



# Effect of distance to urban areas on saproxylic beetles in urban forests

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Effekt av avstånd till bebyggda områden på vedlevande skalbaggar i  
urbana skogsområden

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## Abstract

Urban forests play key roles in animal and plant biodiversity and provide important ecosystem services. Habitat fragmentation and expanding urbanization threaten biodiversity in and around urban areas. Saproxyllic beetles can act as bioindicators of forest health and their diversity may help to explain and define urban-forest edge effects. I explored the relationship between saproxyllic beetle diversity and distance to an urban area along nine transects in the Västra Götaland region of Sweden. Specifically, the relationships between abundance and species richness and distance from the urban-forest boundary, forest age, forest volume, and tree species ratio was investigated. Unbaited flight interception traps were set at intervals of 0, 250, and 500 meters from an urban-forest boundary to measure beetle abundance and richness. A total of 4182 saproxyllic beetles representing 179 species were captured over two months. Distance from the urban forest boundary showed little overall effect on abundance suggesting urban proximity does not affect saproxyllic beetle abundance. There was an effect on species richness, with saproxyllic species richness greater closer to the urban-forest boundary. Forest volume had a very small positive effect on both abundance and species richness likely due to a limited change in volume along each transect. An increase in the occurrence of deciduous tree species proved to be an important factor driving saproxyllic beetle abundance moving closer to the urban-forest. Overall, analysis showed inconsistent effects on both abundance and richness as functions of proximity to the urban-forest boundary. Urban edge effects, forest volume, forest age, and forest tree species make up are all variables that may effect saproxyllic abundance and species richness. Forest managers should consider these variables when making management decisions.

## Sammanfattning

Urbana skogsområden spelar en nyckelroll för mångfalden av djur och växter och de förser omkringliggande områden med viktiga ekosystemtjänster. Fragmentering av habitationer och expanderande urbanisering hotar den biologiska mångfalden i och omkring bebyggda områden. Vedlevande skalbaggar (saproxylic) kan agera som bioindikatorer gällande skogens hälsa och hur mångfalden av dessa arter ser ut kan bidra till att förklara och definiera effekterna av gränsområden mellan bebyggelse och skog. Jag har undersökt förekomsten av dessa skalbaggar i urban miljö i Västra Götalandsregionen, Sverige, utifrån nio tvärsnitt. Oagnade "flight interception" fällor sattes ut med intervall 0, 250, och 500 meter från gränsen till ett urbant skogsområde för att mäta mängd och artrikedom av vedlevande skalbaggar. Under två månader samlades 4182 skalbaggar in och de kunde delas in i 179 olika arter. Mängd och artrikedom jämfördes utifrån avstånd från den urbana skogsgränsen, skogens ålder, skogsvolym och trädartförhållande. Avstånd från skogsgränsen visade liten övergripande effekt på mängden insamlade skalbaggar samt visade en negativ effekt gällande artrikedom. Resultaten föreslagna urbana närhet påverkar inte saproxylbagelöverskott inom 500 meter och saproxyliska artrikedom är större närmare grannskogen. Skogsvolym hade en väldigt liten positiv effekt på både mängd och artrikedom troligtvis beror detta på begränsad förändring i skogsvolym jämsmed tvärsnittet. En ökning i förekomst av lövträd visade sig vara en viktig faktor gällande mängd vedlevande skalbaggar närmare den urbana skogsgränsen. Analysen visade blandad effekt både gällande mängd och artrikedom som funktion av proximitet till den urbana skogsgränsen. Urbana gränseffekter sträcker sig sannolikt längre in i närliggande skogsområden än 500 meter och skogansvarig personal bör ha detta i beaktande när de fattar beslut gällande skogsvård.

## Introduction

Forests are integral parts of social, recreational, and commercial life providing countries and human communities with important ecosystem services. (Dwyer, McPherson, Schroeger, & Rowntree, Rowan, 1992; Rydberg & Falck, 2000; Swanson & Chapin, 2009). Historically, forestry and silvicultural management focused on optimization of stand growth and tree species in relation to commercial forest productivity. During the last century this type of management, combined with

transitioning forests into arable land, drastically changed natural forests throughout Sweden (Fries, Johansson, Pettersson, & Simonsson, 1997; Lämås & Fries, 1995). Starting in 1993, forest management practices in Sweden were modernized to focus on biodiversity, stand maintenance, and deadwood maintenance and retention (Fries et al., 1997; Rydberg & Falck, 2000). Even with such modernization efforts, Sweden is still left with a fraction of its old-growth forests, certain forestry practices continue to be ineffective, and a large number of native plant, animal, and fungal species are threatened as a result (Fries et al., 1997; Gustafsson, Kouki, & Sverdrup-Thygeson, 2010; Gustafsson & Perhans, 2010; Larsson & Danell, 2001; Westling, 2015).

Around the same time Sweden was reviewing production forest management practices, urban forestry management practices were becoming more important in urban areas throughout Europe (Konijnendijk, 2003). Urban forests can include small groups of trees near houses or within neighborhoods, up to large forests on urban fringes used for recreation and/or timber production (Rydberg & Falck, 2000). The focus on urban forests then and now acknowledges the importance these forest have on urban ecosystem services but also recognizes the role they play in plant and animal biodiversity (Gunnarsson, Knez, Hedblom, & Sang, 2016; Konijnendijk, 2003; Kuuluvainen, 2009; Rydberg & Falck, 2000). In an urban forest biodiversity is often altered due to habitat fragmentation, but can also be affected by municipal safety practices (e.g. standing dead wood removal) and urban tree species composition (Carpaneto, Mazziotta, Coletti, Luiselli, & Audisio, 2010; Fujita, Maeto, Kagawa, & Ito, 2008; Gibb & Hochuli, 2002; Horák, 2011). Invertebrate biodiversity, in particular, can respond both positively and negatively, and directly and indirectly to increased urbanization and urban forest management practices (McIntyre, 2000; Sverdrup-Thygeson, Gustafsson, & Kouki, 2014). Specifically, saproxylic invertebrate species are affected in both urban and production forest management by the amount and species diversity of dead wood (Sverdrup-Thygeson et al., 2014).

Saproxylic invertebrates are dependent during at least some of their life cycle, on decaying wood associated with or originating from live, dying, or dead trees (Alexander, 2008; Speight, 1989). Saproxylic insects play an important role in the dead wood cycles in forest landscapes. They consume and break down dead and dying trees through larval development and assist in the spread and colonization of numerous species of obligate saproxylic fungi that also utilize dead wood as a substrate (Speight, 1989). Numerous species of insects, especially beetles (Coleoptera), flies (Diptera) and parasitic wasps (Hymenoptera), are found inhabiting natural dead wood and logging residues throughout Swedish forests and play an important role in forest biodiversity (Hilszczajski et al., 2005; Jonsell, Hansson, & Wedmo, 2007; Økland et al., 2005).

Some researchers in Europe have studied the role and impacts of urban forests and urban trees on saproxylic species. Fattorini and Galassi (2016) suggested that complex saproxylic beetle communities may thrive in well preserved urban forests especially around the periphery of an urban-rural gradient. They showed that greenspace size and forest surface area have positive effects on saproxylic species diversity. Similarly, Horák (2011) showed that tree species composition is an important factor in saproxylic beetle conservation in urban areas. Specifically, that admixed urban forests containing *Quercus* species produce significant numbers of singleton, doubleton, and unique saproxylic species but even urban forests with a high number of a single tree species (e.g. *Fagus*) can support higher saproxylic species abundance versus admix forest stands. Carpaneto et al. (2010) outlined the importance of proper forest management and urban tree removal concerning the conservation of a single saproxylic beetle species (*Osmoderma eremita*). They concluded that urban forests and greenspaces may actually be more important habitats for saproxylic beetles as opposed to the surround rural areas and forests given the number of older trees with decayed hollows found in urban forests as opposed to production forests.

Other researchers have specifically focused on Swedish saproxylic insects (mostly beetles). Some authors focused on environmental factors important for saproxylic beetles (Franc, Götmark, Økland, Nordén, & Paltto, 2007; Hjältén et al., 2007; Widerberg et al., 2012) and spatial and temporal scales relevant for saproxylic conservation (Sverdrup-Thygeson et al., 2014). Other authors focused more on forest management practices such as dead wood management effects on saproxylic beetles (Andersson, Hjältén, & Dynesius, 2015; Ehnström, 2001; Jonsell & Weslien, 2003; Jonsson et al., 2016); use of logging residues by saproxylic beetles (Hjältén, Stenbacka, & Andersson, 2010; Jonsell, 2008; Jonsell et al., 2007); and silvicultural practices (Hjältén et al., 2017).

