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Relative importance of habitat characteristics at multiple spatial scales for wood-dependent beetles in boreal forest

Thomas Ranius, Victor Johansson, Martin Schroeder, Alexandro Caruso

Address to authors (same for all authors):

Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, SE-750 07

Uppsala, Sweden

Corresponding author:

Thomas Ranius

Department of Ecology

Swedish University of Agricultural Sciences (SLU)

Box 7044, SE-750 07 Uppsala, Sweden

Phone: +46-18-672334

E-mail: thomas.ranius@slu.se

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1 **Abstract**

2 **Context:** Species distributions are influenced by habitat conditions and ecological processes at
3 multiple spatial scales. An understanding of the importance of habitat characteristics at different
4 spatial scales is important when developing biodiversity conservation measures.

5 **Objectives:** We investigated the effect of habitat characteristics or amount at three spatial scales
6 on the occurrence of saproxylic (= dead wood-dependent) beetles.

7 **Methods:** Saproxylic beetles were sampled under the bark of dead wood in a managed forest
8 landscape in central Sweden. We modelled the occurrence probability in dead wood items of 44
9 species (all species occurring in >2% of the items), based on dead wood item characteristics,
10 forest stand characteristics, and habitat connectivity (i.e. area of potentially suitable forest stands
11 in the surrounding of each stand), using hierarchical Bayesian regression.

12 **Results:** For the majority of species, dead wood item characteristics (especially tree species and
13 whether standing or downed) were more important than measured stand characteristics and
14 habitat connectivity. Whether the stands were clear-cuts, mature forests, or reserves affected
15 some species, whereas the stand-level amount of dead wood per hectare was not important for
16 any species. Habitat connectivity improved the occurrence models for about a half of the species,
17 but there were both positive and negative relationships, and they were generally weak.

18 **Conclusions:** Forest management should include creation and retention of a high diversity of
19 dead wood to sustain habitat for all species. In a forest-dominated landscape, the spatial
20 distribution of dead wood is of little importance for common saproxylic beetle species.

21

22 Key words: connectivity; dead wood; hierarchical Bayesian regression; island effect; occurrence
23 patterns; sampling effect; saproxylic beetles; threshold

24 **Introduction**

25 Species distributions are influenced by habitat conditions and ecological processes at multiple
26 spatial scales (Wiens 1989; Levin 1992). Human modifications of natural systems also occur at
27 several scales, and a big challenge in conservation biology is to identify the appropriate spatial
28 scales at which conservation actions most likely will balance the negative effects of human
29 impacts (Wiens 1989; Saunders et al. 1991). An understanding of the relative importance of key
30 habitat characteristics at different spatial scales is therefore important when developing
31 biodiversity conservation measures in human-modified landscapes.

32 Commercial logging has turned large regions of the natural boreal forest ecosystem of
33 Europe and North America into forest landscapes dominated by monospecific even-aged stands,
34 where the multi-aged and structurally more diverse natural forest stands are rare and scattered
35 (Esseen et al. 1992; Bergeron et al. 2002). This has raised concerns about how to efficiently
36 extract forest products and still maintain biodiversity. For conservation measures to be applied at
37 the scale where they are most probable to improve persistence of naturally occurring species,
38 knowledge of the relative importance of key habitat characteristics at different spatial scales on
39 species occurrence is needed. However, for forest species such knowledge is generally limited
40 (reviews of epiphytic lichens: Nascimbene et al. 2013, and dead-wood associated species:
41 Sverdrup-Thygeson et al. 2014; see however bird studies, e.g., Saab 1999; Rolstad et al. 2000).

42 About 20% of all multicellular organisms in boreal forests are saproxylic, i.e. dependent on
43 dead wood, or on other saproxylic organisms (Stokland et al. 2012). Fungi and beetles are the
44 largest groups among the saproxylic organisms. These organisms have been given much
45 attention in nature conservation, because intensive forest management strongly decreases the
46 quantity and diversity of coarse dead wood (Siitonen 2001). For instance, more than a half of all

47 red-listed forest species in Fennoscandia are saproxylic. Saproxylic species are often associated
48 with certain characteristics of the dead wood items (e.g. Lindhe et al. 2005; Berglund et al.
49 2011). At the stand scale, a higher amount of dead wood have been found to increase species
50 richness (Lassauce et al. 2011), but its effect on the probability of occurrence of individual
51 species has rarely been studied. Since forest habitats are dynamic, species occurrence relies on
52 colonisation from dispersal sources in the surrounding landscape (Ranius et al. 2014).
53 Consequently, the composition of the surrounding landscape may influence the occurrence
54 patterns of saproxylic organisms (e.g. Gu et al. 2002; Ranius et al. 2010). Most studies that
55 investigate the effect of variables at various spatial scales on saproxylic organisms in forests
56 have, however, either ignored the importance of habitat connectivity (Stenbacka et al. 2010;
57 Berglund et al. 2011) or focused on single species (e.g. Sverdrup-Thygeson and Midtgaard 1998;
58 Schroeder et al. 2007; Jackson et al. 2012; Rubene et al. 2014). Therefore, more knowledge is
59 needed on the relative importance of dead wood quality, stand characteristics, and surrounding
60 landscape on a larger range of saproxylic species.

61 Hierarchical Bayesian modelling could be used for fitting species distribution models with
62 complex multilevel structures to properly model the influence of different explanatory variables
63 at their hierarchical level and account for different sources of variation across different spatial
64 scales (Gelman and Hill 2007). Recently, such approaches have been used for quantifying habitat
65 requirements of individual species in whole communities, based on the relative influence of local
66 and larger-scale explanatory variables. Such analyses have been done on saproxylic fungi
67 (Berglund et al. 2011; Nordén et al. 2013) but to our knowledge not on any other forest-dwelling
68 groups.

