



Veteranised oak cavities attract saproxylic beetles within two years

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Received: 25 November 2025 / Accepted: 31 May 2026
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Abstract Veteran oaks are vitally important for saproxylic beetles due to the diversity of tree-related microhabitats they contain which have developed over centuries. Veteran oaks are however in decline across Europe. Veteranisation is a conservation tool that aims to create or speed up the formation of these rare microhabitats, potentially helping to mitigate losses, although empirical studies on the effectiveness of veteranisation are still very rare. We compared flight interception trapped beetle assemblages from 2-year old veteranised cavities in young oaks (2 methods: ‘nestbox with topping’ – NBT ($n=28$) and ‘woodpecker hole’ – WPH ($n=26$), with untreated control trees ($n=29$) across 14 sites in southern Sweden. In total, 13010 individuals representing 493 beetle species were identified, of which 315 were saproxylic. The trapped beetles were assigned into one of four guilds with respect to their ecological association with wood (‘wood-living’, ‘partly wood-living’, ‘associated with wood living fungi’ and ‘other, non-saproxylic’). Both NBT and WPH supported significantly higher numbers of species and individuals than controls, particularly within the wood-living guild. Species such as *Cryptarcha undata*, *Haploglossa villosula*, and *Quedius mesomelinus* were abundant, reflecting an early-successional community. The presence of *Lymexylon navale* (NT) and *Carphacis striatus* (VU) indicates that the cavities provide ecologically relevant cues, even though reproduction could not yet be confirmed. No significant differences were detected between the two cavity types, suggesting that exposure of fresh wood and cavity creation alone are key drivers of early attraction. Our findings demonstrate that artificial cavities can rapidly increase habitat value for saproxylic beetles in young oaks, contributing to the restoration of oak sites.

Implications for insect conservation Artificially created cavities in young oaks can rapidly attract saproxylic beetles. Such interventions can help alleviate the current scarcity of natural tree hollows, thereby reducing future extinction risks for saproxylic beetles associated.

Keywords Veteranisation · Artificial tree microhabitats · Hollows · Biodiversity conservation · Oak restoration · Chainsaw carved cavities

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Introduction

Large old trees are in decline globally, yet they serve as ‘keystone structures’ for a vast range of species (Lindenmayer et al. 2012; Cálix et al. 2018; Cannon et al. 2022), particularly saproxylic beetles (Speight 1989; Parmain and Bouget 2017), due to their diversity of tree-related microhabitats - TreMs (Siitonen 2012) such as cracks, cavities, and exposed heartwood. Among deciduous trees in Sweden, oaks (*Quercus* spp.) host the highest number of associated species (Sundberg et al. 2019). However, the loss of old oaks is severe in Sweden, where at least 82% were lost between 1790 and 1820 (Eliasson and Nilsson 2002), and with continued losses thereafter due to felling and loss of oak dominated wood pastures (Cousins et al. 2015; Jacobsen et al. 2023). In addition, the lack of trees available to replace old trees as they die, with the resulting gap in suitable habitat (e.g. hollows) has been identified as a problem for saproxylic beetles across Europe (Pilskog et al. 2016; Cálix et al. 2018; Jacobsen et al. 2023; Ranius et al. 2024). Tree microhabitat diversity increases with age and size (Kraus et al. 2016; Kõrkjas et al. 2021), however not in a linear fashion since certain features, such as hollows in oaks, may take over 200 years or more to develop (Ranius et al. 2009a). Kõrkjas et al. (2021) also highlight the fact that it is not enough to just retain existing live trees rich in microhabitats and suggest that actively creating TreMs should be considered.

Veteranisation is a conservation management technique that aims to increase the number of TreMs in living young (60–120 years) trees using tools. The aim with this method is to create valuable habitats suitable for saproxylic species, such as cavities, dysfunctional sapwood, and exposed heartwood, earlier than they would occur normally in natural conditions (Read 2000; Pilskog et al. 2016; Hedin et al. 2018; Cizek et al. 2025). In addition to enhancing habitat diversity, veteranisation may help mitigate both the missing cohorts and the long-term effects of old tree loss on biodiversity (Bengtsson and Wheeler 2021) and it has been undertaken in several countries across the world in recent decades, but more rarely focusing on invertebrates (Best et al. 2026).

Early efforts to create artificial tree cavities primarily aimed to benefit threatened birds (Carey and Sanderson 1981; Best et al. 2026). More recently, research on artificial tree cavities has expanded to include other vertebrates (e.g. Ruegger 2017; Griffiths et al. 2018; Griffiths et al. 2020; Bengtsson and Wheeler 2021; Best et al. 2026), insects (e.g. Cavalli and Mason 2003; Hedin et al. 2018; van Steenis 2023; Cizek et al. 2025), and fungi (e.g. Menkis et al. 2022; Wainhouse and Boddy 2022; Pyne et al. 2023). Despite these recent studies, the field of veteranisation of trees for

conservation purposes is still at its infancy, with major knowledge gaps remaining.

In 2011 and 2012, the authors established an international research trial to test veteranisation treatments on oak (*Quercus robur*) in 20 sites (16 in Sweden, 1 in Norway, and 3 in England) to evaluate the potential biodiversity benefits of veteranisation in young, live oaks (Bengtsson et al. 2012). Utilising this international research trial, in this study we compared flight interception trapped beetles (Coleoptera) attracted by the two artificially created hollows with beetles trapped from untreated control oaks (without any microhabitats) in the same sites. We conducted the study two years after the holes were made in 14 sites in the south of Sweden (Fig. 1). We hypothesised that the two types of artificial hollows would attract a higher proportion of saproxylic beetles compared to the fauna attracted to the control oak trees without veteranisation treatments.

Method

Veteranisation trial sites and treatments

Only oak trees lacking biologically important natural microhabitats and with a diameter at breast height of between 25 and 60 cm were selected in the original trial set up and before treatments. Stratified random sampling was used to decide which tree would have which treatment and which trees would be controls. The two types of cavities that were created at 4 m height, were a ‘woodpecker hole’ (WPH) and a ‘nestbox with topping’ (NBT) (see Fig. 2 and S2). The WPH was made by carving out an oval-shaped cavity with a chainsaw to a depth of 10 cm, with a width of 8 cm and height of 12 cm. The resulting cavity replicates the dimensions of a black woodpecker hole (Fig. 2b; and S2). For the NBT, using a chainsaw a rectangular cavity was cut out. The width of the cavity opening measured approximately one third of the stem diameter (typically c. 10 cm) and the length of the cavity was 50 cm (see Fig. 2c and S2). A vertical cut was made in the side of the tree, perpendicular to the front to allow removal of the resulting rectangular piece of wood. From the extracted piece of wood, still using a chainsaw, the heartwood and the upper 10–15 cm was cut off. The remaining piece of wood, with bark intact was then put back into its original position, secured with two nails, thereby creating a large cavity inside the tree, as well as an opening (See S2 for more details). As mentioned above, this treatment was combined with topping of the tree, whereby the upper third of the live crown was removed, to reduce the risk of the tree failing at the ‘nestbox’. At the point of topping, the cut was made to look like a natural breakage (see Fig. 2d). There were 7 WPH, 7 NBT and 14 control

Fig. 1 Map showing the locations of the 14 sites included in this study. The distances are approximately 460 km from north (59.60, 17.02) to south (55.97, 13.63) and 260 km from east (56.69, 16.62) to west (56.12, 12.69)

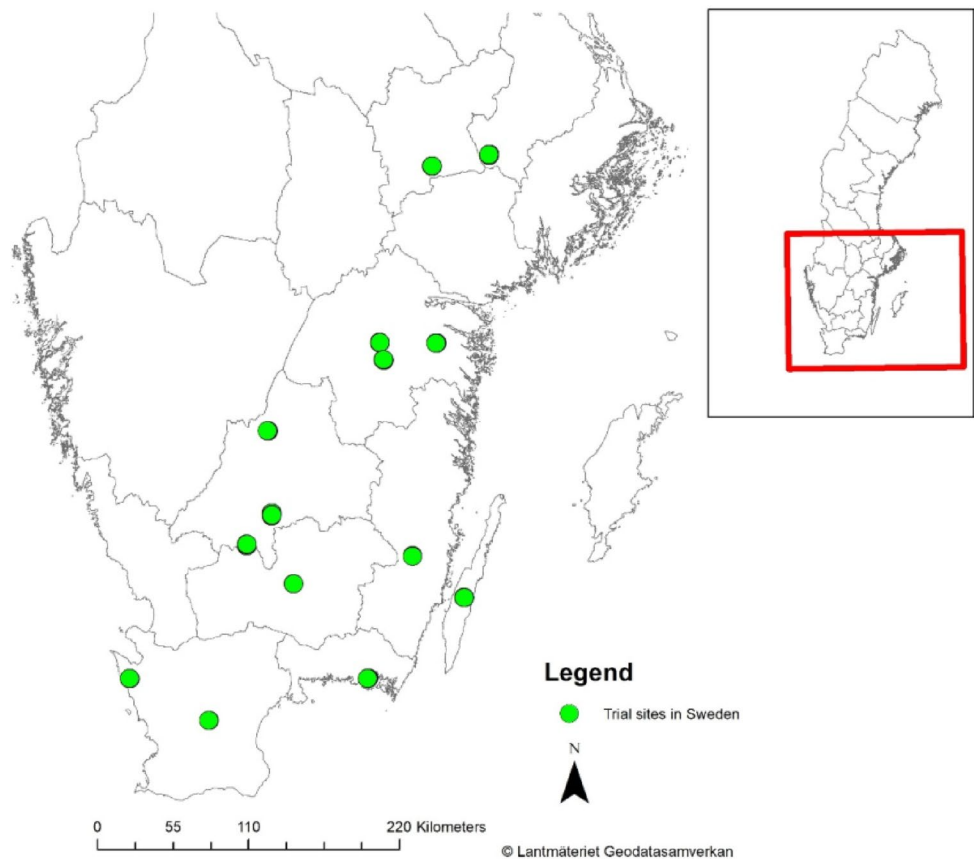


Fig. 2 **a** control tree, **b** woodpecker hole, **c** nestbox, **d** topping made in combination with the nestbox and made to look like storm damage



(C) trees, 28 oaks in total at each site potentially available for monitoring. The cardinal orientation of the veteranisation treatments was not randomly selected, but was chosen by the arborists undertaking the work, ensuring that each cardinal point was represented at least once (N, S, E, W) if possible. However, the safety and logistics for the arborists were the primary drivers for the orientation of veteranisation treatments (i.e. where it was possible to climb and undertake the work safely). The original study was initiated in 2011 and 2012 and further details are available in Bengtsson et al. (2012).

In this study, we evaluated these two types of artificial chainsaw cavities WPH, NBT in comparison with untreated

control trees (C) (Fig. 2), in 14 of the 20 sites (practical and resource limitations), 2 years after their creation.

Insect sampling

Two years after the treatments were created, in 2014, we randomly selected six trees at each of the 14 sites included in this study (Fig. 1; Table 1): two control trees (from 14), two WPH trees (from 7) and two NBT trees (from 7). A flight interception trap was put up (Fig. 3) on each tree, at a 90-degree angle to the treatments or in a random direction at 4 m above ground on the control trees, primarily driven by where it was safe to climb the tree and possible to attach it. Cardinal position did not therefore form a part of our study;

Table 1 The number of actual traps deployed per treatment and site

Site name	C	NBT	WPH	Comments
Bondberget	2	2	2	
Brunnstorp	2	1	2	1 NBT trap only included because Coleoptera samples were lost from the 1 trap
Ekenäs	2	2	1	1 WPH trap only, because 1 was storm damaged
Fulltofta	2	2	2	
Haga Ekbackar	2	2	2	Veteranisation done 2011
Harsbo	2	2	2	
Sverkersholm				
Hjälmskult	2	3	1	Extra trap on NBT instead of WPH, in error
Huseby	3	2	2	3 controls with traps (1 extra set up in error)
Strömsholm	2	2	2	
Tinnerö	2	2	2	Second period of sampling spoiled
Toftaholm	2	2	2	
Tromtö	2	2	2	Second period of sampling spoiled
Vanserum	2	2	2	
Västerby	2	2	2	
Total	29	28	26	83 traps

NBT nestbox and topping, *WPH* Woodpecker Hole, *C* Control, *RDB* Red DataBook



Fig. 3 A flight interception traps as used in this study showing how it was mounted adjacent to a chainsaw carved Woodpecker Hole (WPH), with a tray containing propylene glycol, water and washing up liquid. The colour is extra detergent (washing up liquid) used here to show the level of fluid in the trap

other factors influencing trap position are usually cited as being of more importance (van Achterberg et al. 2010). The flight interception trap was made from a pane (30 cm x 40 cm) of polycarbonate sheeting and a plastic tray (20 cm x 30 cm x 10 cm). The traps were attached to the tree using two small screws and an angle iron. The tray was attached to the polypropylene sheet using two long nails threaded through a pre-drilled hole. Due to storm damage and the resultant tree failure, our data is represented by 83 traps

out of the 84 deployed (see Table 1). The trays were filled with 500 ml propylene glycol and 50 ml water, with a drop of detergent (washing-up liquid) to reduce surface tension. This ensured that the insects falling into the trap would be killed and conserved. The trays were emptied into jars using a funnel, filters and water to rinse them properly, ensuring all material captured was transferred to the jars, which were then filled with ethanol. Due to the long distances between sites, the traps were put up over a three-week period, with all traps installed by the 15 May. Each trap was emptied once between 2 June and 15 July. They were then emptied and taken down between the 15 August and 19 September. The jars were labelled with the tree number, treatment, trap type and date and sent to specialists for sorting and then identification of the Coleoptera fauna.

