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8 **Colonisation of ephemeral forest habitats by specialised species: beetles**
9 **and bugs associated with recently dead aspen wood**

10

11 Short title: Colonisation of recently dead aspen wood

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22

23 **Abstract**

24 The most appropriate strategy for preserving fragmented populations depends on a species'
25 ability to colonise distant habitat patches. Insects associated with early decay stages of dead
26 wood are expected to have a high capacity to colonise new habitat patches. To study the
27 dispersal ranges of beetles (Coleoptera) and flat bugs (Hemiptera: Aradidae) dependent on
28 recently dead aspen (*Populus tremula*) wood in Finland, we set out 58 piles of recently cut
29 aspen logs at various distances up to 1.6 km from forests that contained a high density of old
30 aspen trees. We captured insects by trunk window-traps, and counted beetles' exit holes.
31 Habitat connectivity was measured in terms of the amount of suitable aspen-wood in the
32 surrounding environment, with the closest dead wood items up-weighted by a negative-
33 exponential function.

34 The log-piles attracted many saproxylic insects including four red-listed aspen-
35 specialist species. The exposure of log-piles to the sun, and high levels of habitat
36 connectivity increased the species richness of aspen-specialists, whereas bark peeling by
37 moose decreased richness. The spatial scale at which species richness had its strongest
38 response to habitat was 93 m. Among individual species there was a wide variability in
39 spatial scale of response.

40 This study supports the view that conservation efforts in boreal forests should be
41 concentrated on sites where colonisation by target species is most likely. Restoration of
42 habitat by re-locating logs may be useful at localities with a rich and specialised fauna but
43 which have too low rate of formation of dead wood by natural processes.

44

45 Keywords: bark, dispersal, habitat connectivity, restoration, saproxylic insects

46

47

48 **Introduction**

49 Many organisms associated with dead wood are thought to be threatened as a result of
50 habitat loss and fragmentation (Berg et al. 1995; Nieto and Alexander 2010). The most
51 effective conservation strategy for preserving this fauna and flora depends to some extent on
52 species' dispersal ranges. For species with a limited dispersal range, it is important that
53 conservation efforts are directed within, or close to, sites where the target species are present
54 (Huxel and Hastings 1999), while to protect species that are able to colonise over long

55 distances, efforts can be directed at more distant sites where restoration efforts may be less
56 expensive and where they may improve habitat quality quickly (Ranius and Kindvall 2006).
57 Items of dead wood are ephemeral habitats that, for some species, remain suitable for only
58 one or a few years. Theoretical and empirical studies suggest that species adapted to such
59 short-lived habitats are generally more dispersive than species of more stable habitats
60 (Southwood 1962; Johnson and Gaines 1990; Travis and Dytham 1999).

61 The use of tethered flight to test the physiological capacity for dispersal has shown
62 that beetles living on the fruiting bodies of bracket fungi are able to fly tens of kilometres
63 (Jonsson 2003). However, reproductive success is usually compromised when significant
64 amounts of resources are spent on dispersal (Gibbs and van Dyck 2010); instead, a better
65 strategy can be to avoid risks and save energy by moving shorter distances. Consequently,
66 the distances that an organism actually moves in the field may differ widely from its
67 physiological capacity determined in laboratory experiments (Forsse and Solbreck 1985) and
68 can only be revealed by field studies. Observing the colonisation of artificially created
69 habitat patches in field conditions has been found to be a fruitful yet practically challenging
70 approach when studying dispersal of saproxylic insects. The method has been used on
71 beetles in bracket fungi (Whitlock 1992; Jonsell et al. 1999; Jonsson and Nordlander 2006),
72 and bark beetles on logs (Nuorteva and Nuorteva 1968; Nilssen 1984). In the present study,
73 we experimentally assessed the dispersal and colonisation of aspen-associated beetles and
74 bugs by setting out piles of recently cut aspen logs at sites differing in habitat connectivity.

75 In many regions, aspen (*Populus tremula*, in Northern America: *P. tremuloides*) is
76 considered an important tree species for saproxylic insects (e.g., Canada: Hammond et al.
77 2004; Finland: Kouki et al. 2004; UK: Rotheray et al. 2009). In Finland, aspen has until
78 recently been killed because it is an intermediate host for pine rust, a pest fungus that
79 damages economically valuable pine trees. However, today it is recommended that aspens
80 should be promoted in forest landscapes for enhancing biodiversity (Gustafsson et al. 2010).
81 The efficiency of such conservation measures depends on the ability of aspen-associated
82 species to colonize patches. Several beetle species that specialise on dead aspen wood occur
83 in a larger proportion of items of dead wood where these are present in large aspen stands
84 than in smaller stands (Sahlin and Schroeder 2010). This pattern may be because only large
85 aspen patches are able to continuously provide habitat availability during forest succession
86 (e.g. Vehmas et al. 2009). As the same amount of wood produce more individuals of target
87 species in larger patches, efforts to create and maintain aspen dead wood should be directed

88 towards creating a few larger patches of living and dead aspen trees rather than many small
89 patches.

90 In the present study we set out piles of recently cut aspen logs and captured insects in
91 trunk window-traps during the following three years. After three and five years we counted
92 the number of exit holes of aspen-associated species on the logs. The strongest positive
93 relationship between number of individuals and the amount of aspen dead wood probably
94 occurs at a spatial scale corresponding to the distance over which colonisations most
95 frequently take place. Furthermore, a species' abundance may be related to characteristics of
96 the logs that affects its suitability as breeding substrate. The first aim of this study was to
97 evaluate to what extent transported aspen logs may be useful for aspen-associated insects.
98 The second aim was to test the effect of habitat connectivity and identify the spatial scale
99 with the strongest response to habitat, as this affects which spatial distribution of habitat that
100 is desirable. To test this, we analysed the species richness of aspen-associated insects and
101 abundance of individual species in relation with habitat connectivity and also other log
102 characteristics.

103

104 **Methods**

105 *Study area and experimental design*

106 The experiment was conducted in the Kakonsalo Natura 2000 area in Savonranta (62° 15' N,
107 29° 00' E), eastern Finland. Although most of the Kakonsalo area has been converted to
108 forest managed by clear-cutting during recent decades, three protected areas with aspen-rich
109 forest remain, which together total 160 hectares (Fig. 1). These include clear-cuts with many
110 large retained aspen-trees and old-growth forests. Numerous rare beetle species have been
111 found in these areas, many of which are associated with aspen (Martikainen and Kouki
112 2003). Managed forests surrounding the protected areas contain only small amounts of dead
113 wood and few large aspen trees.

