



# Defining stump harvesting retention targets required to maintain saproxylic beetle biodiversity<sup>☆</sup>



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## ABSTRACT

Stumps comprise up to 80% of the residual deadwood following clear cutting and are a significant source of biomass for bioenergetic applications. However, stump harvesting may pose significant conservation risks for saproxylic organisms that occur in residual deadwood. To define retention targets for stump harvesting operations, we compared abundance and species richness of saproxylic beetles within individual stumps as well as species accumulation curves in replicated pairs of clear cuts with and without stump harvesting in northern Sweden. Using 20 stands, we sampled 1049 stumps using eclector traps and collected 9821 beetles representing 253 species with known saproxylic biology. Nineteen of these species were red-listed in Sweden. We hypothesized that individual stumps left following stump harvesting would contain higher densities and species richness than in clear cuts without stump removal due to crowding of beetles into increasingly limited habitats. However, we found no difference in density or richness within individual stumps between control clear cuts and stumped stands. We also compared species richness between control and stumped treatments using rarefaction within individual stands and across all stands and found no difference. As with density and richness, beetle composition at the stand-level did not differ between control and stumped stands. Thus, the density of surrounding stumps within a stand had very little effect on beetle assemblages in residual stumps. We estimated the effect of stump harvest on species richness at the stand level by combining all samples and extrapolating a rarefaction curve derived from the landscape-level species pool to an accumulated sample volume of 48 m<sup>3</sup> which corresponds to the total volume of stumps on average-sized clear cuts in Northern Sweden. Using this curve, we compared differences in species richness in average-sized clear cuts with 100% (48 m<sup>3</sup>) and 25% (12 m<sup>3</sup>) stump retention and found that stump harvest resulted in a 26% (95% C.I. 7–41%) loss of species. While the absolute scaling of the landscape-derived rarefaction does not reflect species loss at the stand-level because the combined curve reflects all rare species in the landscape, the relative species loss derived from this curve may serve as credible benchmark for species loss at the stand level following current stump harvesting practices. This benchmark may be further calibrated with additional information on number of singleton species and estimates of maximum species richness.

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## 1. Introduction

The desire to offset fossil fuel consumption with renewable sources such as forest biomass has spurred interest in the recovery of additional logging residues such as stumps in Fennoscandia (Björheden, 2006). Slash and stumps in combinations with other wood fuels could theoretically provide 40 TW h of energy in Sweden by 2020, which is more than twice the industry use of fossil

fuels (Oljekommissionen, 2006). The demand for renewable energy has led to extensive implementation of stump harvesting throughout Finland (Hakkila, 2004) as cited in Walmsley and Godbold (2010) and significant trials within Sweden which are estimated to provide ca. 2 TW h in the near future (Skogsstyrelsen, 2009). However, in Finland and Sweden, coarse deadwood has already been greatly reduced through sustained, intensive harvest (Siitonen, 2001; Stenbacka et al., 2010) and stumps now comprise much of the deadwood (Eräjää, 2010; Rabinowitsch-Jokinen and Vanha-Majamaa, 2010). For saproxylic organisms that rely on dead and decaying wood to complete their life cycle, many of which are currently red-listed (Nieter and Alexander, 2010; Gärdenfors, 2015), stumps may serve an important habitat legacy in intensively

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managed stands (Hedgren, 2007; Caruso and Rudolph, 2009; Hjaltn et al., 2010; Jonsell and Hansson, 2011; Jonsell and Schroeder, 2014). Thus stump harvesting can be viewed as an important ecological trade-off that pits long-term potential benefits of climate mitigation strategies against short-term (Geijer et al., 2014) or long-term (Johansson et al., 2016) impacts of biodiversity loss.

Although stumps have been identified as an important substrate for saproxylic organisms (beetles: (Jonsell and Schroeder, 2014); lichens: (Svensson et al., 2016)), we have limited understanding on how stump harvest might influence these species. Recent empirical studies have suggested that in the short term, stump harvesting may have limited, negative impacts on saproxylic species. Within individual stumps, Victorsson and Jonsell (2012) found no differences in saproxylic beetle density between control clear cuts and stump removal plots suggesting that initially following stump harvesting beetles are not crowding into residual stumps. This suggests that the total number of beetles will be proportional to the number of stumps left within the stand and beetle abundance (and presumably species richness) will be lower at the stand-level (Victorsson and Jonsell, 2012). Using the same experiment, these authors demonstrated that species richness of saproxylic beetles was marginally lower in stands where stumps had been removed (Victorsson and Jonsell, 2013). These authors also demonstrated that piles of harvested stumps left to dry at the edge of stands served as ecological traps attracting 4 species in relatively high densities (Victorsson and Jonsell, 2013). However, when longer-term impacts of stump harvesting were evaluated on saproxylic beetle assemblages at the stand-level using flight intercept traps, few differences in species composition, species richness or relative abundance were observed 21–28 years post harvest (Andersson et al., 2012). Together, these studies provide initial benchmarks defining a potential range of impacts caused by stump harvesting. However elaboration of more clearly defined retention targets for stump harvesting requires additional information that quantifies biodiversity impacts as a function of stump biomass removed.

Here we evaluated the effect of stump harvest on saproxylic beetles at both the scale of individual residual stumps and at the stand level. We hypothesized that stump harvesting would initially lead to greater densities of both individuals and species within individual stumps at sites immediately or soon after stumps had been removed due to reduced dead wood availability. We also hypothesized that overall species richness at stand level would be lower following stump harvesting and that species composition following stump harvest would represent a subset of assemblages found in stands where stumps had been retained. We also compared species accumulation curves based on emergence patterns of saproxylic beetles between clear cuts where stumps were removed or retained to define retention targets for stump harvesting operations.

