

Boxing for biodiversity: evaluation of an artificially created decaying wood habitat

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Abstract Many saproxylic species are threatened in Europe because of habitat decline. Hollow trees represent an important habitat for saproxylic species. Artificial habitats may need to be created to maintain or increase the amount of habitat due to natural habitat decline. This study investigated the extent to which saproxylic beetles use artificial habitats in wooden boxes. The boxes were placed at various distances (0–1800 m) from known biodiversity hotspots with hollow oaks and studied over 10 years. Boxes were mainly filled with oak saw dust, oak leaves, hay and lucerne flour. In total, 2170 specimens of 91 saproxylic beetle species were sampled in 43 boxes. The abundance of species associated with tree hollows, wood rot and animal nests increased from the fourth to the final year, but species richness declined for all groups. This study shows that wooden boxes can function as saproxylic species habitats. The artificial habitats developed into a more hollow-like environment during the decade long experiment with fewer but more abundant tree hollow specialists.

Keywords Artificial habitats · Hollow trees · Intervention · Saproxylic beetles · Succession · Wood mould

Introduction

Hollows form when trees age (Gibbons and Lindenmayer 2002; Ranius et al. 2009a, b). These hollows are successively colonized by a wide range of taxa, such as birds (Kosinski 2006), mammals (Manning et al. 2013), reptiles (Bryant et al. 2012), beetles (Ranius and Jansson 2000) and other invertebrates [e.g., (mites Taylor and Ranius 2014) and

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pseudoscorpions (Ranius and Wilander 2000)]. Many invertebrates require that hollows contain wood mould (Ranius et al. 2009a, b; Hagen 2015), i.e. residual woody debris that is mixed with insect fragments, dead leaves, bird and mammal remains.

The number of large old trees is declining in many parts of the world (Lindenmayer et al. 2012). Europe has experienced a substantial deciduous forest reduction compared to pre-historic levels (Hannah et al. 1995; Björse and Bradshaw 1998; Lindbladh and Bradshaw 1998), greatly affecting the tree species most likely to form hollows (Remm and Löhmus 2011). In addition, forestry has reduced the old tree density because trees are often cut before hollows are formed (Eliasson and Nilsson 2002; Andersson and Östlund 2004; Lindenmayer et al. 2012). Trees in agricultural landscapes are also declining because they are not useful in agriculture practices (Dubois et al. 2009). The decrease in hollow trees has caused associated species populations to decline and even become red-listed (Ranius and Jansson 2000). Management practices have been devised in many countries to promote the formation of hollows in trees (Fritz and Heilmann-Clausen 2010; Sebek et al. 2013) or create compensatory habitats, such as artificial hollows (Jansson et al. 2009a; Goldingay and Stevens 2009). Wooden boxes filled with suitable substrates can function as habitats for saproxylic invertebrates (Jansson et al. 2009a; Hilszczański et al. 2014). Although these boxes attract and harbour saproxylic beetles during the first few years of deployment, their durability over time remains unknown. Continued migration over time is often assumed, which may result in species accumulation and late arrivals of certain species (e.g., predators after prey become established Weslien et al. 2011; Lee et al. 2014). Moreover, a later artificial wood mould decay stage, implying a fungal species composition change, could also cause shifts in the species composition and species richness (Kaila et al. 1994; Økland et al. 1996; Müller et al. 2014). However, the artificial wood mould is expected to decrease over time in the boxes due to larval consumption and fungal activity, reducing the total habitat volume of the box. This process contrasts that of a natural hollow, in which wood mould is continuously added as the hollow grows. A more thorough understanding and evaluation of these wood boxes is needed to efficiently manage the boxes.

This study investigated the extent to which boxes serve as artificial habitats for saproxylic beetles. More specifically, the study aimed to answer the following questions:

- (1) How do species richness, abundance and composition change over time?
- (2) How is species composition affected by the distance from dispersal sources (i.e., sites with hollow oaks)?
- (3) How is the species composition and richness affected by the original content of the boxes?

These questions were assessed by surveying saproxylic beetle fauna up to 10 years after boxes were placed. An earlier study (Jansson et al. 2009a) examined saproxylic beetle fauna in these boxes over the first 4 years.

Materials and methods

Field trial

The box dimensions were $0.70 \times 0.30 \times 0.30$ m, yielding a volume of approximately 60 L. The boxes were constructed of oak, with 25 mm thick walls and roof and a 50 mm thick bottom. An 80 mm diameter hole was cut into the front (Fig. 1). The roof could be opened and included a milled cross with four drilled holes (8 mm in diameter) at the

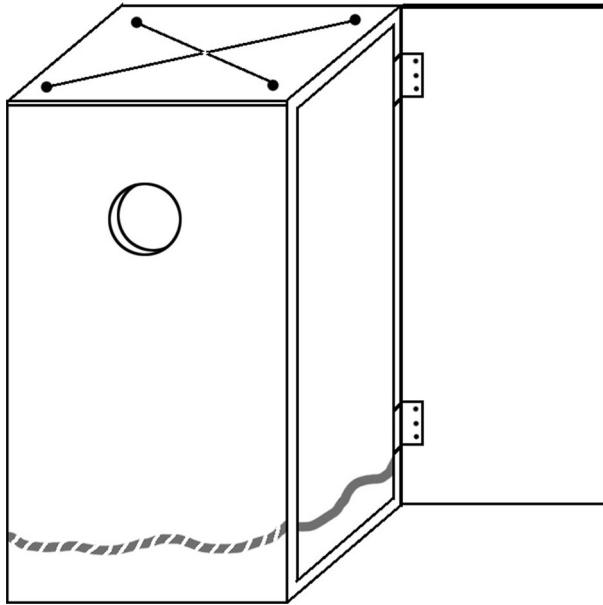


Fig. 1 A wooden box with a milled cross and holes drilled in the roof. Bowl-shaped clay on the bottom of the box and a transparent window with a door to the right

endpoints of the cross, which allowed rain water penetration. The bottom of the box was covered with 50 mm of clay formed into a bowl shape to retain moisture.