12,964 out of a total of 13,010 Coleoptera individuals collected from 83 traps were identified to species (46 remaining to genus) and entered into an Excel database. The species data were then uploaded to www.artportalen.se (project ‘Ekveteraniseringsförsök’, open access). Each Coleoptera species was allocated one of four broad ecological guilds based on current knowledge (e.g. Palm 1953; Speight 1989; Bouget et al. 2019) and the authors’ experience: ‘wood-living’ (WL), ‘partly wood-living’ (PWL), ‘associated with wood-living fungi’ (WLF), and ‘other, not saproxylic’ (OTH) (see Table 8).

Statistical analyses

The site effect was modelled using a negative-binomial GLM with treatment, site and the interaction between treatment and site as fixed factors. The site effect was then tested with a type 2 chi-square test. Pairwise comparisons between sites were tested using Tukey tests. Following examination of the GLM, the number of species and the number of individuals were analysed with generalised linear mixed models (GLMM). The treatment was included as a fixed effect and the site, and treatment nested within site, were included as random effects. The response distribution was set to a negative-binomial and the estimated model was checked for under and overdispersion using the simulation approach from the DHARMA R package. Treatment effects were tested with a type 2 Wald chi-square test for overall differences and a Tukey test for pairwise comparisons between treatments. Models were estimated both for the full set of captured Coleoptera and for each of the four guilds. Statistical analysis used R version 4.5.3 (Reassured Reassurer) and Rstudio 2026.01.1 + 403. The packages tidyverse, lme4, car, DHARMA, emmeans and vegan were used.

Table 2 Overview of the numbers of taxa per site and Red Data Book (RDB) taxa according to the Red Data Book 2020, (Ljungberg et al. 2020), see also S3b for the results of analysis

Site	Total taxa per site	RDB total taxa per site
Strömsholm	99	10
Hjälmslult	100	3
Fulltofta	100	4
Brunnstorp	107	2
Västerby	108	4
Toftaholm	110	4
Haga Ekbackar	112	4
Huseby	113	4
Ekenäs	117	7
Tinnerö	117	7
Tromtö	120	14
Vanserum	121	7
Bondberget	121	4
Harsbo Sverkersholm	162	2

See Table 1 for numbers of traps per sites

Table 3 Overview of the total numbers of individuals per site and Red Data Book (RDB) individuals according to the Red Data Book 2020, (Ljungberg et al. 2020), see also S3c for the results of analysis

Site	Total individuals per site	RDB individuals per site
Tromtö	447	44
Fulltofta	606	33
Ekenäs	622	11
Hjälmslult	640	5
Strömsholm	711	45
Haga Ekbackar	755	6
Bondberget	849	11
Toftaholm	918	9
Vanserum	932	18
Brunnstorp	1010	7
Tinnerö	1071	38
Harsbo Sverkersholm	1466	2
Huseby	1486	9
Västerby	1497	18

See Table 1 for numbers of traps per sites

Results

In total, 13,010 individuals were identified (46 to genus only) representing 493 beetle species. The mean number of species per site was 114 (range 99–162, see also Table 2) and the mean number of individuals per site was 929 (range 447–1497, see also Table 3). The five most abundant species were *Atheta vaga* ($n=1586$, 13 sites, PWL), *Cryptarcha undata* ($n=832$, 14 sites, WL), *Quedius mesomelinus* ($n=735$, 13 sites, PWL), *Haploglossa villosula* ($n=622$, 13 sites, WL) and *Athous subfuscus* ($n=612$, 13 sites, OTH). Three species in addition to *C. undata* were recorded from all 14 sites: *Dalopius marginatus* ($n=277$, 14 sites, PWL),

Table 4 Tukey pairwise comparisons between treatments

Measure	Pairwise comparisons	z ratio	P value
Number of individuals	C/NBT	-2.775	0.0153
	C/WPH	-2.436	0.0394
	NBT/WPH	0.284	0.9565
Number of taxa	C/NBT	-3.215	0.0037
	C/WPH	-3.251	0.0033
	NBT/WPH	-0.093	0.9952

C control, WPH woodpecker hole, NBT nestbox and topping

Athous haemorrhoidalis ($n=225$, 14 sites, OTH) and *Dasytes plumbeus* ($n=67$, 14 sites, WL). For the full list of species, guild assignment and numbers see Annex 8 and Supplementary Information Table S1.

The GLM tests for Coleoptera individuals and taxa revealed significant differences between sites (individuals $DF=13$, $P<0.0001$; taxa $DF=13$, $P=0.0003$, Table S3a). The significant groupings of sites for both taxa and individuals are in Table S3b and S3c. There were also significant treatment effects (individuals $DF=2$, $P=0.0001$; taxa $DF=2$, $P<0.0001$, Table S3a). There were no significant interactions between site and treatment.

The GLMM Anovas show significant differences between treatments for both individual Coleoptera (chi-square=9.279, $DF=2$, $P=0.0097$) and taxa (chi-square=13.928, $DF=2$, $P=0.0009$). Pairwise comparisons indicate that both the NBT and the WPH treatments had significantly more individuals and taxa of Coleoptera than did the controls (Table 4). There were no significant differences between the two treatments.

Guilds

315 of the Coleoptera species identified were saproxylic (i.e. WL, PWL and WLF). The analysis of Coleoptera by guild identified significant effects for WL for both numbers of individuals (chi-square=22.352, $DF=2$, $P<0.0001$) and taxa (chi-square=18.134, $DF=2$, $P=0.0001$) and for PWL for numbers of individuals (chi-square=11.346, $DF=2$, $P=0.0034$), but not for number of taxa. For the other guilds (WLF and OTH) there were no significant differences between treatments either in terms of taxa or individuals (Table S3d). Pairwise comparisons (Table 5 and S3e) indicate that for WL there were significantly more individuals and taxa in the NBT and WPH than the C, although no significant differences between the two treatments were found. For the PWL guild there were significantly more individuals in both the NBT and WPH than the C, but not between the treatments.

For the saproxylic guilds (WL, WLF, PWL), the results showed that the NBT has 1.73 as many individuals as the control, and WPH 1.59 times as many individuals as the

Table 5 Tukey pairwise comparisons between treatments within guilds

Measure	Pairwise comparisons	z ratio	P value
Number of individuals for WL	C/NBT	-4.362	<0.0001
	C/WPH	-3.759	0.0005
	NBT/WPH	0.550	0.8463
Number of taxa for WL	C/NBT	-3.945	0.0002
	C/WPH	-3.486	0.0014
	NBT/WPH	0.421	0.9071
Number of individuals for PWL	C/NBT	-3.171	0.0043
	C/WPH	-2.561	0.0282
	NBT/WPH	0.551	0.8461

Significant results shown here, full results presented in S3e

C control, WPH woodpecker hole, NBT nestbox and topping, WL wood-living guild, PWL partly wood-living

control. When looking at a species level comparison between the treatments, we found that just under half (40.8%) of the species were found only in the WPH or NBT traps (bold in Table 6) and just over a quarter (26.4%) were saproxylic (italics in Table 6). Around 15% of the species were unique to each of the treatments and 33.5% were ubiquitous (found in both treatments and the controls – see Table 6 and Table S1).

47 species are listed on the Swedish Red Data Book (RDB) (Ljungberg et al. 2020) of which 45 are saproxylic (Table 7). The total number of individuals of RDB species collected was 256, mean number of RDB species per site was 5.4 (range 2–14) and mean number of RDB individuals per site was 18.3 (range 2–45) (Tables 2 and 3, Annex 9). 4 RDB species *Calambus bipustulatus* ($n=18$, 5 sites, WL), *Carphacis striatus* ($n=38$, 4 sites, WL), *Ischnomera cinerascens* ($n=15$, 7 sites, WL) and *Lymexylon navale* ($n=93$, 7 sites, WL) were found from 4 or more sites and in larger numbers. Almost all the remaining 43 RDB species were found from only one or two sites and with only one or two individuals (Annex 9).

Table 7 Number of taxa (total and RDB) as recorded by guild and their respective percentage

Guild allocated (*saproxylic)	Number of taxa	Percentage (%)	Red data book taxa (2020)
WL *	221	44.8	35
PWL *	32	6.5	2
WLF *	62	12.6	8
OTH	178	36.1	2
Total	493		47

OTH other, non-saproxylic, PWL partly wood-living, WL wood-living, WLF associated with wood-living fungi

Discussion

This study provides the first quantitative evidence that artificially created cavities in oaks can attract a diverse assemblage of saproxylic beetles shortly after treatment (2 years). Both veteranisation techniques tested (Fig. 2) supported significantly more wood-living individuals and species of Coleoptera than untreated control trees. Almost two thirds (63.9%) of all species recorded were saproxylic and of these 14% were RDB species.

Attraction of saproxylic beetles to newly created cavities

Although the trees in this study were much younger and without existing natural microhabitats prior to treatment (estimated mean age c. 80 yrs) the veteranisation treatments, based on the beetles caught, appear to mimic several microhabitats associated with naturally occurring hollows, including exposed heartwood and sapwood, accumulation of frass and organic material (Ranius et al. 2009b, 2024; Quinto et al. 2014). Many saproxylic beetles, particularly the early successional species are known to be attracted to volatile compounds released from fresh wounds or decaying sapwood (Dajoz 2000; Wainhouse and Boddy 2022). Attraction itself is ecologically meaningful, as it does indicate that the treatments produce cues strong enough to attract dispersing beetles within a short time (Siitonen and Ranius

Table 6 Percentages of species by guild and treatment

Treatment	OTH	PWL	WL	WLF	Total %
C	6.09	1.42	6.69	1.01	15.21
C+NBT	1.83	0.00	2.84	0.20	4.87
C+NBT+WPH	11.36	2.84	14.81	4.46	33.47
C+WPH	2.43	0.20	2.03	1.01	5.68
NBT	5.88	0.81	5.48	1.83	14.00
NBT+WPH	2.64	0.61	6.29	1.42	10.95
WPH	5.88	0.61	6.69	2.64	15.82
Total %	36.11	6.49	44.83	12.58	100.00

C control, NBT Nestbox and topping, WPH woodpecker hole, OTH other, non-saproxylic, PWL partly wood-living, WL wood-living, WLF associated with wood-living fungi) highlighting those that were specific to one treatment or ubiquitous

2015; Cizek et al. 2025). In addition, it cannot be excluded that some of our trapped species were already breeding in the dead wood substrate in and around the created cavities in line with similar investigations by Sverdrup-Thygeson and Birkemoe (2009) who showed that flight interception traps also reflect species colonising the substrate where the trap is attached.

Based on the high abundance of early-successional taxa such as *Cryptarcha undata* (larvae develop under bark in association with sap), *Quedius mesomelinus* (often associated with birds' nests in cavities) and *Haploglossa villosula* (Pilskog et al. 2016 found this abundantly in hollow-oak assemblages) supports our interpretation that the beetle assemblage reflects an early successional community (see S1) (Palm 1953; Speight 1989; Koch et al. 2012; SLU Artdatabanken 2025b).

Our data shows that for the WL guild there were significantly more individuals and taxa in the traps at the treatments, whereas there was no such difference for the WLF and OTH guilds, further supports the fact that the veteranised trees appear to specifically attract wood-living species. That there was no similar significant result for those species associated with fungi (WLF) is not surprising given that the decay processes were at only a very early stage (Menkis et al. 2022; Wainhouse and Boddy 2022). Menkis et al. (2022) showed that six years after the treatments were done, there were few heartwood decay fungal species found in the veteranised trees. A similar pattern for the OTH guild indicates that the treatments are not attracting species without a saproxylic ecology.