## 2. Methods

### 2.1. Study sites

We collected beetles from 20 clear cuts in northern Sweden where half of the clear cuts had been stump harvested and half had been left as controls (Fig. 1). Control and stump harvested clear-cuts were paired based on proximity and harvest date and were treated as 10 replicated experimental blocks. In stump removal clear-cuts, ca. 25% of the stumps were retained according to current recommendations. Stumps were harvested randomly throughout stands within 1-year of clear cutting. Stumps were harvested using a Pallari hydraulic head consisting of opposing blades which is used to first shear and then pull out the entire

stump (Karlsson, 2007). Size of clear cuts, month and year of clearcutting and spatial distance between paired sites within each block are reported in Table 1. Prior to harvesting the stands were all dominated by Norway spruce (*Picea abies* (L.) Karst.). The surrounding forest mainly constituted of managed stands dominated by Norway spruce and Scots pine (*Pinus sylvestris* L.) in various age classes. In both control and stumped sites, most individual stumps had volumes less than 0.02 m<sup>3</sup> (Fig. 2). In control sites 88% of the stumps were less than 0.02 m<sup>3</sup> and the largest stumps did not surpass 0.05 m<sup>3</sup>. In stumped sites 83% of the residual stumps were less than 0.02 m<sup>3</sup> but the range of volumes were greater than control sites with a small proportion (less than 1%) of stumps exceeding 0.05 m<sup>3</sup>.

### 2.2. Sampling

We collected beetles using eclector traps that covered the exposed portion of spruce stumps above the roots (Fig. 3). Each eclector consisted of a mesh bag (ca. 1.5 × 1.5 m) fitted with a support wire that allowed emerging insects to reach a collection bottle filled to 1/3 with 50% propylene glycol (diluted with water) and a small quantity of detergent to break the surface tension. Eclector traps were attached to stumps at soil level using plastic polystrapping placed over the mesh and a thin foam strip used to prevent insects from escaping through furrows in the bark. Traps were set between 2013-05-29 and 2013-06-10 and collected between 2013-09-11 and 2013-09-24 (between 2 and 3.5 years after over-story trees had been removed and stump harvesting occurred). All beetle specimens were identified to species by Stig Lundberg and Jacek Hilszczanski. Within each experimental block, we randomly placed 60 eclector traps on stumps in control clear cuts and 60 eclector traps on residual stumps in stump harvested plots. In total we deployed 1200 eclector traps and recovered 1049 samples following trap losses.

### 2.3. Data treatment

We limited our analysis to species that could be characterized as facultatively or obligatorily saproxylic based on an extensive review of existing literature on life history of both adult and larval stages according to Speight (1989) and the saproxylic database (Anonymous, 2007) to which species confined to the northern part of Sweden were added (Hilszczanski, J., Pettersson R. and Lundberg S., pers. comm.). Species were assigned to functional groups if either larvae or adult could be confidently described as (i) predators, (ii) fungivores, or (iii) cambium and wood feeders. Eighteen species had life stages that were a combination of these three principal functional groups and were defined as predator-fungivore (11 species), fungivore-cambium/wood feeder (6 species), predator-cambium wood-feeder (1 species). Species with both larval and adult life stages other than these three principal functional groups were grouped as 'other'.

We evaluated whether stump harvesting would lead to greater beetle abundance or beetle species richness within stumps using non-linear least squares regression. Both abundance and species richness were characterized as a function of stump volume for each treatment. We selected non-linear least squares regression and a Michaelis–Menten model for our analysis because linear and generalized linear models consistently overestimated both beetle abundance and richness in larger stumps and visual inspection of data clearly suggests a non-linear relationship between both beetle abundance and richness and individual stump volume. The Michaelis–Menten model fits an asymptotic curve using a parameter ( $V_m$ ) to determine the maximum value for the asymptote and a second parameter to determine one-half of the maximum value, referred to as the Michaelis parameter ( $K$ ). Non-linear

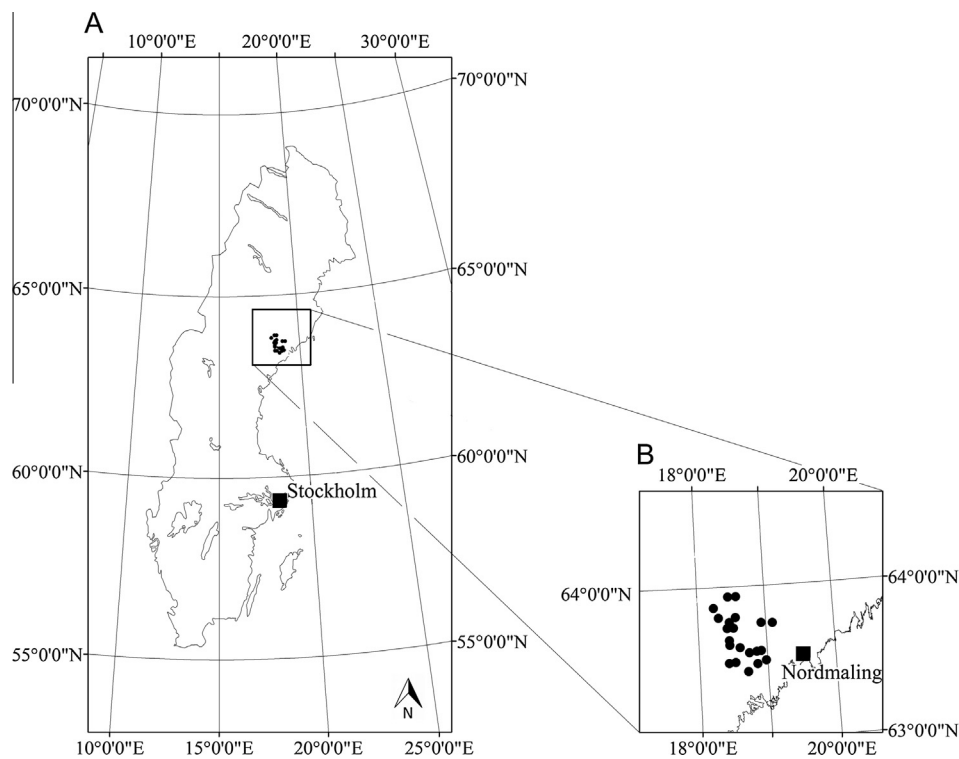


Fig. 1. Location of 20 stands used in the study. Control sites and stumped sites were paired in 10 localities.

