7

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

12

13 Thomas Ranius[a],*, Petri Martikainen[b] and Jari Kouki[c]

14

15 [a] Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

16 [b] School of Forest Sciences, University of Eastern Finland, Joensuu, Finland, Email:
17 petri.martikainen@uef.fi

18 [c] School of Forest Sciences, University of Eastern Finland, Joensuu, Finland, Email:
19 jari.kouki@uef.fi

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

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 (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 (62º 15' N,

107 29º 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-

4

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 m^3, 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 >

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

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

Collection of aspen data

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

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

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

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

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

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

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

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

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

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

Statistical analyses

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

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

where S_i = habitat connectivity of log-pile i; d_{ij} = distance between the log pile i and j; n =
total number of dead wood items in the Kakonsalo area; V_j = volume of dead wood item j;
and α is a parameter related with the spatial scale of the connectivity. Within a radius < 100
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 m³ / 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 m³ / 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

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

Discussion

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

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

In this study, we analysed the abundance of species based on exit holes on the logs, as well as on adults collected with window-traps. Counting exit holes gives reliable information on the extent to which dead wood items are used by insects, while window-traps give data that is more difficult to interpret. The effect of habitat connectivity on abundance from window-trapping data was higher during the second and third year (when trapped 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

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) Insektsgnag 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, Ekbom 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

484

485

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.

490

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

491

[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.
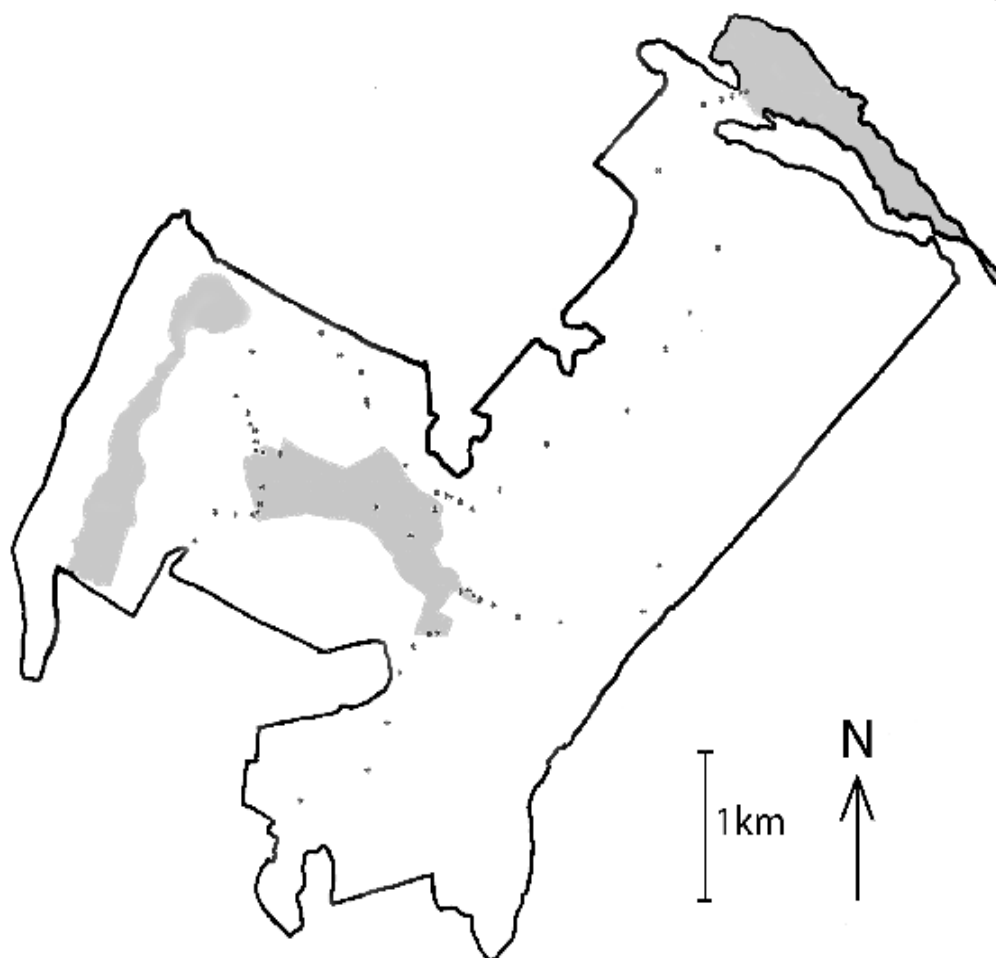[3] Exit holes were not counted every year in 2005-2007, and consequently only one summary value is given.
[4] Number of log-piles with exit holes present.