Differences between veteranisation treatments

Both the WPH and NBT treatments supported significantly higher beetle richness and abundance than untreated controls, yet no significant differences emerged between the two cavity types. However, the species comparison does suggest potential differences that could be further explored, given that around 15% of the species were in fact unique to each of the treatments. *Oxyptoda brevicornis* and *Haploglossa marginalis* were both species only found in the NBT, and which are known to use cavities for hunting and have also been connected with the nests of tree ants and birds (Palm 1953; Pilskog et al. 2016; SLU Artdatabanken 2025e). The presence of these two species in the NBT treatment is possibly due to it being a much larger cavity. The NBT cavities more commonly contained both tree ants and bird nesting material which might also explain the occurrence of these species (Bengtsson and Wheeler 2021). This is somewhat in line with Quinto et al. (2014) who found that natural hollow volume was the main determining factor for saproxylic guild richness and abundance, with large

hollow volume being usually related to higher diversity. We also found that 26% of species only found in the treatments (WPH and NBT) and not in control trees, were saproxylic. Some of these are known deciduous dead wood specialists such as the two click beetles *Ampedus nigroflavus* and *Melasis buprestoides* (SLU Artdatabanken 2025d, 2025f).

Several other species, whilst having been recorded as ubiquitous, were much more abundant from the veteranised cavities. The RDB *Lymexylon navale* (NT) is a good example of this where only one individual was recorded from a C (3% traps), 65 from NBT (35% traps) and 27 from WPH (27% traps). We hypothesized that this species would be favoured by veteranisation because its larvae develop in hard exposed parts of standing or living large oaks, a substrate which in our study has been created in relatively large quantities in association with the NBT treatment (Palm 1953). This species can live in sun-exposed wood on living trees for decades and has been caught from 7 of the studied sites and in good numbers. Both *Cryptarcha undata* (28 C 41% traps, 363 NBT 75% traps, 441 WPH 65% traps) and *Haploglossa villosula* (80 C 59% traps, 398 NBT 68% traps, 144 WPH 73% traps) were more common in the veteranised cavity treatments compared to the controls (see S1). Another such example is the RDB *Carphacis striatus* (VU) where only one was recorded from a C (3% traps), 33 from NBT (18% traps) and 4 from WPH (12% traps). This is a species associated with large old broadleaved trees and lives in association with sap runs and fungi such as *Laetiporus sulphureus*. It is also interesting to note that two of the chafers *Protaetia marmorata* and *Cetonia aurata*, which were ubiquitous (see Table S1), had relatively similar numbers in each of the C, NBT and WPH. This is likely a reflection on the fact that they search for pollen during their imago stage and are thus relatively easily caught in flight interception traps. Both species are usually associated with later stages of decay in large hollow trees, so would not be expected in the artificial cavities after only two years.

The fact that no significant differences emerged between the two treatments at this stage may indicate that the availability of newly exposed wood and open cavities is more important than the exact geometry or volume of the cavity during early colonisation (Griffiths et al. 2020; Cizek et al. 2025). Nevertheless, some ecological differences between the treatments are plausible, not least due to the volume (Quinto et al. 2014) and the 'lid' left in place in the NBT treatment, which is a discrete piece of dead wood that in itself may attract species. In addition, the fact that the larger NBT may retain more moisture and collect more organic material such as birds' nests and tree ants' nests could also have an impact (Grüebler et al. 2013; Griffiths et al. 2020; Bengtsson and Wheeler 2021). Such differences between treatments could, in the longer term contribute to

heterogeneity in beetle assemblages, as different species respond to microclimatic variation and decay development (Jansson et al. 2009; Quinto et al. 2014; Wainhouse and Boddy 2022; Ranius et al. 2024). To verify if these artificial cavities are suitable for reproduction, future surveys employing emergence traps (Goux and Brustel 2011) would be required.

Over time, these cavities are expected to decay due to fungal succession and colonisation, leading to the development of heartwood decay and internal detritus (Schwartz et al. 2000; Boddy 2021; Wainhouse and Boddy 2022; Marcu-llynas et al. 2023). Menkis et al. (2022) found that six years after veteranisation, oaks were dominated by endophytic rather than decay fungi, suggesting that it may require one or more decades for the veteranised cavities to develop decay suitable for later successional species (Ranius et al. 2009a, 2009b; Pyne et al. 2023). Further monitoring is therefore needed to determine whether differences in community composition will emerge as decay progresses.

The amount of overlap in terms of numbers of individuals and taxa between sites given their geographic spread, climate, topography, local landscapes, and logistical sampling issues was surprising. In addition the loss of samples such as at Tromtö, and uneven numbers of traps (due to storm damage), could also have contributed to differences between sites. However, although there were significant differences found, there was a large degree of overlap, and the site differences did not interact with the treatment. Landscape-level factors such as the density of existing hollow oaks, dispersal ability and the availability of decaying wood will likely influence colonisation dynamics (Ranius and Jansson 2000; Pilskog et al. 2016; Miklin et al. 2017; Wetherbee et al. 2020; Weatherbee et al. 2021) and would be an interesting focus for future study.

Conservation and management implications

The demonstrated attraction of saproxylic beetles to artificial cavities underscores the potential of veteranisation as a practical tool for biodiversity management. In landscapes where old oaks are scarce and the connectivity and quantity of hollow tree habitats has declined, such interventions can help ‘bridge the gap’ between existing veteran trees and younger generations (Bengtsson and Wheeler 2021). The technique presented here therefore complements other restoration measures aimed at increasing the availability of tree-related microhabitats (TreMs) (Spînu et al. 2022; Cizek et al. 2025). Given the great diversity of naturally occurring TreMs in old trees our methods will likely emulate only a few (Bütler et al. 2020). Thus, it is also important to use several

different methods when creating artificial microhabitats and over time to ensure a wide variety of tree microhabitats in different successional stages (Stokland et al. 2012; Quinto et al. 2014; Platek et al. 2019; Großmann et al. 2020). Many studies highlight the fact that to support a range of species, particularly rarer ones, a large population of hollow trees is necessary (Ranius 2007; Larsson and Svensson 2011; Lindenmayer and Laurance 2016). Importantly, veteranisation should never be applied to veteran trees or those that already have natural microhabitats or decay, as this could damage existing features (Read 2000; Lonsdale 2013; Wainhouse and Boddy 2022).

Future research

Future monitoring of these same trees in our study will provide valuable insight into the changes in beetle communities over time and may shed light on more specific questions such as if or when obligate old-oak cavity specialists establish and if they reproduce, as the artificial cavities age and decay develops. Future comparative studies repeating the use of flight interception traps and emergence traps could help clarify the link between attraction and reproduction. It would also be interesting to study if trees with artificial cavities can develop decay at higher rates if they have also been inoculated with fungi (Wainhouse and Boddy 2022). It would also be interesting to know at what age the artificial cavities host similar species richness and diversity to natural cavities.

Conclusions

Our results demonstrate that artificially created cavities in young oaks rapidly attracted diverse assemblages of saproxylic beetles, including species of conservation concern. The lack of interaction between site and treatment implies that these methods could be widely applicable. Such interventions can thus help alleviate the current scarcity of natural tree hollows, thereby reducing future extinction risks for saproxylic species associated with natural tree hollows. Future monitoring will clarify the long-term effectiveness of artificial hollows and veteranisation as a restoration tool to mitigate the loss of ancient oaks.

Annex

See Tables 8, 9 and 10.

Table 8 Full species list with the guild assigned in this study

Coleoptera species	Guild assigned
<i>Acanthocinus aedilis</i>	Wood-living
<i>Acrotrichis</i> sp.	Wood-living
<i>Adalia decempunctata</i>	Other
<i>Agabus congener</i>	Other
<i>Agathidium laevigatum</i>	Associated with wood-living fungi
<i>Agathidium rotundatum</i>	Associated with wood-living fungi
<i>Agrilus angustulus</i>	Wood-living
<i>Agrilus laticornis</i>	Wood-living
<i>Agrilus sulcicollis</i>	Wood-living
<i>Agrypnus murinus</i>	Other
<i>Aleochara curtula</i>	Other
<i>Aleochara lanuginosa</i>	Other
<i>Aleochara moerens</i>	Partly wood-living
<i>Alosterna tabacicolor</i>	Wood-living
<i>Amara aenea</i>	Other
<i>Amara familiaris</i>	Other
<i>Ampedus balteatus</i>	Wood-living
<i>Ampedus cardinalis</i>	Wood-living
<i>Ampedus cinnabarinus</i>	Wood-living
<i>Ampedus nigrinus</i>	Wood-living
<i>Ampedus nigroflavus</i>	Wood-living
<i>Ampedus pomorum</i>	Wood-living
<i>Ampedus rufipennis</i>	Wood-living
<i>Ampedus sanguinolentus</i>	Wood-living
<i>Anaglyptus mysticus</i>	Wood-living
<i>Anaspis flava</i>	Wood-living
<i>Anaspis frontalis</i>	wood-living
<i>Anaspis marginicollis</i>	Wood-living
<i>Anaspis rufilabris</i>	Wood-living
<i>Anaspis</i> sp.	Wood-living
<i>Anaspis thoracica</i>	Wood-living
<i>Anchomenus dorsalis</i>	Other
<i>Anisandrus dispar</i>	Wood-living
<i>Anisotoma axillaris</i>	Associated with wood-living fungi
<i>Anobium punctatum</i>	Wood-living
<i>Anomognathus cuspidatus</i>	Wood-living
<i>Anostirus castaneus</i>	Wood-living
<i>Anotylus rugosus</i>	Other
<i>Anthonomus phyllocola</i>	Other
<i>Anthrenus museorum</i>	Partly wood-living
<i>Anthribus nebulosus</i>	Wood-living
<i>Aphidecta oblitterata</i>	Other
<i>Aphthona euphorbiae</i>	Other
<i>Aplocnemus nigricornis</i>	Partly wood-living
<i>Archarius pyrrhoceras</i>	Other
<i>Archarius salicivorus</i>	Other
<i>Atheta crassicornis</i>	Partly wood-living
<i>Atheta fungi</i>	Partly wood-living
<i>Atheta graminicola</i>	Other
<i>Atheta nidicola</i>	Partly wood-living
<i>Atheta</i> sp.	Other
<i>Atheta vaga</i>	Partly wood-living
<i>Athous haemorrhoidalis</i>	Other
<i>Athous subfuscus</i>	Other
<i>Athous vittatus</i>	Other

Table 8 (continued)

Coleoptera species	Guild assigned
<i>Atomaria diluta</i>	Associated with wood-living fungi
<i>Atomaria hislopi</i>	Partly wood-living
<i>Atomaria morio</i>	Partly wood-living
<i>Atomaria nigripennis</i>	Partly wood-living
<i>Atomaria pusilla</i>	Associated with wood-living fungi
<i>Atomaria rubella</i>	Partly wood-living
<i>Atomaria</i> sp.	Other
<i>Atomaria turgida</i>	Associated with wood-living fungi
<i>Atomaria wollastoni</i>	Partly wood-living
<i>Attagenus pello</i>	Partly wood-living
<i>Aulonothroscus brevicollis</i>	Other
<i>Bembidion obtusum</i>	Other
<i>Betulapion simile</i>	Other
<i>Biblopectus spinosus</i>	Partly wood-living
<i>Bibloporus bicolor</i>	Wood-living
<i>Bibloporus minutus</i>	Wood-living
<i>Bisnius subuliformis</i>	Wood-living
<i>Bitoma crenata</i>	Associated with wood-living fungi
<i>Bolitophagus reticulatus</i>	Associated with wood-living fungi
<i>Bryaxis bulbifer</i>	Partly wood-living
<i>Byrrhus pilula</i>	Other
<i>Byturus tomentosus</i>	Other
<i>Cacotemnus rufipes</i>	Wood-living
<i>Calambus bipustulatus</i>	Wood-living
<i>Calathus rotundicollis</i>	Other
<i>Calosoma inquisitor</i>	Other
<i>Calvia quatuordecimguttata</i>	Other
<i>Cantharis figurata</i>	Other
<i>Cantharis fusca</i>	Other
<i>Cantharis nigra</i>	Other
<i>Cantharis nigricans</i>	Other
<i>Cantharis obscura</i>	Other
<i>Cantharis pellucida</i>	Other
<i>Cantharis quadripunctata</i>	Other
<i>Cantharis rufa</i>	Other
<i>Cantharis rustica</i>	Other
<i>Carabus hortensis</i>	Other
<i>Carcinops pumilio</i>	Partly wood-living
<i>Carpelimus elongatulus</i>	Other
<i>Carphacis striatus</i>	Wood-living
<i>Carpophilus marginellus</i>	Partly wood-living
<i>Cartodere nodifer</i>	Wood-living
<i>Cerylon ferrugineum</i>	Wood-living
<i>Cerylon histeroideus</i>	Wood-living
<i>Cetonia aurata</i>	Partly wood-living
<i>Ceutorhynchus obstrictus</i>	Other
<i>Ceutorhynchus pallidactylus</i>	Other
<i>Ceutorhynchus typhae</i>	Other
<i>Chaetocnema picipes</i>	Other
<i>Chilocorus bipustulatus</i>	Other
<i>Chilocorus renipustulatus</i>	Other
<i>Cimberis attelaboides</i>	Other
<i>Cis comptus</i>	Associated with wood-living fungi
<i>Cis dentatus</i>	Associated with wood-living fungi