Table 1  
Stand area and harvest date of 20 clearcut control and stump harvested stands located across 10 localities in Northern Sweden.

Locality	Control			Stumped			Distance between control and stumped sites (km)
	Stand Area (ha)	Harvest date (Month-Year)	Months between harvest and sampling	Stand Area (ha)	Harvest date (Month-Year)	Months between harvest and sampling	
1	3.3	4-2011	26	5.1	8-2010	34	6.2
2	7	9-2010	33	7.3	1-2011	29	20.6
3	14	8-2010	34	6.3	9-2010	33	4.9
4	19.8	8-2010	34	19.9	12-2009	42	17.5
5	3.9	8-2010	34	5.8	5-2010	37	7.9
6	2.6	8-2010	34	6.1	12-2009	42	21.4
7	9.8	1-2011	29	4.6	4-2011	26	7.78
8	11.8	8-2010	34	7.3	12-2009	42	43
9	13.1	8-2009	46	5.8	8-2009	46	15.9
10	4.9	8-2009	46	13.5	12-2009	42	13.9

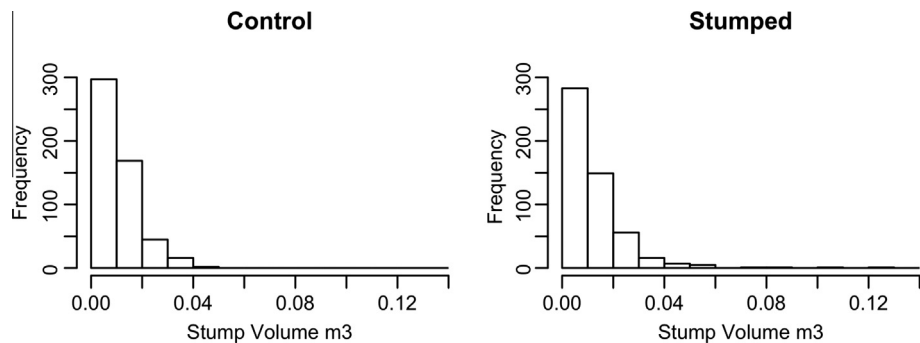


Fig. 2. Frequency of sampled stumps arranged by 0.01 m³ classes.

regression was used to estimate parameter values for each treatment using the nls function in R (R Core Team, 2014). The nls function tests whether the two parameters differ from 0. We then compared 95% confidence intervals for corresponding parameters

between models fitted for control and stumped sites. In five stumps (2 from control sites and 3 from stumped sites), abundances were very large compared with most stumps. High abundances in these stumps ( $n = 103, 90, 153, 504$  and  $128$ ) were

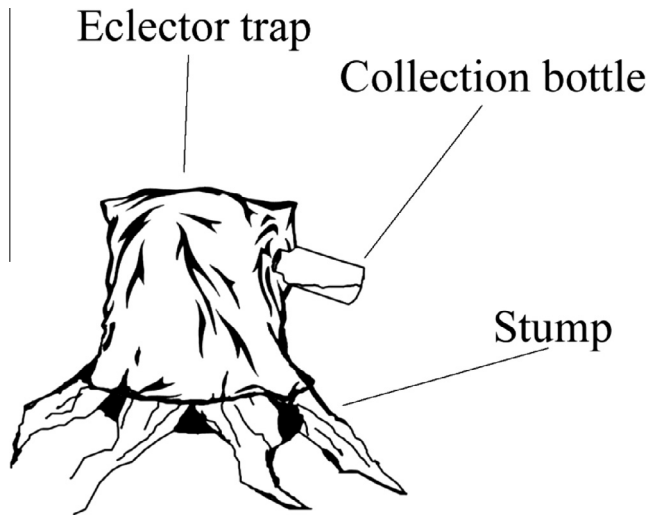


Fig. 3. Illustration of an eclector trap placed over residual stump with collection bottle for capturing saproxylic beetles emerging from the stump above the root collar.

attributable to large numbers of *Crypturgus pusillus* (Gyllenhal) which made up at least 84% of the catch in these sites. We eliminated these five stumps as outliers from non-linear regressions comparing abundances and stump volume, but left these stumps in non-linear regressions comparing species richness to stump volume.

Species composition of beetle assemblages was compared between control and stumped sites using non-metric multidimensional scaling (NMS) with Bray-Curtis distances. For this analysis we pooled all samples within an individual locality  $\times$  treatment combination to represent composition at the stand level ( $n = 20$ ). Prior to the analysis, species abundances were transformed to presence-absence. All singleton species were left in the analysis. We further tested whether composition varied between treatments using multi-response permutation process (MRPP). In MRPP differences in species composition between treatment groups are evaluated based on comparisons of the observed and expected weighted mean within-group distance ( $\delta$ ) using a test statistic  $T$  similar to Student's  $t$ -test. When the observed  $\delta$  falls within the range of possible values  $\delta$  derived from permutations ( $p > 0.05$ ), the null hypothesis that the composition of treatment groups are similar cannot be rejected (McCune and Grace, 2002). Effect size in MRPP is evaluated using the chance-corrected within group agreement ( $A$ ) (McCune and Grace, 2002). Small values of  $A$  suggest that differences in composition are due to chance rather than systematic differences between treatment groups (McCune and Grace, 2002). All multivariate analyses were done using the vegan package in R (R Core Team, 2014).