69 The aim of this study was to investigate the relative importance of habitat characteristics at
70 multiple spatial scales for explaining the occurrence of saproxylic beetles. Specifically, we
71 modelled the occurrence probability of individual beetle species on dead wood items, based on
72 characteristics of dead wood items, stand characteristics, and habitat connectivity, using the
73 hierarchical Bayesian framework. To evaluate the relative importance of spatial scale, we
74 compared average differences in deviance information criterion (DIC) between models that
75 included different sets of variables.

76

77 **Methods**

78 *Study landscape and stand selection*

79 The study was conducted in a 20 000 ha study landscape (Fig. 1) in the Swedish province of
80 Hälsingland (Fig. 1; 62° N, 16° E), situated in the southern boreal vegetation zone (Sjörs 1999).
81 Data on dead wood amounts are available from this landscape (Ekbom et al. 2006). The forest
82 land in the study landscape is owned by one forest company, Holmen Skog AB. Since the 1950's,
83 the forest has been managed more intensively and harvested at thinnings and by clear-felling.
84 Therefore, the landscape is today mainly composed of even-aged management blocks (stands)
85 covering the entire rotation period of about 100 years. There are also three large, legally
86 protected nature reserves, covering 3.1% of the landscape. Norway spruce (*Picea abies* (L.)
87 Karsten) and Scots pine (*Pinus sylvestris* L.) dominate the forests, followed by birch (*Betula*
88 *pendula* Roth and *B. pubescens* Ehrh.) and aspen (*Populus tremula* L.). Productive forest (i.e.
89 with a potential forest growth $> 1 \text{ m}^3 \text{ ha}^{-1}$) covers 83.0% of the landscape. In the managed stands,
90 deciduous trees rarely constitute $> 20\%$ of the standing volume.

91 We surveyed beetles in 56 forest stands, which all were productive forests dominated by
92 Scots pine or Norway spruce. We used databases from the forest owner to randomly select these
93 stands, interspersed across the study landscape and classified into three stand types (Table 1). 1)
94 “Clear-cuts” were 3-7 years old canopy-open stands; 2) “mature” stands (≥ 60 years old) were
95 canopy-closed, managed stands; and 3) “reserves” were canopy-closed, unmanaged forests that
96 are legally protected. These three stand types are potentially important habitat for saproxylic
97 beetles living under bark, since they are characterized by large volumes of dead wood with bark,
98 compared to managed stands 8 – 59 years old, where the dead wood recruitment is low and most
99 of the remaining dead wood items have lost their bark (Ekbom et al. 2006). Due to large sizes of
100 the included three reserves (427, 242, and 82 ha), we divided them into 6, 6, and 2 equally sized
101 sub-areas, respectively. The sub-areas were treated as individual stands in the analyses, and this
102 treatment was supported by low levels of spatial autocorrelation of the residuals from the best
103 full models (see *Statistical analyses*) for all species tested (Moran’s I, $p_{\min} = 0.07$). More mature
104 stands were surveyed than clear-cuts (27 vs. 15), which reflects the difference in total area
105 between these two stand types in the study landscape.

106

107 *Beetle sampling*

108 We aimed at sampling saproxylic beetles in 10 dead wood items per forest stand. We only
109 selected items with a diameter > 10 cm and a length > 0.5 m with bark left, but avoided the
110 youngest decay stage in which bark beetles are typically dominating. In each forest stand, the
111 selection was done randomly from logs (downed CWD) and snags (standing CWD) that occurred
112 within one of four 20 m \times 100 m sampling rectangles. If fewer than 10 dead wood items were
113 found in this way, we searched in the remaining parts of the stand for suitable dead wood items.

114 If there still were fewer than 10 available items, we sampled all available items. During two
115 years (2002 and 2003), 383 dead wood items were sampled. For each item we sieved 1 m² of
116 bark through a coarse net (Wikars et al. 2005), and the resulting fine fraction was placed into
117 Tullgren funnels (30 cm wide, 8 mm mesh size) where beetles were extracted under a lamp
118 (Southwood and Henderson 2000). We used 60 W light bulbs as heat and light source, and
119 extraction lasted for at least 24 h. We identified all adult Coleoptera to species or genus level, but
120 in the analyses we only included species known to be obligate saproxylic (Dahlberg and
121 Stokland 2004). Nomenclature of beetles follows Silfverberg (2004).

122

123 *Explanatory variables*

124 We measured variables that may affect the occurrence of saproxylic beetles on three spatial
125 scales: dead wood items, stands, and surrounding landscape. For each dead wood item we
126 recorded five explanatory variables: diameter, tree species, position (standing or downed), degree
127 of shade, and decay stage. We estimated the degree of shade on a four-level scale: exposed to
128 direct sunlight during 1) > 75%, 2) 50-75%, 3) 25-50%, and 4) < 25% of the day. The decay
129 stage was estimated on a six-level scale based on the hardness of the wood (Siitonen and Saaristo
130 2000).

131 We analysed three stand variables: stand size, amount of coarse dead wood, and stand type.
132 We obtained stand size using databases from the forest owner, and amount of coarse dead wood
133 (both logs and snags) from a previous study in the same forest stands (Ekbohm et al. 2006). For
134 coarse dead wood amount, we used volume (m³) dead wood · ha⁻¹, including dead wood items
135 with a diameter > 10 cm (7 cm for deciduous trees) and a length > 0.5 m. We included stand type

136 because clear-cuts, mature stands, and reserves differ from each other regarding, e.g., forest age
137 and exposure to sun and wind (Table 1).