The boxes were filled to 70 % capacity with a mix of oak saw dust (50 %), oak leaves (25 %), hay (10 %), 1 L lucerne flour (2.5 %) (*Medicago falcata*) and 5 L water (12.5 %) at the start of the experiment, emulating the wood mould conditions in hollow trees. In addition, one of four different substrates was added: 1) a dead hen (*Gallus domesticus*), 2) 1 L of chicken dung, 3) 1 L additional lucerne flour plus 1 L of oat flakes or 4) five potatoes (Table 1). The dead hen and chicken dung were used to mimic the habitat in trunk cavities with bird nests. The lucerne flour and oat flakes increased the protein content and the potatoes created a moist environment. The boxes were suspended on oak trunks,

Table 1 Number of boxes per distance from sites with hollow oaks and the different added substrates used in the artificial wood mould

Distances (m)	Dead hen	Chicken dung	Lucerne flour and oat flakes	Potatoes	Total number of boxes
0	3	3	3	3	12
100	2 ^a	2	2	2 ^a	8
200	1 ^a	1	1	1	4
300	1	1	1	1	4
400	1	1	1	1	4
600	2 ^a	2	2	2	8
1800	2	2 ^a	2	2	8

^a One of these boxes was broken during the course of the study, and hence excluded from the analyses

approximately 4 m from the ground. The boxes were positioned on the shadiest side of each oak to mimic a more stable environment over time.

The study locations included Bjärka-Säby, Brokind and Grebo, which are situated approximately 15–20 km south of Linköping, Sweden (Fig. 2). The distance between the locations ranges from 10 to 20 km. These locations were selected because they are known to harbour species-rich saproxylic invertebrate fauna associated with old hollow oaks (Ranius and Jansson 2000). Approximately 50–100 hollow oaks exist in the core areas of each of the three locations. Old hollow oaks were absent in one or more directions, which allowed us to study the effect of the distance from a dispersal source.

Boxes were placed in the core area and at two or three surrounding sites with younger oaks. The surrounding sites were between 100 and 1800 m from the core area (Table 1), but in different directions. This range of distances was used because it is similar to the observed dispersal distances of saproxylic beetles (Ranius 2006). Boxes were spaced at a distance of 10–200 m at each site. Core area boxes were placed on old hollow oaks, while boxes at other sites were placed on younger oaks. Each core area was confirmed as the nearest dispersal source for wood mould dependent species by searching for hollow trees before box placement. No hollow trees that could contain large amounts of wood mould existed around the study sites, including *Quercus robur*, *Fraxinus excelsior*, *Tilia cordata*, *Acer platanoides*, *Aesculus hippocastanum* and *Ulmus glabra*.

The box experiments lasted for either ten (Brokind, Bjärka Säby) or nine years (Grebo), but had different starting years (2002, 2003 and 2004, respectively). Henceforth, the term “final year” is used for the 10th and 9th years. Five of 48 boxes were broken and discarded during the study period (Table 1).

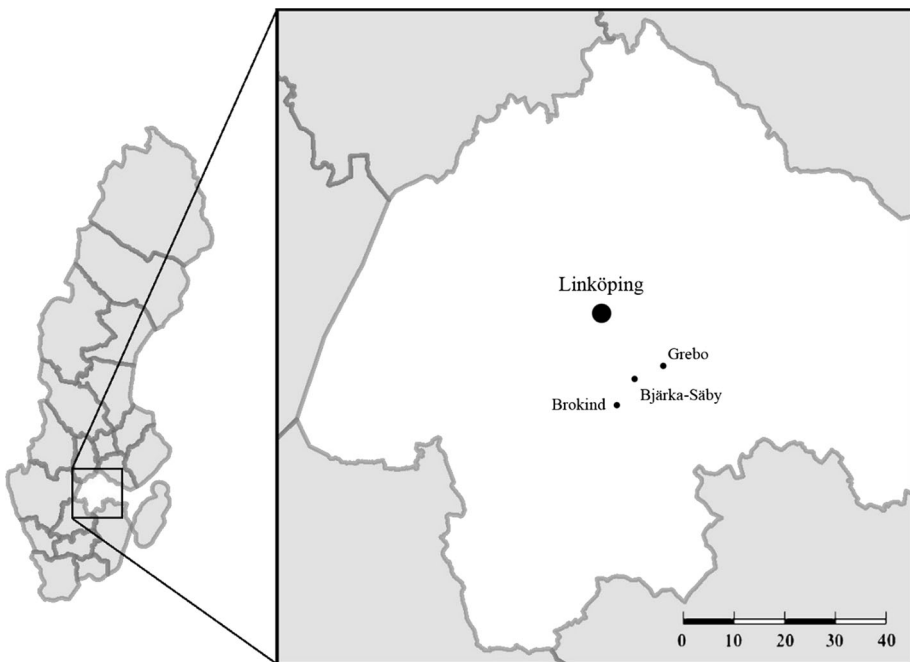


Fig. 2 The locations of the three study sites, south by south-east of Linköping, Sweden (distance in kilometres)

