Ecological Bulletins 53: 131–139, 2010

A comparison of the saproxylic beetle fauna between lowland and upland beech forests in southern Sweden

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The aim of this study was to compare the saproxylic beetle fauna between lowland and upland beech *Fagus sylvatica* forests in southern Sweden and to relate differences in species composition to gradients in site conditions and dead wood characteristics. Beetle surveys conducted with window traps close to snags (naturally broken high stumps with fungal fruiting bodies) were analysed from 10 lowland and 25 upland sites, respectively. Lowland beech forests contained larger proportions of species developing in well decayed wood and in rot holes, whereas the proportions of fungicolous species and of species dependent on fresh dead wood were higher in upland beech forests. Complete surveys of beech snags in the lowland forest of Torup and the upland forest in Söderåsen National Park revealed that the snags in the lowland forest had a larger diameter (median dbh 71 cm and 49 cm, respectively) and were taller than the snags in the upland forest at Söderåsen. The lowland area also had a lower proportion of snags with fruiting bodies of *Fomes fomentarius*. Larger wood dimensions and lower humidity in lowland beech forests imply a slower decay of coarse woody debris. This may explain the higher proportion of beetle species developing in well decayed coarse wood and in rot holes, e.g. the red-listed species *Ampedus rufipennis*, *Anoplodera scutellata* and *Dorcus paralellepipedus*. Snags and logs in the less productive upland forests are of smaller, less persistent dimensions. The humid climate of the uplands also favours the activity of decomposing wood fungi. Such conditions are probably the reason for the higher proportion of fungicolous beetles species found, e.g. *Latridius brevicollis* and *Oplocephala haemorrhoidalis*. We conclude that a balanced conservation of beech forests in both lowland and upland areas is necessary in order to maintain the existing diversity of saproxylic beetles in beech forests.

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The Swedish beech *Fagus sylvatica* forests can be divided into two main groups 1) lowland beech forests on cambisols (Asperulo-Fagetum), where old trees usually reach a large stem diameter (>80 cm) and 2) upland beech forests on podzols (Luzulo-Fagetum) with trees of smaller dimensions (Naturvårdsverket 1997, Andersson and Löfgren 2000). Although differences in elevation are relatively small between these types, the upland stands are characterized by a more humid climate with higher precipitation and lower temperatures than the lowland beech forests.

These differences may influence the properties of the dead wood, especially the decay of the coarse woody debris (CWD). One might, for example expect a higher decay rate with increasing humidity (Mackensen et al. 2003). Gradients in size and decay of CWD between lowland and upland forests may also influence the composition of the saproxylic fauna. It could be assumed that the guild of the fungicolous species is favoured by a higher fungal activity in the more humid climate of the upland forests, whereas species adapted to large dimensions of dead wood are more frequent in old lowland stands.

Such general differences in species composition may also have implications for the conservation of the saproxylic fauna, which constitutes a large part of the total biodiversity in beech forests (Dahlberg and Stokland 2004). If there are large differences between assemblages of saproxylic species in lowland and upland forests, then a bias of forest reserves towards only one of these types will be insufficient to maintain overall species diversity.

The habit of creating reserves on less productive sites has been a relatively widespread practice in Sweden and elsewhere (Nilsson and Götmark 1992, Pressey 1994). In Swedish beech forests, management intensity has long been higher in lowland beech stands due to the fact that they offer better conditions to produce valuable timber (Brunet 2007). A long-term separation of the beech forest habitat into production units on highly productive lowland sites and most conservation units on relatively unproductive upland sites may therefore be favoured by the forestry sector.

Saproxylic beetles (Coleoptera) are, together with the Diptera, the most important group of saproxylic insects in temperate forests (Dahlberg and Stokland 2004). Our knowledge however, of factors influencing the distribution of saproxylic beetle species in Swedish beech forests has been rather limited (Nilsson and Baranowski 1997a). The basic hypothesis of this study was that there are general differences in the saproxylic beetle fauna of lowland and upland beech forests respectively, that can be explained by differences in dead wood characteristics and site conditions. The data analysis in this paper contained two steps: 1) detailed surveys of beech snags were conducted in a lowland and an upland beech forest and related to the composition of the beetle fauna in small window traps attached to the snags; 2) other recent beetle surveys in Swedish beech forests were reviewed in order to test whether the results found in the first study reflected general differences between lowland and upland beech forests. Based on the results, we discuss implications for the conservation of the saproxylic fauna in beech forests.