However, there have been no studies that focus specifically on saproxylic beetles and urban forests in Sweden. The silvicultural practices that affect saproxylic beetles in large, rural production forests may be translated to urban forests. But urban forests differ from large, rural production forests in their direct impact of ecosystem services on local populations (Barthel, Colding, Elmqvist, & Folke, 2005; Konijnendijk, 2003) and the unique forest environments created in urban areas that effect insect biodiversity (Sverdrup-Thygeson et al., 2014). Urban forests can be significant reservoirs for saproxylic beetles due to the occasional occurrence of old growth or monumental trees (Carpaneto et al., 2010). In turn the occurrence of specific species of saproxylic beetles can act as forest health and age bioindicators possibly helping foresters make more focused decisions regarding forest management (Schuck et al., 2004). It is important to better understand the ecology of saproxylic beetles in urban forests and specifically the effects of the urban-forest boundary on saproxylic beetle diversity.

Management of dead wood in and around urban areas can vary greatly depending on the types of surrounding forests, the environmental and ecological goals of municipalities, and how local businesses and individuals manage the landscape of their own private property. For example, the city of Gothenburg works to keep dead wood available in cases where it does not pose a safety risk, but also must balance the amount of dead wood with creating economically viable production forests and accessible recreational forests (Fastighetskontoret, 2014; Fastighetskontoret, 2015). These types of specific dead wood policies and goals relate only to forests, parks, and property directly controlled by the city. It is possible that significant amounts of dead wood may be present in urban areas, on private property, or in areas not controlled or considered by city foresters or park managers. With this in mind it is important to explore other indicators and variables that affect saproxylic insect diversity other than complete reliance on dead wood abundance and availability.

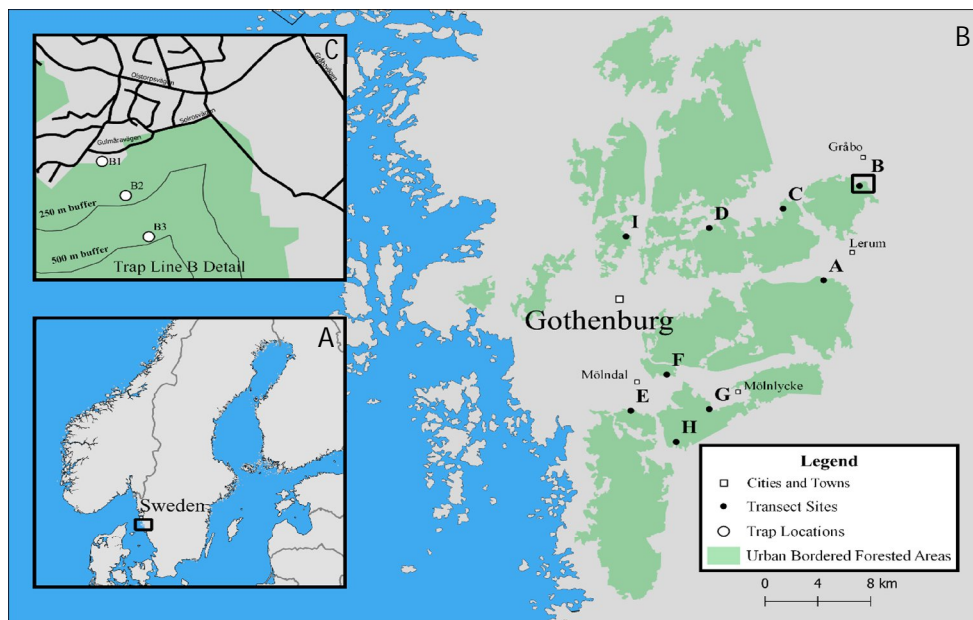
Some authors have suggested a large range of forest and habitat biotic and abiotic variables may be important to saproxylic beetle diversity (Franc et al., 2007; Økland, Bakke, Hågvar, & Kvamme, 1996). But studying dozens of variables unnecessarily complicates data collection and statistical models and may not compensate for collinearity. Analyzing only a few forest variables will keep this study focused. Forest age has been shown to be an important factor when estimating saproxylic beetle species abundance and richness and as a proxy of the amount of deadwood present (Hjältén et al., 2017; Martikainen, Siitonen, Puntila, Kaila, & Rauh, 2000; Stenbacka, Hjältén, Hilszczański, & Dynesius, 2010). Forest volume (includes bark, but not branches and roots) may also explain saproxylic beetle diversity (Franc et al., 2007; Rocca, Stefanelli, Pasquaretta, Campanaro, & Bogliani, 2014) through sunlight coverage and as an estimate for the amount of dead wood attached to live trees. Finally, saproxylic beetle diversity may be affected by the species of trees associated with the study area (Horák, 2011).

In this study I explored saproxylic beetle species richness and abundance along transects set up at defined urban-forest boundaries within urban forests of western Sweden. Urban proximity is the main focus of the following study, but environmental factors within the urban and forested areas likely play a role in saproxylic beetle species richness and abundance. I hypothesized that saproxylic beetle species richness and abundance would be positively correlated with distance from a defined urban-

forest boundary considering the forest age, forest volume, and the tree species composition along each trapping transect.

## Materials and Methods

The study was carried out in the west Swedish county of Västra Götaland in the municipalities of Gothenburg, Mölndal, Härryda, and Lerum (Figure 1). The trapping sites, referred to as sites A-I, were selected based on the following criteria: location of a defined urban-forest boundary; a sufficient



**Figure 1** Study area: A) Sweden, B) Gothenburg area trapping locations, and C) trap line B detail near Gräbo. Traps were set as close to the 250- and 500-meter buffers as possible and/or within the accuracy of the GPS equipment.

buffer allowing traps to be placed at 250, and 500 meters from the urban-forest boundary, and accessibility. Avoiding proximity to large bodies of water and forest clearing activities was also considered but not prioritized. I specifically chose to avoid trapping sites in defined conservation areas and Natura 2000 Habitats. These areas are specially managed for conservation purposes (Kremer, Van der Stegen, Gomez-Zamalloa, & Szedlak, 2015; Naturvårdsverket, 2012) and trapping is either prohibited or requires permission that can take over a year to be granted. Other researchers have tried to keep variables similar between trapping sites (Franc et al., 2007; Nordén, Götmark, Tönnerberg, & Ryberg, 2004; Schiegg, 2000), however that was not attempted for this study due to time and transportation constraints. Urban and forested areas were defined (Table 1) and selected using the 2012 Coordination of Information on the Environment (CORINE) Land Cover data (CLC) (EEA, 2012). Selected urban boundaries consisted of one or more of the following: continuous urban fabric, discontinuous urban fabric, industrial or commercial units,

**Table 1** CORINE Land Cover nomenclature categories and definitions for artificial surfaces and forest areas chosen to represent urban and forested areas for trapping lines.

Level 1	Level 2	Level 3	Definition
Artificial surfaces	<ul style="list-style-type: none"> <li>▪ Urban fabric</li> </ul>	<ul style="list-style-type: none"> <li>▪ Continuous urban fabric</li> <li>▪ Discontinuous</li> </ul>	<ul style="list-style-type: none"> <li>▪ Most of the land is covered by buildings, roads, and artificially surfaced area cover almost all the ground. Non-linear areas of vegetation and bare soil are exceptional.</li> <li>▪ Most of the land is covered by structures.</li> </ul>

		urban fabric	Buildings, roads and artificially surfaced areas associated with vegetated areas and bare soil, which occupy discontinuous but significant surfaces.
	▪ Industrial, commercial, and transport units	▪ Industrial or commercial units	▪ Artificially surfaced areas (with concrete, asphalt, tarmacadam, or stabilized, e.g. beaten earth) devoid of vegetation, occupy most of the area in question, which also contains buildings and/or vegetated areas
		▪ Road and rail networks	▪ Motorways, railways, including associated installations.
		▪ Port areas	▪ Infrastructure of port areas, including quays, dockyards and marinas.
		▪ Airports	▪ Airport installations: runways, buildings and associated land.
	▪ Artificial non-agricultural vegetated areas	▪ Green urban areas	▪ Areas with vegetation within urban fabric. Includes parks and cemeteries with vegetation.
		▪ Sport and leisure facilities	▪ Camping grounds, sports grounds, leisure parks, golf courses, racecourses, etc. Includes formal parks not surrounded by urban zones.
Forests and semi-natural areas	▪ Forests	▪ Broad-leaved forest	▪ Vegetation formation composed principally of trees, including shrub and bush understories, where broadleaved species predominate.
		▪ Coniferous forest	▪ Vegetation formation composed principally of trees, including shrub and bush understories, where coniferous species predominate.
		▪ Mixed forest	▪ Vegetation formation composed principally of trees, including shrub and bush understories, where broadleaved and coniferous species co-dominate.

road and rail networks, maritime port areas, airports, green urban areas, and/or sports and leisure facilities. Selected forested areas consisted of one or more of the following: broad-leaved forests, coniferous forests, and/or mixed forests. The forest manager from the Gothenburg city property office (Fastighetskontoret) provided significant city forest information and assisted in trapping site identification (T. Andersen, personal communication, May 29, 2018). Potential sites were scouted during May 2018, nine trapping sites were chosen, and transects of 500 meters were drawn with buffers of 250 and 500 meters parallel from the urban-forest boundary (Figure 1).