138 At the landscape scale, we estimated the amount of habitat in the surrounding landscape by
139 summing the area of all stand types defined as habitat (i.e. clear-cuts, mature stands, and
140 reserves, since they have larger volumes of dead wood with bark; Ekbom et al. 2006) within four
141 buffer circles (500, 1000, 2000, and 4000 m radius, respectively) around each target stand. We
142 used a measure based only on habitat availability since that could potentially be used in forest
143 planning, whereas connectivity measures that require data about individual species' occurrence
144 patterns and biology are not feasible in most landscapes due to lack of information. We used a
145 buffer metric, since for saproxylic beetles it performs equally well as measures that up-weight
146 closer patches (Ranius et al. 2010). The estimation of surrounding habitat amount was done in
147 ArcMAP 10, and the maximum radius (4000 m) was the maximum distance for which we had
148 available information of stand characteristics for all surrounding stands. Six of the analysed
149 species were identified as canopy-closed species, since they either did not occur in clear-cuts or
150 were associated with closed stands according to statistical analyses (i.e. negative 95% credible
151 intervals for clear-cut did not overlap 0; Fig. 2). For these six species, we used the summed area
152 of only mature stands and reserves as the habitat connectivity variable. In the analyses, we tested
153 the four spatial scales (radii) for the habitat connectivity one by one in separate models. For
154 stands situated spatially close, the buffer circles overlapped, and we hence to some extent pseudo-
155 replicate the connectivity measure. However, that is a minor problem as the spatial
156 autocorrelation was low for the model residuals (see *Study landscape and stand selection*).

157 We checked all continuous explanatory variables for cross-correlations prior to the
158 analyses. The highest Pearson correlation coefficient, $r = 0.3$, was found between stand size and

159 dead wood amount $\cdot \text{ha}^{-1}$. For tests of associations between categorical and continuous variables,
160 we performed one-way ANOVA's with Tukey's Honestly Significant Differences post-hoc test.
161 Reserve stands were larger than both clear-cuts and mature stands, and their dead wood amounts
162 $\cdot \text{ha}^{-1}$ were also higher (Table 1). Individual dead wood items were less shaded in clear-cuts
163 compared to both mature stands and reserves, and more shaded in mature stands than in reserves
164 (Table 1). Dead wood diameter was greater in clear-cuts compared to both mature stands and
165 reserves (Table 1).

166

167 *Statistical analyses*

168 We modelled occurrence probability of individual beetle species based on dead wood
169 characteristics, stand characteristics, and habitat connectivity, while accounting for the
170 hierarchical structure of the data. Analyses were conducted for the most frequent 44 species,
171 which had occurrences in at least eight ($> 2\%$) of the sampled dead wood items. Specifically, we
172 analysed the probability of occurrence on individual dead wood items, using Bayesian
173 hierarchical generalized linear models (Gelman and Hill 2007) with a logit link function (logistic
174 regression) and varying intercepts. The hierarchical Bayesian framework enables the utilization
175 of explanatory variables measured at the stand level (i.e. at the higher hierarchical level), as they
176 are used to model the stand-specific intercepts (Gelman and Hill 2007). We assumed a Bernoulli
177 probability distribution of the binary response variable (y_{ij} ; species presence/absence) and
178 modelled species occurrence probability on dead wood item i in stand j , i.e. $P(y_{ij} = 1)$ as:

$$\text{logit} \left(P(y_{ij} = 1) \right) = \alpha_j + \sum_{k=1}^n \beta_k X_{ijk}$$

179

180 where α_j is the stand-specific intercept (see below), X_{ijk} is the dead wood item-level explanatory
181 variable k for dead wood item i in stand j and β_k is the dead wood item-level effect-size
182 parameter of explanatory variable k (n in total). The stand-specific intercepts (α_j) were modelled
183 as:

$$\alpha_j \sim N(\mu_{\alpha_j}, \sigma_{\alpha})$$

184 where σ_{α} is the standard deviation of a normal distribution with a mean (μ_{α_j}) modelled based on
185 the stand-level explanatory variables as:

$$\mu_{\alpha_j} = \gamma + \sum_{m=1}^h \rho_m Z_{jm}$$

186
187 where γ is an intercept parameter, Z_{jm} is the stand-level explanatory variable m for stand j and ρ_m
188 the associated effect-size parameter (h in total). Hence, the intercepts vary between stands and σ_{α}
189 determines the between-stand variation (here called random error). The landscape-scale variable
190 (habitat connectivity at four spatial scales) was treated as a stand variable in the model, but was
191 added separately at the end of the model-building procedure.

192 We constructed hierarchical Bayesian models for each species using different sets of
193 variables, but always with a hierarchical structure (i.e. with varying intercepts). First, we
194 parameterized one model containing only dead wood variables (henceforth, dead wood model).
195 Then we selected the model with the lowest DIC (deviance information criterion) among models
196 with all combinations of the five dead wood variables. DIC is analogous to the Akaike
197 information criterion (AIC), and is well-suited for Bayesian hierarchical modelling
198 (Spiegelhalter et al. 2002). Second, we repeated the same model selection procedure, but with
199 only stand variables included (henceforth, stand model). Third, we constructed full models with

200 both dead wood and stand variables included in the model selection procedure. The variables
201 included in these full models could be only dead wood, only stand, both dead wood and stand, or
202 no variables, depending on the species tested. To evaluate the relative importance of dead wood
203 and stand variables, we compared the average differences in DIC between the hierarchical null
204 model (i.e. including stand identity as a random factor but no explanatory variables) and the dead
205 wood, stand, and full model, respectively. Finally, we tested whether adding habitat connectivity
206 at four spatial scales, one by one, to the full models improved the models by reducing DIC.