Table 8 (continued)

Coleoptera species	Guild assigned
<i>Cis fagi</i>	Associated with wood-living fungi
<i>Cis</i> sp.	Associated with wood-living fungi
<i>Cis submicans</i>	Associated with wood-living fungi
<i>Coeliodes rana</i>	Other
<i>Coeliodes</i>	Other
<i>transversealbofasciatus</i>	
<i>Coeliodinus rubicundus</i>	Other
<i>Conopalpus testaceus</i>	Wood-living
<i>Contacyphon coarctatus</i>	Other
<i>Contacyphon ochraceus</i>	Other
<i>Contacyphon padi</i>	Other
<i>Contacyphon variabilis</i>	Other
<i>Corticaria</i> sp.	Other
<i>Corticarina minuta</i>	Associated with wood-living fungi
<i>Corticarina similata</i>	Associated with wood-living fungi
<i>Corticeus linearis</i>	Wood-living
<i>Cortinicara gibbosa</i>	Associated with wood-living fungi
<i>Crepidodera aurata</i>	Other
<i>Cryptarcha strigata</i>	Wood-living
<i>Cryptarcha undata</i>	Wood-living
<i>Cryptocephalus labiatus</i>	Other
<i>Cryptocephalus querceti</i>	Other
<i>Cryptocephalus sexpunctatus</i>	Other
<i>Cryptolestes ferrugineus</i>	Wood-living
<i>Cryptophagus</i> sp.	Other
<i>Cryptophagus badius</i>	Associated with wood-living fungi
<i>Cryptophagus confusus</i>	Associated with wood-living fungi
<i>Cryptophagus dentatus</i>	Associated with wood-living fungi
<i>Cryptophagus denticulatus</i>	Associated with wood-living fungi
<i>Cryptophagus distinguendus</i>	Associated with wood-living fungi
<i>Cryptophagus fuscicornis</i>	Associated with wood-living fungi
<i>Cryptophagus labilis</i>	Associated with wood-living fungi
<i>Cryptophagus micaceus</i>	Associated with wood-living fungi
<i>Cryptophagus reflexus</i>	Associated with wood-living fungi
<i>Cryptophagus scanicus</i>	Associated with wood-living fungi
<i>Crypturgus subcribrosus</i>	Wood-living
<i>Ctenicera pectinicornis</i>	Other
<i>Ctesias serra</i>	Wood-living
<i>Curculio nucum</i>	Other
<i>Curculio venosus</i>	Other
<i>Curculio villosus</i>	Other
<i>Cychramus luteus</i>	Associated with wood-living fungi
<i>Cypha apicalis</i>	Associated with wood-living fungi
<i>Dacne bipustulata</i>	Associated with wood-living fungi
<i>Dalopius marginatus</i>	Partly wood-living
<i>Dasytes aeratus</i>	Wood-living
<i>Dasytes caeruleus</i>	Wood-living
<i>Dasytes niger</i>	Wood-living
<i>Dasytes plumbeus</i>	Wood-living
<i>Dendrophilus punctatus</i>	Wood-living
<i>Dendroxena quadrimaculata</i>	Other
<i>Denticollis linearis</i>	Wood-living
<i>Dermestes lardarius</i>	Other
<i>Dermestes murinus</i>	Other
<i>Diaperis boleti</i>	Associated with wood-living fungi

Table 8 (continued)

Coleoptera species	Guild assigned
<i>Diplocoelus fagi</i>	Associated with wood-living fungi
<i>Dircaea australis</i>	Wood-living
<i>Dorcatoma chrysomelina</i>	Associated with wood-living fungi
<i>Dorcatoma dresdensis</i>	Associated with wood-living fungi
<i>Dorcatoma flavicornis</i>	Associated with wood-living fungi
<i>Dorcatoma robusta</i>	Associated with wood-living fungi
<i>Dromius agilis</i>	Other
<i>Dromius fenestratus</i>	Other
<i>Dromius quadrimaculatus</i>	Other
<i>Dropephylla gracilicornis</i>	Wood-living
<i>Dropephylla ioptera</i>	Wood-living
<i>Dryocoetes alni</i>	Wood-living
<i>Dryocoetes villosus</i>	Wood-living
<i>Elateroides dermestoides</i>	Associated with wood-living fungi
<i>Enicmus fungicola</i>	Associated with wood-living fungi
<i>Enicmus rugosus</i>	Associated with wood-living fungi
<i>Enicmus testaceus</i>	Associated with wood-living fungi
<i>Ennearthron cornutum</i>	Associated with wood-living fungi
<i>Epuraea aestiva</i>	Wood-living
<i>Epuraea biguttata</i>	Wood-living
<i>Epuraea boreella</i>	Wood-living
<i>Epuraea guttata</i>	Wood-living
<i>Epuraea melina</i>	Wood-living
<i>Epuraea muehli</i>	Wood-living
<i>Epuraea neglecta</i>	Wood-living
<i>Epuraea pallescens</i>	Wood-living
<i>Epuraea</i> sp.	Other
<i>Epuraea unicolor</i>	Wood-living
<i>Epuraea variegata</i>	Wood-living
<i>Ernobius nigrinus</i>	Wood-living
<i>Ernoporus tiliae</i>	Wood-living
<i>Eucnemis capucina</i>	Wood-living
<i>Euglenes oculatus</i>	Wood-living
<i>Euplectus karstenii</i>	Wood-living
<i>Euplectus piceus</i>	Wood-living
<i>Euplectus punctatus</i>	Wood-living
<i>Exochomus quadripustulatus</i>	Other
<i>Gabrius splendidulus</i>	Wood-living
<i>Gastrophysa polygoni</i>	Other
<i>Gaurotes virginea</i>	Other
<i>Geodromicus plagiatus</i>	Other
<i>Glaphyra umbellatarum</i>	Wood-living
<i>Glischrochilus hortensis</i>	Wood-living
<i>Glischrochilus quadriguttatus</i>	Wood-living
<i>Glischrochilus quadripunctatus</i>	Wood-living
<i>Gnathoncus buyssoni</i>	Wood-living
<i>Gnathoncus rotundatus</i>	Wood-living
<i>Gnorimus nobilis</i>	Wood-living
<i>Grammoptera ustulata</i>	Wood-living
<i>Grynocharis oblonga</i>	Wood-living
<i>Gymnetron veronicae</i>	Other
<i>Hapalaraea pygmaea</i>	Wood-living
<i>Haploglossa gentilis</i>	Wood-living
<i>Haploglossa marginalis</i>	Wood-living

Table 8 (continued)

Coleoptera species	Guild assigned
<i>Haploglossa picipennis</i>	Wood-living
<i>Haploglossa villosula</i>	Wood-living
<i>Harpalus latus</i>	Other
<i>Hemicoelus canaliculatus</i>	Wood-living
<i>Hemicoelus fulvicornis</i>	Wood-living
<i>Hemicrepidius hirtus</i>	Wood-living
<i>Hemicrepidius niger</i>	Wood-living
<i>Homalota plana</i>	Wood-living
<i>Hydraena britteni</i>	Other
<i>Hylastes brunneus</i>	Wood-living
<i>Hylesinus crenatus</i>	Wood-living
<i>Hylesinus wachtl</i>	Wood-living
<i>Hylis cariniceps</i>	Wood-living
<i>Hylis olexai</i>	Wood-living
<i>Hylis procerulus</i>	Wood-living
<i>Hylobius abietis</i>	Wood-living
<i>Hylobius excavatus</i>	Wood-living
<i>Hylurgops palliatus</i>	Wood-living
<i>Hypera meles</i>	Other
<i>Hypera nigrirostris</i>	Other
<i>Hypoganus inunctus</i>	Wood-living
<i>Ipidia binotata</i>	Wood-living
<i>Ips typographus</i>	Wood-living
<i>Ischnomera cinerascens</i>	Wood-living
<i>Korynetes caeruleus</i>	Wood-living
<i>Lagria hirta</i>	Other
<i>Latridius brevicollis</i>	Associated with wood-living fungi
<i>Latridius gemellatus</i>	Associated with wood-living fungi
<i>Latridius hirtus</i>	Associated with wood-living fungi
<i>Latridius minutus</i>	Associated with wood-living fungi
<i>Leiopus linnei</i>	Wood-living
<i>Leiopus nebulosus</i>	Wood-living
<i>Leptura quadrifasciata</i>	Wood-living
<i>Leptusa fumida</i>	Wood-living
<i>Leptusa ruficollis</i>	Wood-living
<i>Limnebius truncatellus</i>	Other
<i>Limonius poneli</i>	Other
<i>Litargus connexus</i>	Associated with wood-living fungi
<i>Lochmaea caprea</i>	Other
<i>Lordithon lunulatus</i>	Associated with wood-living fungi
<i>Lucanus cervus</i>	Wood-living
<i>Lyctus linearis</i>	Wood-living
<i>Lymexylon navale</i>	Wood-living
<i>Magdalis duplicata</i>	Wood-living
<i>Magdalis flavicornis</i>	Wood-living
<i>Malachius bipustulatus</i>	Other
<i>Malthinus facialis</i>	Wood-living
<i>Malthinus flaveolus</i>	Wood-living
<i>Malthinus frontalis</i>	Wood-living
<i>Malthodes brevicollis</i>	Wood-living
<i>Malthodes fibulatus</i>	Wood-living
<i>Malthodes guttifer</i>	Wood-living
<i>Malthodes marginatus</i>	Wood-living
<i>Malthodes minimus</i>	Wood-living

Table 8 (continued)

Coleoptera species	Guild assigned
<i>Malthodes</i> sp.	Wood-living
<i>Margarinotus merdarius</i>	Partly wood-living
<i>Mecinus pascuorum</i>	Other
<i>Megatoma undata</i>	Wood-living
<i>Melanotus castanipes</i>	Wood-living
<i>Melanotus villosus</i>	Wood-living
<i>Melasis buprestoides</i>	Wood-living
<i>Meligethes aeneus</i>	Other
<i>Meligethes pedicularius</i>	Other
<i>Meligethes viridescens</i>	Other
<i>Melinopterus prodromus</i>	Other
<i>Mesosa nebulosa</i>	Wood-living
<i>Metoeus paradoxus</i>	Other
<i>Micrambe abietis</i>	Associated with wood-living fungi
<i>Micrambe woodroffe</i>	Other
<i>Microcara testacea</i>	Other
<i>Microrhagus lepidus</i>	Wood-living
<i>Microrhagus pygmaeus</i>	Wood-living
<i>Molorchus minor</i>	Wood-living
<i>Monotoma longicollis</i>	Partly wood-living
<i>Mordella aculeata</i>	Wood-living
<i>Mordellistena neuwaldeggiana</i>	Wood-living
<i>Mordellochroa abdominalis</i>	Wood-living
<i>Mycetochara axillaris</i>	Wood-living
<i>Mycetochara flavipes</i>	Wood-living
<i>Mycetochara maura</i>	Wood-living
<i>Mycetophagus fulvicollis</i>	Wood-living
<i>Mycetophagus multipunctatus</i>	Wood-living
<i>Mycetophagus piceus</i>	Wood-living
<i>Mycetophagus quadriguttatus</i>	Wood-living
<i>Mycetophagus quadripustulatus</i>	Wood-living
<i>Mycetoporus lepidus</i>	Other
<i>Myzia oblongoguttata</i>	Other
<i>Nargus anisotomoides</i>	Other
<i>Nebria brevicollis</i>	Other
<i>Necrodes littoralis</i>	Other
<i>Necydalis major</i>	Wood-living
<i>Nemadus colonoides</i>	Wood-living
<i>Nemozoma elongatum</i>	Wood-living
<i>Neocoenorrhinus germanicus</i>	Other
<i>Neocoenorrhinus minutus</i>	Other
<i>Nephus redtenbacheri</i>	Other
<i>Nicrophorus humator</i>	Other
<i>Nicrophorus investigator</i>	Other
<i>Nicrophorus vespillo</i>	Other
<i>Nicrophorus vespilloides</i>	Other
<i>Notoxus monoceros</i>	Other
<i>Oenopia conglobata</i>	Other
<i>Oiceoptoma thoracicum</i>	Other
<i>Omalius caesum</i>	Other
<i>Omalius rivulare</i>	Other
<i>Orchesia fasciata</i>	Associated with wood-living fungi
<i>Orchesia micans</i>	Associated with wood-living fungi
<i>Orchesia minor</i>	Associated with wood-living fungi

Table 8 (continued)