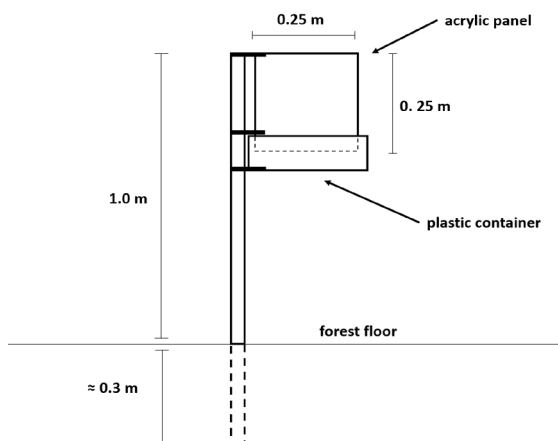
Most forested areas were classified as majority coniferous (Table 2). Common tree species within 125 meters of each trapping location consisted of Scots pine (*Pinus silvestris*, mean = 43.6 m<sup>3</sup>sk/ha, SD = 23.8), Norway spruce (*Picea abies*, mean = 29.1, SD = 21.6), birch (*Betula* spp., mean = 14.8, SD = 7.0), and oak (*Quercus* spp., mean = 5.0, SD = 9.4) (Skogsstyrelsen, 2017). Other broadleaf tree species observed such as European ash (*Fraxinus excelsior*) and maple (*Acer* spp.) were grouped as other deciduous trees (mean = 4.0, SD = 3.4) (Skogsstyrelsen, 2017). The average age of the forest at each site was 41 years (SD = 14.4) (Skogsstyrelsen, 2017).

Insects were sampled using non-baited flight interception traps. The traps were made of a 25 x 25 cm transparent acrylic glass panel above a 3.8 L plastic container filled with 2 L of 50% water and 50% propylene glycol (Figure 2). Each collection container had two holes about 1 cm below the edge to allow for drainage of excess rainwater. The acrylic panel and collection container were attached to a 4.5 x 4.5 x 130 cm wooden pole. At each of the nine sampling sites three traps were set one meter off the ground along each transect at 0, 250, and 500-meter intervals starting on the edge of the selected

urban-forest boundary. A small informational sign in Swedish and English with contact information and asking people to not disturb the study was attached to each trap.

Traps were set on 31 May and 1-2 June, 2018 to coincide with peak beetle emergence in the Västra Götaland region based on locally reported sighting and trapping information between 2000-2017 (SLU, 2018). Each trap line was checked three times during the months of June and July (lines B and C were only checked twice due to time constraints). During checks, all insects were removed, traps were replenished with a fresh water/propylene glycol mix, and were cleaned of debris. Captured insects were pooled by trap number over the entire study duration. Collections were not separated by date and therefore no time effect within trapping lines was analyzed for this study. Traps were removed from 1-4 August. All traps represented a total of 1671 trap-days in the field with an average

of 62 days per trap. No traps were missing, felled, or damaged during the study.



**Figure 2** Trap design consisting of a 25x25 cm acrylic panel above a 3.8 L plastic tray attached to a wooden stake one meter above forest floor.

I identified all collected insects with some assistance. Each pooled trap collection was screened for beetles (Coleoptera). All beetle families, with the exception of the Staphylinidae (see: Parmain et al., 2015), were identified at least to genus, most to species. *Nicrophorus* spp. (Silphidae) were discarded without identification or counts as they were likely attracted to the dead insects in the traps, numbers in the thousands, and were not relevant to this study.

Specimens unable to be identified to a distinct species were compared between trap lines and determined at a morphospecies level (see: Oliver & Beattie, 1996 or Dangerfield et. al., 2003).

Beetles were separated as either saproxylic or non-saproxylic using the Alexander (2001) annotated checklist and the saproxylic beetle list compiled at [saprox.mnhn.fr](http://saprox.mnhn.fr) (SAPROX, 2018). Obligate saproxylic species were analyzed separately and were pooled with facultative species for analysis. Two species of *Anaspis* (Scraptiidae) females were counted for abundance analysis but removed for richness analysis. *Anaspis* females are difficult to identify to species and I could not be sure they were not already represented by identified male *Anaspis*.

Abundance count datum was separated into total abundance and obligate saproxylic only abundance. For richness counts, singletons were removed and data was separated into total richness and obligate saproxylic richness. As pointed out by many authors regarding ecological sampling, observed species counts almost always result in a significant underestimation of the true species richness in the sampled area (Chao & Chiu, 2016; Gotelli & Chao, 2013; Gotelli & Colwell, 2011). To compensate for possible underrepresented richness counts along each trapping transect, I estimated the richness at each trapping location using the average of the iChao1 (Chiu et. al., 2014), ACE-1 (Chao & Lee, 1992), and 2nd order Jack-knife richness model estimates. Estimated richness data was separated into total estimated richness and estimated obligate saproxylic richness.

Saproxylic species abundance, richness, and estimated richness were analyzed using a generalized linear model (GLM). Models built for abundance and estimated richness used a negative binomial distribution. Negative binomial distribution is commonly used for count data with overdispersion (Gardner, Mulvey, & Shaw, 1995) and my abundance and estimated richness data showed significant

**Table 2** Details and characteristics of trapping sites studied in the summer of 2018 in Västra Götaland, Sweden

Trap Line (Location)	Forest Use	Trap #	Coordinates (DMS)	Elevation (m)	Forest Stand Description (avg. within 125 m of each trap)§							
					Forest Type	Avg. Forest Age (years)	Birch <sup>†</sup>	Oak <sup>†</sup>	Other Deciduous <sup>†</sup>	Scots Pine <sup>†</sup>	Norway Spruce <sup>†</sup>	Biomass <sup>†</sup>
<b>A (Lerum)</b>	Production	1	N57° 44' 40.6284" E12° 14' 22.0092"	60	Coniferous	33	22.0	1.4	6.9	36.8	27.5	73.0
		2	N57° 44' 34.008" E12° 14' 21.2316"	106	Coniferous	49	18.0	0.5	2.9	60.1	44.2	100.0
		3	N57° 44' 28.172" E12° 14' 15.601"	111	Coniferous	56	9.0	0.4	1.5	62.6	41.7	66.1
<b>B (Gräbo)</b>	Recreation/ Production	1	N57° 49' 6.298" E12° 16' 31.062"	104	Coniferous	53	7.3	0.4	1.2	66.7	27.9	97.1
		2	N57° 48' 59.926" E12° 16' 39.094"	100	Coniferous	67	7.9	0.4	0.9	72.9	38.5	77.1
		3	N57° 48' 52.222" E12° 16' 47.06"	95	Coniferous	67	7.2	0.2	0.8	77.5	42.4	69.5
<b>C (Olofstorp)</b>	Production	1	N57° 47' 48.095" E12° 10' 44.915"	122	Coniferous	46	22.6	1.8	6.3	78.8	17.0	65.0
		2	N57° 47' 51.972" E12° 10' 59.747"	122	Coniferous	41	12.7	1.3	3.2	55.8	14.2	60.0
		3	N57° 47' 54.708" E12° 11' 12.858"	137	Coniferous	39	8.5	1.0	2.4	47.2	15.1	50.5
<b>D (Gunnlise)</b>	Semi-natural	1	N57° 46' 52.846" E12° 5' 20.141"	72	Mixed	17	16.8	1.2	5.3	5.8	6.4	37.0
		2	N57° 46' 48.151" E12° 5' 32.42"	108	Mixed	28	23.4	1.8	9.1	36.0	7.2	104.5
		3	N57° 46' 41.29" E12° 5' 37.867"	129	Coniferous	56	15.8	1.5	4.8	78.3	19.4	96.2
<b>E (Möhdal)</b>	Semi-natural	1	N57° 38' 23.712" E12° 0' 18.036"	21	Deciduous	21	8.0	44.0	0.0	0.9	1.2	55.5
		2	N57° 38' 18.938" E12° 0' 4.759"	67	Deciduous	22	12.6	22.0	0.9	8.1	7.7	97.3
		3	N57° 38' 16.044" E11° 59' 57.048"	54	Deciduous	23	12.6	20.9	0.7	9.2	8.6	101.3
<b>F (Rådasjön)</b>	Production	1	N57° 40' 2.111" E12° 2' 49.099"	86	Coniferous	38	11.1	0.2	1.4	29.8	49.7	83.5
		2	N57° 40' 8.314" E12° 2' 43.444"	110	Coniferous	50	17.2	0.1	1.3	41.9	69.3	157.9
		3	N57° 40' 12.886" E12° 2' 34.93"	115	Coniferous	19	10.8	0.9	3.3	14.8	8.2	110.5
<b>G (Mölnlycke)</b>	Semi-natural/ Production?	1	N57° 38' 31.769" E12° 5' 56.195"	74	Mixed	40	35.8	11.0	6.8	19.7	16.7	97.7
		2	N57° 38' 26.239" E12° 5' 50.208"	103	Coniferous	52	18.5	5.0	3.5	56.2	48.4	76.9
		3	N57° 38' 19.036" E12° 5' 47.483"	84	Coniferous	50	12.4	4.3	4.2	58.6	43.2	75.3
<b>H (Källered)</b>	Production	1	N57° 36' 55.894" E12° 3' 34.452"	84	Mixed	21	6.8	4.8	4.9	10.4	15.2	102.7
		2	N57° 37' 2.006" E12° 3' 42.156"	93	Coniferous	48	9.5	4.0	3.3	46.6	62.3	136.9
		3	N57° 37' 8.285" E12° 3' 47.153"	101	Coniferous	50	8.3	0.5	1.1	53.2	65.9	106.9
<b>I (Backatorp)</b>	Recreation	1	N57° 46' 21.4" E11° 59' 11.609"	31	Mixed	29	21.7	1.7	11.8	34.0	5.8	80.6
		2	N57° 46' 18.908" E11° 58' 59.07"	56	Mixed	40	26.2	2.7	13.6	59.1	11.3	157.6
		3	N57° 46' 16.172" E11° 58' 47.46"	72	Coniferous	57	18.5	1.2	5.0	56.7	72.9	230.5