207 We estimated the posterior distributions of the Bayesian model parameters in equations (1)
208 and (2), using two Monte Carlo Markov chains of 610 000 iterations each. We discarded 10 000
209 iterations as ‘burn-in’ and then saved every 60th iteration to accumulate 10 000 values from each
210 chain (i.e. 20 000 in total). To improve convergence of the chains and simplify the interpretation
211 of the models, we centred all variables (i.e. subtracted the mean from each measured value) and
212 also standardized (i.e. dividing each measured value by 2·sd) the continuous variables (Gelman
213 and Hill 2007). For categorical dead wood (tree species and position) and stand (stand type)
214 variables, we excluded categories in which the species was not found. Consequently, we
215 excluded birch for seven species, clear-cuts for three species, and both birch and clear-cuts for
216 one species (Table A1).

217 We used uninformative prior distributions for all model parameters. We used normal
218 distributions with mean = 0 and variance = 1000 for all effect size parameters and the intercept γ ,
219 while σ_α was drawn from a uniform distribution between 0 and 100. To evaluate convergence,
220 we visually inspected the trace plots and used the Gelman-Rubin diagnostic (Gelman and Hill
221 2007). Convergence ($R < 0.1$) was reached for all estimated parameters. We summarized the
222 posterior distribution of estimated parameters by calculating the distribution mode and Bayesian

223 50% and 95% credible intervals. For the analyses, we used the statistics software JAGS
224 (Plummer 2003) and R 2.14.0 (R Development Core Team 2011).

225

226 **Results**

227 Characteristics of dead wood items were more important for explaining species' occurrence
228 probability than characteristics measured of the forest stands, as judged by the average reduction
229 in DIC between the hierarchical null models and the dead wood (16.7) and stand (1.7) models,
230 respectively (Fig. 3). When adding habitat connectivity, DIC was reduced by 1.9. The average
231 reduction in DIC between the hierarchical null models and the full models was close to the
232 average reduction between the hierarchical null models and the dead wood models (Fig. 3).

233 Tree species and position (i.e. standing or downed) were the variables that were important
234 for the largest number of species; they were included in the final occurrence models for 22 and
235 21 beetle species, respectively (Fig. 2). However, among the studied species there were no
236 specialists; none occurred only in one tree species or only in either standing or downed dead
237 wood. The majority of the beetles affected by tree species (18 of 21) were associated with
238 conifers (spruce or pine), whereas only three species were associated with birch (i.e. the negative
239 95% credible intervals for both spruce and pine did not overlap 0; Fig. 2). Furthermore, there
240 were eight species that did not occur on birch at all, and consequently the effect of birch was not
241 tested for them (Table A1). Degree of shade, diameter, and decay stage were included in the full
242 models for 13, 10, and 9 species, respectively (Fig. 2).

243 Stand type was the most important stand characteristic for explaining species occurrence,
244 and was included in the final model for seven species. Clear-cuts had a negative effect on several
245 species: four species did not occur on clear-cuts at all (Table A1), and the occurrence probability

246 of two species was lower on clear-cuts compared to reserves (Fig. 2). One species was associated
247 with reserves, whereas for two species the occurrence probability was higher in mature stands
248 compared to reserves (Fig. 2). Stand size affected very few species, whereas the amount of dead
249 wood did not affect any of the species.

250 Adding habitat connectivity to the full model improved the models for 24 species, but in
251 most cases the 95% credible interval included 0 (Fig. 2). For 11 species the relationship was
252 positive, whereas for 13 species it was negative.

253

254 **Discussion**

255 *Relative importance of spatial scales*

256 We found that characteristics of the dead wood items were more important than characteristics
257 measured of the forest stand and surrounding landscape for explaining the occurrence of
258 relatively common saproxylic beetles in a managed boreal forest landscape (Fig. 3). Thus, this
259 beetle community are mainly conforming to what in metacommunity ecology is referred to as the
260 species sorting view, which is defined by the close link between species distributions and local
261 conditions (acting directly or by altering competitive abilities) together with sufficient
262 availability of dispersal sources (Leibold et al. 2004). However, our result may not only be a
263 consequence of the species' biology, but may also reflect that it is easier to measure
264 characteristics relevant for saproxylic species at a dead wood item scale rather than at a stand and
265 landscape scale. The characteristics we used are representative for what is typically measured in
266 biodiversity monitoring and surveys. For that reason our outcome is still relevant for
267 management and conservation, suggesting that strategies should be based more on characteristics
268 of dead wood items rather than stand and landscape characteristics. It should be noted that this

269 study only includes the 44 relatively common saproxylic species, and for rarer and more
270 specialised species, for which the habitat is more fragmented, habitat connectivity is expected to
271 be more important (Fahrig 1998; Nordén et al. 2013).

272 There were correlations between some characteristics of the dead wood items and stand type
273 (Table 1); however, we believe that these correlations have minor influence on our main
274 conclusions since the characteristics that influenced the largest number of species (tree species
275 and position) did not differ between different stand types. Perhaps stand characteristics would
276 have an overall slightly higher relative importance if shade and diameter was not included at the
277 lower hierarchical level.

278

279 *Effects of characteristics of dead wood items*

280 The characteristics of dead wood items were important for explaining occurrence of the majority
281 of the saproxylic beetles (Fig. 2). This agrees with earlier studies of saproxylic beetles (Ulyshen
282 and Hanula 2009; Jackson et al. 2012; see however Wikars 2002) and fungi (Stokland and
283 Kauserud 2004; Berglund et al. 2011). For both beetle larvae and fungi, development takes place
284 in one single dead wood item, which can explain why the conditions in individual logs are
285 important for the recruitment of adult beetles and fruiting bodies of fungi. The most important
286 characteristics of the dead wood items for explaining species occurrence in the present study
287 were tree species, position, decay stage, and degree of shade. Even though there were no true
288 specialists, many species occurred more frequently in certain types of dead wood. These dead
289 wood characteristics may reflect microclimatic conditions (moisture and temperature) as well as
290 nutrient supply (for instance, availability of fungi), and have been shown important for
291 explaining occurrence of saproxylic organisms also in earlier studies (e.g. Ranius and Jansson

292 2000; Jonsell and Weslien 2003; Lindhe et al. 2005; Saint-Germain et al. 2007; Berglund et al.
293 2011). The direction of the impact of dead wood characteristics varied among species, which
294 suggests that a high heterogeneity of microhabitats may increase the diversity of saproxylic
295 species (Davies et al. 2008).