Coleoptera species	Guild assigned
<i>Orchesia undulata</i>	Associated with wood-living fungi
<i>Orchestes fagi</i>	Other
<i>Orchestes hortorum</i>	Other
<i>Orchestes pilosus</i>	Other
<i>Orchestes quercus</i>	Other
<i>Orchestes rusci</i>	Other
<i>Orsodacne cerasi</i>	Other
<i>Orthocis alni</i>	Associated with wood-living fungi
<i>Orthoperus atomus</i>	Partly wood-living
<i>Orthoperus</i> sp.	Partly wood-living
<i>Osmoderma eremita</i>	Wood-living
<i>Otiorhynchus carinatopunctatus</i>	Other
<i>Otiorhynchus singularis</i>	Other
<i>Oxypoda brevicornis</i>	Partly wood-living
<i>Oxypoda exoleta</i>	Partly wood-living
<i>Oxypoda procerula</i>	Other
<i>Oxypoda</i> sp.	Other
<i>Oxypoda spectabilis</i>	Other
<i>Oxytelus laqueatus</i>	Other
<i>Paraphotistus impressus</i>	Other
<i>Paromalus flavicornis</i>	Wood-living
<i>Pediacus depressus</i>	Wood-living
<i>Pedostrangalia revestita</i>	Wood-living
<i>Pelenomus commari</i>	Other
<i>Pella cognata</i>	Other
<i>Pella funesta</i>	Other
<i>Pella laticollis</i>	Other
<i>Pella lugens</i>	Other
<i>Phalacrus corruscus</i>	Other
<i>Philonthus carbonarius</i>	Other
<i>Philonthus cognatus</i>	Other
<i>Philonthus tenuicornis</i>	Other
<i>Phloeonomus punctipennis</i>	Wood-living
<i>Phloeonomus pusillus</i>	Wood-living
<i>Phloeotribus spinulosus</i>	Wood-living
<i>Phloiotrya rufipes</i>	Wood-living
<i>Phyllobius argentatus</i>	Other
<i>Phyllobius glaucus</i>	Other
<i>Phyllobius pyri</i>	Other
<i>Phyllobius virideaeris</i>	Other
<i>Phyllodrepa floralis</i>	Wood-living
<i>Phyllodrepa melanocephala</i>	Wood-living
<i>Phyllodrepa nigra</i>	Wood-living
<i>Phyllodrepa salicis</i>	Wood-living
<i>Phyllopertha horticola</i>	Other
<i>Phyllotreta undulata</i>	Other
<i>Phyllotreta vittula</i>	Other
<i>Phymatodes testaceus</i>	Wood-living
<i>Pityogenes chalcographus</i>	Wood-living
<i>Pityogenes quadridens</i>	wood-living
<i>Pityophagus ferrugineus</i>	Wood-living
<i>Placusa depressa</i>	Wood-living
<i>Placusa</i> sp.	Wood-living
<i>Placusa tachyporoides</i>	Wood-living

Table 8 (continued)

Coleoptera species	Guild assigned
<i>Platycerus caraboides</i>	Wood-living
<i>Platydemus violaceum</i>	Wood-living
<i>Platynus assimilis</i>	Other
<i>Platynus krynickii</i>	Other
<i>Platystomos albinus</i>	Associated with wood-living fungi
<i>Plegaderus caesus</i>	Wood-living
<i>Podabrus alpinus</i>	Other
<i>Podistra rufotestacea</i>	Other
<i>Polydrusus mollis</i>	Other
<i>Polydrusus tereticollis</i>	Other
<i>Prionocyphon serricornis</i>	Wood-living
<i>Prionychus ater</i>	Wood-living
<i>Propylea quatuordecimpunctata</i>	Other
<i>Prosternon tessellatum</i>	Other
<i>Protaetia marmorata</i>	Wood-living
<i>Protaetia metallica</i>	Wood-living
<i>Protapion apricans</i>	Other
<i>Protapion fulvipes</i>	Other
<i>Pseudocistela ceramboidea</i>	Wood-living
<i>Psylliodes affinis</i>	Other
<i>Ptenidium pusillum</i>	Wood-living
<i>Pterostichus diligens</i>	Other
<i>Pterostichus niger</i>	Other
<i>Ptilinus pectinicornis</i>	Wood-living
<i>Ptinomorphus imperialis</i>	Wood-living
<i>Ptinus fur</i>	Partly wood-living
<i>Ptinus rufipes</i>	Partly wood-living
<i>Ptinus subpillosus</i>	Wood-living
<i>Ptomaphagus varicornis</i>	Other
<i>Pyrochroa coccinea</i>	Wood-living
<i>Quedius brevicornis</i>	Wood-living
<i>Quedius cruentus</i>	Wood-living
<i>Quedius dilatatus</i>	Wood-living
<i>Quedius fuliginosus</i>	Partly wood-living
<i>Quedius maurus</i>	Partly wood-living
<i>Quedius mesomelinus</i>	Partly wood-living
<i>Quedius truncicola</i>	Wood-living
<i>Quedius xanthopus</i>	Partly wood-living
<i>Rhagium inquisitor</i>	Wood-living
<i>Rhagium mordax</i>	Wood-living
<i>Rhagonycha lignosa</i>	Other
<i>Rhagonycha lutea</i>	Other
<i>Rhagonycha nigriventris</i>	Other
<i>Rhagonycha testacea</i>	Other
<i>Rhamphus pulicarius</i>	Other
<i>Rhizophagus bipustulatus</i>	Wood-living
<i>Rhizophagus depressus</i>	Wood-living
<i>Rhizophagus dispar</i>	Wood-living
<i>Rhizophagus fenestralis</i>	Wood-living
<i>Rhyncolus ater</i>	Wood-living
<i>Rhyncolus sculpturatus</i>	Wood-living
<i>Salpingus planirostris</i>	Wood-living
<i>Salpingus ruficollis</i>	Wood-living
<i>Saperda scalaris</i>	Wood-living

Table 8 (continued)

Coleoptera species	Guild assigned
<i>Saprinus semistriatus</i>	Wood-living
<i>Scaphisoma agaricinum</i>	Associated with wood-living fungi
<i>Schizotus pectinicornis</i>	Wood-living
<i>Sciaphilus asperatus</i>	Other
<i>Scolytus intricatus</i>	Wood-living
<i>Scraptia fuscula</i>	Wood-living
<i>Scraptia testacea</i>	wood-living
<i>Scydmorephes helvolus</i>	Wood-living
<i>Scymnus silesiacus</i>	Other
<i>Selatosomus aeneus</i>	Other
<i>Selatosomus cruciatus</i>	Other
<i>Sepedophilus testaceus</i>	Other
<i>Serica brunnea</i>	Other
<i>Silvanoprus fagi</i>	Wood-living
<i>Sinodendron cylindricum</i>	Wood-living
<i>Sitona obsoletus</i>	Other
<i>Soronia grisea</i>	Other
<i>Soronia punctatissima</i>	Wood-living
<i>Stagetus borealis</i>	Wood-living
<i>Stenagostus rhombeus</i>	Wood-living
<i>Stenocorus meridianus</i>	Wood-living
<i>Stenostola dubia</i>	Wood-living
<i>Stephostethus lardarius</i>	Associated with wood-living fungi
<i>Stephostethus pandellei</i>	Associated with wood-living fungi
<i>Stictoleptura maculicornis</i>	Associated with wood-living Fungi
<i>Stictoleptura scutellata</i>	Wood-living
<i>Strangalia attenuata</i>	Wood-living
<i>Strophosoma capitatum</i>	Other
<i>Synchita humeralis</i>	Wood-living
<i>Synchita variegata</i>	Wood-living
<i>Tachinus laticollis</i>	Other
<i>Tachyporus chrysomelinus</i>	Other
<i>Tachyporus solutus</i>	Other
<i>Tetrops praeustus</i>	Wood-living
<i>Thamiaraea cinnamomea</i>	Partly wood-living
<i>Thamiaraea hospita</i>	Partly wood-living
<i>Thanasimus femoralis</i>	Wood-living
<i>Thanasimus formicarius</i>	Wood-living
<i>Tillus elongatus</i>	Wood-living
<i>Trechus quadristriatus</i>	Other
<i>Trichius fasciatus</i>	Other
<i>Trichoceble floralis</i>	Wood-living
<i>Trichoceble memnonia</i>	Other
<i>Triphyllus bicolor</i>	Associated with wood-living fungi
<i>Triplax aenea</i>	Associated with wood-living fungi
<i>Triplax rufipes</i>	Associated with wood-living fungi
<i>Triplax russica</i>	Associated with wood-living fungi
<i>Tritoma bipustulata</i>	associated with wood-living fungi
<i>Trixagus carinifrons</i>	Other
<i>Trixagus dermestoides</i>	Other
<i>Trypodendron domesticum</i>	Wood-living
<i>Tychius stephensi</i>	Other
<i>Tytthaspis sedecimpunctata</i>	Other
<i>Xantholinus linearis</i>	Other

Table 8 (continued)

Coleoptera species	Guild assigned
<i>Xestobium rufovillosum</i>	Wood-living
<i>Xyleborinus attenuatus</i>	Wood-living
<i>Xyleborinus saxesenii</i>	Wood-living
<i>Xyleborus monographus</i>	Wood-living
<i>Xyletinus longitarsis</i>	wood-living
<i>Xylotrechus antilope</i>	Wood-living

Table 9 Red data book species listed with the guild, red data book category, numbers of individuals in each trap and total number of sites from which the species was recorded (Ljungberg et al. 2020)

Red-listed species	Guild	RDB	C	NBT	WPH	Total	No of sites
<i>Agrilus laticornis</i>	WL	NT		1		1	1
<i>Ampedus cardinalis</i>	WL	NT	2			2	1
<i>Ampedus rufipennis</i>	WL	VU		4		4	1
<i>Ampedus sanguinolentus</i>	WL	NT	1			1	1
<i>Anaglyptus mysticus</i>	WL	NT	4	3	4	11	3
<i>Atomaria diluta</i>	WLF	NT		1	1	2	1
<i>Atomaria nigripennis</i>	PWL	VU			2	2	1
<i>Calambus bipustulatus</i>	WL	NT	7	4	7	18	5
<i>Carphacis striatus</i>	WL	VU	1	33	4	38	4
<i>Cis submicans</i>	WLF	NT		1		1	1
<i>Cryptophagus fuscicornis</i>	WLF	NT		1		1	1
<i>Cypha apicalis</i>	WLF	NT	1			1	1
<i>Diplocoelus fagi</i>	WLF	NT			1	1	1
<i>Dircaea australis</i>	WL	VU	1	1		2	1
<i>Eucnemis capucina</i>	WL	NT			1	1	1
<i>Gnorimus nobilis</i>	WL	NT		1		1	1
<i>Hemicoelus fulvicornis</i>	WL	NT		1	1	2	1
<i>Hylesinus crenatus</i>	WL	NT			1	1	1
<i>Hylesinus wachtli</i>	WL	NT			1	1	1
<i>Ischnomera cinerascens</i>	WL	NT	2	9	4	15	7
<i>Lyctus linearis</i>	WL	VU		2		2	1
<i>Lymexylon navale</i>	WL	NT	1	65	27	93	7
<i>Malthinus facialis</i>	WL	NT		1	1	2	1
<i>Mesosa nebulosa</i>	WL	NT		1		1	1
<i>Mordellistena neuwaldeggiana</i>	WL	NT	3			3	1
<i>Mycetophagus fulvicollis</i>	WL	NT	1			1	1
<i>Mycetophagus quadriguttatus</i>	WL	NT			1	1	1
<i>Orchesia fasciata</i>	WLF	NT	1		1	2	2
<i>Orchesia minor</i>	WLF	NT			1	1	1
<i>Osmoderma eremita</i>	WL	NT		1		1	1
<i>Pediacus depressus</i>	WL	NT		3		3	1
<i>Pedostrangalia revestita</i>	WL	EN			1	1	1
<i>Phyllodrepa salicis</i>	WL	VU			1	1	1
<i>Platydemus violaceum</i>	WL	NT			1	1	1
<i>Platynus krynickii</i>	Oth	NT			1	1	1
<i>Quedius truncicola</i>	WL	VU	3			3	1
<i>Scymnus silesiacus</i>	Oth	NT		2		2	1
<i>Stagetus borealis</i>	WL	NT		1		1	1
<i>Stenagostus rhombeus</i>	WL	VU	2			2	1
<i>Stictoleptura scutellata</i>	WL	VU	1			1	1
<i>Strangalia attenuata</i>	WL	NT	1	1		2	1
<i>Synchita variegata</i>	WL	NT	1			1	1
<i>Thamaraea hospita</i>	PWL	NT	1	1	4	6	4
<i>Triplax rufipes</i>	WLF	NT	2	3	1	6	4
<i>Xyleborus monographus</i>	WL	NT	2	4	3	9	2
<i>Xyletinus longitarsis</i>	WL	NT	1			1	1
<i>Xylotrechus antilope</i>	WL	NT	1		1	2	1
Total			40	145	71		