Invertebrate sampling

Only eclector trap invertebrate sampling data collected during the fourth year and final year were used in this analysis. Sampling was also conducted by placing pitfall traps in the boxes during the second and third years, and the results have been presented elsewhere (Jansson et al. 2009a). An eclector trap means that boxes are covered and sealed with a dark bag made of cloth with a single exit hole (Økland 1996). The hole was located approximately in front of the orifice, and a half transparent white plastic bottle filled with liquid preservatives was placed at the exit hole. The liquid consisted of 50 % propylene glycol, 50 % water and drops of dish soap to eliminate surface tension. The bottles were changed every third week. The sampling began in early spring (March–April) and continued until there no insects emerged (August). In the final year, boxes were taken down permanently and brought to the laboratory for eclector trapping.

Most invertebrates were identified to the species level the authors, but some difficult genera required experts (Stig Lundberg, Arne Ekström, Gunnar Sjödin and Rickard Andersson). All species considered as saproxylic (facultatively or obligatively), according to Dodelin et al. (2008), were used in the present study. The saproxylic beetle species were also classified into ecological ‘guilds’ based on preferred microhabitat (Ranius and Jansson 2000), including (i) tree-hollow species (occurs exclusively in rotten wood in hollows), (ii) wood rot species (rotten wood in any part of the trunk), (iii) nest species (nests from birds or other animals in tree hollows), (iv) dry wood species (dead, dry wood in trunks) and (v) fungi species (fruiting bodies of saproxylic fungi). The first three classes were of particular interest because they are more commonly associated with large, hollow oaks than other saproxylic species.

Data analyses

Statistical analyses were conducted using the data from year four and the final year because the same species sampling method was used each year.

A Generalized Linear Models for Multivariate Abundance Data (manyGLM) was used to test the effects of time, distance from the core area and substrate type (categorical factor) on the beetle species composition. The model included a negative binomial distribution, unadjusted univariate test and 999 permutations using the mvabund package (Wang et al. 2010). The distance was square root transformed prior to the test and the residual normality was visually checked. Two interactions were analysed in addition to the three main factors (time, distance and substrate type), including time \times distance and time \times substrate. Hence, manyGLM analysed five factors, resulting in nine estimates per model.

Odds ratios were used to compare the species occurrence odds in the box after 4 years and the last year. A meta-analytical tool (Comprehensive Metaanalysis 2.0; Borenstein et al. 2005) was used to calculate the weighted averages for species belonging to different guilds, and for those classified as obligate and facultative. A negative effect was observed for boxes directly placed on hollow trees. Therefore, the odds of finding a species in a box on a hollow oak was compared to a box placed some distance away (using boxes placed in the range of 100–400 m from a core area).

Results

In total, 2170 specimens of 91 saproxylic beetle species were collected from the boxes using eclector traps during the two sampling periods (Table 2).

According to the manyGLM results, there were no statistically significant effects of time ($P = 0.103$), distance (0.164) from the core area or their interaction (0.536). Species-based models included both increasing and decreasing species with age and distance, but among the 10 species contributing most to the overall model, few displayed a significant response (Table 3). In addition, the substrate effect estimates were not significant (substrate, time \times substrate; six P values ranging from 0.134 to 0.233).

Of the 91 saproxylic beetle species sampled in the eclector traps, 62 % exhibited higher odds of occurrence in the fourth year and 31 % higher odds in the final year (Appendix). Among the 15 most frequent species, four and five were significantly affiliated with the 4th year and the final year, respectively (Fig. 3a). Relatively few species occurred in both years (46 %) and many species were singletons (33 %). The guild-wise odds did not change over time, with the exception of fungi species (i.e. feeding on fruiting bodies of saproxylic fungi) that were most frequent during the fourth year (Fig. 3b). Facultative saproxylic species were also most frequent during the fourth year ($\ln(\text{OR}) = -0.545$, $\text{CI}_{95\%} -0.963$, -0.127) in contrast to obligate saproxylic species ($\ln(\text{OR}) = -0.545$, $\text{CI}_{95\%} -0.455$, 0.487).

When contrasting boxes placed on hollow oaks with those placed at some distance from a core area (100–400 m), it was apparent from the meta-analysis of all species, that hollow oaks were less preferred ($\ln(\text{OR}) = -0.321$; $\text{CI}_{95\%} -0.624$, -0.018). No differences existed among guilds or when comparing facultative and obligate saproxylic species (data not shown).

Discussion

This study demonstrates that boxes can function as artificial saproxylic beetle habitats for at least 10 years. Furthermore, the distance to real hollow trees affected colonizing species composition.