296

297 *Effects of stand characteristics*

298 Even if dead wood characteristics explained most of the variation in the occurrence patterns (Fig.
299 3) also stand characteristics were important; for instance, stand type influenced the occurrence
300 probability of 20% of the species. This was mainly because species occurred in lower frequency
301 on clear-cuts compared to the canopy-closed mature and reserve stands. This agrees with earlier
302 findings of similarities in saproxylic beetle communities among mature managed and old-growth
303 boreal stands, but divergent species composition in clear-cuts (McGeoch et al. 2007; Stenbacka
304 et al. 2010; Hjältén et al. 2012). One reason for this divergence is the difference in sun exposure,
305 which affects saproxylic beetles (Similä et al. 2002; Lindhe et al. 2005). Species dependent on
306 forest cover continuity, dead wood, and large trees have been found to be more species rich in
307 unmanaged forests than in managed ones (Paillet et al. 2010). The relatively weak effect of
308 management in our study may be due to that there are relatively small differences in dead wood
309 amounts between mature managed stands and reserves (Table 1) compared to the differences that
310 often occur between old-growth forests and forests that have been managed by clear-felling since
311 a long time (Siitonen 2001).

312 We found no effect of dead wood amount per hectare and only a weak effect of stand size
313 on species occurrence probability per dead wood item. In many studies, higher amounts of dead
314 wood increase species richness and probability of occurrence of saproxylic organisms per forest

315 stand (Lassauce et al. 2011 and references therein). The positive effects of the amount of dead
316 wood on species richness reported in the literature could in most cases be explained by a
317 sampling effect alone, i.e. by the fact that a larger amounts of dead wood will contain more
318 individuals and this will imply more species (Fahrig 2013). This is the case when window traps
319 are used to collect saproxylic beetles, since they capture beetles from a larger volume of dead
320 wood if situated at a spot with a higher density of dead wood. Our study is one of a few in which
321 the amount of dead wood sampled was standardized, which is necessary when disentangling the
322 island effect (i.e. higher species densities on larger habitat islands) and the sampling effect
323 (Fahrig 2013). For saproxylic beetles, such standardized samples are obtained by searching
324 through certain amounts of dead wood (using, for instance, bark sieving and extraction as in the
325 present study) and when using emergence traps (e.g., Wikars et al. 2005). An island effect is
326 expected according to the island biogeography theory (predictions about species richness;
327 MacArthur and Wilson 1967) and the resource concentration hypothesis (predictions about
328 population densities; Root 1973). Our results imply that there is no island effect; however, other
329 studies of saproxylic beetles have revealed an island effect, since they have observed a positive
330 effect of habitat amount at the stand scale on the probability of species occurrence per dead wood
331 item (Komonen et al. 2000; Ranius 2002; Sahlin and Schroeder 2010; Victorsson and Jonsell
332 2013). These studies have mainly focused on species specialised to certain dead wood types with
333 a highly fragmented distribution, while in the present study we analysed the 44 most frequently
334 occurring species in a wide range of dead wood types. Also, a study conducted in the same area
335 as the present study, focusing on certain redlisted saproxylic beetle species, suggested that some
336 species are demanding regarding amounts of certain qualities of dead wood at a local scale
337 (Rubene et al. 2014), but these species were too rare to be analysed in the present study. The lack

338 of relationship in the present study may be explained by the fact that forest stands with at least
339 some dead wood present occurred relatively continuously in the landscape. Consequently, there
340 are many dispersal sources for the relatively common species that were included in the present
341 study. This makes the amount of dispersal sources within each forest stand a less critical factor.
342 Another possible reasons for the weak effect of current dead wood amounts is that saproxylic
343 species richness may be better explained by other factors which are difficult to measure, such as
344 the historical continuity of dead wood. Some studied indicates that historical continuity is
345 important for rare and threatened saproxylic beetles (Nilsson and Baranowski 1997; Siitonen and
346 Saaristo 2000), but little is known about its effect on more common species. It should also be
347 remembered that in the present study, stand size and dead wood amounts differed between the
348 three stand types, and the weak effect could therefore also be because including stand type in the
349 model removes some of the variation in these two explanatory variables. However, this potential
350 bias is still only valid for a few species; only six species had any stand characteristics that did not
351 overlap zero in their final model.

