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

Short title: Colonisation of recently dead aspen wood

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

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

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

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

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

Abstract

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

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

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

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

Introduction

Many organisms associated with dead wood are thought to be threatened as a result of habitat loss and fragmentation (Berg et al. 1995; Nieto and Alexander 2010). The most effective conservation strategy for preserving this fauna and flora depends to some extent on species' dispersal ranges. For species with a limited dispersal range, it is important that conservation efforts are directed within, or close to, sites where the target species are present (Huxel and Hastings 1999), while to protect species that are able to colonise over long distances, efforts can be directed at more distant sites where restoration efforts may be less expensive and where they may improve habitat quality quickly (Ranius and Kindvall 2006). Items of dead wood are ephemeral habitats that, for some species, remain suitable for only one or a few years. Theoretical and empirical studies suggest that species adapted to such short-lived habitats are generally more dispersive than species of more stable habitats (Southwood 1962; Johnson and Gaines 1990; Travis and Dytham 1999).

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

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

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

Methods

Study area and experimental design

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

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

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

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

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

Collection of insect and log pile data

Beetles (Coleoptera) and flat bugs of the genus *Aradus* (Heteroptera) were monitored using trunk window-traps. Traps attached to dead trees usually capture more saproxylic beetles than traps situated away from trees (Hyvärinen et al. 2006; Sverdrup-Thygeson and Birkemoe 2009, see however Saint-Germain et al. 2006), which means that the capture in trunk window traps at least to some extent reflect what is attracted by the trees. In each pile, one trap was attached to the standing log (Fig. 2). The trap consisted of two perpendicular 40 cm × 60 cm transparent plastic panes, with a funnel below the panes leading to a 1 *l* container partly filled with a solution of water, salt and detergent to preserve the captured insects. In this study, the number of individuals decreased during the third year, indicating that aspen wood attracts beetles mainly during the first few years. Consequently, sampling was conducted during three years, 10 June – 14 September 2005, 10 May – 8 August 2006, and 6 May – 14 August 2007. The traps were emptied 2 or 3 times per year. When identifying the trap material, only aspen specialists using dead wood items > 10 cm were 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 m^2-plots per stand. No measurements were made in stands where the total amount of dead wood was visually estimated to < 5 m^3/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.

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

Results

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

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

Abundance of individual species was negatively related with the degree of bark peeling by moose for three species (statistically significant for two); positively related with sun exposure for four species (statistically significant for three); and positively related (significant for all) with habitat connectivity for all seven species for which we had 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 (when only individuals attracted by the logs were trapped; Fig. 4). This is consistent with the view that the relationship with habitat connectivity is indeed reflecting where species are breeding and not only to which log piles flying insects have been attracted.

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

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

Conclusions

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

The spatial distribution of dead wood items affects the extent to which they are used by wood-inhabiting species. Even though we studied a group of species that is probably more dispersive than many other saproxylic insects, we found a clear positive effect of habitat connectivity on species' abundance at a scale of tens to hundreds of metres. The present study therefore lends support to the view that conservation efforts in boreal forests should be concentrated in space, given that the goal is to maintain species richness at a landscape level. Thus, in a stand with a relatively high proportion of older deciduous trees, for instance, it would be desirable to retain all such trees, while single trees of the same quality should be given lower priority, because they would not be used to the same extent by habitat specialists. This conclusion applies to retention tree recommendations (for a recent review on current retention recommendations, see Gustafsson et al. 2010), but also to those cases where aspen is actively restored, for instance, by log transports.

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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						
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

[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.

Table 2. Aspen-specialists analysed in relation with characteristics of logs and their surroundings (including only species with > 10 individuals collected). Generalized linear models with a log-link function (logit-link function for presence/absence of *S. perforata* holes). 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); and species richness of aspen specialists according to Table 1. Explanatory variables: Moose = proportion of bark peeled by moose; Connectivity = habitat connectivity; 1/α = spatial scale of response (in m; see eq. 4). "ns" means that the variable was not included in the most parsimonious model according to Akaike Information Criterion.

	Moose	**Sun exposure**	**Connectivity**	**1/α**
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

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

Figure 1. The Kakonsalo Natura 2000 area with three protected aspen-rich reserves (grey). Asterisks represent experimental log piles.