Table 2 A summary of species and specimens found in 43 boxes with artificial wood mould

	Year four (SD)	Year ten (SD)	Both years (SD)
Total number of saproxylic beetle species	75	42	91
Total number of saproxylic beetle specimens	1089	1081	2170
Total number of redlisted saproxylic beetles species	8	5	11
Mean number of saproxylic beetle species per box	5.7 (4.3)	5.0 (2.8)	10.0 (5.1)
Mean number of saproxylic beetle specimens per box	25.3 (43.2)	25.1 (36.0)	50.5 (54.7)
Total number of HWN species ^a	47	29	55
Total number of HWN specimens ^a	669	922	1591
Mean number of HWN species per box ^a	4.1 (3.3)	3.5 (2.2)	7.0 (3.5)
Mean number of HWN specimens per box ^a	15.5 (18.7)	21.4 (31.3)	37.0 (36.8)
Proportion HWN of saproxylic species/specimens (%) ^a	63/61	69/85	60/73

^a HWN saproxylic beetles associated with tree hollows, wood rot, or animal nests

Table 3 The top 10 saproxylic species that contributed to the time effect and the distance from the core area (DFCA) effect

	% Contribution to time effect (P value; estimate)	% Contribution to DFCA effect (P value; estimate)	Habitat type (saproxylic type) ^a
Top-ranked: time effect			
<i>Liocola marmorata</i>	7.3 (0.039; 0.47)	1.1 (0.775; 0.026)	Hole (O)
<i>Scraptia fuscula</i>	7.2 (0.116; 0.33)	1.4 (0.78; 0.016)	Nest (O)
<i>Ctesias serra</i>	7.0 (0.02; 1.03)	2.9 (0.358; 0.083)	Rot (O)
<i>Hypebaeus flavipes</i>	5.9 (0.063; 0.82)	0.7 (0.884; 0.023)	Rot (O)
<i>Euplectus mutator</i>	5.8 (0.137; 0.31)	2.4 (0.617; 0.026)	(O)
<i>Anaspis thoracica</i>	5.7 (0.113; 2.07)	4.4 (0.215; -0.49)	(O)
<i>Anaspis marginicollis</i>	4.7 (0.156; 0.52)	0.5 (0.853; -0.023)	(O)
<i>Cryptophagus badius</i>	4.7 (0.055; 0.53)	0.7 (0.023; 0.43)	Rot (O)
<i>Ptinus rufipes</i>	4.6 (0.27; 0.27)	1.7 (0.651; -0.055)	Rot (O)
<i>Dasytes cyaneus</i>	4.6 (0.092; 0.58)	1.1 (0.651; -0.062)	(O)
Top-ranked: DFCA effect			
<i>Ptinus fur</i> (♀)	2.8 (0.627; 0.14)	11.9 (0.004; -0.32)	Hole (F)
<i>Trox scaber</i>	0.2 (0.042; -2.04)	9.0 (0.017; 0.13)	Nest (F)
<i>Atomaria morio</i>	3.6 (0.076; 0.49)	7.4 (0.107; -1.58)	Nest (F)
<i>Phyllodrepa melanocephala</i>	0.3 (0.126; -2.63)	6.3 (0.235; 0.18)	(F)
<i>Cryptophagus micaceus</i>	0.6 (0.689; -0.064)	6.0 (0.274; 0.19)	Nest (O)
<i>Prionychus ater</i>	4 (0.485; 0.20)	5.2 (0.2; -0.12)	Hole (O)
<i>Anaspis thoracica</i>	5.7 (0.113; 2.07)	4.4 (0.215; -0.49)	(O)
<i>Anthrenus museorum</i>	4.3 (0.207; -0.25)	4.0 (0.167; -0.13)	Nest (F)
<i>Dropephylla ioptera</i>	0 (0.376; -0.66)	3.9 (0.112; -0.46)	Hole (O)
<i>Ctesias serra</i>	7 (0.02; 1.03)	2.9 (0.358; 0.083)	Rot (O)

Partial results from many generalized linear models for multivariate abundance data (GLM)

^a *Nest* nest species, *hollow* tree-hollow species, *rot* wood rot species, *O* obligate saproxylic species, *F* facultative saproxylic species

Changes over time

The species richness decreased between year four and the final year (Table 2). This decrease may be due to a wood mould decrease, as the wood mould volume had decreased by 65 % after 10 years (data not shown). All saproxylic beetle guilds experienced species richness declines from the fourth to the final year, but the total abundance of species associated with tree hollows, wood rot and animal nests increased (Table 2). Thus, the beetle assemblage became increasingly dominated by specialized hollow tree species. This dominance in the final year may occur because the artificial wood mould becomes increasingly similar to real wood mould. Saproxylic fauna generally changes with succession, and many species occur in the later decay stages (Kaila et al. 1994; Økland et al. 1996; Lassauce et al. 2011; Müller et al. 2014; Milberg et al. 2016). In contrast, the facultative saproxylic species generally decreased over time. Consequently, the species composition developed an increasingly higher degree of specialisation to wood mould. Among the noteworthy species using the boxes was *Osmoderma eremita* (NT, Gärdenfors 2010), of which four specimens were recorded in the last year. *O. eremita* requires old trees