We used binomial mixture based rarefaction to compare species richness between control and stumped sites (Colwell et al., 2004). In this approach, species richness is estimated using presence-absence data from individual samples, in this case individual stumps. For each stand, we also estimated the number of singletons and the Chao 2 estimate of species richness. These measures provide additional information pertinent to the interpretation of stand-level species accumulation curves influencing the slope and asymptote respectively. We compared the number of singletons (based on pooling all samples within a locality  $\times$  treatment combination) and the Chao 2 estimate within each stand between treatments using simple linear models. We then compared species richness between control and stumped sites at individual sampling localities and across the entire study by pooling species incidence across

all sampling localities. When we pooled samples from different localities, rarefaction curves reflect species richness drawn from the larger landscape. These pooled curves are likely to have more species than species accumulation curves derived from individual stands due in large part to the accumulation of singleton species across the landscape. To compare harvesting treatments across a larger range of samples, the overall rarefaction curves were extrapolated for each treatment by a factor of two to estimate the relative number of additional species that would be expected if we doubled sampling effort. We then pooled all samples across both treatment and locality and substituted the mean volume of stumps for the number of samples to estimate of species richness as a function of increasing stump volume. We extrapolated the pooled rarefaction curve to a total cumulative stump volume that would be found on the average sized clear cut in Northern Sweden (6 ha). This extrapolated the 1049 samples that represent a cumulative volume of 12.24 m<sup>3</sup> to 4200 samples representing a cumulative volume of 47.8 m<sup>3</sup>. All rarefaction analyses and Chao 2 estimates were done using EstimateS version 9.1.0 (Colwell, 2013).

### 3. Results

We collected 9821 individuals representing 253 species with known saproxylic biology. Cambium and wood feeders were most abundant (5431 individuals or 55.2% of the total abundance) followed by predators (2076 individuals, 21.1%) and fungivores (1876 individuals, 19.1%). Trends in overall species richness among the principal functional groups were reversed from those observed in abundance, where fungivores accounted for the majority of species (102 species) followed by predators (76 species) and cambium and wood feeders (43 species). Two cambium feeders, *C. pusillus* (3218 individuals) and *Dryocetes autographus* (Ratzeburg) (1283 individuals) dominated the catch while all other species were represented by <500 individuals (Fig. 4). Seventy species were represented as single individuals. Of all the species collected, 19 species were red-listed (3 vulnerable, 15 near threatened and 1 species currently being considered for listing (Appendix A). Red-listed species were primarily fungivorous (9 species) and predatory taxa (8 species). The total abundance of each species collected from control clear cuts and stump harvested sites are presented as Appendix A.

#### 3.1. Beetle abundance, species richness and stump volume

Both beetle abundance and species richness increased with individual stump volume but we observed no differences between control and stumped sites (Fig. 5). All parameter estimates for Michaelis-Menten models in each treatment were significantly different from 0. Confidence intervals for corresponding

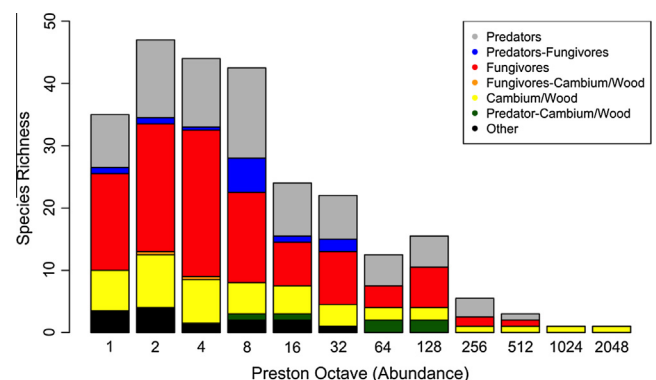
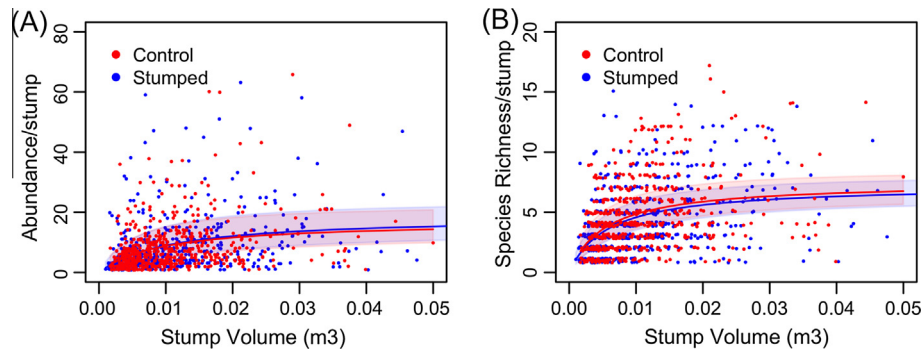


Fig. 4. Frequency distribution of species grouped into Preston octaves (abundance classes grouped by log base 2) and separated by functional groups.



**Fig. 5.** Michealis–Menten models derived from using non-linear least squares depicting changes in abundance/stump (A) and species richness/stump (B) with increases in individual stump volume in control and stumped sites. Colored bands correspond to 95% confidence intervals. Each point corresponds to an individual stump.

parameters between control and stumped treatments overlapped (Table 2). For both treatments, both beetle abundance and species richness increased rapidly with stump volume up to 0.02 m<sup>3</sup> (stumps with diameters ranging from ca. 30–45 cm). For stumps greater than 0.02 m<sup>3</sup>, beetle abundance and species richness was highly variable but remained constant over the remaining range of stump volume (Fig. 5).