† m3sk/ha = forest cubic meter, wood volume of a tree or forest, including bark but excluding branches and roots.

‡ tonnes/hectare

§ Sources = Skogsstyrelsen, 2017 & SLU, 2017



overdispersion (ABN,  $\mu = 51.9$ ,  $\sigma^2 = 2307.6$ ; ABN\_OB,  $\mu = 29.4$ ,  $\sigma^2 = 685.3$ ; ERCH,  $\mu = 49.9$ ,  $\sigma^2 = 984.6$ ; ERCH\_OB,  $\mu = 33.3$ ,  $\sigma^2 = 604.7$ ). Models built for observed richness used a Poisson distribution. I analyzed each dependent variable as a function of the experimental trap distance from the urban-forest boundary and other variables. Other variables were chosen from a range of options considered ecologically or biologically significant to saproxylic beetle abundance and richness (see Table 3 for complete descriptions) in order to create a minimum adequate model. The trap distance from the urban-forest boundary was run as a factored variable in the model. Trap distance and deciduous to coniferous tree species ratio were also tested for an interaction effect within each GLM. Tree species has been shown to affect saproxylic beetle diversity and this variable may change significantly depending on the distance from an urban area.

**Table 3** Correlation matrix and description of dependent variables used in GLM analysis

Variable	Description	p values				Source
		TRAPEX	VOL	AGE	DC_RATIO	
<b>TRAPEX</b>	Categorical variable describing the experimental trap distance along each urban-forest boundary transect line.		0.389	0.010	0.013	N/A
<b>VOL</b>	The average forest volume measured in <i>forest cubic meters</i> ( $m^3$ sk/ha), including bark but excluding branches	0.18		0.515	0.719	Skogsstyrelsen, 2017
<b>AGE</b>	The average forest age measured in years, within 125 m of a trap.	0.52	0.15		< 0.001	SLU, 2017
<b>DC_RATIO</b>	The ratio of total volume of deciduous trees to total volume of coniferous trees, within 125 m of a trap.	-0.50	-0.08	-0.86		Skogsstyrelsen, 2017
		<b>Spearman <math>r_s</math> values</b>				

Each independent variable was checked for collinearity using Spearman's rank-order correlation method (Table 3). Average forest age and deciduous to coniferous tree species ratio showed significant correlation, however there was no obvious biological or other explanation for the correlation and both variables were kept for the analysis. All variables were checked for normality using a Shapiro-Wilk test. Post hoc analysis was carried out using a pairwise comparison of estimated marginal means corrected with Tukey adjustments to account for multiple tests.

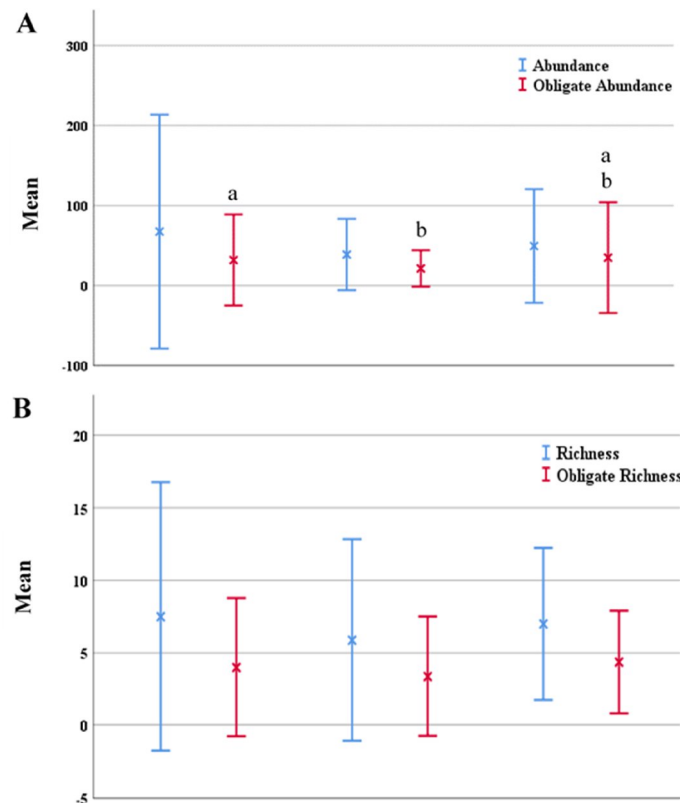
Most, if not all, previous studies regarding saproxylic beetles have relied on deadwood volume, diameter, and/or density as an independent variable used to model abundance and richness. Deadwood variables were left out of this analysis for four reasons. First, data provided by the Swedish National Forest Inventory (NFI) were too coarse of a resolution and would not have been meaningfully accurate at the small scale of this study. Second, even if the NFI data were robust enough to be used at the study scale, there are no data points within urban areas and any conclusions of deadwood effects at the urban-forest boundary would have been misleading. Third, an inventory of available deadwood around the transect lines would have been an intense undertaking for the scope and level of this study. Finally, saproxylic species caught in flight interception traps and the amount of deadwood in proximity to those traps is not necessarily correlated and does not significantly affect the number of different species caught (Siitonen, 1994). Thus using dead wood volume to make conclusions about saproxylic beetle diversity is not necessarily informative (Grove, 2002; Vodka, Konvicka, & Cizek, 2009).

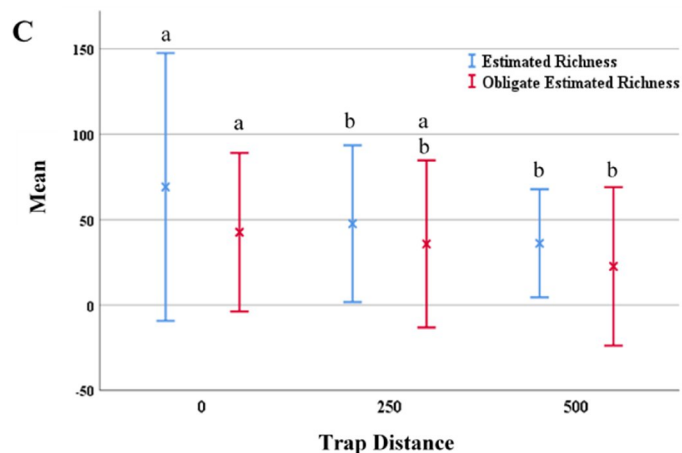
All data analysis was performed using R 3.5.1 (R Core Team, 2018) in R Studio 1.1.463 (R Studio, 2018). Dependent variable distribution fitting was performed with the fitdistplus package (Delignette-Muller & Dutang, 2015). Richness estimates were calculated using the SpadeR package (Chao, Ma, Hsieh, & Chiu, 2016). Negative binomial GLMs were run with the MASS package (Venables & Ripley, 2002) and Poisson GLMs were run with the stats package (R Core Team, 2018). Post hoc analysis was run with the emmeans package (Lenth, 2018).