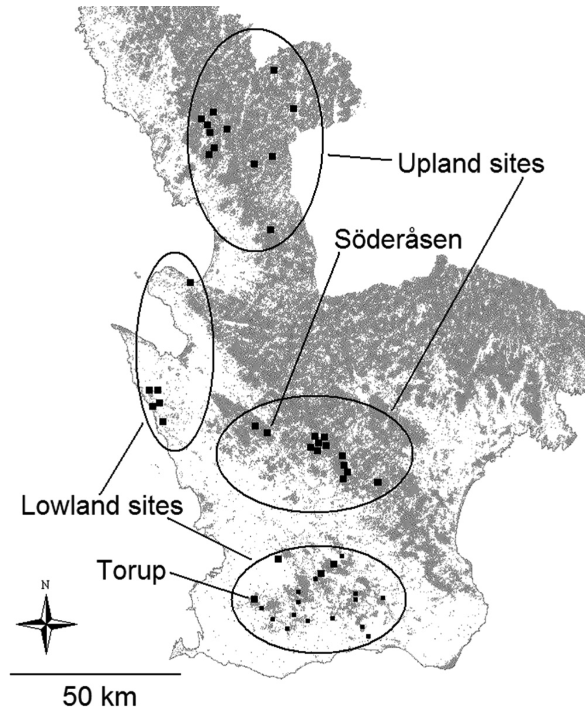

Figure 1. The location of the study sites in the Counties of Skåne and Halland in southern Sweden. Large dots show sites with complete species lists, small dots are sites with data for species of conservation concern only. Grey areas show forests and white areas open land, respectively.

Material and methods

Study 1

The original beetle surveys in the lowland beech forest of Torup and the upland beech forest of Söderåsen were conducted with 30 window traps in each area. In the present study, seven traps from the Torup area (snag decay classes 1 and 4 in Brunet and Isacsson 2008, 2009a) were excluded which were either attached to very old and coarse snags lacking bark and fungal fruiting bodies (4 traps), or to still living snags (3 traps). This was done to make the data set compatible with the other data sets in which most traps were attached to snags of an intermediate stage of decay, including fungal fruiting bodies (snag decay classes 2 and 3 in Brunet and Isacsson 2009a). The northwestern part of the Söderåsen study area (7 traps) was isolated from the rest of the area by a two km wide zone of planted coniferous forest (Brunet et al. 2008, Brunet and Isacsson 2009b). This area was treated separately and included in the data set of other upland beech forests for comparison (see below). Both data sets of study 1 thus included 23 window traps.

The lowland beech forest of Torup

The first study area was the 360 ha forest around Torup castle (Fig. 1). The study area is situated in a hilly landscape created by glacial deposits upon early Tertiary limestone (chalk). Forest soils on well drained sites are mostly eutric and dystric cambisols (Table 1). The core of the area has been broadleaved forest for thousands of years. Beech established in the area >2000 yr ago, but did not attain a dominant role until the 16th century (Hultberg et al. 2010). The forest has probably been used as a wood pasture with varying grazing intensity since the Viking age. Regular shelterwood forestry with natural regeneration started in the mid 19th century, when grazing by domestic animals declined (Brunet 2003). Today, beech stands cover ca 170 ha (excluding 20 ha young plantations on old fields), of which most are rich in herbs and belong to the Asperulo-Fagetum type (Table 1).

The upland beech forest of Söderåsen

The second study area was Söderåsen National Park that was established in 2001 (Fig. 1). The park covers an area of 1625 ha, of which ca 1350 ha are forest, including 830 ha of beech forest surveyed. The climate is slightly cooler and more humid than at Torup (Table 1). Forest soils on well drained sites are mostly podzols and dystric cambisols. The beech forests on these sites usually belong to the Luzulo-Fagetum type (Table 1). The Söderåsen ridge is divided by

Table 1. Characteristics of the study areas Torup forest and Söderåsen National Park in southern Sweden.