OTH other, non-saproxyllic, PWL partly wood-living, WL wood-living, WLF associated with woodlivingfungi, NBT nestbox and topping, WPH Woodpecker Hole, C Control, RDB Red Data Book

Table 10 Numbers of individuals of species per guild, treatment and number of sites, in alphabetical order

Species wood-living	Guild	RDB	C	NBT	WPH	Total	No of sites
<i>Acanthocinus aedilis</i>	WL				1	1	1
<i>Acrotrichis</i> sp.	WL		2			2	1
<i>Agrilus angustulus</i>	WL			1	1	2	2
<i>Agrilus laticornis</i>	WL	NT		1		1	1
<i>Agrilus sulcicollis</i>	WL		1	1		2	2
<i>Alosterna tabacicolor</i>	WL		2	1	2	5	3
<i>Ampedus balteatus</i>	WL		6	5	4	15	5
<i>Ampedus cardinalis</i>	WL	NT	2			2	1
<i>Ampedus cinnabarinus</i>	WL				3	3	1
<i>Ampedus nigrinus</i>	WL		5	5	3	13	4
<i>Ampedus nigroflavus</i>	WL			5	4	9	6
<i>Ampedus pomorum</i>	WL		4	3	1	8	5
<i>Ampedus rufipennis</i>	WL	VU		4		4	1
<i>Ampedus sanguinolentus</i>	WL	NT	1			1	1
<i>Anaglyptus mysticus</i>	WL	NT	4	3	4	11	3
<i>Anaspis flava</i>	WL		1			1	1
<i>Anaspis frontalis</i>	WL		12	20	10	42	11
<i>Anaspis marginicollis</i>	WL			1		1	1
<i>Anaspis rufilabris</i>	WL		14	10	16	40	11
<i>Anaspis</i> sp.	WL		2	1	2	5	2
<i>Anaspis thoracica</i>	WL		28	35	46	109	12
<i>Anisandrus dispar</i>	WL				3	3	1
<i>Anobium punctatum</i>	WL				3	3	1
<i>Anomognathus cuspidatus</i>	WL		1		4	5	4
<i>Anostirus castaneus</i>	WL				1	1	1
<i>Anthribus nebulosus</i>	WL		9	4	6	19	8
<i>Bibloporus bicolor</i>	WL				2	2	1
<i>Bibloporus minutus</i>	WL			1	2	3	2
<i>Bisnius subuliformis</i>	WL		16	59	27	102	13
<i>Cacotemnus rufipes</i>	WL			9	1	10	2
<i>Calambus bipustulatus</i>	WL	NT	7	4	7	18	5
<i>Carphacis striatus</i>	WL	VU	1	33	4	38	4
<i>Cartodere nodifer</i>	WL		1			1	1
<i>Cerylon ferrugineum</i>	WL		2	14	28	44	10
<i>Cerylon histeroideus</i>	WL			2	2	4	4
<i>Conopalpus testaceus</i>	WL		1	2	2	5	4
<i>Corticeus linearis</i>	WL		1			1	1
<i>Cryptarcha strigata</i>	WL		57	194	187	438	13
<i>Cryptarcha undata</i>	WL		28	363	441	832	14
<i>Cryptolestes ferrugineus</i>	WL			1		1	1
<i>Crypturgus subcribrosus</i>	WL		1			1	1
<i>Ctesias serra</i>	WL		45	47	35	127	10
<i>Dasytes aeratus</i>	WL			3		3	2
<i>Dasytes caeruleus</i>	WL		9	9	15	33	9
<i>Dasytes niger</i>	WL			2	2	4	4
<i>Dasytes plumbeus</i>	WL		24	19	24	67	14
<i>Dendrophilus punctatus</i>	WL		2	1	1	4	1
<i>Denticollis linearis</i>	WL			1	1	2	2
<i>Dircaea australis</i>	WL	VU	1	1		2	1
<i>Dropephylla gracilicornis</i>	WL				4	4	3
<i>Dropephylla ioptera</i>	WL		1		2	3	3
<i>Dryocoetes alni</i>	WL		3			3	3
<i>Dryocoetes villosus</i>	WL		1	8	10	19	8
<i>Epuraea aestiva</i>	WL		1			1	1
<i>Epuraea biguttata</i>	WL			1		1	1

Table 10 (continued)

Species wood-living	Guild	RDB	C	NBT	WPH	Total	No of sites
<i>Epuraea boreella</i>	WL				2	2	1
<i>Epuraea guttata</i>	WL		2	20	15	37	6
<i>Epuraea melina</i>	WL			1		1	1
<i>Epuraea muehli</i>	WL		2		2	4	3
<i>Epuraea neglecta</i>	WL			3	1	4	1
<i>Epuraea pallescens</i>	WL				24	24	1
<i>Epuraea unicolor</i>	WL			14	1	15	3
<i>Epuraea variegata</i>	WL			3	134	137	5
<i>Ernobius nigrinus</i>	WL		1			1	1
<i>Ernoporus tiliae</i>	WL				1	1	1
<i>Eucnemis capucina</i>	WL	NT			1	1	1
<i>Euglenes oculatus</i>	WL			1		1	1
<i>Euplectus karstenii</i>	WL			1		1	1
<i>Euplectus piceus</i>	WL		1			1	1
<i>Euplectus punctatus</i>	WL				1	1	1
<i>Gabrius splendidulus</i>	WL		2	5		7	4
<i>Glaphyra umbellatarum</i>	WL		1			1	1
<i>Glischrochilus hortensis</i>	WL		41	91	65	197	12
<i>Glischrochilus quadriguttatus</i>	WL			1	4	5	2
<i>Glischrochilus quadripunctatus</i>	WL		2	6	5	13	5
<i>Gnathoncus buyssoni</i>	WL		7	75	33	115	12
<i>Gnathoncus rotundatus</i>	WL				1	1	1
<i>Gnorimus nobilis</i>	WL	NT		1		1	1
<i>Grammoptera ustulata</i>	WL		4	3	1	8	5
<i>Grynocharis oblonga</i>	WL			2	4	6	4
<i>Hapalaraea pygmaea</i>	WL		1	12	2	15	3
<i>Haploglossa gentilis</i>	WL			16	17	33	6
<i>Haploglossa marginalis</i>	WL			13		13	1
<i>Haploglossa picipennis</i>	WL		6	37		43	6
<i>Haploglossa villosula</i>	WL		80	398	144	622	13
<i>Hemicoelus canaliculatus</i>	WL		1	8	1	10	4
<i>Hemicoelus fulvicornis</i>	WL	NT		1	1	2	1
<i>Hemicrepidius hirtus</i>	WL		1			1	1
<i>Hemicrepidius niger</i>	WL		17	15	112	144	8
<i>Homalota plana</i>	WL		3	3	5	11	5
<i>Hylastes brunneus</i>	WL		63	2	1	66	2
<i>Hylesinus crenatus</i>	WL	NT			1	1	1
<i>Hylesinus wachtli</i>	WL	NT			1	1	1
<i>Hylis cariniceps</i>	WL			2	1	3	2
<i>Hylis olexai</i>	WL			1	1	2	2
<i>Hylis procerulus</i>	WL				3	3	1
<i>Hylobius abietis</i>	WL		2		1	3	1
<i>Hylobius excavatus</i>	WL				1	1	1
<i>Hylurgops palliatus</i>	WL		1			1	1
<i>Hypoganus inunctus</i>	WL		2			2	2
<i>Ipidia binotata</i>	WL				1	1	1
<i>Ips typographus</i>	WL		3			3	1
<i>Ischnomera cinerascens</i>	WL	NT	2	9	4	15	7
<i>Korynetes caeruleus</i>	WL			1		1	1
<i>Leiopus linnei</i>	WL		2	7	4	13	6
<i>Leiopus nebulosus</i>	WL				1	1	1
<i>Leptura quadrifasciata</i>	WL		2	1	3	6	3
<i>Leptusa fumida</i>	WL		5	8	1	14	3
<i>Leptusa ruficollis</i>	WL		5	9	6	20	6

Table 10 (continued)

Species wood-living	Guild	RDB	C	NBT	WPH	Total	No of sites
<i>Lucanus cervus</i>	WL				1	1	1
<i>Lyctus linearis</i>	WL	VU		2		2	1
<i>Lymexylon navale</i>	WL	NT	1	65	27	93	7
<i>Magdalis duplicata</i>	WL		4			4	1
<i>Magdalis flavicornis</i>	WL		1			1	1
<i>Malthinus facialis</i>	WL	NT		1	1	2	1
<i>Malthinus flaveolus</i>	WL		5	2	2	9	5
<i>Malthinus frontalis</i>	WL		5		2	7	3
<i>Malthodes brevicollis</i>	WL		1	1		2	2
<i>Malthodes fibulatus</i>	WL		1			1	1
<i>Malthodes guttifer</i>	WL		1		1	2	2
<i>Malthodes marginatus</i>	WL		19	12	8	39	6
<i>Malthodes minimus</i>	WL		11	14	15	40	7
<i>Malthodes</i> sp.	WL		7	4	5	16	8
<i>Megatoma undata</i>	WL		36	49	32	117	11
<i>Melanotus castanipes</i>	WL		18	13	13	44	12
<i>Melanotus villosus</i>	WL		10	9	4	23	5
<i>Melasis buprestoides</i>	WL			14	4	18	5
<i>Mesosa nebulosa</i>	WL	NT		1		1	1
<i>Microrhagus lepidus</i>	WL		1			1	1
<i>Microrhagus pygmaeus</i>	WL		1	1		2	2
<i>Molorchus minor</i>	WL			1		1	1
<i>Mordella aculeata</i>	WL				1	1	1
<i>Mordellistena neuwaldeggiana</i>	WL	NT	3			3	1
<i>Mordellochroa abdominalis</i>	WL		2			2	2
<i>Mycetochara axillaris</i>	WL			1	18	19	3
<i>Mycetochara flavipes</i>	WL		6	11	1	18	3
<i>Mycetochara maura</i>	WL		29	16	10	55	5
<i>Mycetophagus fulvicollis</i>	WL		1			1	1
<i>Mycetophagus multipunctatus</i>	WL	NT		1	2	3	2
<i>Mycetophagus piceus</i>	WL		1	1	2	4	3
<i>Mycetophagus quadriguttatus</i>	WL	NT			1	1	1
<i>Mycetophagus quadripustulatus</i>	WL				1	1	1
<i>Necydalis major</i>	WL			2	2	4	3
<i>Nemadus colonoides</i>	WL			1		1	1
<i>Nemozoma elongatum</i>	WL		3			3	1
<i>Osmoderma eremita</i>	WL	NT		1		1	1
<i>Paromalus flavicornis</i>	WL		1	1	1	3	2
<i>Pediacus depressus</i>	WL	NT		3		3	1
<i>Pedostrangalia revestita</i>	WL	EN			1	1	1
<i>Phloeonomus punctipennis</i>	WL		1			1	1
<i>Phloeonomus pusillus</i>	WL		1	1		2	2
<i>Phloeotribus spinulosus</i>	WL		2	1		3	1
<i>Phloiotrya rufipes</i>	WL		2	4	5	11	5
<i>Phyllodrepa floralis</i>	WL			2	2	4	2
<i>Phyllodrepa melanocephala</i>	WL			4	5	9	6
<i>Phyllodrepa nigra</i>	WL				1	1	1
<i>Phyllodrepa salicis</i>	WL	VU			1	1	1
<i>Phymatodes testaceus</i>	WL		4	6	12	22	9
<i>Pityogenes chalcographus</i>	WL		10	4	2	16	5
<i>Pityogenes quadridens</i>	WL		29			29	2
<i>Pityophagus ferrugineus</i>	WL		1	1		2	2
<i>Placusa depressa</i>	WL		4	15	4	23	4
<i>Placusa</i> sp.	WL		1		1	2	1

Table 10 (continued)