## Results

At all nine trapping transects a total of 8380 beetles were collected (See Appendix A for a complete list). Of these, 4182 were saproxylic beetles represented by 179 species, and of these 98 species (913 individuals) were obligate saproxylic. Unidentifiable species were removed for the analysis. The F trapping line accounted for 2937 individual saproxylic beetles captured. A follow up survey in the area discovered a previously unknown logging operation that included many stacks of fresh cut logs and an electric company right-of-way that was likely the reason for a significantly skewed trap catch count at the 500-meter position. On this line one species of facultative saproxylic sap beetle, *Glischrochilus hortensis* (Nitidulidae), accounted for over 61% of the total study saproxylic beetle catch. Due to flawed trap placement and the saproxylic beetle catches being significantly skewed because of this trap placement, trapping line F was removed from all data analyses for this study.

The results summarize both observed and estimated species richness. However, the following discussion regarding species richness and its relation to other variables is only in the context of the estimated species richness. Many statisticians and ecologists have pointed out that observed richness counts significantly underestimate the actual species richness (Chao & Chiu, 2016; Gotelli & Chao, 2013; Gotelli & Colwell, 2011). Estimated species richness was greater at all trap distances and a simple paired t-test showed a significant difference in means between the observed and estimated species richness ( $t(27) = -7.78, p < 0.001$ ).





**Figure 3** Mean total saproxylic beetle counts at each trapping distance from the urban-forest boundary. A) abundance, B) observed richness, C) estimated richness. Error bars =  $\pm 2$  SD. Post hoc analysis results denoted above error bars (means with the same letter are not significantly different).

The main effects of trap distance from the urban-forest boundary showed little significance over all. Trap distance showed a negative significance for both estimated richness variables moving further into the forest from the urban-forest boundary (Table 4). Abundance, richness, and obligate richness showed no significance differences along the transect line. Obligate abundance showed a positive significance moving further into the forest from the urban-forest boundary (Table 4). The interaction between deciduous to coniferous tree species ratio and trap distance was significant at both the 250 and 500 m trap distance for abundance and obligate abundance. All other dependent variables showed no significance with the interaction effect.

Average forest volume showed a significant positive effect for all dependent variables except obligate richness. However, this positive effect was minimal based on estimated parameters (Table 4). Average forest age showed a significant negative effect on both abundance variables, both richness variables, and estimated richness, but there was no significant effect on estimated obligate richness (Table 4). Deciduous to coniferous tree species ratio show no significance for all dependent variables (Table 4). However, the significance of the tree species interaction with trap distance in both abundance variables and estimated richness, suggests that the tree species composition along each transect is lowering the effect on those variables based on distance from the urban-forest boundary.

**Table 4** Results of the GLM analysis exploring urban-forest proximity and other forest variables to saproxylic species abundance and richness. Est. = Estimated parameters,  $p$  = p-value. Significant p-values in bold.

	Abundance <sup>†</sup>		Abundance, Obligate <sup>†</sup>		Richness <sup>‡</sup>		Richness, Obligate <sup>‡</sup>		Estimated Richness <sup>†</sup>		Estimated Richness, Obligate <sup>†</sup>	
	Est.	$p$	Est.	$p$	Est.	$p$	Est.	$p$	Est.	$p$	Est.	$p$
<b>VOL</b>	0.004	<b>0.018</b>	0.005	<b>&lt; 0.001</b>	0.003	<b>0.007</b>	0.002	0.099	0.003	<b>0.011</b>	0.004	<b>0.001</b>
<b>AGE</b>	-0.030	<b>0.041</b>	-0.033	<b>0.009</b>	-0.022	<b>0.017</b>	-0.028	<b>0.022</b>	0.003	0.755	0.023	<b>0.033</b>
<b>DC_RATIO</b>	-0.038	0.176	-0.040	0.118	-0.005	0.760	-0.043	0.163	-0.019	0.278	0.026	0.210
<b>TRAPEX(250)</b>	-0.023	0.960	0.109	0.786	0.207	0.494	0.172	0.664	-0.384	0.162	-0.354	0.287
<b>TRAPEX(500)</b>	0.248	0.598	0.083	<b>0.044</b>	0.313	0.306	0.554	0.164	-0.832	<b>0.004</b>	-1.261	<b>&lt; 0.001</b>
<b>DC_RATIO*TRAPEX(250)</b>	-0.897	<b>0.030</b>	-0.729	<b>0.045</b>	-0.612	0.052	-0.413	0.258	-0.424	0.097	-0.302	0.332
<b>DC_RATIO*TRAPEX(500)</b>	-0.905	<b>0.047</b>	-1.215	<b>0.003</b>	-0.371	0.179	-0.493	0.174	-0.139	0.623	-0.086	0.815

<sup>†</sup> generalized linear model fit with negative binomial distribution

<sup>‡</sup> generalized linear model fit with poisson distribution

Post hoc analysis was run for obligate abundance variables and all estimated richness variables (Figure 3). A significant contrast was shown between the 0 m and 250 m traps for both abundance ( $p$

= 0.010) and obligate abundance ( $p = 0.043$ ) counts, but the absence of a significant main effect at the 250 m trap distance for the either variable makes this post hoc significance difficult to interpret. Significant contrasts were shown for two trap distance comparisons for estimated richness (0-250 and 0-500;  $p = 0.002$  and  $0.011$ , respectively). A significant contrast was shown between the 0 m and 500 m traps for estimated obligate richness ( $p = 0.010$ ).

## Discussion

The scope of this study was to determine the main effect of urban proximity on saproxylic beetle abundance and species richness. I hypothesized that saproxylic beetle species abundance and species richness would increase with increasing distance from an urban-forest boundary. Based on my analyses I could not find a consistent pattern for this relationship; in some cases there was a significant positive relationship and in others a negative one with increasing distance from the urban-forest boundary. Unfortunately, the lack of clear-cut significance regarding the abundance and species richness as functions of proximity to the urban-forest boundary make definitive acceptance or outright rejection of my initial hypothesis difficult. However, the variables that did show significant effects on saproxylic beetle abundance and species richness provide for interesting discussion, reflection, and lay a ground work for future studies similar in scope.

Any meaningful conclusions regarding this study would be difficult if the discussion was taken outside of the context of an edge effect. Examining the effects of the edge of two distinct habitats is a core concept that most likely is represented by the above data. The significant positive effect of distance to an urban area on obligate species abundance may suggest a slight increase in saproxylic abundance moving away from urban areas, but post hoc analysis of this significance rejects any meaningful difference between abundance counts at each trap distance. It is most likely that urban proximity, at least within 500 meters, does not affect saproxylic beetle abundance.

The negative effect of estimated obligate richness at the same distance, suggests that species richness may decrease moving away from the urban-forest edge. This is not unprecedented as some authors have shown the combination of species from two different habitats meeting at an edge, may extend further than 400 m from the edge resulting in greater species diversity in the depth-of-edge-influence area (Dangerfield et al., 2003; Sattler, Duelli, Obrist, Arlettaz, & Moretti, 2010). The suggested, although weak, increase in species richness nearer to the urban-forest boundary may be related to edge effect, specifically at an urban edge. The increase in average temperature and sun intensity commonly found on natural and man-made forest edges (Murcia, 1995; Sattler et al., 2010) may explain the increased numbers of insect species (Gibb & Hochuli, 2002; Vodka & Cizek, 2013). Without a concurrent survey of larval stages of saproxylic beetles along each transect, or a methodological adjustment for traps further into the forest, a more accurate estimation of species richness along each trapping line remains difficult to evaluate.

Even though the main effect of trap distance from the urban-forest boundary did not provide conclusive direction about saproxylic beetle abundance and species richness, a distinct interaction effect connecting the ratio of deciduous to coniferous tree species along the transect lines with trap distance from the urban-forest boundary was observed. When accounting for the deciduous to coniferous tree species ratio, abundance and obligate abundance were negatively affected farther away from the urban forest boundary. This shows that tree species composition is an important factor around the edges in this study and suggests that an increase in deciduous tree species may lower the effects of urbanization on saproxylic species abundance. This is appropriate as saproxylic beetle species in Sweden may be affected by the amount of deciduous wood available and the amount added or removed for forest management purposes (Felton, Lindbladh, Brunet, & Fritz, 2010; Franc et al., 2007; Økland et al., 1996).