352

353 *Effects of habitat connectivity*

354 Habitat connectivity affected the occurrence of many species; however, the effect was usually
355 weak and there were nearly as many negative as positive relationships (Fig. 2). The occurrence
356 of both negative and positive effects suggests that the spatial location of the dead wood items had
357 some effect on species' occurrence; however, the spatial pattern was not clearly associated with
358 habitat density. We had expected a clearer positive relationship, due to higher colonization rates
359 when there are higher habitat density, and thus larger dispersal sources nearby (Thomas et al.
360 1992). One reason could be that we mainly analyse rather common species. Several other studies

361 of saproxylic beetles, which have shown clearer positive effect of habitat connectivity, have
362 focused on species specialised to habitats that are more fragmented in comparison to the present
363 study (Økland et al. 1996; Ranius et al. 2010; 2014; Götmark et al. 2011; Bergman et al. 2012).
364 It could be that since all species in our study occur in managed forest, and the study landscape is
365 dominated by managed forest, the landscape is not very fragmented for these species. At such
366 low level of habitat fragmentation, habitat quality has generally a greater influence than habitat
367 connectivity on species occurrence patterns (Fahrig 1998; Andréén 1999). Among saproxylic
368 fungi, specialised species have indeed been found to be more sensitive to habitat fragmentation
369 than generalistic species since they respond more negatively to connectivity (Nordén et al. 2013).
370 Another reason for the weak effect in the present study could be that the importance of habitat
371 connectivity may be underestimated when analysing snapshot data in landscapes where habitat
372 conditions change over time (Hodgson et al. 2009). In our study landscape, the area covered by
373 older forest has clearly decreased during the last 50 years, and therefore the current species
374 occurrence patterns may to some extent reflect historical habitat connectivity (Schroeder et al.
375 2007). Thirdly, we measured connectivity as the amount of habitat in the surroundings, while a
376 measure that includes information on habitat quality or species' occurrences would reflect the
377 amount of dispersal sources better (Ranius et al. 2010). An advantage with the measure we used
378 is that it better reflects what could potentially be used in management, since it only requires data
379 that are widely available.

380

381 **Implications for conservation**

382 We found that for the occurrence of the more common saproxylic beetle species', the quality of
383 dead wood items is more important than their spatial location. The habitat requirements

384 regarding dead wood characteristics (i.e. tree species, position, decay stage and degree of shade)
385 differed among species. Therefore, conservation measures aiming at mitigating negative impacts
386 of forestry should aim at creating not only large amounts, but also a high diversity of dead wood.
387 Attempts have been made to identify "thresholds" in the dead wood amounts that should be
388 exceeded for sustaining biodiversity (Müller and Bütler 2010). However, due to the lack of
389 relationships between amount of dead wood per stand and probability of occurrence per dead
390 wood item, our study does not lend support for any such thresholds at a forest stand level. Our
391 study only included more common species, but it may be that rarer species is more demanding
392 (cf. Penttälä et al. 2004). To some extent, our outcome may also be because we lack detailed data
393 on the amount of dead wood that is suitable for each species. In that sense our study is more
394 similar to the situation for practitioners, who do not have detailed data about all individual
395 species' occurrence patterns and biology. In our study landscape, the amount of dead wood with
396 certain qualities is probably a key factor to allow persistence of the saproxylic fauna. However,
397 in forest habitats that are more fragmented and for rare and demanding species, high
398 concentration of habitat may be important for species' occurrence (e.g. Ranius et al. 2010;
399 Bergman et al. 2012).

400

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408

409 Table 1. Characteristics (mean and standard error) of the sampled dead wood items and stand
 410 types.

	Stand type			ANOVA (df =2)*
	Clear-cut (n = 15)	Mature (n = 27)	Reserve (n = 14)	
<u>Dead wood item characteristics</u>				
Birch (%)	26.5 (6.5)	32.2 (5.8)	20.8 (4.2)	ns
Pine (%)	24.2 (7.5)	29.7 (6.5)	43.1 (7.7)	ns
Spruce (%)	49.3 (8.5)	38.1 (6.0)	36.2 (7.0)	ns
Downed (%)	39.3 (6.9)	45.9 (6.2)	37.9 (5.5)	ns
Degree of shade	1.2 (0.1) ^a	3.4 (0.1) ^b	3 (0.1) ^c	F = 149.8, p < 0.001
Diameter (cm)	26.4 (2.0) ^a	17.6 (0.7) ^b	20.4 (1.0) ^b	F = 14.2, p < 0.001
Decay stage ¹	1.2 (0.1)	1.2 (0.1)	1.2 (0.1)	ns
<u>Stand characteristics</u>				
Age (year) ²	3 (1)	104 (7)	>150	not tested
Size (ha) ²	15 (2) ^a	12 (2) ^a	53 (4) ^b	F = 72.6, p < 0.001
Dead wood amount (m ³ /ha) ³	14 (3) ^a	20 (4) ^a	34 (5) ^b	F = 5.5, p = 0.007

411 * One-way ANOVA with Tukey Honest Significant Differences post-hoc test for tests of associations between stand
 412 type and continuous variables. The p values are adjusted for pairwise comparisons. Different letters (^a, ^b, or ^c) within
 413 a row denote significant differences.

414 ¹According to a six-grade scale made by Siitonen and Saaristo (2000), with 0 being the first and 5 the latest stage

415 ²According to databases provided by the forest company

416 ³Measured as described in Ekbohm et al. (2006)