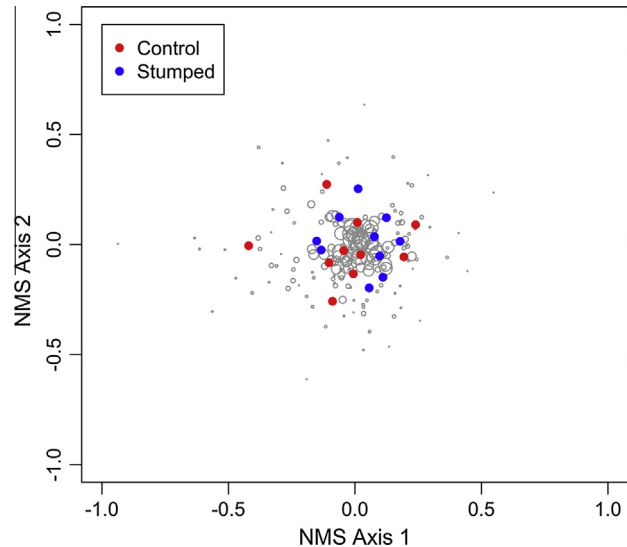
3.2. Species composition at the stand level

We did not observe differences in species composition between harvesting treatments at the stand level (Fig. 6). Beetle composition did not differ at the stand-level between treatments based on comparisons using MRPP (observed delta 0.4429, expected delta 0.4432,  $p = 0.397$ , Chance corrected within-group agreement,  $A = 0.000781$ ). We also compared how the total number of months between harvest and sampling affected beetle composition using overlays on the NMS ordination and found no visible trends related to temporal differences in sampling.

When individual species scores were overlaid on the ordination, commonly occurring species are located at the center and rarer species are located on the periphery of the ordination, suggesting that minor differences in beetle composition among stands are driven primarily by rare species (Fig. 6).

3.3. Species richness

When we compared treatments within experimental localities, 95% confidence intervals of each treatment overlapped throughout the entire range of samples suggesting no difference between treatments (Fig. 7). Variation between treatments between localities was unbiased. Localities 1, 3, 5 and 8 showed increased richness



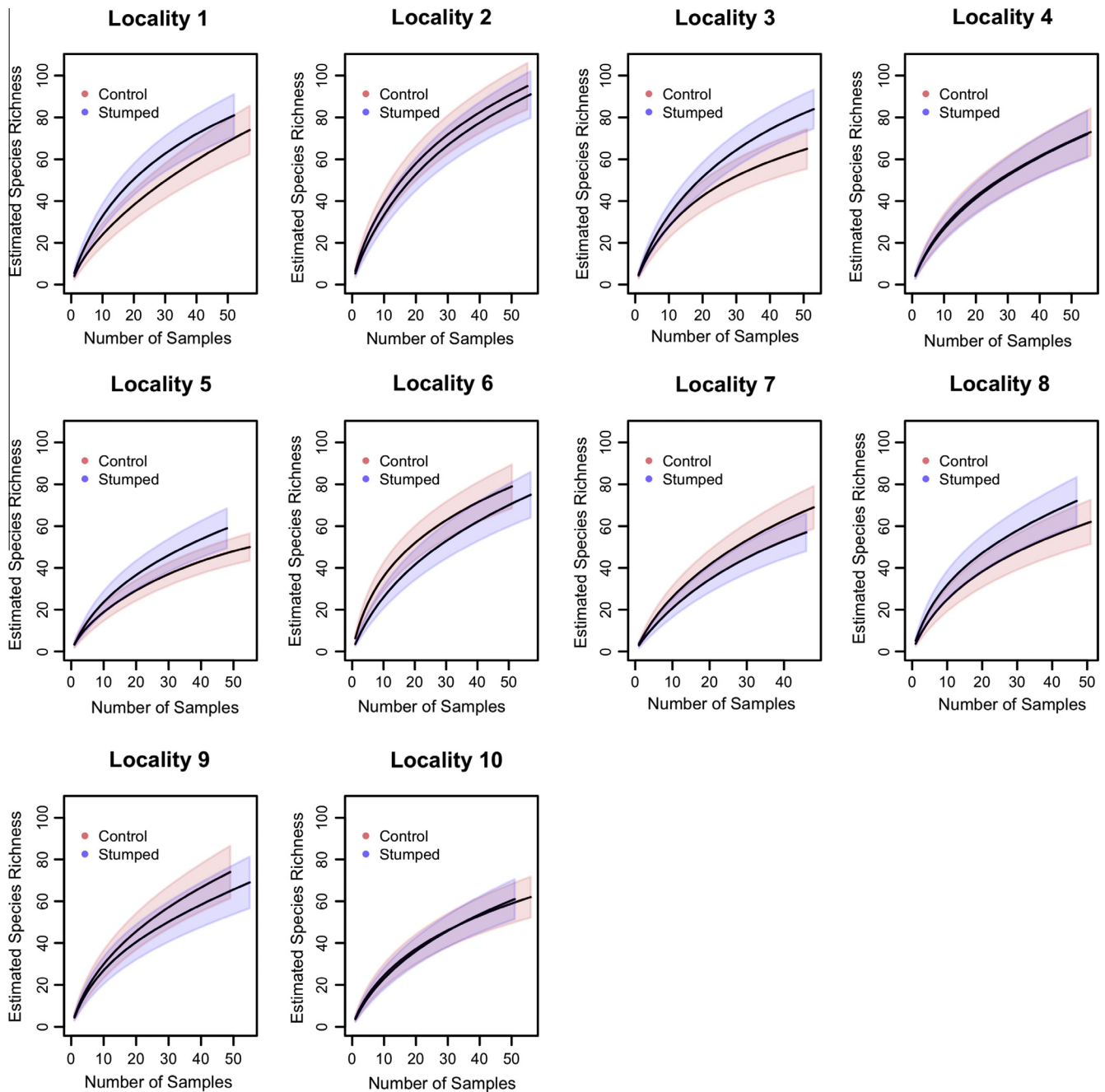
**Fig. 6.** Non-metric scaling ordination (NMS) depicting stand-level differences in species composition (based on presence–absence data) between control and stumped treatments. Individual species scores are plotted as gray circles and scaled to the total frequency of occurrence with large points reflecting commonly occurring species and smaller points reflecting rarer species. The final ordination stress was 0.23.

in stumped stands while localities 2, 6, 7 and 9 showed increased richness in control stands. Trends in species richness between control and stumped stands were nearly identical at localities 4 and 11. The number of singletons in each stand did not differ between treatment ( $F_{1,18} = 0.236$ ,  $p = 0.63$ ) and overall mean number of singletons expected within any given stand was 31.2 (Table 3).