Average forest age seemed to explain some variation in the abundance and estimated obligate species richness along the trapping lines. Although, surprisingly, the negative correlation suggested an increase in age would result in a decrease in saproxylic abundance. My results directly contradict other research that shows a positive link between stand age (often separated broadly as “recently felled forests”, “actively managed forests”, “mature forests”, and/or “old-growth forest”, or derivatives thereof) and saproxylic beetle abundance (Hjältén et al., 2017; Martikainen et al., 2000; Stenbacka et al., 2010). However, the positive correlation between age and estimated obligate species richness agreed with the same authors. These positive links are always applied as functions of the amount of deadwood that is/might be present because of stand age, which holds true in most Swedish forests (Fridman & Walheim, 2000). It is possible that the city of Gothenburg and production forest managers are making efforts to retain enough deadwood in and around the city and county to make the impact on saproxylic beetles unaffected by forest age. It is also likely that these results reflect the populations of early successional species (Horn, 1974; Swanson et al., 2011). Comparing older forests may show a positive relationship between saproxylic species diversity and age as the above authors have shown.

Average forest age showed no significant effect on estimated richness. These results partially agreed with at least one study that showed standardized species richness counts were not significantly related to stand age (Langor, Spence, Hammond, Jacobs, & Cobb, 2006). However, many studies (including those mentioned above) show strong positive effects of forest age on saproxylic beetle richness (Cocciufa et al., 2014; Lassauce, Larrieu, Paillet, Lieutier, & Bouget, 2013; Wermelinger, Flukiger, Obrist, & Duelli, 2007)

Volume had a slight positive effect on all tested variables. Since most saproxylic studies focus on dead wood, few analyze how the volume of living trees affect saproxylic abundance and richness. But the studies that do, associate a negative effect on saproxylic beetle richness on increased living forest volume likely due to decreased sunlight exposure (Franc et al., 2007; Rocca et al., 2014). The slight positive effect recorded here might indicate an extremely small change in forest volume along each transect which is often the case in managed forests.

The above results may seem somewhat contradictory or confusing, but I believe that they show a definite edge effect related to the urban-forest boundary with the consideration that analyzing species gradients related to urban areas risks simplifying highly complex urban-rural and urban-forest interactions (Mckinney, 2008). My data from this edge effect may be confounded by at least two variables and insufficient sampling. The two variables include forest fragmentation and the compounding effects of multiple edges. Forest fragmentation can have positive or negative effects on species abundance and richness (Bolger, Suarez, Crooks, Morrison, & Case, 2000; Fahrig, 2003; Mckinney, 2008) depending on the reason and extent of the fragmentation (Hunter, 2002; Radeloff, Hammer, & Stewart, 2005) I did not explore any measurements of fragmentation related to the transect lines, but any follow up studies should include this in the analysis or should standardize trapping locations to negate any such effect. The effects of multiple edges could have resulted in an additive increase of the edge effects along each trapping transect (Ewers & Didham, 2007; Ewers, Thorpe, & Didham, 2007).

There is good reason to believe that the depth-of-edge influence related to the urban forests in this study may extend further than the 500 m explored here. Many authors place the effects of edges related to forests between 20 m and 500 m (Broadbent et al., 2008; Dantas de Paula, Groeneveld, & Huth, 2016; Ewers et al., 2007) but this is almost exclusively in the context of natural edges or edges created through deforestation. Combined with the above-mentioned ecological complexity of urbanization, I hypothesize that edge effects related to urban-forest boundaries extend significantly farther than the analyzed 500 m. This is supported by at least one author that suggests forest edge effects can extend over 1 km into the forest interior (Ewers & Didham, 2008). Urbanization

contributes to extensive fragmentation, which in turn increases the number and length of urban-forest edges (Ewers & Didham, 2007; Ries, Fletcher, Battin, & Sisk, 2004). Urban areas provide diverse green spaces and tree species richness not found in the surrounding forests that often contribute to an increase in species abundance and richness (Gibb & Hochuli, 2002; Gunnarsson et al., 2016; McIntyre, 2000). One author suggests that saproxylic beetle desire for sunny habitats combined with a poor flying ability for some species might encourage congregation and greater species diversity near forest edges and away from closed forests with dense growth (Vodka & Cizek, 2013). One could imagine that saproxylic beetles may move toward urban-forest edges from deeper than 500 m into the forest to exploit the urban habitat and take advantage of the forest edge habitat. Any follow up studies should include sampling methods that extend farther than 500 m from the urban-forest boundary.

It should be noted that this study suffers from pseudoreplication as a result of the sampling sites being in the same general area. The results presented here cannot be generalized outside the study area. As noted by Murcia (1995), pseudoreplication is a significant issue in studies regarding forest edge effects. However, as also pointed out by many ecologists, pseudoreplication should not be considered a hindrance to ecological studies especially in the face of limited resources and/or time (Davies & Gray, 2015).

The data presented above shows inconsistent significance and only minor overall effects, but the analysis of urban-forest boundaries on saproxylic beetle abundance and richness in this study has implications for the management of urban forests and the urban-forest edge. Urban areas and urban-forest edges have been shown to have unique arthropod arrangements compared to surrounding forests and local agricultural areas (Sattler, Obrist, Duelli, & Moretti, 2011). This is likely true within Gothenburg as the city has a high urban tree species diversity index (Sjöman, Östberg, & Bühler, 2011). This level of diversity likely provides many different habitats for a significant range of invertebrates including saproxylic beetles. If saproxylic beetle species richness and abundance is greater near urban-forest edges, then city managers and foresters should take this into account. If the deciduous to coniferous tree species ratio is a significant factor affecting saproxylic beetle diversity, increasing this ratio could prove to be an easier focus for managers rather than dealing directly with dead wood management and retention. If tree volume positively directly or indirectly affects saproxylic beetle diversity, increasing this should also be a main part of forest management practices.

Although it should not be completely discounted, results of this study suggest that dead wood management does not necessarily need to be the main focus of forest management regarding saproxylic beetles. With proper and focused maintenance of urban forests, specifically the urban-forest boundary, forest managers can provide continued ecosystem service benefits for urban populations without negatively affecting saproxylic beetle diversity and have the potential to create biodiversity hotspots that extend along forest edges.

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**Appendix A.** List of all collected Coleoptera. Abundance is the total number collected. % Trap Occurrence is out of 27 traps. Unidentified, unidentifiable, and Staphylinidae species were not included in the data analysis regardless of their possible saproxylic status (See Materials and Methods).

Family	Species	Saproxylic Category*	Abundance	% Trap Occurrence
<b>Aderidae</b>	<i>Anidorus nigrinus</i>	SxF	1	4%
	<i>Euglenes pygmaeus</i>	SxO	2	7%
<b>Anobiidae</b>	<i>Dryophilus pusillus</i>	SxO	6	11%
	<i>Ernobius mollis</i>	SxO	1	4%
	<i>Hadrobregmus pertinax</i>	SxO	1	4%
	<i>Ptilinus pectinicornis</i>	SxO	3	11%
	<i>Pinus rufipes</i>	SxO	1	4%
	<i>Pinus subpillosus</i>	SxF	2	4%
<b>Anthribidae</b>	<i>Dissoleucas niveirostris</i>	SxO	1	4%
<b>Apionidae</b>	<i>Kalcapion pallipes</i>	NS	1	4%
	<i>Protapion apricans</i>	NS	1	4%
	<i>Protapion fulvipes</i>	NS	1	4%
	Unidentified	NS	7	22%
<b>Buprestidae</b>	<i>Trachys minuta</i>	NS	1	4%
<b>Byturidae</b>	<i>Byturus ochraceus</i>	NS	1	4%
<b>Cantharidae</b>	<i>Cantharis decipiens</i>	NS	2	7%
	<i>Cantharis figurata</i>	NS	9	15%
	<i>Cantharis flavilabris</i>	NS	1	4%
	<i>Cantharis livida</i>	NS	1	4%
	<i>Cantharis nigra</i>	NS	2	7%
	<i>Cantharis nigricans</i>	NS	18	30%
	<i>Cantharis obscura</i>	NS	2	7%
	<i>Cantharis paludosa</i>	NS	1	4%
	<i>Cantharis pellucida</i>	NS	5	15%
	<i>Cantharis quadripunctata</i>	NS	1	4%
	<i>Cantharis rufa</i>	NS	2	7%
	<i>Malthinus biguttatus</i>	SxF	1	4%
	<i>Malthinus flaveolus</i>	SxO	11	19%
	<i>Malthodes brevicollis</i>	SxO	2	4%
	<i>Malthodes crassicornis</i>	SxO	2	4%
	<i>Malthodes fibulatus</i>	SxO	3	7%
	<i>Malthodes flavoguttatus</i>	SxO	1	4%
	<i>Malthodes fuscus</i>	SxO	12	15%
	<i>Malthodes guttifer</i>	SxO	10	19%
	<i>Malthodes marginatus</i>	SxO	3	11%
	<i>Malthodes maurus</i>	SxO	1	4%
	<i>Malthodes</i> sp. 1	SxO	5	7%
	<i>Malthodes</i> sp. 2	SxO	1	4%
	<i>Malthodes spathifer</i>	SxO	1	4%
	<i>Malthodes</i> spp.	SxO	88	81%
	<i>Podistra rufotestacea</i>	NS	6	19%
	<i>Podistra schoenherri</i>	NS	6	19%
	<i>Rhagonycha fulva</i>	NS	18	11%
	<i>Rhagonycha lignosa</i>	NS	4	15%
	<i>Rhagonycha nigriventris</i>	NS	1	4%
<i>Rhagonycha testacea</i>	NS	3	7%	