	Torup	Söderåsen
Annual mean temperature (°C)	7.5	7.0
Annual precipitation (mm)	650	800
Elevation a.s.l. (m)	25–75	50–210
Bedrock	chalk	granite
Soil type	dystric cambisol	podzol
Soil acidity	moderately acidic	strongly acidic
Forest type (Natura 2000 code)	Asperulo-Fagetum (9130)	Luzulo-Fagetum (9110)
Total beech forest area (ha)	170	830

deep fissure valleys. The largest of them, Skäralid Ravine, forms the central part of the national park and harbours the finest stands of old-growth beech forest in Sweden. Beech immigrated to the area ca 200–600 AD and gradually replaced the previously dominating mixed oak forests (Bergman 2000). The contemporary beech forests outside the ravines often originate from semi-open wood pastures which were converted to high forest by natural regeneration in the late 19th century after cattle grazing had ceased (Bergman 2000).

The stand structure in large parts of the two study areas is representative of the predominantly even-aged managed beech forests of northwestern Europe. The protection of the beech forest within the national park and within certain woodland key habitats in the Torup area has however, initiated a recent accumulation of CWD.

Survey of snags

In both study areas, beech snags (naturally broken high stumps) with a diameter at breast height (dbh) of ≥30 cm and a height of >1.5 m were surveyed with regard to dbh (cm), height (m), presence–absence of fruiting bodies of tinder bracket fungus (*Fomes fomentarius*) and vitality (dead or still living). In Torup forest, only four snags with a dbh <30 cm were found. Additional surveys of snags <30 cm dbh and of uprooted trees were made in parts of the Söderåsen area. These data showed that snags ≥30 cm dbh and their logs made up ca 85% of the total volume of dead wood of beech (Brunet et al. 2008).

Sampling of saproxylic beetles

Beetles were caught with small window traps (flight interception traps) with a plexiglass window of 10 × 20 cm. The traps were attached to beech snags at two (Söderåsen) and three metres (Torup) height perpendicular and close to the southern face of the stem. The density of visitors is much higher at Torup forest and the higher position on the snag was chosen in order to reduce the risk of the traps being vandalized. An aluminium vessel on a wooden console below the window was filled with equal amounts of isopropylglykol and water and some drops of a detergent. The traps were operated between 19 April and 2 September 2004 at Torup (137 d) and between 12 April and 19 August 2005 at Söderåsen (130 d). The vessels were emptied five times during that period.

Comparative studies show that trunk window traps relatively well reflect the insect fauna of snags (Sverdrup-Thygeson and Birkemoe 2009). Trapped beetles may originate from the snag itself or were attracted by the snag. The small size of the traps and the close attachment to the stem were chosen to reduce the risk of catching specimens that accidentally pass the snags.

Beetles were separated from other insects in the lab and stored in 70% ethanol. Species determination was done by Gunnar Isacsson and Rickard Andersson. Species were classified as saproxylic according to an unpublished species list by Rickard Andersson. All obligate and selected facultative saproxylic species are included in this list. Nomenclature is according to Lundberg and Gustafsson (1995).

Study 2

Recent surveys with window traps of the saproxylic beetle fauna in other southern Swedish beech forests were compared with the results from study 1. Complete data sets were available from an additional 9 lowland sites and 24 upland sites in the Counties of Halland and Skåne (Table 2, Fig. 1). The lowland sites were situated on sedimentary bedrock <100 m a.s.l. and with an annual precipitation of 550–700 mm. The upland sites were situated on granite bedrock >100 m a.s.l. with an annual precipitation of 700–1500 mm (Raab and Vedin 1995). Similar to our study, the window traps used in these surveys were mostly placed at or close to beech snags. The traps were however, larger than those in our study (Table 2). In certain upland areas, the published lists also include species from pitfall traps and sieving of beech wood mould (Table 2).

Table 2. Sampling effort in the beetle surveys using window traps that were reviewed in this study.

Source	No. window traps/no. areas	Size (cm)	Sampling period	Additional sampling
Lowland beech forest				
This study: Torup	23/1	10 × 20	April–Sept 2004	–
Malmqvist 2004	2/5	30 × 40	May–July 2004	–
Malmqvist 2005	2/2	30 × 40	May–July 2005	–
Malmqvist 2006	2/1	30 × 40	July–Aug 2006	–
Sörensson 2009	4/1	30 × 40	May–Aug 2008	–
Upland beech forest				
This study: Söderåsen	23/1	10 × 20	April–Aug 2005	–
Brunet and Isacsson 2009b	7/1	10 × 20	April–Aug 2005	–
Andersson 2001	4/2	35 × 60	1997–1999	–
Malmqvist 2002	2/11	30 × 40	April–Aug 2002	sieving
Jansson 2004	4–7/10	35 × 60	April–Aug 2002	pitfall traps