Species wood-living	Guild	RDB	C	NBT	WPH	Total	No of sites
<i>Placusa tachyporoides</i>	WL				3	3	1
<i>Platycerus caraboides</i>	WL		1	1		2	2
<i>Platydemus violaceum</i>	WL	NT			1	1	1
<i>Plegaderus caesus</i>	WL				1	1	1
<i>Prionocyphon serricornis</i>	WL		3	4	7	14	6
<i>Prionychus ater</i>	WL		3	5		8	2
<i>Protaetia marmorata</i>	WL		12	14	9	35	5
<i>Protaetia metallica</i>	WL		7	3		10	5
<i>Pseudocistela ceramboides</i>	WL			1		1	1
<i>Ptenidium pusillum</i>	WL				1	1	1
<i>Ptilinus pectinicornis</i>	WL		5	66	19	90	5
<i>Ptinomorphus imperialis</i>	WL		1	2	3	6	5
<i>Ptinus subpillosus</i>	WL		17	6	21	44	9
<i>Pyrochroa coccinea</i>	WL		13	2	14	29	5
<i>Quedius brevicornis</i>	WL		7	3	4	14	5
<i>Quedius cruentus</i>	WL			7	16	23	5
<i>Quedius dilatatus</i>	WL		2	20	11	33	8
<i>Quedius truncicola</i>	WL	VU	3			3	1
<i>Rhagium inquisitor</i>	WL		1	2	1	4	4
<i>Rhagium mordax</i>	WL		3	4	7	14	9
<i>Rhizophagus bipustulatus</i>	WL		9	18	38	65	11
<i>Rhizophagus depressus</i>	WL				1	1	1
<i>Rhizophagus dispar</i>	WL			4	2	6	2
<i>Rhizophagus fenestralis</i>	WL		2	1		3	3
<i>Rhyncolus ater</i>	WL			1		1	1
<i>Rhyncolus sculpturatus</i>	WL				4	4	3
<i>Salpingus planirostris</i>	WL			2	3	5	3
<i>Salpingus ruficollis</i>	WL		4	8	10	22	10
<i>Saperda scalaris</i>	WL			2	3	5	2
<i>Saprinus semistriatus</i>	WL		1			1	1
<i>Schizotus pectinicornis</i>	WL		2	9	5	16	10
<i>Scolytus intricatus</i>	WL		29	27	3	59	8
<i>Scraptia fuscula</i>	WL			5		5	4
<i>Scraptia testacea</i>	WL			2		2	1
<i>Scydmorephes helvolus</i>	WL			1		1	1
<i>Silvanoprus fagi</i>	WL			1	2	3	3
<i>Sinodendron cylindricum</i>	WL				1	1	1
<i>Soronia punctatissima</i>	WL		98	131	117	346	13
<i>Stagetus borealis</i>	WL	NT		1		1	1
<i>Stenagostus rhombeus</i>	WL	VU	2			2	1
<i>Stenocorus meridianus</i>	WL		5	1	5	11	5
<i>Stenostola dubia</i>	WL			1	1	2	2
<i>Stictoleptura scutellata</i>	WL	VU	1			1	1
<i>Strangalia attenuata</i>	WL	NT	1	1		2	1
<i>Synchita humeralis</i>	WL			1		1	1
<i>Synchita variegata</i>	WL	NT	1			1	1
<i>Tetrops praeustus</i>	WL			1	2	3	3
<i>Thanasimus femoralis</i>	WL		1			1	1
<i>Thanasimus formicarius</i>	WL		3		1	4	3
<i>Tillus elongatus</i>	WL			1		1	1
<i>Trichocelebe floralis</i>	WL			1		1	1
<i>Trypodendron domesticum</i>	WL		2		2	4	2
<i>Xestobium rufovillosum</i>	WL		5	4	2	11	8
<i>Xyleborinus attenuatus</i>	WL			1	1	2	2

Table 10 (continued)

Species wood-living	Guild	RDB	C	NBT	WPH	Total	No of sites
<i>Xyleborinus saxesenii</i>	WL		3	5	1	9	5
<i>Xyleborus monographus</i>	WL	NT	2	4	3	9	2
<i>Xyletinus longitarsis</i>	WL	NT	1			1	1
<i>Xylotrechus antilope</i>	WL	NT	1		1	2	1
Total			1029	2283	2032	5344	
Species associated with wood-living fungi	Guild	RDB	C	NBT	WPH	Total	No of sites
<i>Agathidium laevigatum</i>	WLF				1	1	1
<i>Agathidium rotundatum</i>	WLF				1	1	1
<i>Anisotoma axillaris</i>	WLF			4	1	5	3
<i>Atomaria diluta</i>	WLF	NT		1	1	2	1
<i>Atomaria pusilla</i>	WLF		1			1	1
<i>Atomaria turgida</i>	WLF		2	2		4	2
<i>Bitoma crenata</i>	WLF			1		1	1
<i>Bolitophagus reticulatus</i>	WLF		1			1	1
<i>Cis comptus</i>	WLF			1		1	1
<i>Cis dentatus</i>	WLF		1	1	1	3	2
<i>Cis fagi</i>	WLF				1	1	1
<i>Cis</i> sp.	WLF		1			1	1
<i>Cis submicans</i>	WLF	NT		1		1	1
<i>Corticarina minuta</i>	WLF		1	10	5	16	4
<i>Corticarina similata</i>	WLF			3	5	8	1
<i>Corticinara gibbosa</i>	WLF		16	5	12	33	9
<i>Cryptophagus badius</i>	WLF		4	13	17	34	8
<i>Cryptophagus confusus</i>	WLF		1	1	1	3	1
<i>Cryptophagus dentatus</i>	WLF				3	3	1
<i>Cryptophagus denticulatus</i>	WLF			1		1	1
<i>Cryptophagus distinguendus</i>	WLF		1			1	1
<i>Cryptophagus fuscicornis</i>	WLF	NT		1		1	1
<i>Cryptophagus labilis</i>	WLF			1		1	1
<i>Cryptophagus micaceus</i>	WLF		11	75	59	145	12
<i>Cryptophagus reflexus</i>	WLF				5	5	2
<i>Cryptophagus scanicus</i>	WLF		21	65	28	114	8
<i>Cychramus luteus</i>	WLF		9	7	11	27	8
<i>Cypha apicalis</i>	WLF	NT	1			1	1
<i>Dacne bipustulata</i>	WLF		71	73	44	188	13
<i>Diaperis boleti</i>	WLF		163	100	186	449	13
<i>Diplocoelus fagi</i>	WLF	NT			1	1	1
<i>Dorcatoma chrysomelina</i>	WLF		15	6	2	23	6
<i>Dorcatoma dresdensis</i>	WLF		2	1	5	8	4
<i>Dorcatoma flavicornis</i>	WLF			1	1	2	2
<i>Dorcatoma robusta</i>	WLF				1	1	1
<i>Elateroides dermestoides</i>	WLF		1		1	2	2
<i>Enicmus fungicola</i>	WLF				4	4	2
<i>Enicmus rugosus</i>	WLF		17	39	33	89	13
<i>Enicmus testaceus</i>	WLF		1	3	6	10	5
<i>Ennearthron cornutum</i>	WLF		2		2	4	3
<i>Latridius brevicollis</i>	WLF			3		3	1
<i>Latridius gemellatus</i>	WLF			1		1	1
<i>Latridius hirtus</i>	WLF			3	5	8	4
<i>Latridius minutus</i>	WLF				4	4	1
<i>Litargus connexus</i>	WLF			1	1	2	1
<i>Lordithon lunulatus</i>	WLF		3		3	6	4
<i>Micrambe abietis</i>	WLF				1	1	1

Table 10 (continued)

Species associated with wood-living fungi	Guild	RDB	C	NBT	WPH	Total	No of sites
<i>Orchesia fasciata</i>	WLF	NT	1		1	2	2
<i>Orchesia micans</i>	WLF		1	2	1	4	3
<i>Orchesia minor</i>	WLF	NT			1	1	1
<i>Orchesia undulata</i>	WLF		1	4	1	6	4
<i>Orthocis alni</i>	WLF			2		2	1
<i>Platystomos albinus</i>	WLF		12	9	10	31	8
<i>Scaphisoma agaricinum</i>	WLF		2	3	3	8	5
<i>Stephostethus lardarius</i>	WLF				2	2	2
<i>Stephostethus pandellei</i>	WLF		97	34	109	240	8
<i>Stictoleptura maculicornis</i>	WLF		6	4	1	11	6
<i>Triphyllus bicolor</i>	WLF			2	1	3	3
<i>Triplax aenea</i>	WLF				1	1	1
<i>Triplax rufipes</i>	WLF	NT	2	3	1	6	4
<i>Triplax russica</i>	WLF		1		2	3	2
<i>Tritoma bipustulata</i>	WLF		2	3	2	7	3
Total			471	490	588	1549	
Species - other, non wood-living	Guild	RDB	C	NBT	WPH	Total	No of sites
<i>Adalia decempunctata</i>	OTH		1	3	1	5	4
<i>Agabus congener</i>	OTH		1			1	1
<i>Agrypnus murinus</i>	OTH			1		1	1
<i>Aleochara curtula</i>	OTH		2	1		3	2
<i>Aleochara lanuginosa</i>	OTH		1			1	1
<i>Amara aenea</i>	OTH				1	1	1
<i>Amara familiaris</i>	OTH		1			1	1
<i>Anchomenus dorsalis</i>	OTH			1		1	1
<i>Anotylus rugosus</i>	OTH			2		2	2
<i>Anthonomus phyllocola</i>	OTH		2			2	2
<i>Aphidecta oblitterata</i>	OTH				1	1	1
<i>Aphthona euphorbiae</i>	OTH		1	4	2	7	3
<i>Archarius pyrrhoceras</i>	OTH		4	4	2	10	4
<i>Archarius salicivorus</i>	OTH		3	2	1	6	5
<i>Atheta graminicola</i>	OTH			1		1	1
<i>Atheta</i> sp.	OTH			1	1	2	2
<i>Athous haemorrhoidalis</i>	OTH		49	108	68	225	14
<i>Athous subfuscus</i>	OTH		485	60	67	612	13
<i>Athous vittatus</i>	OTH			5	7	12	5
<i>Atomaria</i> sp.	OTH		1	2	2	5	4
<i>Aulonothroscus brevicollis</i>	OTH			3	1	4	2
<i>Bembidion obtusum</i>	OTH				1	1	1
<i>Betulapion simile</i>	OTH		1	1		2	1
<i>Byrrhus pilula</i>	OTH			1		1	1
<i>Byturus tomentosus</i>	OTH		10		4	14	1
<i>Calathus rotundicollis</i>	OTH			1		1	1
<i>Calosoma inquisitor</i>	OTH		18	9	14	41	3
<i>Calvia quatuordecimguttata</i>	OTH				4	4	4
<i>Cantharis figurata</i>	OTH		1	1	2	4	2
<i>Cantharis fusca</i>	OTH		1			1	1
<i>Cantharis nigra</i>	OTH		1		3	4	2
<i>Cantharis nigricans</i>	OTH		1			1	1
<i>Cantharis obscura</i>	OTH		6	8	2	16	6
<i>Cantharis pellucida</i>	OTH		8	6	7	21	6
<i>Cantharis quadripunctata</i>	OTH				1	1	1
<i>Cantharis rufa</i>	OTH			1		1	1
<i>Cantharis rustica</i>	OTH		4	5	5	14	7

Table 10 (continued)

Species - other, non wood-living	Guild	RDB	C	NBT	WPH	Total	No of sites
<i>Carabus hortensis</i>	OTH		1		3	4	2
<i>Carpelimus elongatulus</i>	OTH		2			2	1
<i>Cetonia aurata</i>	OTH		21	13	19	53	12
<i>Ceutorhynchus obstrictus</i>	OTH		2	2	3	7	2
<i>Ceutorhynchus pallidactylus</i>	OTH		2	7	8	17	3
<i>Ceutorhynchus typhae</i>	OTH			2		2	1
<i>Chaetocnema picipes</i>	OTH			4		4	3
<i>Chilocorus bipustulatus</i>	OTH				1	1	1
<i>Chilocorus renipustulatus</i>	OTH		1	1	2	4	2
<i>Cimberis attelaboides</i>	OTH		5		1	6	1
<i>Coeliodes rana</i>	OTH				2	2	2
<i>Coeliodes transversealbofasciatus</i>	OTH			1		1	1
<i>Coeliodinus rubicundus</i>	OTH		1			1	1
<i>Contacyphon coarctatus</i>	OTH		6	6	11	23	6
<i>Contacyphon ochraceus</i>	OTH		1	8	2	11	4
<i>Contacyphon padi</i>	OTH		13	21	32	66	9
<i>Contacyphon variabilis</i>	OTH				1	1	1
<i>Corticaria</i> sp.	OTH			1		1	1
<i>Crepidodera aurata</i>	OTH			1	1	2	1
<i>Cryptocephalus labiatus</i>	OTH			1	1	2	1
<i>Cryptocephalus querceti</i>	OTH			1	1	2	1
<i>Cryptocephalus sexpunctatus</i>	OTH		1			1	1
<i>Cryptophagus</i>	OTH		1	5	3	9	4
<i>Ctenicera pectinicornis</i>	OTH				3	3	3
<i>Curculio nucum</i>	OTH				1	1	1
<i>Curculio venosus</i>	OTH		2	5	6	13	9
<i>Curculio villosus</i>	OTH		10	1	4	15	3
<i>Dendroxena quadrimaculata</i>	OTH		11	1	12	24	8
<i>Dermestes lardarius</i>	OTH			1		1	1
<i>Dermestes murinus</i>	OTH		4	4	1	9	2
<i>Dromius agilis</i>	OTH		37	29	28	94	13
<i>Dromius fenestratus</i>	OTH		1		4	5	4
<i>Dromius quadrimaculatus</i>	OTH		15	10	15	40	11
<i>Epuraea</i> sp.	OTH		1			1	1
<i>Exochomus quadripustulatus</i>	OTH			1	1	2	1
<i>Gastrophysa polygoni</i>	OTH				1	1	1
<i>Gaurotes virginea</i>	OTH				1	1	1
<i>Geodromicus plagiatus</i>	OTH		3			3	1
<i>Gymnetron veronicae</i>	OTH				1	1	1
<i>Harpalus latus</i>	OTH		1	2	1	4	4
<i>Hydraena britteni</i>	OTH		1			1	1
<i>Hypera meles</i>	OTH				1	1	1
<i>Hypera nigrirostris</i>	OTH		1			1	1
<i>Lagria hirta</i>	OTH		3		2	5	4
<i>Limnebius truncatellus</i>	OTH			1		1	1
<i>Limonium poneli</i>	OTH				1	1	1
<i>Lochmaea caprea</i>	OTH		1	1	2	4	3
<i>Malachius bipustulatus</i>	OTH		11	11	9	31	10
<i>Mecinus pascuorum</i>	OTH		1		1	2	1
<i>Meligethes aeneus</i>	OTH		13	12	21	46	11
<i>Meligethes pedicularius</i>	OTH				3	3	1
<i>Meligethes viridescens</i>	OTH		4	4	2	10	3
<i>Melinopterus prodromus</i>	OTH		1			1	1
<i>Metoecus paradoxus</i>	OTH		1			1	1
<i>Micrambe woodroffeii</i>	OTH		1			1	1