	Unidentifiable	----	3	7%
<b>Carabidae</b>	<i>Dromius quadrimaculatus</i>	SxF	1	4%
	<i>Dromius</i> sp.	SxF	1	4%
<b>Cerambycidae</b>	<i>Alosterna tabacicolor</i>	SxO	1	4%
	<i>Anastrangalia reyi</i>	SxO	2	7%
	<i>Anastrangalia sanguinolenta</i>	SxO	20	22%
	<i>Clytus arietis</i>	SxO	12	19%
	<i>Grammoptera ruficornis</i>	SxO	1	4%
	<i>Leptura quadrifasciata</i>	SxO	5	15%
	<i>Molorchus minor</i>	SxO	1	4%
	<i>Oxymirus cursor</i>	SxO	2	7%
	<i>Phymatodes testaceus</i>	SxO	1	4%
	<i>Rhagium mordax</i>	SxO	2	7%
	<i>Stenurella melanura</i>	SxO	3	11%
	<i>Stictoleptura maculicornis</i>	SxO	22	26%
	<i>Stictoleptura rubra</i>	SxO	3	11%
	<i>Xylotrechus rusticus</i>	SxO	1	4%
<b>Cerylonidae</b>	<i>Cerylon ferrugineum</i>	SxO	10	26%
<b>Chrysomelidae</b>	<i>Crepidodera aurata</i>	NS	1	4%
	<i>Crepidodera fulvicornis</i>	NS	5	4%
	<i>Cryptocephalus labiatus</i>	NS	1	4%
	<i>Cryptocephalus</i> sp.	NS	2	7%
	<i>Luperus longicornis</i>	NS	2	7%
	<i>Pyrrhalta viburni</i>	NS	1	4%
	Unidentified	NS	1	4%
<b>Ciidae</b>	<i>Cis boleti</i>	SxO	16	26%
	<i>Cis dentatus</i>	SxO	1	4%
	<i>Cis submicans</i>	SxO	1	4%
	<i>Ennearthron cornatum</i>	SxO	3	7%
	<i>Octotemnus glabriculus</i>	SxO	1	4%
	<i>Orthocis alni</i>	SxO	1	4%
<b>Cleridae</b>	<i>Thanasimus formicarius</i>	SxO	2	4%
<b>Coccinellidae</b>	<i>Psyllobora vigintiduopunctata</i>	NS	1	4%
	<i>Chilocorus bipustulatus</i>	NS	1	4%
	<i>Chilocorus renipustulatus</i>	NS	4	11%
	<i>Coccinella septempunctata</i>	NS	6	7%
<b>Corylophidae</b>	<i>Sericoderus lateralis</i>	SxF	2	7%
	<i>Orthoperus</i> sp.	SxF	1	4%
<b>Cryptophagidae</b>	<i>Atomaria apicalis?</i>	SxF	1	4%
	<i>Atomaria lewisi</i>	SxF	1	4%
	<i>Atomaria nigrirostris?</i>	SxF	2	4%
	<i>Atomaria nigriventris</i>	SxF	1	4%
	<i>Atomaria pulchra?</i>	SxF	1	4%
	<i>Atomaria</i> sp. 1	SxF	9	15%
	<i>Atomaria</i> sp. 2	SxF	2	7%
	<i>Atomaria</i> sp. 3	SxF	1	4%
	<i>Atomaria turgida</i>	SxF	14	26%
	<i>Atomaria umbrina?</i>	SxF	1	4%
	<i>Atomaria wollastoni?</i>	SxF	2	4%

	<i>Caenoscelis subdeplanata</i>	SxF	1	4%
	<i>Cryptophagus cylindrus</i>	SxO	2	4%
	<i>Cryptophagus dentatus</i>	SxF	4	15%
	<i>Cryptophagus micaceus</i>	SxF	1	4%
	<i>Cryptophagus parallelus</i>	SxF	2	4%
	<i>Cryptophagus pubescens</i>	SxF	5	7%
	<i>Cryptophagus</i> sp.	SxF	1	4%
	<i>Micrambe abietis</i>	SxF	1	4%
	<i>Micrambe woodroffei</i>	SxF	1	4%
	<i>Pteryngium crenulatum</i>	SxO	1	4%
	<i>Telmatophilus schoenherrii</i>	SxF	1	4%
	Unidentifiable	----	5	11%
<b>Curculionidae</b>	<i>Anisandrus dispar</i>	NS	1	4%
	<i>Anoplus plantaris</i>	NS	2	7%
	<i>Archarius pyrrhoceras</i>	NS	1	4%
	<i>Archarius salicivorus</i>	NS	1	4%
	<i>Brachonyx pineti</i>	NS	1	4%
	<i>Crypturgus hispidulus</i>	SxO	1	4%
	<i>Crypturgus subcribrosus</i>	SxO	8	7%
	<i>Dryocoetes</i> sp.	SxO	3	7%
	<i>Hylobius abietis</i>	SxO	2	4%
	<i>Ips typographus</i>	SxO	1	4%
	<i>Orchestes quercus</i>	NS	1	4%
	<i>Orchestes rusci?</i>	NS	1	4%
	<i>Otiorhynchus singularis</i>	NS	1	4%
	<i>Phyllobius</i> spp.	NS	10	19%
	<i>Pityogenes chalcographus</i>	SxO	4	11%
	<i>Pityophthorus pubescens</i>	SxO	1	4%
	<i>Polydrusus</i> spp.	NS	3	7%
	<i>Rhamphus</i> sp.	NS	1	4%
	<i>Rhinoncus</i> sp.	NS	1	4%
	<i>Romualdius scaber?</i>	NS	1	4%
	<i>Scolytus intricatus</i>	SxO	1	4%
	<i>Simo hirticornis</i>	NS	1	4%
	<i>Strophosoma</i> spp.	NS	50	30%
	<i>Tomicus minor</i>	SxO	1	4%
	Unidentifiable	UNK	2	7%
	Unidentified	NS	2	4%
	<i>Strophosoma</i> spp.	NS	17	7%
	(Entiminae) Unidentified	NS	2	7%
<b>Dasytidae</b>	<i>Dasytes niger</i>	SxO	1	4%
	<i>Dasytes plumbeus</i>	SxO	139	56%
<b>Dermestidae</b>	<i>Ctesias serra</i>	SxF	1	4%
<b>Elateridae</b>	<i>Actenicerus sjaelandicus</i>	NS	3	7%
	<i>Adrastus pallens</i>	NS	1	4%
	<i>Ampedus balteatus</i>	SxO	10	33%
	<i>Ampedus nigrinus</i>	SxO	3	11%
	<i>Ampedus</i> sp.	SxO	1	4%
	<i>Ampedus tristis</i>	SxO	1	4%
	<i>Athous haemorrhoidalis</i>	NS	1	4%
	<i>Athous subfuscus</i>	NS	51	78%



