\}$.

738

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