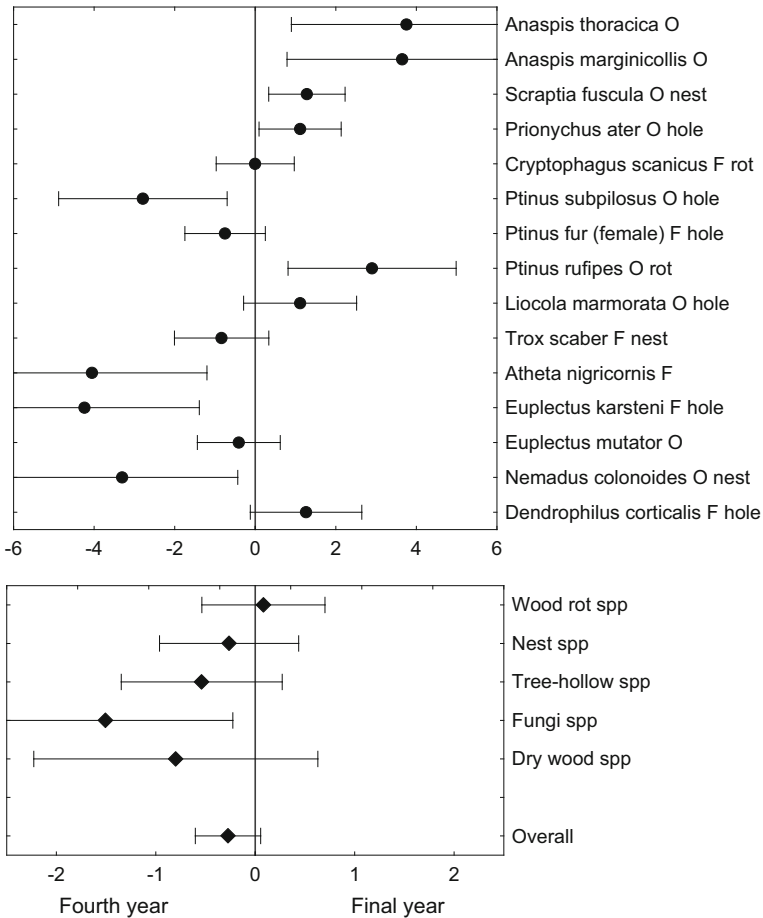


Fig. 3 In (Odds ratios) for: **a** 15 of the most frequent saproxylic beetle species found in boxes with artificial wood mould, comparing the fourth year and final year occurrences. Bars indicate 95 % confidence intervals, the zero reference line indicates no difference and positive values indicate that the species was more common during the last year. O and F refer to obligate and facultative saproxylic species. Guild type is also given as rot, nest, hollow, fungi and dry. **b** Weighted average of ln(OR) per guild, based on all species classified as belonging to a guild (N = 66). “Overall” refers to the outcome when analysing all saproxylic beetle species identified (N = 91)

with large amounts of wood mould (Ranius et al. 2009a, b). The species is an indicator of high saproxylic beetle species richness (Ranius 2002; Jansson et al. 2009b) and has been proposed as an umbrella species for saproxylic environments.

Distance from dispersal sources

Steady species declines were expected with distance from core areas based on previously observed beetle dispersal limitations in hollow oaks (Ranius and Hedin 2001; Ranius 2006; Jansson et al. 2009a). However, such a trend was not apparent in the data. This result may suggest that hollow oaks do not constitute the main source habitats of some species. In

addition, the boxes placed on the trunks of hollow oaks may directly ‘compete’ with hollow trees for migrating beetles, while boxes placed at a distance from the hollow oaks might attract a larger proportion of the dispersing beetles (cf Ranius et al. 2010). This assumption was confirmed by comparing the odds of finding a species in a box on a hollow oak in a core area with that of finding a species in a box on a non-hollow oak at some distance away. Hence, a box’s benefit may improve if not placed directly on hollow oaks, but on other trees, possibly at a distance from a hollow oak core area.

Original box contents

Neither the different artificial wood mould additives nor the the interactions between time and the additives suggested any influence on composition of the saproxylic beetle species composition (manyGLM). Jansson et al. (2009a) reported differences in the number of specimens between substrate types for some groups after 4 years, suggesting that potential initial benefits decrease as the decay process continues.

Box usage in conservation management

91 saproxylic beetle species, including a saproxylic environment umbrella species, were detected in this analysis, suggesting that boxes with sawdust are sufficient artificial habitats. With some modification in box design, and a strategy for refilling boxes, they could fulfil their intended role in conservation of saproxylic species. The goals of such projects may be to increase the available habitat or to connect isolated sites. Mature boxes may also be used to translocate saproxylic beetle assemblages.

Five boxes were broken during the 10 year period (Table 1). The metallic band holding the box was only attached to the back side of the box and a whole side could come loose. Therefore, the box suspension should be improved so that all sides of the box are held together by the metallic band if used in future conservation management projects. Moreover, some of the boxes began to leak wood mould after the 10 year period when the wood had begun to disintegrate due to larvae consumption, wasp gnawing or other reasons. Therefore, the bottom of a box should be covered with a non-consumable substance, such as a plastic sheet. The boxes could also benefit from being larger to obtain a more stable micro-climate. Finally, material that can develop into wood mould must eventually be added to the boxes. Small, annual additions would mimic the dynamics in a tree hollow, but longer intervals can be used for practical and logistical reasons.

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Appendix

See Table 4.