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

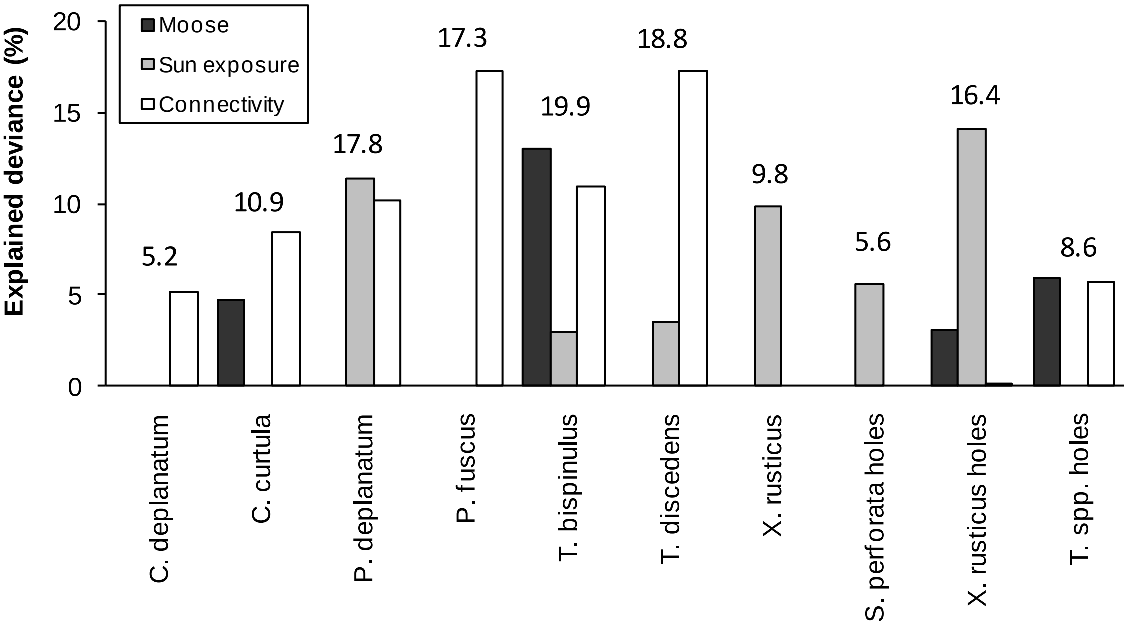

Figure 3. The increase in explained deviance (%) of Poisson regression models when adding different independent variables to the most parsimonious model but with this variable absent. Response variables: number of individuals collected with trunk window-traps 2005-2007; presence/absence of exit holes 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.