498
499

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.

511

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

512

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

514
515

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

517   Asterisks represent experimental log piles.

518

519

520
521

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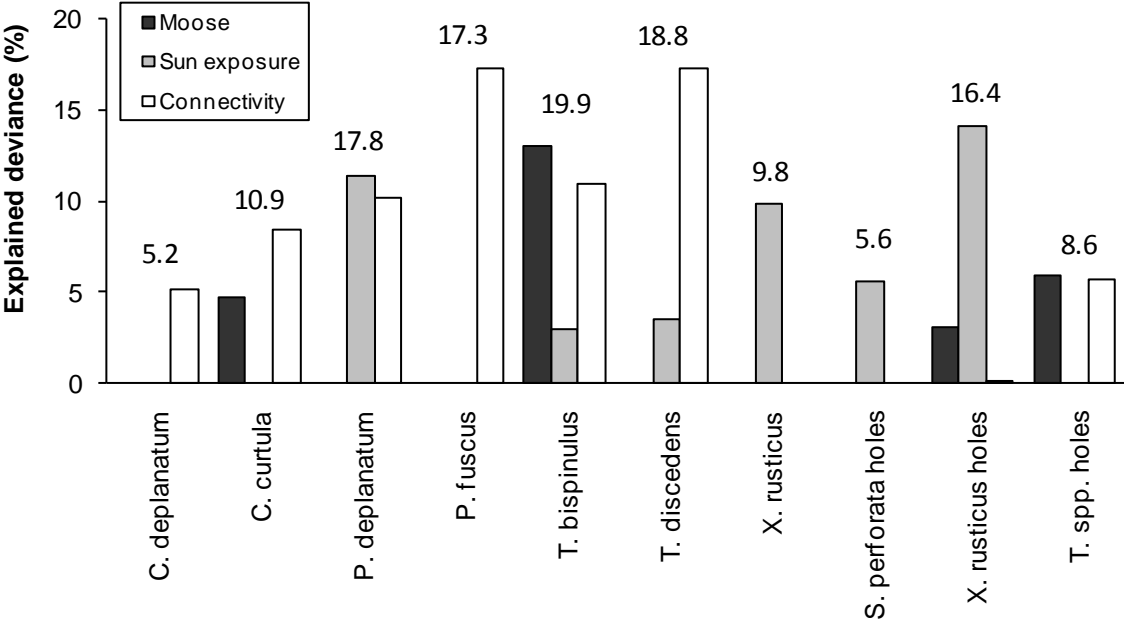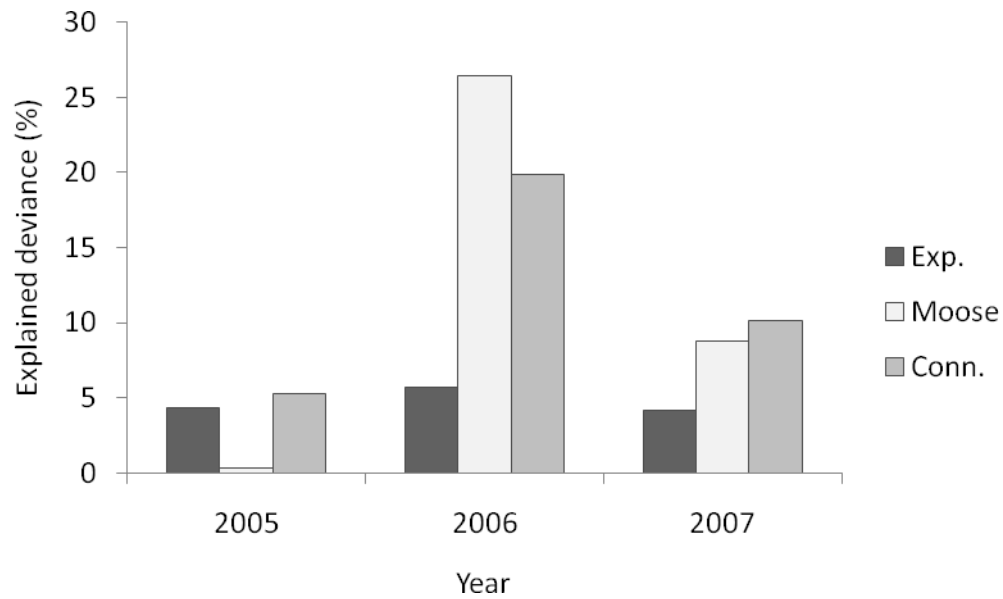
Photo by P. Martikainen.