Table 10 (continued)

Species - other, non wood-living	Guild	RDB	C	NBT	WPH	Total	No of sites
<i>Microcara testacea</i>	OTH		3	1	1	5	4
<i>Mycetoporus lepidus</i>	OTH		2			2	2
<i>Myzia oblongoguttata</i>	OTH		1			1	1
<i>Nargus anisotomoides</i>	OTH		1			1	1
<i>Nebria brevicollis</i>	OTH		2	1		3	2
<i>Necrodes littoralis</i>	OTH		1		1	2	2
<i>Neocoenorrhinus germanicus</i>	OTH		1			1	1
<i>Neocoenorrhinus minutus</i>	OTH		1	1		2	1
<i>Nephus redtenbacheri</i>	OTH				1	1	1
<i>Nicrophorus humator</i>	OTH			1		1	1
<i>Nicrophorus investigator</i>	OTH		3	2	6	11	4
<i>Nicrophorus vespillo</i>	OTH		1	1	2	4	2
<i>Nicrophorus vespilloides</i>	OTH		39	40	26	105	12
<i>Notoxus monoceros</i>	OTH			1		1	1
<i>Oenopia conglobata</i>	OTH		1	1		2	1
<i>Oiceoptoma thoracicum</i>	OTH		4	8	4	16	6
<i>Omalium caesum</i>	OTH			1		1	1
<i>Omalium rivulare</i>	OTH			1		1	1
<i>Orchestes fagi</i>	OTH		2	14	5	21	5
<i>Orchestes hortorum</i>	OTH		1	2	2	5	3
<i>Orchestes pilosus</i>	OTH		12	12	7	31	9
<i>Orchestes quercus</i>	OTH		93	21	39	153	9
<i>Orchestes rusci</i>	OTH		1			1	1
<i>Orsodacne cerasi</i>	OTH			1		1	1
<i>Otiorhynchus carinatuspunctatus</i>	OTH				1	1	1
<i>Otiorhynchus singularis</i>	OTH		5	1	4	10	3
<i>Oxypoda procerula</i>	OTH		2	3	1	6	2
<i>Oxypoda</i> sp.	OTH		1			1	1
<i>Oxypoda spectabilis</i>	OTH		1			1	1
<i>Oxytelus laqueatus</i>	OTH		2		1	3	2
<i>Paraphotistus impressus</i>	OTH		2	2	1	5	4
<i>Pelenomus commari</i>	OTH		1			1	1
<i>Pella cognata</i>	OTH			3		3	1
<i>Pella funesta</i>	OTH				3	3	1
<i>Pella laticollis</i>	OTH		1			1	1
<i>Pella lugens</i>	OTH				1	1	1
<i>Phalacrus corruscus</i>	OTH			1		1	1
<i>Philonthus carbonarius</i>	OTH				1	1	1
<i>Philonthus cognatus</i>	OTH			1		1	1
<i>Philonthus tenuicornis</i>	OTH				1	1	1
<i>Phyllobius argentatus</i>	OTH				1	1	1
<i>Phyllobius glaucus</i>	OTH			1		1	1
<i>Phyllobius pyri</i>	OTH		84	95	63	242	12
<i>Phyllobius virideaeris</i>	OTH			3		3	1
<i>Phyllopertha horticola</i>	OTH				1	1	1
<i>Phyllotreta undulata</i>	OTH			2	1	3	3
<i>Phyllotreta vittula</i>	OTH			13	7	20	2
<i>Platynus assimilis</i>	OTH		3	17	8	28	3
<i>Platynus krynickii</i>	OTH	NT			1	1	1
<i>Podabrus alpinus</i>	OTH		1	1	1	3	3
<i>Podistra rufotestacea</i>	OTH				1	1	1
<i>Polydrusus mollis</i>	OTH			4	1	5	3
<i>Polydrusus tereticollis</i>	OTH		2		1	3	2
<i>Propylea quatuordecimpunctata</i>	OTH		1	1	1	3	3
<i>Prosternon tessellatum</i>	OTH		3	1		4	3

Table 10 (continued)

Species - other, non wood-living	Guild	RDB	C	NBT	WPH	Total	No of sites
<i>Protapion apricans</i>	OTH			1		1	1
<i>Protapion fulvipes</i>	OTH			4	7	11	7
<i>Psylliodes affinis</i>	OTH		1			1	1
<i>Pterostichus diligens</i>	OTH				1	1	1
<i>Pterostichus niger</i>	OTH			2	2	4	1
<i>Ptomaphagus varicornis</i>	OTH				1	1	1
<i>Rhagonycha lignosa</i>	OTH		3	5	3	11	7
<i>Rhagonycha lutea</i>	OTH		4	1	2	7	5
<i>Rhagonycha nigriventris</i>	OTH		1	2	3	6	2
<i>Rhagonycha testacea</i>	OTH		3	3	2	8	5
<i>Rhamphus pulicarius</i>	OTH			1		1	1
<i>Sciaphilus asperatus</i>	OTH		5		2	7	2
<i>Scymnus silesiacus</i>	OTH	NT		2		2	1
<i>Selatosomus aeneus</i>	OTH		17	16	15	48	9
<i>Selatosomus cruciatus</i>	OTH			2	1	3	1
<i>Sepedophilus testaceus</i>	OTH				1	1	1
<i>Serica brunnea</i>	OTH		1			1	1
<i>Sitona obsoletus</i>	OTH		2			2	2
<i>Soronia grisea</i>	OTH		33	52	47	132	11
<i>Strophosoma capitatum</i>	OTH		65	84	88	237	12
<i>Tachinus laticollis</i>	OTH		3	27	9	39	4
<i>Tachyporus chrysomelinus</i>	OTH		1			1	1
<i>Tachyporus solutus</i>	OTH			1		1	1
<i>Trechus quadristriatus</i>	OTH		1	1		2	2
<i>Trichius fasciatus</i>	OTH		1			1	1
<i>Trichoceble memnonia</i>	OTH		1	1		2	1
<i>Trixagus carinifrons</i>	OTH		2		1	3	1
<i>Trixagus dermestoides</i>	OTH		10	8	18	36	10
<i>Tychius stephensi</i>	OTH			1		1	1
<i>Tytthaspis sedecimpunctata</i>	OTH			1		1	1
<i>Xantholinus linearis</i>	OTH		1	1		2	2
Total			1215	862	807	2884	
Species—partly wood-living	Guild	RDB	C	NBT	WPH	Total	No of sites
<i>Aleochara moerens</i>	PWL		51	148	139	338	12
<i>Anthrenus museum</i>	PWL			2		2	2
<i>Aplocnemus nigricornis</i>	PWL		3	1	1	5	3
<i>Atheta crassicornis</i>	PWL			1	2	3	3
<i>Atheta fungi</i>	PWL			2	5	7	2
<i>Atheta nidicola</i>	PWL		1	7	2	10	4
<i>Atheta vaga</i>	PWL		495	538	553	1586	13
<i>Atomaria hislopi</i>	PWL		1			1	1
<i>Atomaria morio</i>	PWL				2	2	2
<i>Atomaria nigripennis</i>	PWL	VU			2	2	1
<i>Atomaria rubella</i>	PWL		2			2	1
<i>Atomaria wollastoni</i>	PWL		1			1	1
<i>Attagenus pellio</i>	PWL		6	16	6	28	5
<i>Biblopectus spinosus</i>	PWL			1		1	1
<i>Bryaxis bulbifer</i>	PWL		1			1	1
<i>Carcinops pumilio</i>	PWL		1			1	1
<i>Carpophilus marginellus</i>	PWL		1	4	9	14	5
<i>Dalopius marginatus</i>	PWL		109	99	69	277	14
<i>Margarinotus merdarius</i>	PWL		1	1	5	7	4
<i>Monotoma longicollis</i>	PWL			1		1	1
<i>Orthoperus atomus</i>	PWL		8	18	9	35	2
<i>Orthoperus</i> sp.	PWL				1	1	1

Table 10 (continued)

Species—partly wood-living	Guild	RDB	C	NBT	WPH	Total	No of sites
<i>Oxyptoda brevicornis</i>	PWL			12		12	1
<i>Oxyptoda exoleta</i>	PWL		1			1	1
<i>Ptinus fur</i>	PWL		5	14	4	23	9
<i>Ptinus rufipes</i>	PWL		4		1	5	4
<i>Quedius fuliginosus</i>	PWL		1			1	1
<i>Quedius maurus</i>	PWL			1	1	2	2
<i>Quedius mesomelinus</i>	PWL		143	376	216	735	13
<i>Quedius xanthopus</i>	PWL		2	13	11	26	11
<i>Thamiaraea cinnamomea</i>	PWL		5	38	54	97	11
<i>Thamiaraea hospita</i>	PWL	NT	1	1	4	6	4
Total			843	1294	1096	3233	

OTH other, non-saproxyllic, PWL partly wood-living, WL wood-living, WLF associated with woodlivingfungi, NBT nestbox and topping, WPH Woodpecker Hole, C Control, RDB Red Data Book

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10841-026-00788-7>.

Acknowledgements This manuscript has been produced with support of the EAC-R&D Grant Scheme, funding project number EAC-R&D 2024 Veteranisation. The support from the EAC Research & Development Grant Scheme to produce this article reflects the views of the authors. The EAC Research & Development Grant Scheme cannot be held responsible for any use that may be made of the information contained therein. Financial support via a grant has been provided by Eklandskapsstiftelsen. Financial support and time have also been provided by the County Administrative Boards of Blekinge, Jönköping, Kalmar, Kronoberg, Östergötland, Västmanland, Skåne, Uppsala, Statens Fastighetsverk, Municipalities of Jönköping and Linköping, Stiftelsen Skånska Landskap, Swedish Environmental Protection Agency, and Stiftelsen Pro Natura. A special thanks to Olof Persson who sorted all the samples and Hans-Erik Wanner who identified the beetles, and to Erik Hellberg Meshaks who ensured support for set-up of the project. We would also like to thank Adam Flöhr who helped with the updated analysis in the second revision. Finally, we would like to thank the two anonymous reviewers for their helpful comments, which much improved the manuscript.

Author contributions Mats Niklasson, Jonas Hedin and Vikki Bengtsson conceptualized the study. Mats Niklasson and Jonas Hedin designed the study. Data collection was coordinated by Vikki Bengtsson and performed by Pro Natura, Naturecentrum and Vikki Bengtsson. Vikki Bengtsson and Phil Wheeler performed the data analysis. Vikki Bengtsson wrote the first draft. Thomas Appelqvist allocated guilds to the Coleoptera. All authors commented on the first version of the manuscript, as well as read and approved the final manuscript.

Funding Open access funding provided by Swedish University of Agricultural Sciences.

Data availability The data supporting the findings of this study are available within the paper, its Supplementary Information and as open access in www.artportalen.se, project “Ekveteraniseringsförsök”.

Declarations

Competing interests The authors declare no competing interests.

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