	<i>Cardiophorus ruficollis</i>	SxF	1	4%
	<i>Dalopius marginatus</i>	NS	69	74%
	<i>Denticollis linearis</i>	SxF	7	26%
	<i>Ectinus aterrimus</i>	NS	3	11%
	<i>Melanotus castanipes</i>	SxO	3	7%
	<i>Paraphotistus impressus</i>	SxF	1	4%
	<i>Prosternon tessellatum</i>	NS	6	15%
	<i>Selatosomus aeneus</i>	SxF	1	4%
	Unidentifiable	----	1	4%
<b>Erotylidae</b>	<i>Dacne bipustulata</i>	SxO	2	7%
	<i>Triplax russica</i>	SxO	31	44%
	<i>Triplax aenea</i>	SxO	1	4%
<b>Eucnemidae</b>	<i>Hylis cariniceps</i>	SxO	1	4%
	<i>Hylis fovecollis</i>	SxO	11	33%
	<i>Hylis olexai</i>	SxO	11	30%
	<i>Hylis procerulus</i>	SxO	2	7%
	<i>Microrhagus pygmaeus</i>	SxO	10	30%
	<i>Xylophilus corticalis</i>	SxO	6	22%
<b>Geotrupidae</b>	<i>Anoplotrupes stercorosus</i>	NS	2	4%
<b>Histeridae</b>	<i>Hister unicolor</i>	NS	5	11%
	<i>Margarinotus merdarius</i>	SxF	1	4%
	<i>Margarinotus striola</i>	NS	73	26%
	<i>Myrmetes paykulli</i>	NS	1	4%
	<i>Platysoma lineare</i>	SxO	1	4%
<b>Hydrophilidae</b>	<i>Enochrus?</i> sp.	NS	1	4%
	<i>Megasternum concinnum</i>	NS	1	4%
	Unidentified	NS	8	15%
<b>Kateretidae</b>	<i>Kateretes pusillus</i>	NS	1	4%
	<i>Kateretes rufilabris</i>	NS	1	4%
<b>Latridiidae</b>	<i>Cartodere constricta</i>	SxF	7	4%
	<i>Cartodere nodifer</i>	SxF	11	33%
	<i>Corticaria</i> sp. 1	SxF	1	4%
	<i>Corticaria</i> sp. 2	SxF	1	4%
	<i>Corticarina minuta</i>	SxF	5	19%
	<i>Corticarina parvula</i>	SxF	1	4%
	<i>Corticarina similata</i>	SxF	1	4%
	<i>Corticinara gibbosa</i>	SxF	6	19%
	<i>Enicmus fungicola</i>	SxF	2	4%
	<i>Enicmus rugosus</i>	SxF	51	74%
	<i>Enicmus testaceus</i>	SxF	158	74%
	<i>Enicmus transversus</i>	SxF	1	4%
	<i>Latridius hirtus</i>	SxF	1	4%
	Unidentifiable	----	4	11%
<b>Leiodidae</b>	<i>Agaricophagus cephalotes</i>	NS	1	4%
	<i>Agathidium arcticum</i>	SxF	1	4%
	<i>Agathidium atrum</i>	SxF	2	7%
	<i>Agathidium pisanum</i>	SxF	2	7%
	<i>Agathidium rotundatum</i>	SxO	2	7%
	<i>Agathidium seminulum</i>	SxF	4	15%
	<i>Agathidium</i> sp. 1	SxF	1	4%

	<i>Anisotoma axillaris</i>	SxF	2	7%
	<i>Anisotoma castanea</i>	SxO	3	11%
	<i>Anisotoma glabra</i>	SxO	2	7%
	<i>Anisotoma humeralis</i>	SxF	61	44%
	<i>Anisotoma orbicularis</i>	SxO	3	11%
	<i>Catops?</i> sp.	NS	1	4%
	<i>Leiodes</i> sp.	SxF	1	4%
	<i>Sciodrepoides watsoni</i>	NS	3	4%
	Unidentifiable	----	2	4%
<b>Melandryidae</b>	<i>Orchesia micans</i>	SxO	1	4%
	<i>Orchesia undulata</i>	SxO	1	4%
	<i>Wanachia triguttata</i>	SxO	1	4%
<b>Monotomidae</b>	<i>Monotoma longicollis</i>	SxF	3	7%
	<i>Rhizophagus bipustulatus</i>	SxO	1	4%
	<i>Rhizophagus dispar</i>	SxO	4	7%
	<i>Rhizophagus nitidulus</i>	SxO	1	4%
<b>Mordellidae</b>	<i>Mordella aculeata</i>	SxO	1	4%
	<i>Mordellistena</i> sp.	UNK	1	4%
<b>Mycetophagidae</b>	<i>Mycetophagus atomarius</i>	SxO	1	4%
	<i>Mycetophagus quadripustulatus</i>	SxF	1	4%
<b>Nitidulidae</b>	<i>Carpophilus marginellus</i>	SxF	2	4%
	<i>Cychramus luteus</i>	SxF	19	15%
	<i>Cychramus variegatus</i>	SxF	2	7%
	<i>Eपुरaea aestiva</i>	SxF	5	11%
	<i>Eपुरaea biguttata</i>	SxF	3	11%
	<i>Eपुरaea marseuli</i>	SxF	2	7%
	<i>Eपुरaea pallescens</i>	SxF	2	7%
	<i>Eपुरaea</i> sp.	SxF	10	26%
	<i>Eपुरaea unicolor</i>	SxF	6	11%
	<i>Eपुरaea variegata</i>	SxF	1	4%
	<i>Glischrochilus hortensis</i>	SxF	2744	56%
	<i>Glischrochilus quadriguttatus</i>	SxF	13	26%
	<i>Ipidia binotata</i>	SxO	1	4%
	<i>Meligethes atramentarius</i>	NS	2	7%
	<i>Meligethes bidens</i>	NS	1	4%
	<i>Meligethes</i> sp.	NS	1	4%
	<i>Omosita depressa</i>	NS	3	11%
	<i>Soronia grisea</i>	SxF	6	15%
	<i>Soronia punctatissima</i>	SxF	1	4%
	Unidentifiable	----	6	7%
<b>Oedemeridae</b>	<i>Chrysanthia geniculata</i>	SxO	61	30%
	<i>Chrysanthia viridissima</i>	SxO	1	4%
<b>Ptiliidae</b>	<i>Acrotrichis cognata</i>	NS	9	15%
	<i>Acrotrichis dispar</i>	SxF	1	4%
	<i>Acrotrichis fascicularis</i>	SxF	13	15%
	<i>Acrotrichis insularis</i>	SxF	7	15%
	<i>Acrotrichis intermedia</i>	SxF	5	11%
	<i>Acrotrichis rosskotheni</i>	NS	1	4%
	<i>Acrotrichis rulugosa</i>	NS	12	11%
	<i>Acrotrichis silvatica</i>	NS	1	4%

	<i>Acrotrichis sitkaensis?</i>	NS	1	4%
	<i>Acrotrichis</i> sp. 1	NS	4	15%
	<i>Ptenidium fuscicorne?</i>	SxF	1	4%
	<i>Ptenidium nitidum</i>	SxF	6	11%
	<i>Ptenidium</i> sp.	SxF	2	4%
	<i>Ptilium myrmecophilum?</i>	NS	2	4%
	Unidentifiable	-----	23	33%
<b>Rhynchitidae</b>	<i>Deporaus betulae</i>	NS	1	4%
<b>Salpingidae</b>	<i>Salpingus planirostris</i>	SxO	3	4%
<b>Scarabaeidae</b>	<i>Aphodius</i> sp.	NS	1	4%
	<i>Cetonia aurata</i>	SxF	2	7%
	<i>Phyllopertha horticola</i>	NS	3	7%
	<i>Protaetia metallica</i>	NS	99	41%
	<i>Serica brunnea</i>	NS	1	4%
	<i>Trichius fasciatus</i>	SxO	10	11%
<b>Scirtidae</b>	<i>Contacyphon</i> spp.	NS	165	93%
	<i>Elodes minuta</i>	NS	1	4%
	<i>Microcara testacea</i>	NS	2	4%
<b>Scraptiidae</b>	<i>Anaspis flava</i>	SxO	3	7%
	<i>Anaspis frontalis</i>	SxO	10	19%
	<i>Anaspis marginicollis</i>	SxO	3	11%
	<i>Anaspis</i> sp. 1	SxO	230	52%
	<i>Anaspis</i> sp. 2 ♀	SxO	21	19%
	<i>Anaspis</i> sp. 3 ♀	SxO	4	11%
	<i>Anaspis thoracica</i>	SxO	5	7%
	<i>Scraptia fuscula</i>	SxO	3	7%
	Unidentifiable	-----	10	22%
<b>Silvanidae</b>	<i>Silvanoprus fagi</i>	SxO	1	4%
<b>Sphindidae</b>	<i>Sphindus dubius</i>	SxF	5	11%
	<i>Aspidiphorus orbiculatus</i>	SxF	13	30%
<b>Staphylinidae</b>	<i>Bibloporus</i> spp.	-----	2	4%
	<i>Habrocerus capillaricornis</i>	-----	1	4%
	<i>Megarthus depressus</i>	-----	1	4%
	<i>Megarthus</i> spp.	-----	4	4%
	<i>Scaphidium quadrimaculatum</i>	-----	1	4%
	<i>Scaphisoma</i> spp.	-----	30	67%
	Unidentified	-----	3199	100%
<b>Tenebrionidae</b>	<i>Lagria hirta</i>	NS	7	15%
	<i>Diaperis boleti</i>	SxO	8	22%
	<i>Palorus depressus</i>	SxF	1	4%
<b>Tetratomidae</b>	<i>Hallomenus binotatus</i>	SxO	3	11%
<b>Throscidae</b>	Unidentifiable	-----	1	4%
	<i>Trixagus carinifrons</i>	NS	20	19%
	<i>Trixagus dermestoides</i>	NS	117	52%
<b>Total individuals</b>			<b>8380</b>	

\*NS, non-saproxyllic; SxF, facultative saproxyllic, can develop in dead wood or other substrates; SxO, obligate saproxyllic, development is exclusively in dead wood; UNK, saproxyllic status is unknown.