**Table 2**  
Parameter estimates ( $V_m$  and  $K$ ) from Michaelis–Menten models characterizing changes in beetle abundance and species richness as a function of individual stump volume in control and stumped sites.

	Estimate	Std. error	t-value	Pr> t	Confidence interval 2.5%	Confidence interval 97.5%
<b>Abundance</b>						
<b>Stumped</b>						
$V_m$	18.5879	2.2759	8.1672	0.0000	14.6486	24.3531
$K$	0.0107	0.0030	3.6146	0.0003	0.0059	0.0189
<b>Control</b>						
$V_m$	17.0670	2.2633	7.5407	0.0000	13.3237	22.9727
$K$	0.0095	0.0028	3.3932	0.0007	0.0051	0.0173
<b>Species Richness</b>						
<b>Stumped</b>						
$V_m$	7.2398	0.4482	16.1520	0.0000	6.4125	8.2328
$K$	0.0058	0.0010	5.5897	0.0000	0.0040	0.0083
<b>Control</b>						
$V_m$	7.4936	0.5265	14.2341	0.0000	6.5618	8.6577
$K$	0.0055	0.0011	5.0122	0.0000	0.0036	0.0080





**Fig. 7.** Incidence-based rarefaction curves for control and stumped treatment within individual sampling localities. Colored bands correspond to 95% confidence intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Likewise, the upper limit of species richness within each stand as measured by the Chao 2 estimate also did not differ between treatments (Chao 2,  $F_{1,18} = 0.046$ ,  $p = 0.83$ ). The mean richness measured by the Chao 2 index across all stands was 116.6. When samples were pooled across localities within treatments, we observed extensive overlap of confidence intervals for individual curves suggesting no difference in species richness in individual stumps between harvesting treatments even when rarefaction curves were extrapolated to twice the sampling effort (Fig. 8).

Over this study, we sampled a total stump volume of 12.24 m<sup>3</sup>. Extrapolating the entire sampled volume to the volume that would be found on the averaged size clear cut in Northern Sweden (ca. 48 m<sup>3</sup> or 6 ha) resulted in a rarefaction curve derived from the species pool found across the landscape (Fig. 9). Coincidentally, the

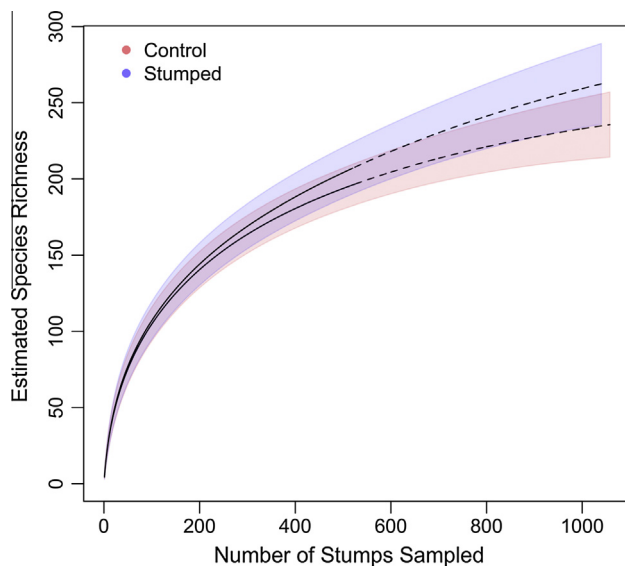
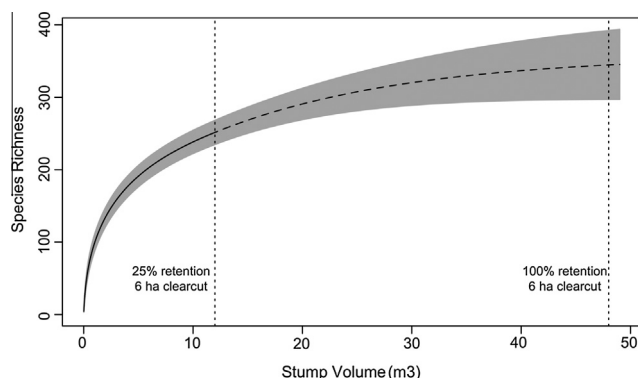
actual volume of stumps sampled corresponded closely with the recommended upper limit volume of residual stumps left following stump harvesting (12 m<sup>3</sup> or 25% of residual stumps that would be found in a 6 ha clear cut). Interpolating backwards from 48 m<sup>3</sup> to 12 m<sup>3</sup> on this curve results in a mean difference of ca. 93 species or 26% of the total species that would be predicted on a 6 ha clear cut if species were drawn from the entire landscape-level species pool. Using the entire range of 95% confidence intervals between 48 m<sup>3</sup> to 12 m<sup>3</sup> provides however a wide range of species differences ranging from ca. 158 species to ca. 27 species.

These extreme ranges in the confidence intervals correspond to 40% and 7% respectively of the total species that would be predicted on a 6 ha clearcut if species were drawn from the entire landscape-level species pool.

**Table 3**

Number of singletons and Chao 2 estimate with associated confidence intervals for control and stumped stands in individual localities.