524

525

526

527

528
529

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

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

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

2007; presence/absence of exit holes of *S. perforata* in 2009; number of exit holes of *X.*

rusticus and *Trypophloeus* spp. (in 2007). Explanatory variables: Moose = proportion of

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

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

value, the explained deviance was reported as 0.

540

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.
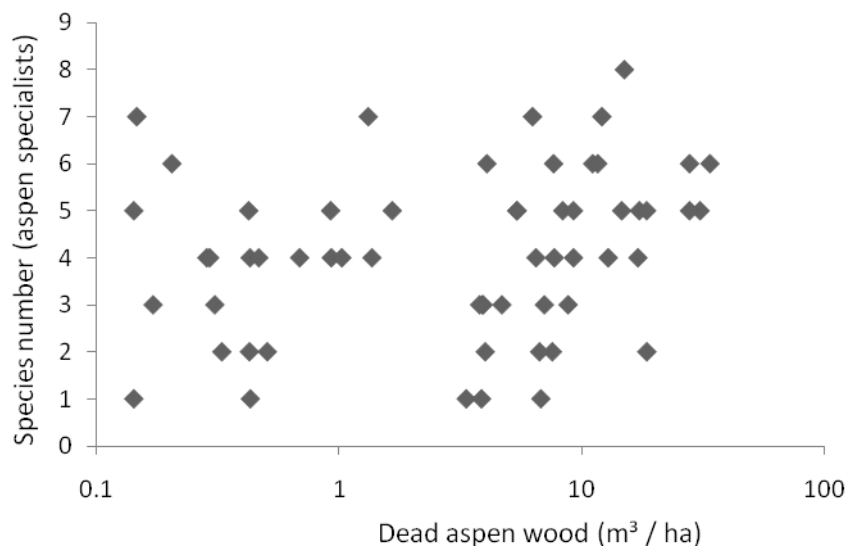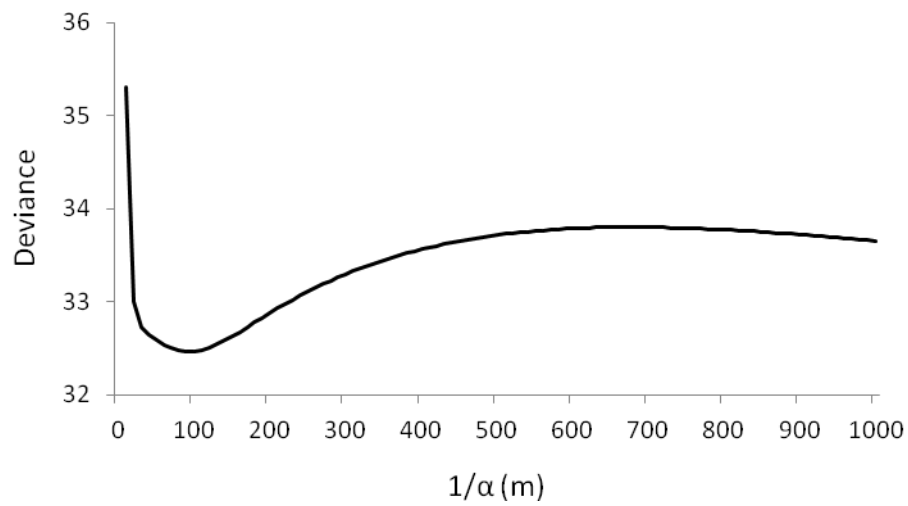
546

547

548

Figure 5. Total number of aspen-specialist beetle and bug species collected per log-pile

during three years, in relation to the amount of dead aspen wood (dead trees and dead parts

of living trees) within a radius of 232 m. This radius was chosen because it resulted in the

strongest statistical relationship ($p = 0.010$, linear regression analysis).

553

554

555

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.