114 We set out 58 piles of aspen logs in a way that generated a high variability in habitat
115 connectivity among log-piles. They were set out along six forest roads, starting from
116 different borders of two of the protected areas with a high density of aspen. At each forest
117 road we identified a starting point, which was the outermost large aspen in the margin of the
118 protected area. Where possible, one log-pile was located inside the protected area within 50
119 m of the starting point, and the other piles were set outside the protected area at distances
120 from the starting point of 0 – 25 m, 25 – 50 m, 50 – 100 m, 100 – 200 m, 200 – 400 m, 400-

121 800 m, and 800 – 1600 m. In some cases, dense young forest or difficult terrain along the
122 forest road forced us to place the log piles at sites that differed slightly (usually less than 15
123 m) from this rule. Five additional log-piles were located in the core areas of the protected
124 areas.

125 Each of the 58 piles consisted of six aspen-logs with two each in the following three
126 diameter classes: 5 – 15 cm, 15 – 25 cm, and 25 – 35 cm (Fig. 2). The bottom layer
127 comprised one log from each diameter class; the upper layer comprised one thin and one
128 thick log, placed crosswise above the first layer; the remaining 15 – 25 cm log was
129 positioned vertically against the other logs and secured by boards and nails. Horizontally
130 laid logs were all 3 m long; the standing logs were all 2 m long. The volume of each pile
131 was approximately 0.6 m³, which corresponds to a medium-sized aspen-tree.

132 All experimental aspen logs were sourced from managed forests outside the study area.
133 The trees were harvested and distributed to the locations of the piles in February 2005, when
134 no colonization by insects would have been possible. Only fresh, healthy-looking logs were
135 accepted, i.e. with no heart-rot, visible polypores or old wounds. The logs were arranged
136 into piles in spring. Before spring many logs (44 %) had to some extent been debarked by
137 moose, *Alces alces* (L.).

138

139 *Collection of insect and log pile data*

140 Beetles (Coleoptera) and flat bugs of the genus *Aradus* (Heteroptera) were monitored using
141 trunk window-traps. Traps attached to dead trees usually capture more saproxylic beetles
142 than traps situated away from trees (Hyvärinen et al. 2006; Sverdrup-Thygeson and
143 Birkemoe 2009, see however Saint-Germain et al. 2006), which means that the capture in
144 trunk window traps at least to some extent reflect what is attracted by the trees. In each pile,
145 one trap was attached to the standing log (Fig. 2). The trap consisted of two perpendicular 40
146 cm × 60 cm transparent plastic panes, with a funnel below the panes leading to a 1 l
147 container partly filled with a solution of water, salt and detergent to preserve the captured
148 insects. In this study, the number of individuals decreased during the third year, indicating
149 that aspen wood attracts beetles mainly during the first few years. Consequently, sampling
150 was conducted during three years, 10 June – 14 September 2005, 10 May – 8 August 2006,
151 and 6 May – 14 August 2007. The traps were emptied 2 or 3 times per year. When
152 identifying the trap material, only aspen specialists using dead wood items > 10 cm were
153 considered (Table 1). Aspen specialists were defined as species for which we estimate that >

154 95 % of the population in our study area to develop in aspen wood or bark (Palm 1959;
155 Ehnström and Axelsson 2002; personal observations). The species may use dead trees or
156 rotten parts of trees that still are alive. To obtain evidence of reproduction, we assessed the
157 occurrence of exit holes for those aspen-specialist beetles which have characteristic holes:
158 *Xylotrechus rusticus* (Cerambycidae), *Saperda perforata* (Cerambycidae) and *Trypophloeus*
159 spp. (*Trypophloeus bispinulus* and *T. discedens*; Curculionidae). For *X. rusticus* and
160 *Trypophloeus* spp. the number of exit holes was counted, while for *Saperda perforata* only
161 presence/absence was assessed since it is impossible to identify *S. perforata* holes without
162 destroying the substrate. The logs were inspected for exit holes at 14 August 2007, when the
163 majority of beetles developing in the logs had already emerged from the logs, which were by
164 then too old for further colonization by these species. Exit holes formed by *S. perforata* were
165 screened again two years later on 28 August 2009, in logs where the species were absent in
166 2007. Because sporadic holes of *Trypophloeus* spp. are difficult to recognize, a positive
167 record was only made if groups of at least five holes were found.

168 On 14 August 2007, we measured two characteristics of the log-piles that may affect
169 their suitability for insects – their degree of exposure to the sun (Martikainen 2001;
170 Sverdrup-Thygeson and Ims 2002; Sahlin and Ranius 2009), and the extent to which bark
171 had been stripped by moose (Sahlin 2009). We visited the piles regularly to empty the traps,
172 and then we observed that this bark stripping took place before the sampling started in the
173 first year. We categorised dead wood items according to sun exposure into six subjective
174 classes from 0 (totally shaded) to 5 (in full sun). We estimated bark stripping in terms of the
175 proportion of the total area of bark that had been lost.

176

177 *Collection of aspen data*

178 We estimated habitat connectivity from the amount and position of potential dispersal
179 sources in the whole Kakonsalo study area. As our study species specialise on dead aspen
180 wood, we defined dead aspen trees (laying and standing), and dead parts of living aspen
181 trees, as suitable habitat. We obtained habitat data for the whole Kakonsalo area, either by
182 own surveys, or from data collected by Metsähallitus (the forest manager). All log-piles
183 were situated within the Kakonsalo forest estate at least 75 m from the border. Because
184 mature aspen is rare in the intensively managed forest surrounding Kakonsalo, it probably
185 has a negligible influence on the estimate of habitat connectivity that we only included data
186 from the Kakonsalo area in our estimate.