417

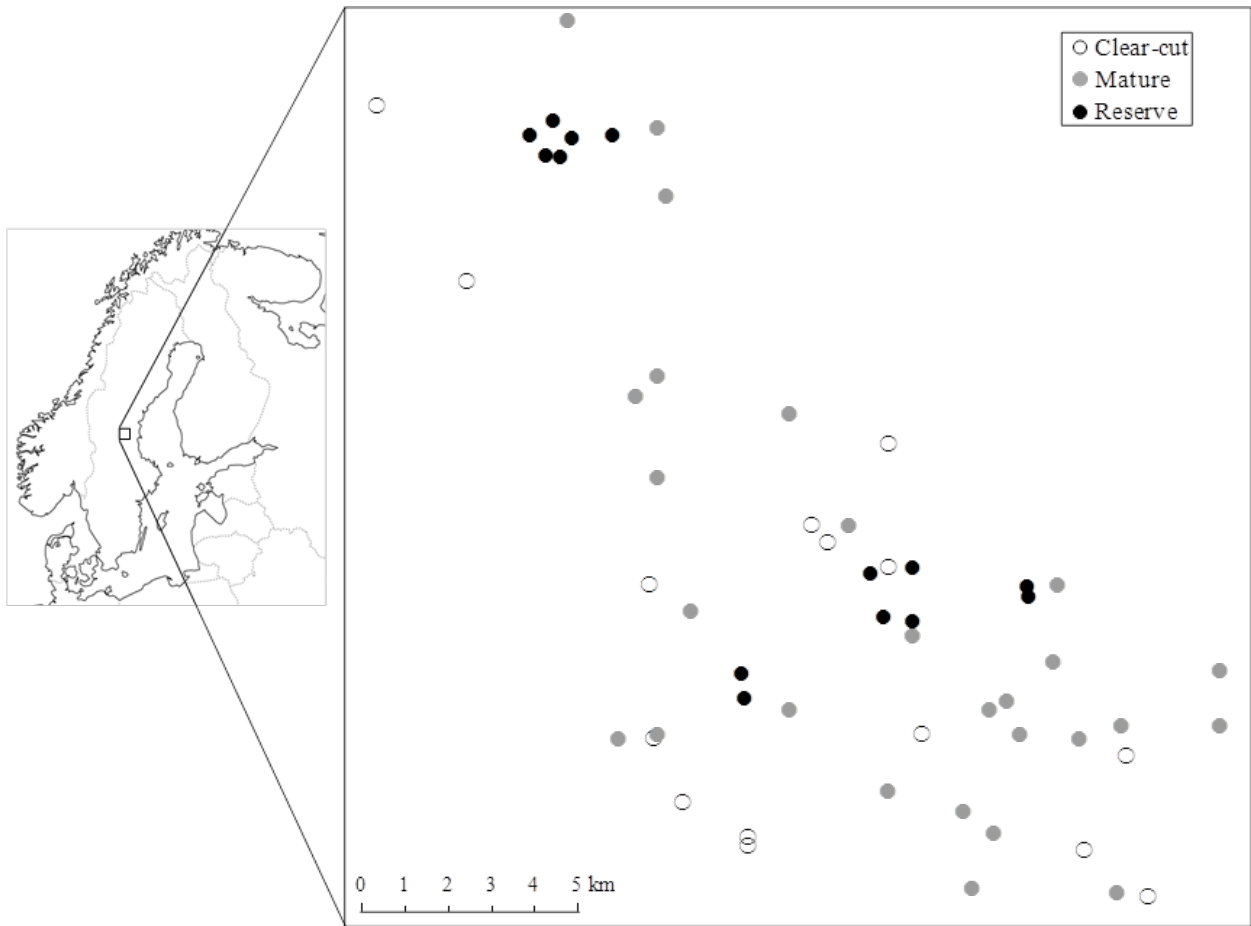
418 Figure 1. Location of the 56 forest stands where beetles were sampled, in a study landscape
419 situated in central Sweden. The distance to the nearest neighbour was, on average, 965 m.

420

421 Figure 2. Estimates of parameters in Bayesian generalized linear models for occurrence
422 probability of saproxylic beetle species on individual dead wood items. The modes (short vertical
423 lines), 50% (thick horizontal lines) and 95% (thin horizontal lines) credible intervals are shown
424 for the full models including or excluding habitat connectivity. Grey lines indicate that the 95%
425 credible interval includes 0, black lines that it does not. * denotes that parameter estimates are,
426 for visibility reasons, scaled by a factor 10. ¹ and ² denote effects of habitat connectivity at 500
427 and 4000 m, respectively. For the categorical variables “tree species”, “dead wood position”, and
428 “stand type”, only parameters for categories other than the reference category (birch, downed,
429 and reserves, respectively) are given. Dead wood amount was also tested, but that is not shown
430 here since it was not included in the final model for any of the species. Standard deviation of
431 random error (σ) is the parameter associated with unexplained between-stand variation.