For red-listed and formerly red-listed species, here called species of conservation concern, which in the study area mainly occur in beech forests (according to information in the studies reviewed and at <www.artdata.slu.se>), additional surveys from 15 sites within the core area of the Swedish lowland beech forest in southern Skåne were evaluated (Fig. 1, Bellinga, Bergsjöholm, Bökeberg, Börringe, Häckeberga, Havgård, Husarahagen, Idala, Krageholm, Övedskloster, Röddinge, Slätteröd, Snogeholm, Svaneholm, Sövdeborg). These surveys were mainly carried out with manual search methods and focused on species of conservation concern (Hägg 1995, 1997, Blomberg 2001, Andersson 2006). When comparing the results of these surveys with the other 10 lowland and 25 upland beech forests, available records of species in these sites with other methods than window traps were included (Table 6).

Data analysis

Saproxylic beetles were divided into red-listed species, formerly red-listed species (Gärdenfors 2000, 2005) and other species.

Species were also classified into larval habitat guilds according to Schmidl and Bußler (2004): 1) species living in fresh dead wood and bark (Fresh wood species); 2) species living in older, decayed dead wood (Decayed wood species); 3) species living in fruiting bodies and mycelium of wood fungi (Fungicolous species); 4) species living in rot holes and wood mould (Rot hole species); 5) other species, including species dependent on other saproxylic insects. Species missing from Schmidl and Bußler (2004) were classified using information from Palm (1959) and Ehnström and Axelsson (2002).

Data on the volume of the beech snags were taken from Brunet and Isacsson (2008, 2009a, b) and Brunet et al. (2008).

Characteristics of the beech snags were compared with the Mann-Whitney test and the χ^2 test. Frequencies of beetle species of conservation concern in lowland and upland forests were compared with the χ^2 test. Frequencies of different species should be largely independent of each other and no Bonferroni correction of p-values was applied. The sampling effort differed between the beetle surveys reviewed (Table 2). Proportions of species within larval habitat guilds are therefore analysed instead of absolute species numbers. The number of species in traps (species richness) and proportions of species within groups showed normal distributions and were compared with the two sample t-test. All statistical analyses were conducted with Minitab 15.

Results

Study 1

Beech snags

The Torup area contained 130 beech snags in 2004 with a dbh ≥30 cm, corresponding to 0.8 snags per ha beech forest. Snag density in Söderåsen National Park was much higher with 3.0 snags per ha (Table 3). The snags at Torup however, had a much larger dbh and they were also significantly taller. There was therefore, only a relatively small difference in the volume of snags per ha between the two study areas, despite the large difference in snag density (Table 3). The proportion of snags which were still alive was

Table 3. Characteristics of beech snag populations in the study areas Torup forest (lowland) and Söderåsen National Park (upland). P-values are according to the Mann-Whitney U-test (median dbh and height) and the χ^2 test (proportion of snags alive and with *F. fomentarius*).

	Torup	Söderåsen	p-value
All beech snags			
Total no. of surveyed snags	130	2428	
Mean no. snags/ha beech forest	0.8	3.0	
Mean snag volume m^3 ha^{-1} beech forest	1.9	2.2	
Median dbh of snags, cm	71	49	0.001
Median height of snags, m	6	5	0.001
Proportion of snags still alive (%)	31	21	0.005
Proportion of snags with *F. fomentarius* (%)	52	89	0.001
Snags with beetle traps			
Minimum–median–maximum dbh, cm	51–84–97	47–60–97	0.001
Minimum–median–maximum height, m	4–6–20	2–6–9	0.157
Snags with *F. fomentarius*, %	87	96	0.295
Minimum–median–maximum bark loss, %	0–20–90	1–25–80	0.948

significantly higher at Torup forest, and this area also had a much lower proportion of snags with fruiting bodies of the white rot fungus *Fomes fomentarius* (52%, Table 3). At Söderåsen, almost 90% of the snags had such fruiting bodies. The snags with traps were somewhat coarser than the local snag populations in both areas (Table 3).

Saproxylic beetles

Almost twice as many individuals were caught at Torup (3685) when compared to Söderåsen (2069). The total number of species and the number of red-listed species were however, only slightly higher at Torup (Table 4). Most of the species caught are known to develop in beech and the remaining species may develop in beech at least occasionally. Nine bark beetle species (16 individuals caught) are known only from coniferous tree species and were not included in the above figures. At Torup, species of decayed wood formed the largest group, whereas fungicolous species were most numerous at Söderåsen (Table 4).