187 For forest stands situated within 100 m of the log-piles, we made a detailed survey of
188 living and dead aspens in October and November 2009. We surveyed the whole of smaller
189 stands when some part of it was within 100 m of the log-piles, but for large stands we only
190 surveyed the area within a 100 m radius of the log-pile. The positions of living and dead
191 aspen trees were measured with a GPS with a maximum error of about 20 m. We surveyed
192 dead trees with diameters > 10 cm at either breast height of standing dead wood, or in the
193 middle of laying dead wood. Items of dead wood were classified into three different decay
194 classes: ‘fresh’ - those that appeared to be less than three years old; ‘suitable’ - estimated to
195 be 3 – 10 years old, i.e. those that potentially hosted source populations of species that may
196 have dispersed to the log-piles when the beetle data were collected, 2 – 4 years ago; and
197 ‘old’ - estimated to be older than ten years. The volume of downed and standing dead aspen
198 wood was calculated by using length and diameter data assuming the shape to be a cylinder.

199 We also surveyed all living aspens with a diameter at breast height > 20 cm. For each
200 tree, we estimated the volume (in m³), V , based on the breast height diameter (in cm), d , and
201 tree height (in m), h , using the following equation (Eriksson 1973):

202
203
$$V = (0.01548d^2 + 0.03255d^2h - 0.000047d^2h^2 - 0.01333dh + 0.004859dh^2)/1000 \quad \text{eq. (1)}$$

204
205 For living trees we only had field data on diameter. Therefore, we estimated tree heights
206 using the following equation:

207
208
$$h = 1.016d - 0.009d^2 \quad \text{eq. (2)}$$

209
210 We derived this equation from data on mean diameters and heights of aspens collected in the
211 study area by Metsähallitus. In this data set, trees had diameters up to 51 cm. With this
212 equation, the height reached a maximum (28.7 m) when tree diameter was 56 cm. Therefore,
213 when the tree diameter exceeded 56 cm, we assumed tree height to be constant at 28.7 m.
214 For living trees, we obtained a proxy of the amount of dead wood by multiplying the tree
215 volume with the proportion of the trunk surface area without bark.

216 For forests not included in our detailed survey, i.e. those with no part < 100 m from
217 any log-pile, and the distant parts of those stands which were only partly (< 100 m from a
218 log-pile) surveyed, we used stand-level data of living and dead aspen from Metsähallitus.
219 Data on living trees was based on at least three relascope plots per stand, and on dead wood

220 on at least three 50 m²-plots per stand. No measurements were made in stands where the
 221 total amount of dead wood was visually estimated to < 5 m³/ha. For all aspen wood, the
 222 midpoint of the stand was used as the position. We multiplied the volume of dead wood by
 223 0.20, as that was the proportion that we found to be in a suitable decay class (3 – 10 years) in
 224 our field data. For living trees, we estimated a proxy of dead wood amount by multiplying
 225 the proportion of trunk surface area without bark with the total volume of aspen per stand as
 226 measured by Metsähallitus. We estimated the proportion of trunk surface area without bark,
 227 P , using the mean diameter of aspens, and the following equation derived from our own
 228 field data on living aspen trees:

$$229 \quad P = 0.00366 + 0.00068d \quad \text{eq. (3)}$$

230

231 *Statistical analyses*

232 We analysed the number of individuals of each species (for species with > 10 individuals),
 233 and species richness, in relation to the characteristics of each log pile and its surroundings.
 234 For all analyses we used a generalized linear model with a log-link function, assuming a
 235 Poisson distribution. We identified the most parsimonious statistical model using Akaike's
 236 Information Criterion (AIC). The AIC value was calculated as $-2 \log\text{-likelihood} + 2k$,
 237 where k is the number of parameters in the model plus the spatial scale parameter, as that
 238 was also estimated in the statistical test. When building the model, 'sun exposure' and 'bark
 239 peeled by moose' were added in order of explained deviance, after which we added the
 240 habitat connectivity variable. Variables were added only when they generated a decrease in
 241 the AIC value. There were no statistically significant relationships between these three
 242 variables ($p < 0.05$; for connectivity, $1/\alpha$ was set to 93 m), which implies that there is little
 243 risk that observed relationships with species occurrence are due to confounding effects of
 244 these variables. We estimated habitat connectivity using the following equation:

245

$$246 \quad S_i = \sum_{j=1}^n \exp(-\alpha d_{ij}) V_j, \text{ for all } j \neq i \quad \text{eq. (4)}$$

247 where S_i = habitat connectivity of log-pile i ; d_{ij} = distance between the log pile i and j ; n =
 248 total number of dead wood items in the Kakonsalo area; V_j = volume of dead wood item j ;
 249 and α is a parameter related with the spatial scale of the connectivity. Within a radius < 100
 250 m, j are individual dead wood items, and at further distances midpoints of the forest stands.

251 This function is based on the assumption that all dead wood items are potential dispersal
252 sources, and items that are large-sized and situated closely are up-weighted in comparison to
253 those that are small and far away. This function has been found to be useful in connectivity
254 measures for animal species (Moilanen and Nieminen 2002; Prugh 2009). The volumes of
255 dead wood items were calculated as described above (*Collection of aspen data*). We
256 identified the scale that generated the minimum residual deviance for the total statistical
257 model by graphically comparing spatial scales (i.e. $1/\alpha$, in whole meters) within an interval
258 from 10 to 1,000 m. For each independent variable, we calculated the explained deviance
259 (%), which is an analogue to R^2 .

260

261 **Results**

262 We collected 13 aspen specialists: 12 beetle species and one flat bug species (Table 1). For
263 *Xylotrechus rusticus* and *Trypophloeus* spp. the number of exit holes was counted, which
264 revealed that the number of individuals that had emerged from the log-piles during three
265 years (666 and 685) was one order of magnitude higher than the number of individuals
266 captured in traps during the same period (35 and 49, respectively).

267 Species richness of aspen specialists was positively related with sun exposure and
268 habitat connectivity and negatively related with the degree of bark peeling by moose (Table
269 2, Fig. 3). The effect of habitat connectivity and degree of bark peeling was stronger during
270 the second and third year than the first (Fig. 4). Even though the relationship between
271 species richness and amount of aspen dead wood in the surrounding was clearly significant
272 ($p = 0.010$, linear regression analysis), the explained deviance was rather moderate (Fig. 4).
273 Where log-piles were surrounded by very small amounts of aspen dead wood ($< 1 \text{ m}^3 / \text{ha}$),
274 the number of aspen-specialist species sampled was usually between 2 and 5, while for those
275 surrounded by large amounts of aspen dead wood ($> 10 \text{ m}^3 / \text{ha}$), the number of aspen-
276 specialist species sampled was usually between 4 and 6 (Fig. 5). The spatial scale at which
277 species richness had its strongest response to habitat was 93 m (Fig. 6).