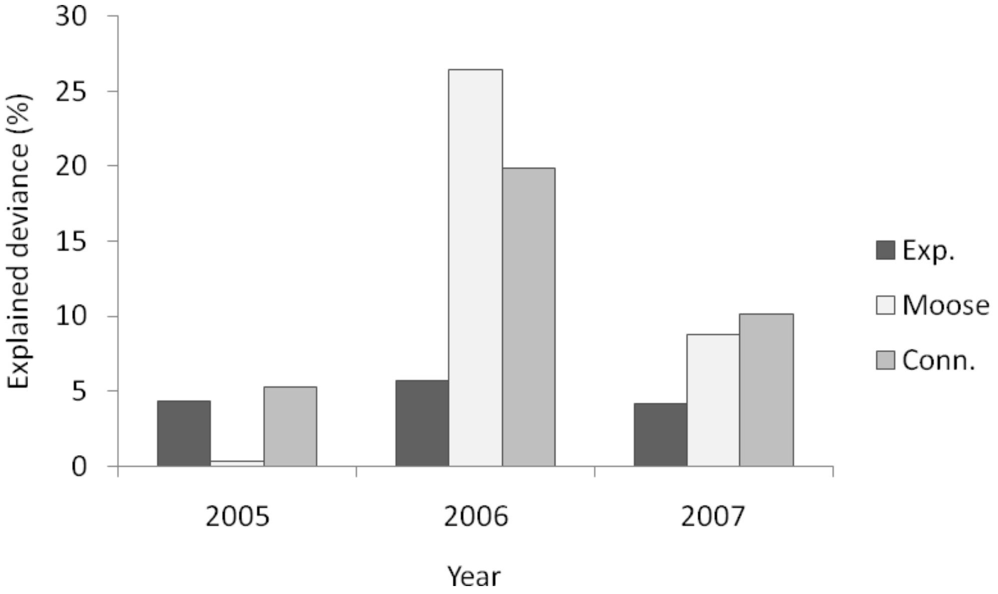

Figure 4. Explained deviance (%) of the three predictor variables estimated as (deviance with the other two predictor variables – deviance with all predictor variables) / (deviance with the other two predictor variables). Response variables: species richness per year of aspen specialists according to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

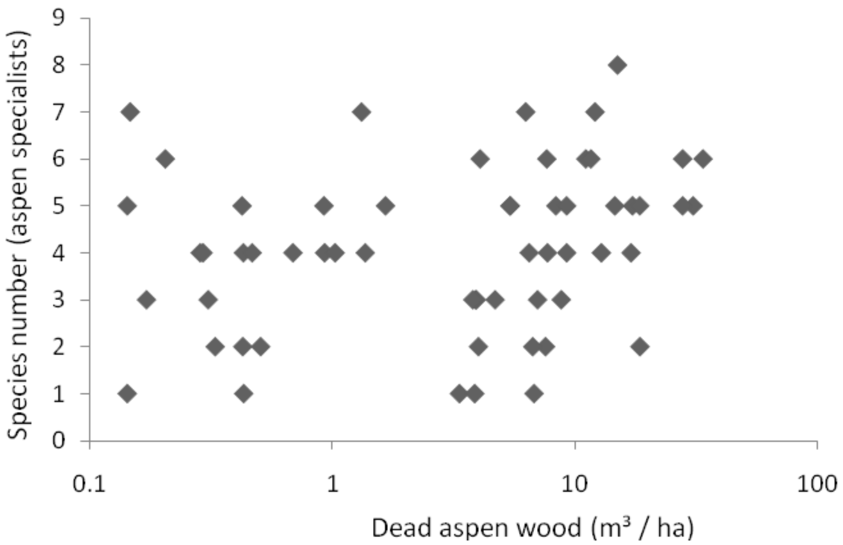

Figure 5. Total number of aspen-specialist beetle and bug species collected per log-pile during three years, in relation to the amount of dead aspen wood (dead trees and dead parts of living trees) within a radius of 232 m. This radius was chosen because it resulted in the strongest statistical relationship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

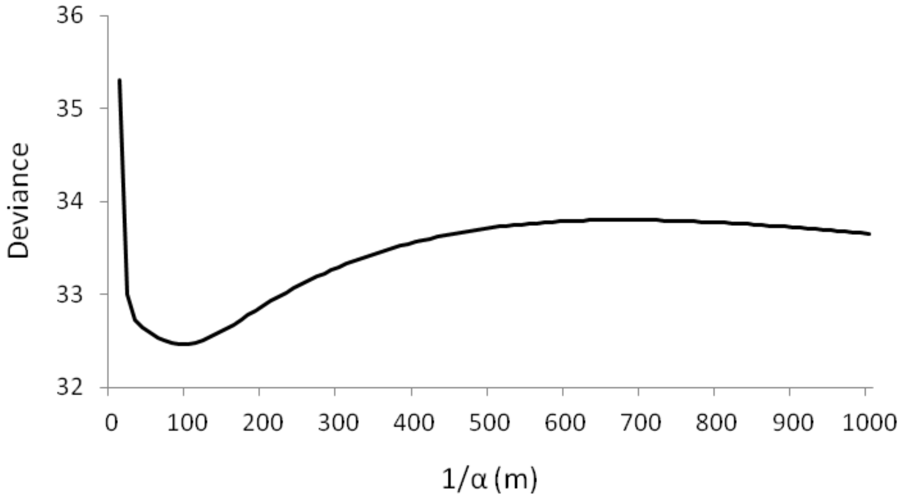

Fig. 6. The relationship between the spatial scale of the connectivity measure (1/α in eq. (4)) and the deviance between the statistical model and data. The deviance reached its minimum at 1/α = 93 m.