Study 2

Regional distribution patterns (35 sites with window traps)

The lowland beech forests contained significantly larger proportions of species developing in well decayed wood and in rot holes, whereas the proportions of fungicolous species and of species depending on fresh dead wood were larger in the upland beech forests (Table 5, Fig. 2). Species depending on well decayed wood were the largest group in lowland beech forests, and the fungicolous species were the largest group in the upland forests, a pattern that confirmed the results of study 1 from Torup and Söderåsen (Table 4).

A total of 63 red-listed species were recorded in the surveys reviewed, including Torup forest and Söderåsen National Park. The proportion of red-listed species ranged from 0 to 26% among the surveys. Lowland beech forests had a significantly higher proportion of red-listed species

Table 4. Number of saproxylic beetle species (proportion) within different groups that were caught in Torup forest and Söderåsen National Park.

Species group	Torup	Söderåsen
No. species	174	164
No. red-listed species	22 (13%)	19 (12%)
No. VU species	4	4
No. NT species	18	15
Fresh wood species	26 (15%)	21 (13%)
Fungicolous species	55 (32%)	67 (41%)
Decayed wood species	72 (41%)	60 (37%)
Rot hole species	5 (3%)	1 (1%)
Other species	16 (9%)	15 (9%)

Red-list categories: VU = vulnerable, NT = near threatened.

Table 5. Proportion (%) of species within larval habitat guilds out of total number of species, and out of number of red-listed species in southern Swedish lowland and upland beech forests. Mean values (SD) are given for 10 lowland (red-listed species n=8) and 25 upland areas, respectively. P-values are according to the two-sample t-test (including normality and variance testing).

Habitat guild	Lowland beech	Upland beech	p-value
All species			
Fresh wood	11.6 (4.5)	15.3 (3.1)	0.009
Fungicolous	32.6 (7.4)	42.5 (4.6)	0.002
Decayed wood	45.9 (7.6)	36.1 (4.6)	0.003
Rot hole	2.5 (2.0)	0.5 (0.8)	0.012
Other	7.4 (3.8)	5.6 (2.1)	0.192
Red-listed species			
Fresh wood	8.0 (7.1)	12.1 (12.2)	0.378
Fungicolous	20.1 (13.0)	37.6 (26.4)	0.083
Decayed wood	52.5 (11.2)	46.2 (26.9)	0.529
Rot hole	9.5 (2.4)	2.1 (4.5)	0.001
Other	9.6 (9.4)	1.9 (6.8)	0.017

(13%) than upland beech forests (6%, p=0.024), although two lowland sites were lacking red-listed species.

In both lowland and upland beech forests, the guild of decayed wood was the largest group among red-listed species, followed by fungicolous species (Table 5). Red-listed species of the guilds rot hole and other species were significantly more common in lowland forests (Table 5).

Species of conservation concern in beech forests (50 sites)

Within the study area (Skåne and Halland), a number of species of conservation concern have most of their locations in beech forests, but may differ in their frequency between lowland and upland sites (Table 6). The species being more common in lowland forests mainly develop in decayed wood (e.g. *Ampedus rufipennis*, *Anoplodera scutellata*, *Dorcus parallelepipedus*) or in rot holes (*Allecula rhenana*, *Cryptophagus labilis*, *Quedius truncicola*). Species without a preference for forest type belong to the guilds fresh wood and decayed wood. Three fungicolous species typical for beech in the study area were significantly more common in upland sites (*Latridius brevicollis*, *Oplocephala haemorrhoidalis*, *Stephostethus alternans*, Table 6).