278 Abundance of individual species was negatively related with the degree of bark
279 peeling by moose for three species (statistically significant for two); positively related with
280 sun exposure for four species (statistically significant for three); and positively related
281 (significant for all) with habitat connectivity for all seven species for which we had
282 abundance data. The spatial scale at which species had their strongest response to habitat

283 varied widely among species (between 10 m and 1000 m, which were the minimum and
284 maximum values tested, respectively).

285

286 **Discussion**

287 For all species, there was a positive relationship between habitat connectivity and abundance
288 (except *S. perforata*, for which individuals per pile were not counted; for *X. rusticus* the
289 relationship was statistically significant for one of two response variables tested). Thus,
290 items of dead wood attract more aspen-specialists if they are situated close to (within a few
291 hundred metres) rather than further away from dispersal sources. However, aspen logs
292 several hundred metres from other aspen logs are also used by saproxylic insects; our data
293 shows that even when the amount of habitat in the surrounding area is very low, several
294 aspen-specialists can be present (Fig. 5). Furthermore, isolated aspen logs may be colonised
295 by a higher proportion of dead wood generalists (Sahlin and Schroeder 2010), but such
296 species were not analysed in the present study.

297 The spatial scale at which species respond to habitat was smaller or similar in this
298 study in comparison to previous studies of saproxylic beetles (Holland et al. 2005; Gibb et
299 al. 2006; Schroeder et al. 2006; Franc et al. 2007; Ranius et al. 2010; Saint-Germain and
300 Drapeau 2011). For three taxa out of nine, the strongest relationship was obtained using the
301 largest spatial scale tested (1000 m; Table 2). This indicates that these taxa may respond to
302 habitat connectivity even stronger at a larger scale than tested in this study, while for the
303 majority of the species, the limitation in the spatial scale in this study does not seem to be a
304 problem. Given that the study species are restricted to using a brief stage in the decay of
305 wood, we expect that they belong to the more dispersive species among saproxylic insects.
306 Although the studied species may very well be able to move tens of kilometres, as has been
307 shown for other saproxylic beetles (Jonsson 2003), our results show that the spatial
308 distribution of dead wood at a rather small scale may be important for how much it is used
309 by these species.

310 In this study, we analysed the abundance of species based on exit holes on the logs, as
311 well as on adults collected with window-traps. Counting exit holes gives reliable
312 information on the extent to which dead wood items are used by insects, while window-traps
313 give data that is more difficult to interpret. The effect of habitat connectivity on abundance
314 from window-trapping data was higher during the second and third year (when trapped
315 individuals may include those emerging from the aspen piles) than during the first year

316 (when only individuals attracted by the logs were trapped; Fig. 4). This is consistent with the
317 view that the relationship with habitat connectivity is indeed reflecting where species are
318 breeding and not only to which log piles flying insects have been attracted.

319 As far as we are aware, this is the first study to report a negative effect of bark peeling
320 by moose on saproxylic insects. The effect was only found during the second and third years
321 (Fig. 4), which suggests that it is not the attraction to the log piles, but the development of
322 insects that is affected. Other studies have found that when moose populations are high, the
323 regeneration of aspen and other deciduous trees may be rendered impossible by the high
324 grazing pressure (Edenius and Ericsson 2007; Kouki et al. 2004). Consequently, the high
325 moose population density that currently prevails means that there will be less aspen wood in
326 the future. Bark peeling is probably a smaller problem than grazing: in our study 25 % of the
327 bark was peeled, which is similar to the levels observed in an area in central Sweden (Sahlin
328 2009). However, in contrast to grazing, bark peeling has an immediate effect on the
329 population sizes of threatened insects that specialise on aspen wood.

330 Sun exposure increased total species richness and for *Platysoma deplanatum*,
331 *Trypophloeus bispinulus*, and *Xylotrechus rusticus* there was a positive relationship between
332 sun exposure of logs and abundance (Table 2). Also previous studies have revealed that sun
333 exposure affects the species composition of beetles associated with dead aspen and several
334 species are favoured by sun exposure (Martikainen 2001, Sverdrup-Thygeson and Ims 2002,
335 Jonsell et al. 2004, Lindhe et al. 2005, Sahlin and Ranius 2009, Schroeder et al. 2011). One
336 reason why the effect of sun exposure was relatively weak in this study may be that there
337 was a relatively limited variability in sun exposure among the piles studied.

338

339 **Conclusions**

340 In this study we transported aspen logs from managed forests with a limited number of
341 aspen specialists in their fauna, to an area known to be a hotspot for this fauna. The
342 transported logs were shown to attract threatened saproxylic insects. Restoration by log
343 transportation may therefore be useful at localities that harbour a rich and specialised fauna,
344 but which have too low a rate of formation of new dead wood habitat.

345 The spatial distribution of dead wood items affects the extent to which they are used
346 by wood-inhabiting species. Even though we studied a group of species that is probably
347 more dispersive than many other saproxylic insects, we found a clear positive effect of
348 habitat connectivity on species' abundance at a scale of tens to hundreds of metres. The

349 present study therefore lends support to the view that conservation efforts in boreal forests
350 should be concentrated in space, given that the goal is to maintain species richness at a
351 landscape level. Thus, in a stand with a relatively high proportion of older deciduous trees,
352 for instance, it would be desirable to retain all such trees, while single trees of the same
353 quality should be given lower priority, because they would not be used to the same extent by
354 habitat specialists. This conclusion applies to retention tree recommendations (for a recent
355 review on current retention recommendations, see Gustafsson et al. 2010), but also to those
356 cases where aspen is actively restored, for instance, by log transports.