Table 4 Saprophytic beetle species recorded in boxes with artificial wood mould evaluated as an intervention method

Species name	Obligate or facultative saprophytic species	Guild	Red listed 2010	Ln (OR)	Lower CI _{95%}	Upper CI _{95%}	Number of occurrences in boxes (max 2 × 43)
<i>Plegaderus caesus</i>	O	Hole		-1.66	-4.72	1.41	2
<i>Gnathoncus buyssoni/nannetensis</i>	F	Nest		0.00	-2.80	2.80	2
<i>Dendrophilus corticalis</i>	F	Hole		1.26	-0.12	2.65	12
<i>Paromalus flavicornis</i>	O	Rot		-1.12	-4.35	2.11	1
<i>Margarinotus striola</i>	F	Hole		-1.12	-4.35	2.11	1
<i>Nemadus colonoides</i>	O	Nest		-3.31	-6.18	-0.43	10
<i>Stenichnus bicolor</i>	F			-1.12	-4.35	2.11	1
<i>Stenichnus godarti</i>	O	Hole		-1.66	-4.72	1.41	2
<i>Scydmaenus hellwigii</i>	F	Nest		-1.12	-4.35	2.11	1
<i>Velleius dilatatus</i>	F	Nest		-1.12	-4.35	2.11	1
<i>Bisnius subuliformis</i>	O	Nest		-2.71	-5.62	0.20	6
<i>Bibloporus bicolor</i>	O	Rot		-1.12	-4.35	2.11	1
<i>Gabrius splendidulus</i>	F			-1.12	-4.35	2.11	1
<i>Thamiaraea hospita</i>	O		NT	-1.66	-4.72	1.41	2
<i>Quedius brevicornis</i>	O	Nest		-1.66	-4.72	1.41	2
<i>Quedius mesomelinus</i>	F	Nest		-0.72	-3.16	1.72	3
<i>Quedius cruentus</i>	F	Nest		-2.02	-5.01	0.98	3
<i>Quedius xanthopus</i>	F	Fungi		-1.12	-4.35	2.11	1
<i>Euplectus nanus</i>	F	Hole		-2.52	-5.45	0.41	5
<i>Euplectus mutator</i>	O			-0.41	-1.44	0.62	19
<i>Euplectus karsteni</i>	F	Hole		-4.24	-7.09	-1.39	19
<i>Hapalaraea pygmaea</i>	O	Nest		1.66	-1.41	4.72	2
<i>Phyllodrepa melanocephala</i>	F			0.31	-1.25	1.87	7
<i>Dropephylla ioptera</i>	O	Hole		0.00	-2.80	2.80	2
<i>Hapalaraea nigra</i>	F	Fungi		-2.29	-5.25	0.66	4
<i>Hapalaraea floralis</i>	F	Nest		-1.66	-4.72	1.41	2
<i>Haploglossa villosula</i>	F	Nest		-2.71	-5.62	0.20	6
<i>Atheta nigricornis</i>	F			-4.05	-6.90	-1.20	17
<i>Atheta crassicornis</i>	F			-1.66	-4.72	1.41	2
<i>Atheta euryptera</i>	F			-1.12	-4.35	2.11	1
<i>Trox scaber</i>	F	Nest		-0.83	-2.00	0.34	15
<i>Liocola marmorata</i>	O	Hole		1.11	-0.29	2.52	11
<i>Osmoderma eremita</i>	O	Hole	NT	1.66	-1.41	4.72	2
<i>Ampedus nigrinus</i>	O			-1.66	-4.72	1.41	2
<i>Ampedus nigroflavus</i>	O	Rot	NT	0.00	-1.46	1.46	8
<i>Ampedus tristis</i>	O			-1.12	-4.35	2.11	1
<i>Ampedus pomorum</i>	O	Rot		-1.12	-4.35	2.11	1
<i>Ampedus hjorti</i>	O	Hole		-1.66	-4.72	1.41	2
<i>Ampedus balteatus</i>	O	Rot		-2.02	-5.01	0.98	3
<i>Melanotus castanipes</i>	O	Rot		-1.12	-4.35	2.11	1