432

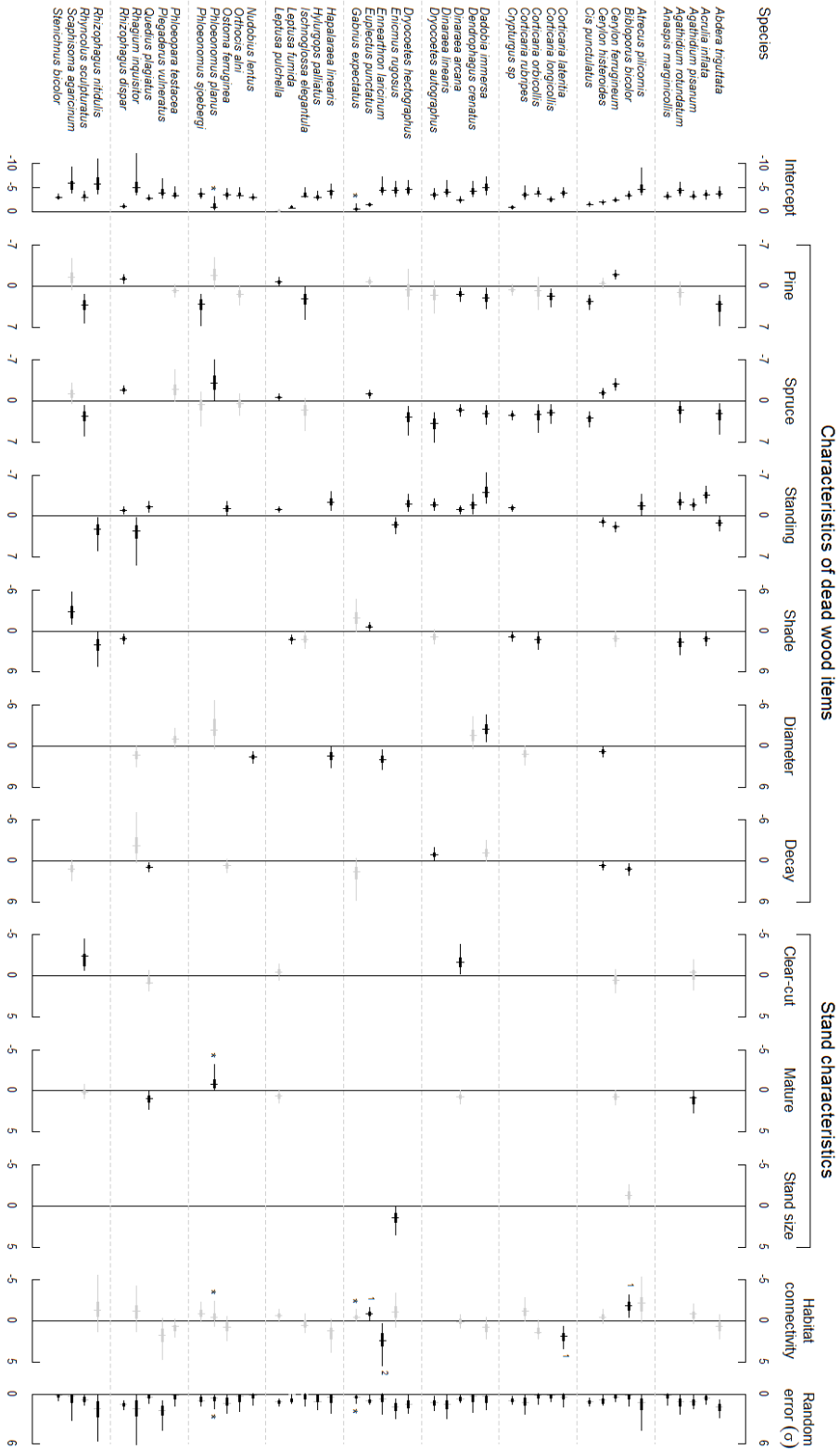
433 Figure 3. Change in DIC (\pm SE) between models including explanatory variables at different
434 spatial scales and a null model with only the random stand effect included. Variables included in
435 the full models can be only dead wood, only stand, both dead wood and stand, or no variables
436 (see Fig. 2 for species-specific details). hc = habitat connectivity.



437

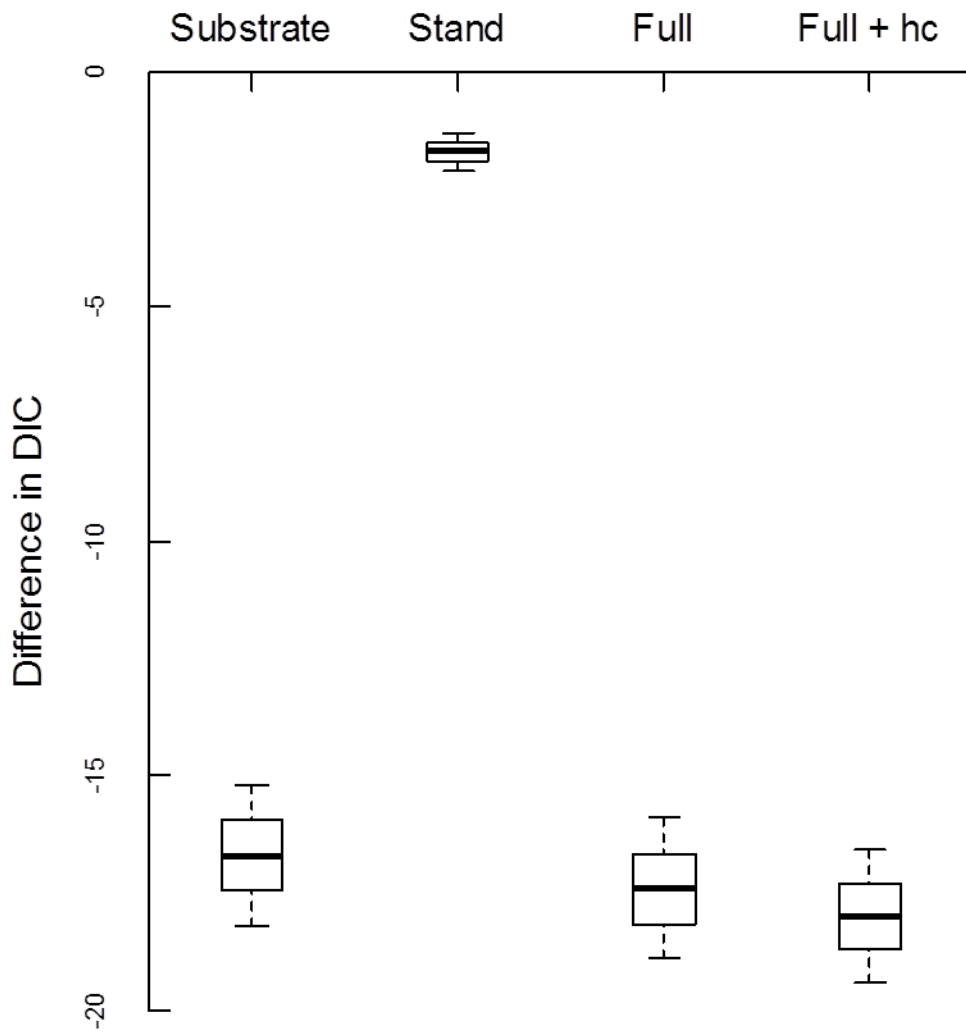
438

439 Fig. 1



440

441 Fig. 2



442

443

444 Fig. 3

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