357

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370

371 **References**

- 372 Berg Å, Ehnström B, Gustafsson L, Hallingbäck T, Jonsell M, Weslien J (1995) Threat
373 levels and threats to red-listed species in Swedish forests. *Conserv Biol* 9:1629–1633
- 374 Edenius L, Ericsson G (2007) Aspen demographics in relation to spatial context and
375 ungulate browsing: implications for conservation and forest management. *Biol*
376 *Conserv* 135:293–301
- 377 Ehnström B, Axelsson R (2002) *Insektsnag i bark och ved*. Swedish Species Information
378 Centre, Uppsala
- 379 Eriksson H (1973) *Volymfunktioner för stående träd av ask, asp, klibbal och contorta-tall*.
380 *Rapporter och uppsatser 26*. Institutionen för skogsproduktion, Skogshögskolan,
381 Stockholm

382 Forsse E, Solbreck C (1985) Migration in the bark beetle *Ips typographus* L.: duration,
383 timing and height of flights. *Z Angew Entomol* 100:47–57

384 Franc N, Götmark F, Økland B, Nordén B, Paltto H (2007) Factors and scales potentially
385 important for saproxylic beetles in temperate mixed oak forest. *Biol Conserv* 135:86–
386 98

387 Gibb H, Hjältén J, Ball JP, Atlegrim O, Pettersson RB, Hilszczański, Johansson T, Danell K
388 (2006) Effects of landscape composition and substrate availability on saproxylic
389 beetles in boreal forests: a study using experimental logs for monitoring assemblages.
390 *Ecography* 29:191–204

391 Gibbs M, van Dyck H (2010) Butterfly flight activity affects reproductive performance and
392 longevity relative to landscape structure. *Biol Conserv* 163:341–350

393 Gustafsson L, Kouki J, Sverdrup-Thygeson A (2010) Tree retention as a conservation
394 measure in clear-cut forests of northern Europe: a review of ecological consequences.
395 *Scand J For Res* 25:295–308

396 Hammond HEJ, Langor DW, Spence JR (2004) Saproxylic beetles (Coleoptera) using
397 *Populus* in boreal aspen stands of western Canada: Spatiotemporal variation and
398 conservation of assemblages. *Can J For Res* 34:1–19

399 Holland JD, Fahrig L, Cappuccino N (2005) Body size affects the spatial of habitat-beetles
400 interactions. *Oikos* 110:101–108

401 Huxel GR, Hastings A (1999) Habitat loss, fragmentation and restoration. *Restor Ecol*
402 7:309–315

403 Hyvärinen E, Kouki J, Martikainen P (2006) A comparison of three trapping methods used
404 to survey forest-dwelling Coleoptera. *Eur J Entomol* 103:397–407

405 Johnson ML, Gaines MS (1990) Evolution of dispersal: theoretical models and empirical
406 tests using birds and mammals. *Annu Rev Ecol Syst* 21:449–480

407 Jonsell M, Nordlander G, Jonsson M (1999) Colonization patterns of insects breeding in
408 wood-decaying fungi. *J Insect Conserv* 3:145–161

409 Jonsell M, Nittérus K, Stighäll K (2004) Saproxylic beetles in natural and man-made
410 deciduous high stumps retained for conservation. *Biol Conserv* 118:163–173

411 Jonsson M (2003) Colonisation ability of the threatened tenebionid beetle *Oplocephala*
412 *haemorrhoidalis* and its common relative *Bolitophagus reticulatus*. *Ecol Entomol*
413 28:159–167

- 414 Jonsson M, Nordlander G (2006) Insect colonisation of fruiting bodies of the wood-decaying
415 fungus *Fomitopsis pinicola* at different distances from an old-growth forest. *Biodiv*
416 *Conserv* 15:295–309
- 417 Kouki J, Arnold K, Martikainen P (2004) Long-term persistence of aspen – a key host for
418 many threatened species – is endangered in old-growth conservation areas in Finland.
419 *J Nat Conserv* 12:41–52
- 420 Larsson S, Danell K (2001) Science and the management of boreal forest diversity. *Scand J*
421 *For Res Suppl* 3:5–9
- 422 Lindhe A, Lindelöw Å, Åsenblad N (2005) Saproxylic beetles in standing dead wood
423 density in relation to substrate sun-exposure and diameter. *Biodiv Conserv* 14:3033–
424 3053
- 425 Martikainen P (2001) Conservation of threatened saproxylic beetles: significance of retained
426 aspen *Populus tremula* on clearcut areas. *Ecol Bull* 49:205–218
- 427 Martikainen P, Kouki J (2003) Sampling the rarest: threatened beetles in boreal forest
428 biodiversity inventories. *Biodiv Conserv* 12:1815–1831
- 429 Moilanen A, Nieminen M (2002) Simple connectivity measures in spatial ecology. *Ecology*
430 83:1131–1145
- 431 Nieto A, Alexander KNA (2010) European Red List of Saproxylic Beetles. Publications
432 Office of the European Union, Luxembourg
- 433 Nilssen AC (1984) Long-range aerial dispersal of bark beetles and bark weevils (Coleoptera,
434 Scolytidae and Curculionidae) in northern Finland. *Ann Entomol Fenn* 50:37–43
- 435 Nuorteva M, Nuorteva P (1968) The infestation of timber by bark beetles (Col., Scolytidae)
436 and their enemies in different zones of the Finnish south-western archipelago. *Ann*
437 *Entomol Fenn* 34:56–65
- 438 Palm T (1959) Die Holz- und Rindenkäfer der Süd- und Mittelschwedischen Laubbäume.
439 *Opuscula Entomologica Supplementum XVI*, Lund
- 440 Prugh LR (2009) An evaluation of patch connectivity measures. *Ecol Appl* 19:1300–1310
- 441 Ranius T, Kindvall O (2006) Extinction risk of wood-living model species in forest
442 landscapes as related to forest history and conservation strategy. *Landscape Ecol* 21:
443 687–698
- 444 Ranius T, Johansson V, Fahrig L (2010) A comparison of patch connectivity measures using
445 data on invertebrates in hollow oaks. *Ecography* 33:971–978

446 Rassi P, Hyvärinen E, Juslén A, Mannerkoski I (eds) (2010) The 2010 Red List of Finnish
447 species. Ministry of the Environment and Finnish Environment Institute, Helsinki. 685
448 pp

449 Rotheray EL, MacGowan I, Rotheray GE, Sears J, Elliott A (2009) The conservation
450 requirements of an endangered hoverfly, *Hammerschmidtia ferruginea* (Diptera,
451 Syrphidae) in the British Isles. *J Insect Conserv* 13:569–574

452 Sahlin E (2009) Habitat requirements of saproxylic beetles on aspen. Doctoral thesis.
453 Swedish University of Agricultural Sciences, Uppsala