Locality	Control				Stumped			
	Estimated number of singletons	Chao 2 estimate	Chao 2 lower 95% CI	Chao 2 upper 95% CI	Estimated number of singletons	Chao 2 estimate	Chao 2 lower 95% CI	Chao 2 upper 95% CI
1	42	135.96	102.42	209.11	33	117.47	96.68	165.81
2	38	139.73	115.36	193.23	39	137.98	112.55	193.43
3	25	96.86	77.01	149.56	32	113.19	96.65	151.33
4	33	127.51	96.34	200.28	34	126.49	95.34	199.24
5	18	62.89	54.49	87.02	29	94.49	73.24	147.48
6	31	118.82	95.58	174.62	35	123.53	96.51	184.51
7	32	110.13	86.78	164.12	29	87.4	69.31	132.08
8	28	109.39	80.53	183.15	28	130.23	96.09	212.77
9	33	154.65	107.87	266.05	33	150.74	102.35	269.35
10	26	99.13	76.35	158.04	26	96.07	75.3	146.98

**Fig. 8.** Incidence-based rarefaction curves for control and stumped treatments based on samples pooled across all localities. Colored bands represent 95% confidence intervals. Solid lines represent estimates of species richness based on interpolations. Dashed lines represent estimates of species richness based on extrapolations to twice the sampling effort. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)**Fig. 9.** Incidence based rarefaction curve derived from data pooled from all stands (with 95% confidence intervals) which depicts increases in species richness with increasing stump volume if species were drawn from the entire landscape species pool. Solid and dashed lines indicate actual volume sampled and extrapolated region of the rarefaction curve respectively. Dotted lines demark stump volume found on 6 ha clearcut in Northern Sweden where 25% and 100% of the stumps have been retained.

#### 4. Discussion

After an unprecedented and extensive sampling effort, we found little evidence in support of our first hypothesis that stump harvesting affected saproxylic beetle density, richness or composition in residual stumps. Other authors have observed similar responses in saproxylic beetle density (Victorsson and Jonsell, 2012, 2013) but reported reduced species richness both at the level of individual stumps and across multiple stump harvested stands (Victorsson and Jonsell, 2012). Similar beetle density in residual stumps in stands with and without stump removal provides a simple maxim for stump harvesting- that overall abundance of beetles will simply be proportional to the number of stumps retained (Victorsson and Jonsell, 2013). We did not observe decreases in species richness within individual stumps nor the decreases in species richness when samples were pooled across stands in stump harvested sites that were reported by Victorsson and Jonsell (2012) despite that both studies produced remarkably similar estimates of species richness within individual stumps (4–6 species/stump) in both treatments.

Beetle density increased in individual stumps with volume up to 0.02 m<sup>3</sup> (stumps with diameters ranging from ca. 30–45 cm). This supports Grove's adage, 'bigger deadwood is better [for conservation]' (Grove, 2002) but only up to 0.02 m<sup>3</sup>. Thus retaining stumps larger than 0.02 m<sup>3</sup> in stump harvested sites should provide no additional benefits for maintaining beetle density than stumps with volumes of 0.02 m<sup>3</sup>. Still this relationship holds for the majority of stumps left following commercial harvest. The positive relationship between beetle density and stump volume below 0.02 m<sup>3</sup> provides a means to calibrate the effects of stump harvesting in younger stands or stands with poor productivity. Stump harvesting in younger stands or stands with poor productivity that have smaller stumps will have smaller effects on absolute beetle density than stump harvesting in older or more productive stands if stump densities are similar.

Given this positive relationship between stump volume and species richness, differences in the size of stumps between stands with and without stump removal may explain discrepancies in species richness between our outcome and Victorsson and Jonsell (2013). Victorsson and Jonsell (2013) show that stump harvesting treatments in their study reduced mean stump diameter 0.34–0.27 m. Our results suggest that reducing the average size of stumps would result in decreased species richness in smaller volume stumps. In our study, stumps were not smaller in stumped sites. Rather, we observed relatively equal distributions of individual stump volumes up to 0.04 m<sup>3</sup> and several very large stumps (>0.04 m<sup>3</sup>) that were left in stump harvested plots. Differences in size of stumps between treatments in Victorsson and Jonsell's study may also account for discrepancies between species richness when samples were pooled across stands as bigger stumps will

likely harbor more singleton species which in turn would inflate the control curve relative to the stumped curve. Taken together these studies demonstrate that careful consideration of average stump volume is warranted when setting targets for stump retention and selective 'high-grading' of large stumps should be avoided.

We failed to observe evidence for either species loss or species packing in residual stumps as a result of stump harvesting. The relation between species richness and habitat amount has rarely been studied on clear-cuts, but there are some evidence for both negative (Ericksson et al., 2006) as well as positive (Rubene et al., 2014) relationships. Failure to detect a decline in species richness in residual stumps in stump removal sites suggests that the amount of surrounding stumps within the clear cut is not a limiting factor for colonization. In one other study of saproxylic beetles, no effect of the amount of dead wood within stands on species occurrence per individual dead wood substrate was observed, suggesting that at least for the more frequently occurring species much of the immigration occurs over longer distances (Ranius et al., 2015). However, the importance of these factors may change over time as immigration will likely be more important immediately after harvesting.