Table 4 continued

Species name	Obligate or facultative saproxylic species	Guild	Red listed 2010	Ln (OR)	Lower CI _{95%}	Upper CI _{95%}	Number of occurrences in boxes (max 2 × 43)
<i>Aulonothroscus brevicollis</i>	F			-1.12	-4.35	2.11	1
<i>Dermestes lardarius</i>	F	Nest		-1.12	-4.35	2.11	1
<i>Globicornis nigripes</i>	O	Nest	NT	1.12	-2.11	4.35	1
<i>Megatoma undata</i>	F	Rot		-0.74	-2.50	1.01	6
<i>Anthrenus scrophulariae</i>	F	Nest		1.71	-0.48	3.90	6
<i>Anthrenus museorum</i>	F	Nest		0.00	-1.66	1.66	6
<i>Ctesias serra</i>	O	Rot		1.20	-0.460	2.86	8
<i>Ptinus rufipes</i>	O	Rot		2.90	0.81	4.99	14
<i>Ptinus fur (female)</i>	F	Hole		-0.75	-1.75	0.25	22
<i>Ptinus subpilosus</i>	O	Hole		-2.79	-4.88	-0.70	13
<i>Xestobium rufovillosum</i>	O	Dry		-1.66	-4.72	1.41	2
<i>Gastrallus immarginatus</i>	O	Dry		-1.12	-4.35	2.11	1
<i>Hemicoelus canaliculatus</i>	O	Dry		1.12	-2.11	4.35	1
<i>Lyctus linearis</i>	O	Dry	VU	-1.12	-4.35	2.11	1
<i>Lymexylon navale</i>	O	Dry	NT	-1.12	-4.35	2.11	1
<i>Hypebaeus flavipes</i>	O	Rot	VU	0.31	-1.25	1.87	7
<i>Dasytes cyaneus</i>	O			3.04	0.15	5.92	8
<i>Trichoceble memnonia</i>	O	rot		1.12	-2.11	4.35	1
<i>Rhizophagus cribratus</i>	O	Rot		-1.12	-4.35	2.11	1
<i>Cryptophagus acutangulus</i>	F			-1.12	-4.35	2.11	1
<i>Cryptophagus badius</i>	O	Rot		0.00	-2.80	2.80	2
<i>Cryptophagus confusus</i>	F	Hole		-2.02	-5.01	0.98	3
<i>Cryptophagus micaceus</i>	O	Nest		0.00	-1.46	1.46	8
<i>Cryptophagus quercinus</i>	O	Hole	NT	1.66	-1.41	4.72	2
<i>Cryptophagus dentatus</i>	F	Fungi		-2.02	-5.01	0.98	3
<i>Cryptophagus scanicus</i>	F	Rot		0.00	-0.97	0.97	22
<i>Cryptophagus reflexus</i>	F			-1.12	-4.35	2.11	1
<i>Cryptophagus scutellatus</i>	F			-1.12	-4.35	2.11	1
<i>Atomaria morio</i>	F	Nest		1.92	-0.24	4.08	7
<i>Dacne bipustulata</i>	O	Fungi		-1.12	-4.35	2.11	1
<i>Cerylon histerooides</i>	O	Rot		-1.12	-4.35	2.11	1
<i>Latridius minutus</i>	F			1.15	-1.16	3.45	4
<i>Latridius nidicola</i>	F			0.72	-1.72	3.16	3
<i>Latridius consimilis</i>	F			-1.12	-4.35	2.11	1
<i>Corticaria serrata</i>	F			-1.71	-3.90	0.48	6
<i>Corticaria longicollis</i>	F			1.12	-2.11	4.35	1
<i>Corticarina minuta</i>	F			1.12	-2.11	4.35	1
<i>Corticarina similata</i>	F			1.66	-1.41	4.72	2
<i>Mycetophagus 4-guttatus</i>	F	Fungi	NT	-1.12	-4.35	2.11	1
<i>Diaperis boleti</i>	O	Fungi		-1.12	-4.35	2.11	1
<i>Tenebrio opacus</i>	O	Hole	VU	-1.12	-4.35	2.11	1
<i>Tenebrio molitor</i>	F	Nest		2.02	-0.98	5.01	3

Table 4 continued

Species name	Obligate or facultative saproxylic species	Guild	Red listed 2010	Ln (OR)	Lower CI _{95%}	Upper CI _{95%}	Number of occurrences in boxes (max 2 × 43)
<i>Prionychus ater</i>	O	Hole		1.11	0.096	2.13	23
<i>Pseudocistela ceramboides</i>	O	Hole		1.12	-2.11	4.35	1
<i>Mycetochara humeralis</i>	O	Hole	NT	-1.66	-4.72	1.41	2
<i>Mycetochara linearis</i>	O	Rot		-1.66	-4.72	1.41	2
<i>Scraptia fuscula</i>	O	Nest		1.28	0.34	2.23	30
<i>Anaspis marginicollis</i>	O			3.65	0.79	6.51	13
<i>Anaspis rufilabris</i>	O			2.71	-0.20	5.62	6
<i>Anaspis thoracica</i>	O			3.76	0.90	6.61	14
<i>Malachius bipustulatus</i>	O	Rot		3.18	0.30	6.01	9

In total, 43 boxes were sampled after 4 and 9 or 10 years in the field. Ln(OR) is the ln(odds ratio) contrasting these two time points; a positive value means an increase over time

References

- Andersson R, Östlund L (2004) Spatial patterns, density changes and implications on biodiversity for old trees in the boreal landscape of northern Sweden. *Biol Conserv* 118:443–453
- Björse G, Bradshaw R (1998) 2000 years of forest dynamics in southern Sweden: suggestions for forest management. *For Ecol Manag* 104:15–26
- Borenstein M, Hedges L, Higgins J, Rothstein H (2005) Comprehensive meta-analysis version 2. Biostat, Englewood. www.meta-analysis.com
- Bryant G, Dundas S, Fleming P, Bennett N (2012) Tree hollows are of conservation importance for a Near-Threatened python species. *J Zool* 286:81–92
- Dodelin B, Ballot P, Stokland J (2008) The saproxylic database checklist of beetles, vers. 8/2008. <http://radon.uio.no/WDD/Login.aspx?ReturnUrl=%2fwdd%2fDefault.aspx>. Accessed 10 Dec 2010
- Dubois G, Vignon V, Delettre YR, Rantier Y, Vernon P, Burel F (2009) Factors affecting the occurrence of the endangered saproxylic beetle *Osmoderma eremita* (Scopoli, 1763) (Coleoptera: Cetoniidae) in an agricultural landscape. *Landsc Urban Plan* 91:152–159
- Eliasson P, Nilsson S (2002) You should hate young oaks and young noblemen: the environmental history of oaks in eighteenth- and nineteenth-century Sweden. *Environ Hist* 7:659–677
- Fritz Ö, Heilmann-Clausen J (2010) Rot holes create key microhabitats for epiphytic lichens and bryophytes on beech (*Fagus sylvatica*). *Biol Conserv* 143:1008–1016
- Gärdenfors U (ed) (2010) The 2010 red list of Swedish species. Swedish Species Information Center, SLU, Uppsala, p 592
- Gibbons P, Lindenmayer D (2002) Tree hollows and wildlife conservation in Australia. CSIRO Publishing, Collingwood, p 211. ISBN 9780643067059
- Goldingay RL, Stevens JR (2009) Use of artificial tree hollows by Australian birds and bats. *Wildl Res* 36:81–97
- Hagen S (2015) The significance of tree, site and landscape variables on eight saproxylic beetles in hollow oaks. MSc thesis, Norwegian University of Life Sciences, Department of Ecology & Natural Resources
- Hannah L, Carr J, Lankerani A (1995) Human disturbance and natural habitat: a biome level analysis of a global data set. *Biodivers Conserv* 4:128–155
- Hilszczański J, Jaworski T, Plewa R, Jansson N (2014) Surrogate tree cavities: boxes with artificial substrate can serve as temporary habitat for *Osmoderma barnabita* (Motsch.) (Coleoptera, Cetoniinae). *J Insect Conserv* 18:855–861
- Jansson N, Larsson A, Milberg P, Ranius T (2009a) Boxes mimicking tree hollows can help conservation of saproxylic beetles. *Biodivers Conserv* 18:3891–3908
- Jansson N, Bergman K-O, Jonsell M, Milberg P (2009b) An indicator system for identification of sites of high conservation value for saproxylic oak (*Quercus* spp.) beetles in southern Sweden. *J Insect Conserv* 13:399–412