454 Sahlin E, Ranius T (2009) Habitat availability in forests and clearcuts for saproxylic beetles
455 with aspen. *Biodivers Conserv* 18:621–638

456 Sahlin E, Schroeder M (2010) Importance of habitat patch size for occupancy and density of
457 aspen-associated saproxylic beetles. *Biodiv Conserv* 19:1325–1339

458 Saint-Germain M, Drapeau P (2011) Response of saprophagous wood-boring beetles
459 (Coleoptera: Cerambycidae) to severe habitat loss due to logging in an aspen-
460 dominated boreal landscape. *Landscape Ecology* 26:573–586

461 Saint-Germain M, Buddle CM, Drapeau P (2006) Sampling saproxylic Coleoptera: scale
462 issues and the importance of behavior. *Environ Entomol* 35:478–487

463 Schroeder LM, Ranius T, Ekbohm B, Larsson S (2006) Recruitment of saproxylic beetles in
464 high stumps created for maintaining biodiversity in a boreal forest landscape. *Can J*
465 *For Res* 36:2168–2178

466 Schroeder LM, Sahlin E, Paltto H (2011) Retention of aspen (*Populus tremulae*) at final
467 cuttings – The effect of dead wood characteristics on saproxylic beetles. *Forest Ecol*
468 *Manage* 262:853–862

469 Southwood TRE (1962) Migration of terrestrial arthropods in relation to habitat. *Biol Rev*
470 37:171–214

471 Sverdrup-Thygeson A, Ims RA (2002) The effect of forest clearcutting in Norway on the
472 community of saproxylic beetles on aspen. *Biol Conserv* 106:347–357

473 Sverdrup-Thygeson A, Birkemoe T (2009) What window traps can tell us: effect of
474 placement, forest openness and beetle reproduction in retention trees. *J Insect Conserv*
475 13:183–191

476 Travis JMJ, Dytham C (1999) Habitat persistence, habitat availability and the evolution of
477 dispersal. *Proc R Soc Lond B* 266:723–728

- 478 Vehmas M, Kouki J, Eerikäinen K (2009) Long-term spatio-temporal dynamics and
479 historical continuity of European aspen (*Populus tremula* L.) stands in the Koli
480 National Park, eastern Finland. *Forestry* 82:135–148
- 481 Whitlock MC (1992) Nonequilibrium population structure in forked fungus beetles:
482 extinction, colonization and the genetic variance among populations. *Am Nat*
483 139:952–970
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Table 1. Aspen specialists using large diameter (> 10 cm) dead wood items observed in 2005-2007, including 12 beetle species and one flat bug (*Aradus truncatus*). Red-list categories according to Rassi et al. (2010). Total number of individuals captured with trunk window-traps and number of exit holes, and percentage of piles with the species present.

Species ¹	Red-list ²	Number of individuals			Piles (%)	
		2005	2006	2007	Sum	
Collected beetles						
<i>Aradus truncatus</i> Fieber, 1861	NT	0	1	2	3	5.2
<i>Cerylon deplanatum</i> Gyllenhal, 1827	LC	64	45	17	126	89.7
<i>Cyphea curtula</i> (Erichson, 1837)	LC	2	42	17	61	62.1
<i>Enicmus lundbladi</i> Palm, 1956	LC	1	0	0	1	1.7
<i>Obrium cantharinum</i> (Linnaeus, 1767)	LC	0	2	0	2	3.4
<i>Platysoma deplanatum</i> (Gyllenhal, 1808)	LC	9	4	2	15	20.7
<i>Ptilinus fuscus</i> Geoffroy, 1785	LC	17	27	10	54	56.9
<i>Quedius microps</i> Gravenhorst, 1847	NT	1	0	0	1	1.7
<i>Saperda perforata</i> (Pallas, 1773)	LC	1	3	0	4	6.9
<i>Trypophloeus bispinulus</i> Eggers, 1927	LC	3	31	1	35	36.2
<i>Trypophloeus discedens</i> Palm, 1950	NT	8	6	0	14	20.7
<i>Xyletinus tremulicola</i> Y.Kangas, 1958	VU	0	1	0	1	1.7
<i>Xylotrechus rusticus</i> (Linnaeus, 1758)	LC	16	10	9	35	34.5
Sum		122	172	58	352	
Observed exit holes						
<i>Saperda perforata</i> ³	LC	x	x	x	19 ⁴	32.8
<i>Xylotrechus rusticus</i> ³	LC	x	x	x	666	53.4
<i>Trypophloeus spp</i> ³		x	x	x	685	41.4

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¹ In addition to the aspen-specialists above, we also made observations of another threatened species: *Xylomya czekanovskii* Pleske, 1925.

² VU = vulnerable; NT = near threatened; LC = least concern.

³ Exit holes were not counted every year in 2005-2007, and consequently only one summary value is given.

⁴ Number of log-piles with exit holes present.