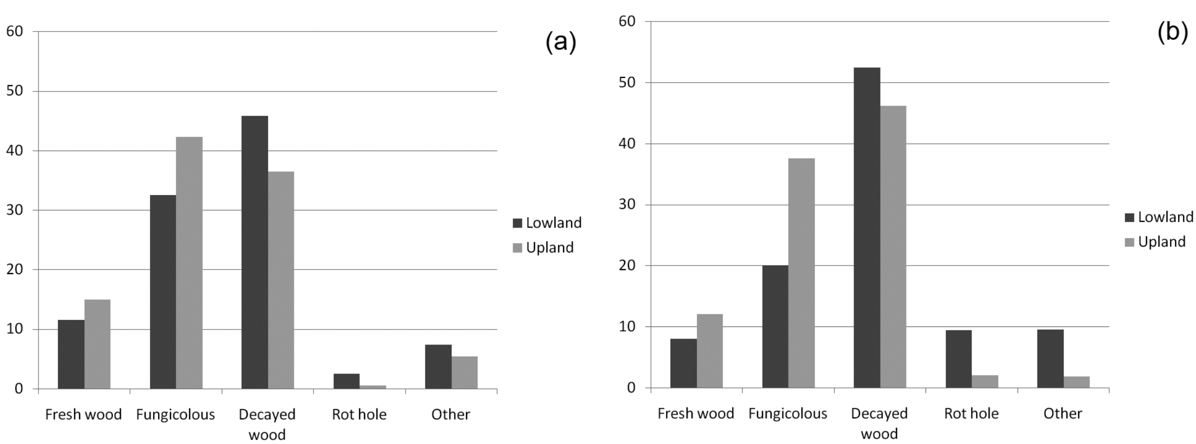

Figure 2. Saproxylic beetle species from five larval habitat guilds. The proportion (%) of each guild out of total number of species (a), and the proportion of each guild among red-listed species (b) are shown. Mean values of 10 lowland beech forests and 25 upland beech forests, respectively. See Table 5 for statistically significant differences between lowland and upland areas.

Table 6. Frequency (no. of records) of species of conservation concern mainly confined to beech in the study area. Data from 25 lowland and 25 upland sites are included. Red-list category according to Gärdenfors (2005). Larval habitat guild according to Schmidl and Bußler (2004). Only species with at least four records were included in the analyses.

Species	Red list	Guild	Lowland	Upland	p-value
Aeletes atomarius	NT	Other	15	1	0.001
Allecula rhenana	EN	Rot hole	6	0	0.009
Ampedus rufipennis	VU	Decayed	11	2	0.004
Anoplodera scutellata	VU	Decayed	13	3	0.002
Cryptophagus labilis	NT	Rot hole	15	5	0.004
Dorcus parallelepipedus	NT	Decayed	15	0	0.001
Mycetochara axillaris	LC	Decayed	9	0	0.001
Platysoma compressum	VU	Decayed	8	1	0.010
Plegaderus dissectus	NT	Decayed	20	10	0.004
Quedius truncicola	EN	Rot hole	7	1	0.021
Anobium costatum	NT	Decayed	7	3	0.157
Corticeus unicolor	LC	Decayed	15	13	0.569
Ernoporus fagi	NT	Fresh	4	6	0.480
Melasis buprestoides	LC	Fresh	10	13	0.395
Plectophloeus nubigena	NT	Decayed	6	7	0.747
Stenagostus rhombeus	VU	Decayed	2	4	0.384
Oplocephala haemorrhoidalis	LC	Fungi	0	8	0.002
Platycis cosnardi	VU	Decayed	2	9	0.017
Rhizophagus brancsiki	NT	Decayed	1	10	0.002
Stephostethus alternans	NT	Fungi	3	14	0.001
Latridius brevicollis	LC	Fungi	5	25	0.001

Red-list categories: EN = endangered, VU = vulnerable, NT = near threatened, LC = least concern.

Discussion

The surveys reviewed in this study show a general difference in the saproxylic beetle fauna between Swedish lowland and upland beech forests. Differences in climate, site productivity and forest history are probably all affecting dead wood characteristics which in turn influence the relative abundance of species with different larval habitats.

The snag surveys suggest that beech snags at upland sites are smaller and colonized by the white rot fungus *Fomes fomentarius* to a larger extent than snags at lowland sites. This probably results in a faster decay process as well as the snags falling down earlier in the uplands, the decay being additionally accelerated by a more humid climate (Mackensen et al. 2003, Müller-Using and Bartsch 2003, Garrett et al. 2007). These differences probably explain the higher relative importance of fungicolous saproxylic species in upland beech forests. The large tineid moth *Scardia boletella*, which develops in *F. fomentarius*, also mainly occurs in humid upland beech forests in Halland and Skåne (Fritz 2004).

The occurrence of snags and logs of large dimensions and the relatively dry climate in the lowland stands result in a longer process of wood decay and a higher variability of dead wood qualities. This provides suitable conditions for a higher diversity of species developing in decayed wood, rot holes and wood mould than in the uplands. The habitat guild of other species, including beetles depending on other saproxylic insects, may also be favoured by the variation of dead wood under lowland conditions.