- Kaila L, Martikainen P, Punttila P, Yakovlev E (1994) Saproxyllic beetles (Coleoptera) on dead birch trunks decayed by different polypore species. *Ann Zool Fenn* 31:97–107
- Kosinski Z (2006) Factors affecting the occurrence of middle spotted and great spotted woodpeckers in deciduous forests—a case study from Poland. *Ann Zoologici Fenn* 43:198–210
- Lassauce A, Paillet Y, Jactel H, Bouget C (2011) Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxyllic organisms. *Ecol Indic* 11:1027–1039
- Lee SI, Spence JR, Langor DW (2014) Succession of saproxyllic beetles associated with decomposition of boreal white spruce logs. *Agric For Entomol* 16:391–405
- Lindbladh M, Bradshaw R (1998) The origin of present forest composition and pattern in southern Sweden. *J Biogeogr* 25:463–477
- Lindenmayer D, Laurance W, Franklin J (2012) Global decline in large old trees. *Science* 338:1305–1306
- Manning A, Gibbons P, Fischer J, Oliver D, Lindenmayer D (2013) Hollow futures? Tree decline, lag effects and hollow-dependent species. *Anim Conserv* 16:395–403
- Milberg P, Bergman K-O, Sancak K, Jansson N (2016) Assemblages of saproxyllic beetles on large downed trunks of oak. *Ecology & Evolution* 6. doi:10.1002/ece3.1935
- Müller J, Jarzabek-Müller A, Bussler H, Gossner MM (2014) Hollow beech trees identified as keystone structures for saproxyllic beetles by analyses of functional and phylogenetic diversity. *Anim Conserv* 17:154–162
- Økland B (1996) A comparison of three methods of trapping saproxyllic beetles. *Eur J Entomol* 93:195–209
- Økland B, Bakke A, Hågvar S, Kvamme T (1996) What factors influence the diversity of saproxyllic beetles? A multiscaled study from a spruce forest in southern Norway. *Biodivers Conserv* 5:75–100
- Ranius T (2002) *Osmoderma eremita* as an indicator of species richness of beetles in tree hollows. *Biodivers Conserv* 11:931–941
- Ranius T (2006) Measuring the dispersal of saproxyllic insects: a key characteristic for their conservation. *Popul Ecol* 48:177–188
- Ranius T, Hedin J (2001) The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. *Oecologia* 126:363–370
- Ranius T, Jansson N (2000) The influence of forest regrowth, original canopy cover and tree size on saproxyllic beetles associated with old oaks. *Biol Conserv* 95:85–94
- Ranius T, Wilander P (2000) Occurrence of *Larca lata* H.J. Hansen (Pseudoscorpionida: Garypidae) and *Allochernes wideri* C.L. Koch (Pseudoscorpionida: Chernetidae) in tree hollows in relation to habitat quality and density. *J Insect Conserv* 4:23–31
- Ranius T, Niklasson M, Berg N (2009a) Development of tree hollows in pedunculate oak (*Quercus robur*). *For Ecol Manag* 257:303–310
- Ranius T, Svensson GP, Berg N, Niklasson M, Larsson MC (2009b) The successional change of hollow oaks affects their suitability for an inhabiting beetle, *Osmoderma eremita*. *Ann Zoologici Fenn* 46:205–216
- Ranius T, Johansson V, Fahrig L (2010) A comparison of patch connectivity measures using data on invertebrates in hollow oaks. *Ecography* 33:971–978
- Remm J, Löhmus A (2011) Tree cavities in forests: the broad distribution pattern of a keystone structure for biodiversity. *For Ecol Manag* 262:579–585
- Sebek P, Altman J, Platek M, Cizek L (2013) Is active management the key to the conservation of saproxyllic biodiversity? Pollarding promotes the formation of tree hollows. *PLoS ONE* 8:e60456
- Taylor A, Ranius T (2014) Tree hollows harbour a specialised oribatid mite fauna. *J Insect Conserv* 18:39–55
- Wang Y, Naumann U, Wright S, Warton D (2010) mvabund: statistical methods for analysing multivariate abundance data. R package version 3.9.3
- Weslien J, Djupström LB, Schroeder M, Widenfalk O (2011) Long-term priority effects among insects and fungi colonizing decaying wood. *J Anim Ecol* 80:1155–1162