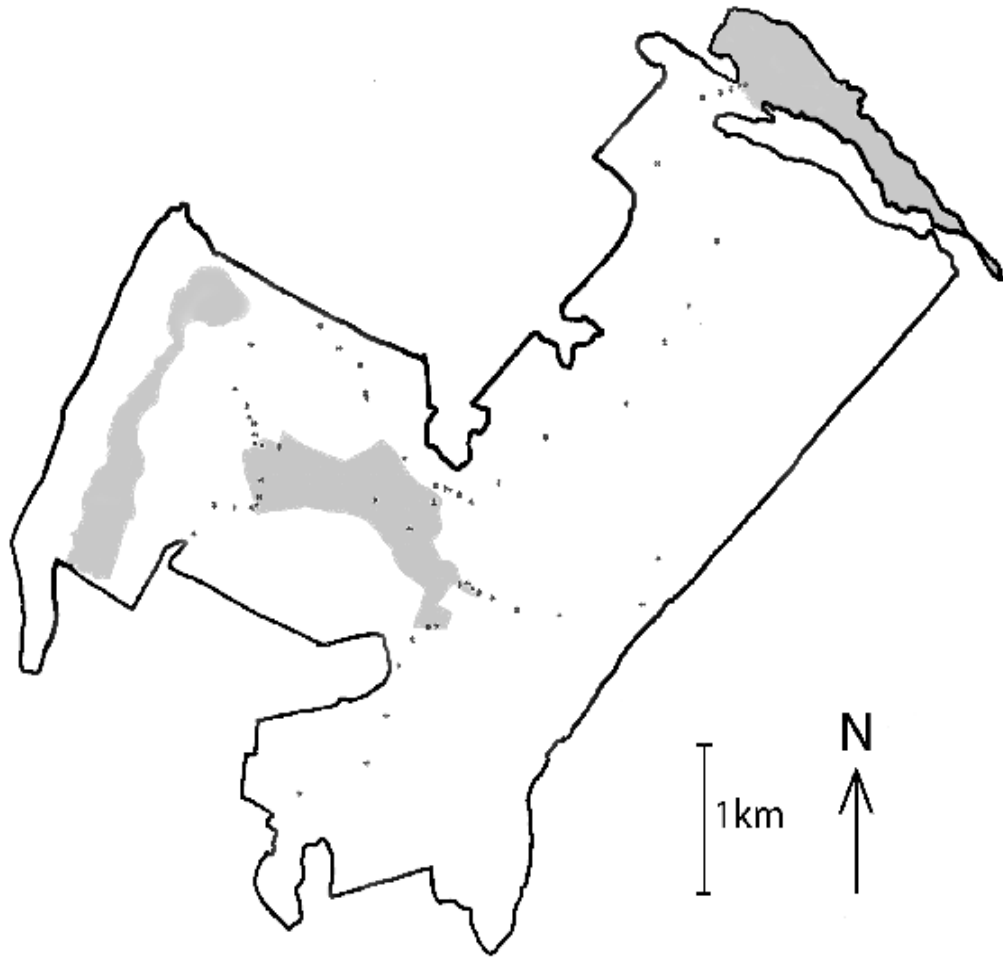
500
501 Table 2. Aspen-specialists analysed in relation with characteristics of logs and their
502 surroundings (including only species with > 10 individuals collected). Generalized linear
503 models with a log-link function (logit-link function for presence/absence of *S. perforata*
504 holes). Response variables: number of individuals collected with trunk window-traps 2005-
505 2007; presence/absence of exit holes of *S. perforata* in 2009; number of exit holes of *X.*
506 *rusticus* and *Trypophloeus* spp. (in 2007); and species richness of aspen specialists
507 according to Table 1. Explanatory variables: Moose = proportion of bark peeled by moose;
508 Connectivity = habitat connectivity; $1/\alpha$ = spatial scale of response (in m; see eq. 4). “ns”
509 means that the variable was not included in the most parsimonious model according to
510 Akaike Information Criterion.

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	Moose	Sun exposure	Connectivity	1/α
<i>C. deplanatum</i>	ns	ns	0.00348***	1000
<i>C. curtula</i>	-1.06	ns	0.00797**	274
<i>P. deplanatum</i>	ns	0.612*	0.0103*	1000
<i>P. fuscus</i>	ns	ns	0.0120***	282
<i>T. bispinulus</i>	-3.20***	0.282*	0.00926***	481
<i>T. discedens</i>	ns	0.349	0.0182***	306
<i>X. rusticus</i>	ns	0.486***	ns	(14)
<i>S. perforata</i> holes	ns	0.578	ns	(88)
<i>X. rusticus</i> holes	-2.64***	0.636***	0.521***	10
<i>T. spp.</i> holes	-2.73***	ns	0.00699***	1000
Species richness	-0.654*	0.149*	0.0125*	93

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513 Significance levels: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$



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516 Figure 1. The Kakonsalo Natura 2000 area with three protected aspen-rich reserves (grey).

517 Asterisks represent experimental log piles.

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522 Figure 2. A pile of six aspen logs, with a trunk window-trap attached to the standing log.

523 Photo by P. Martikainen.

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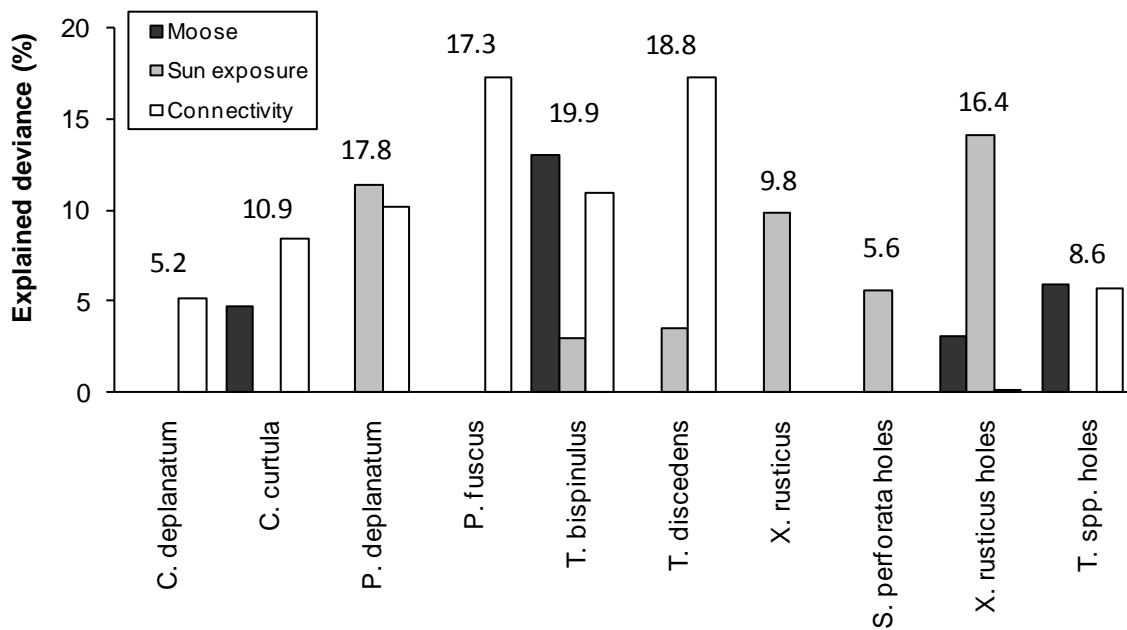
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532 Figure 3. The increase in explained deviance (%) of Poisson regression models when adding

533 different independent variables to the most parsimonious model but with this variable

534 absent. Response variables: number of individuals collected with trunk window-traps 2005-