Many of the forest stands where the beetle surveys were conducted are unmanaged key habitats or nature reserves. In the uplands, these areas are to a larger extent surrounded by production forests of both conifers and broadleaves than in the less wooded lowlands (Brunet 2005, Brunet et al. 2005). Larger amounts of logging residue could explain the relatively greater importance of species depending on fresh dead wood in the uplands.

Some species occur on the northern edge of their distribution range in our study area (Ehnström and Axelsson 2002). They may find a more suitable micro-climate in the relatively dry and warm lowland sites but are absent from the cool and humid uplands. *Dorcus parallelepipedus* is a good representative of the species which may be particularly favoured by the combination of CWD and lowland climate. It has been recorded from many sites in the lowland beech forests of southern and eastern Skåne and along the coast of Blekinge, but it is absent from the humid uplands along the west coast (Ehnström and Axelsson 2002). Swedish beech forests show a high degree of fragmentation today (Fritz et al. 2008). In the lowlands, they are often surrounded by agricultural land and in the uplands by plantations of Norway spruce *Picea abies*. The occurrence of saproxylic species with a limited dispersal ability may therefore depend on the continuous presence of suitable habitat (Nilsson and Baranowski 1997a, Brunet and Isacsson 2009b). Historical sources show that lowland beech forest areas have a continuous presence of old and large beech trees to a higher degree than upland forests (Brunet 2003, 2005, 2007). This may partly explain the current distribution pattern of certain rare species that depend on relatively large standing dead wood, e.g. *Ampedus rufipennis* and *Anoplodera scutellata* (Nilsson and Baranowski 1995, 1997b). The rare click beetles *Denticollis rubens* and *Stenagostus rhombeus* which mainly develop in coarse logs however, have only survived in the very few remnants of old-growth beech forests with a continuous availability of logs (Malmqvist et al. 2006).

Bearing in mind that there is a gradual transition from lowland to upland beech forest sites in southern Sweden, and that sampling efforts, sampling years and trap size were different, the results provide surprisingly clear evidence for general differences in abundance of species guilds between the lowlands and uplands. The full data set for the lowlands was relatively small and, except for Torup, did not include surveys from the lowland beech forest core area in southern Skåne (Brunet 2005). The additional analysis of the 15 lowland surveys restricted to species of conservation concern supports however, the results from the full data set analyses. The comparison between 25 sites of each forest type confirm that several redlisted species of coarse decayed wood (*Ampedus rufipennis*, *Anoplodera scutellata* and *Dorcus parallelepipedus*) and of rot holes (*Allecula rhenana, Quedius truncicola*) have their main distribution in lowland beech forests. Fungicolous species of conservation concern, on the other hand, find more suitable habitat in the upland beech forests. *Latridius brevicollis* and *Oplocephala haemorrhoidalis* develop in *Fomes fomentarius*. *Rhizophagus brancsiki*, another rare species typical for upland beech forests, develops in moist and soft wood decayed by *F. fomentarius.*

Conclusions

The largest conservation efforts to date have focused on the most valuable upland beech forests in Sweden (Biskopstorp in Halland, Söderåsen in Skåne). The results of this study support recent efforts to protect the most important core areas for saproxylic beetles in Swedish lowland beech forests (e.g. Häckeberga and Torup in Skåne, Tromtö in Blekinge) and to increase the amount of CWD in managed lowland stands. The survey of beech snags in this study showed that previously managed, old beech forests that are set aside for conservation may accumulate relatively large numbers of snags and logs as quickly as within the first 20 yr after protection. We conclude that a balanced conservation of beech forests in both lowland and upland areas is necessary in order to maintain the existing diversity of saproxylic beetles in beech forests.

Acknowledgements – We would like to thank Rickard Andersson for the determination of critical beetle species at Torup and of all species at Söderåsen. Rickard Andersson also determined the species in many of the other studies reviewed. We thank Georg Andersson, Karin Bengtsson, Emma Holmström and Prisca Schäffer for help with the field and lab work. We would also like to thank Oddvar Fiskesjö, Mikael Lang, Staffan Pettersson, Carina Zätterström, Anders Ekstrand and Bo Edlund for providing information and access to the study areas. Thanks also to the reviewers whose comments helped to improve the paper and to Vikki Bengtsson for correcting the English. The study was financed by the research program Sustainable Management in Hardwood Forests.

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