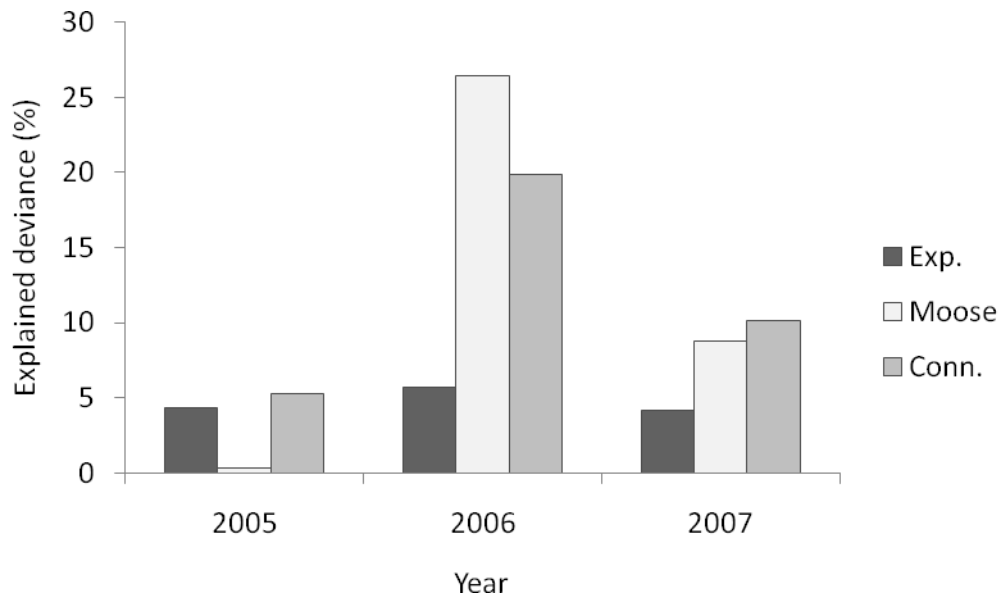
535 2007; presence/absence of exit holes of *S. perforata* in 2009; number of exit holes of *X.*536 *rusticus* and *Trypophloeus* spp. (in 2007). Explanatory variables: Moose = proportion of

537 bark peeled by moose. All relationships with Moose were negative, and all with sun

538 exposure and connectivity were positive. If inclusion of the variable did not lower the AIC

539 value, the explained deviance was reported as 0.

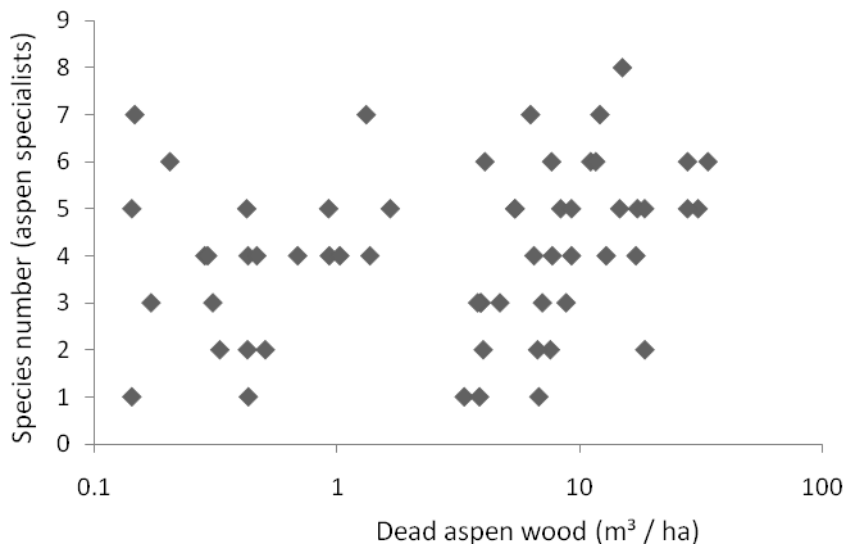
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 542 Figure 4. Explained deviance (%) of the three predictor variables estimated as (deviance
 543 with the other two predictor variables – deviance with all predictor variables) / (deviance
 544 with the other two predictor variables). Response variables: species richness per year of
 545 aspen specialists according to Table 1.

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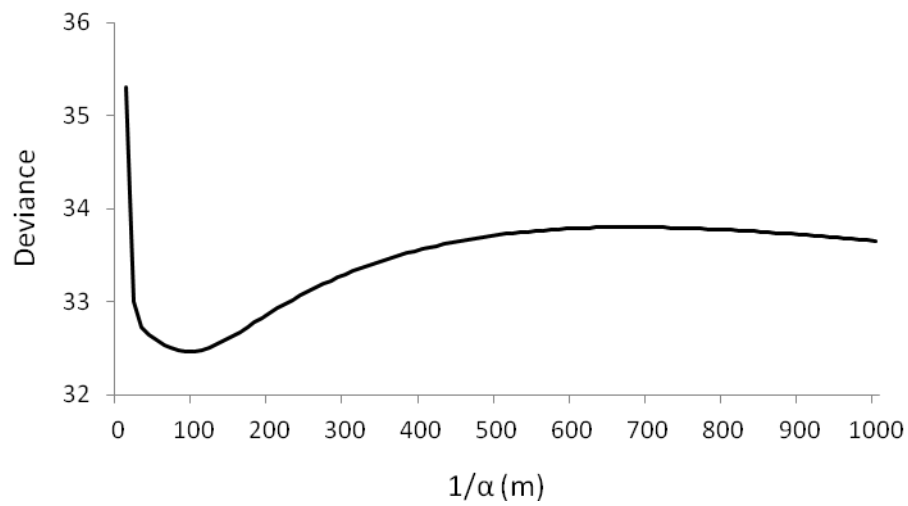


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549 Figure 5. Total number of aspen-specialist beetle and bug species collected per log-pile
550 during three years, in relation to the amount of dead aspen wood (dead trees and dead parts
551 of living trees) within a radius of 232 m. This radius was chosen because it resulted in the
552 strongest statistical relationship ($p = 0.010$, linear regression analysis).

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556 Fig. 6. The relationship between the spatial scale of the connectivity measure ($1/\alpha$ in eq. (4))
557 and the deviance between the statistical model and data. The deviance reached its minimum
558 at $1/\alpha = 93$ m.