Stand-level composition of beetles in control and stumped sites were statistically indistinguishable with minor differences attributable primarily to singleton species. Lack of compositional differences between treatments justifies pooling all data and creating a single species accumulation curve with sufficient sample size to extrapolate confidently to the total stump volume on the average clear cut in Northern Sweden. Because the combined rarefaction curve draws from the species pool sampled on the entire landscape it would be inappropriate to draw conclusions on the absolute difference in species between different stump volumes at the stand-level. In the way the combined curve most likely overestimates the absolute number of species found in a single stand due in part to the large number of singleton species found across the landscape. However because each stand is a subset of the larger landscape species pool, relative differences in species richness between the total cumulative volume expressed in the extrapolation and smaller volumes representative of the effects of stump harvesting may apply to all stands. Based on this extrapolation, a 75% reduction in stump volume, which is the lowest harvest level recommended in current stump harvesting operations in Sweden (Skogsstyrelsen, 2009), would reduce species richness on average by 26% (95% C.I. 7–41%). It should be noted that at retention levels lower than 25%, the reduction in species richness will be relatively high, resulting from the steep decline in the rarefaction curve at lower retention levels. At 15%, which is the lowest recommended retention level, species richness will be reduced by an average 37% (95% C.I. 21–48%). While we believe that our results provide a credible benchmark to measure the relative impacts of stump harvesting on local beetle species richness, it would be useful to be able to estimate absolute number of species loss in individual stands. We suggest as a pragmatic approach that absolute species

loss could be translated to the stand-level using both relative species loss estimated from the landscape species pool and the Chao 2 estimate of maximum species richness. In our study, the average species richness estimated for individual stands was ca. 116 which when discounted by 26% species loss that occurs following stump harvesting would predict the loss of ca. 30 species within an individual stand.

As with all empirical studies, we stress that these results must be interpreted within the limitations of our study. While the sampling effort in our study was intense, our data only reflects the initial responses of beetles following stump harvesting, 2–3 years following harvest. While this timeframe should have been sufficient to capture beetles that have had an opportunity to colonize stumps post-harvest, we fully expect compositional changes to occur as residual phloem is utilized by cambium feeding insects or as wood quality changes as stumps dry and decompose with time. While we anticipate that higher trophic consumers such as fungivores will become increasingly important as stumps are colonized by fungi and decompose, longer term inferences will necessitate longer term study of the effects of stump harvesting. Likewise we were unable to directly assess impacts of landscape surrounding stump harvested sites in this study. However, a theoretical study suggests that there will take several decades before landscape-scale effect on biodiversity are shown, which makes empirical studies difficult (Johansson et al., 2016).

## 5. Conclusions

Similarity of beetle density, richness and composition within residual stumps between control clear cuts and stump removal plots greatly simplifies our approach to conservation in the context of stump harvesting. Similarities in beetle assemblages at the stump level suggest limited effects of surrounding deadwood within the stand on residual stumps. Thus when considered at the level of individual deadwood substrates, residual stumps left after stump removal are not marginalized habitats for beetles. There will however be less of them per ha within the stand following stump harvest. Thus the impacts, while relatively straightforward, are far from trivial. Current recommendations for stump removal in Sweden will likely reduce species richness by ca. ¼ within individual stands. These species will likely include infrequently encountered species, species at their distribution limits and possibly red listed species. Improving conservation within stump-harvested stands will necessitate increasing retention targets

## Acknowledgements

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## Appendix A

List of all species and total abundances in control and stumped treatments for saproxylic beetles collected from 20 clearcuts in Northern Sweden.

Family	Species	Control	Stumped	Total	IUCN Red-Listed Category
Aderidae	<i>Euglenes pygmaeus</i>	29	32	61	
Anobiidae	<i>Hadrobregmus pertinax</i>	20	17	37	
Anobiidae	<i>Ptinus fur</i>	6	4	10	
Anobiidae	<i>Ptinus villiger</i>	9	5	14	

(continued on next page)



## Appendix A (continued)

Family	Species	Control	Stumped	Total	IUCN Red-Listed Category
Buprestidae	<i>Buprestis haemorrhoidalis</i>	1		1	Near-threatened
Buprestidae	<i>Buprestis rustica</i>	1	1	2	
Buprestidae	<i>Chrysobothris chrysostigma</i>	2		2	
Cantharidae	<i>Malthinus biguttatus</i>	5	1	6	
Cantharidae	<i>Malthinus flaveolus</i>	1	1	2	
Cantharidae	<i>Malthodes brevicollis</i>	8	3	11	
Cantharidae	<i>Malthodes fuscus</i>	23	22	45	
Cantharidae	<i>Malthodes guttifer</i>	30	31	61	
Cantharidae	<i>Malthodes marginatus</i>		1	1	
Cantharidae	<i>Podistra rufotestacea</i>	23	17	40	
Cantharidae	<i>Podistra schoenherri</i>	11	15	26	Near-threatened
Carabidae	<i>Pterostichus niger</i>	1		1	
Carabidae	<i>Pterostichus oblongopunctatus</i>	32	40	72	
Carabidae	<i>Pterostichus strenuus</i>	1		1	
Cerambycidae	<i>Alosterna tabacicolor</i>		1	1	
Cerambycidae	<i>Gnathacmaeops pratensis</i>		1	1	
Cerambycidae	<i>Judolia sexmaculata</i>	5	2	7	
Cerambycidae	<i>Leptura quadrifasciata</i>		2	2	
Cerambycidae	<i>Lepturobosca virens</i>	19	23	42	
Cerambycidae	<i>Oxymirus cursor</i>		3	3	
Cerambycidae	<i>Pogonocherus fasciculatus</i>		1	1	
Cerambycidae	<i>Rhagium inquisitor</i>	8	7	15	
Cerambycidae	<i>Stenurella melanura</i>	9	2	11	
Cerambycidae	<i>Tetropium castaneum</i>	53	60	113	
Cerylonidae	<i>Cerylon ferrugineum</i>		1	1	Near-threatened
Cerylonidae	<i>Cerylon histeroides</i>	40	41	81	
Ciidae	<i>Cis boleti</i>	12	1	13	
Ciidae	<i>Cis lineatocribratus</i>	1		1	
Ciidae	<i>Cis micans</i>	3	5	8	
Ciidae	<i>Cis punctulatus</i>	1		1	
Ciidae	<i>Cis rugulosus</i>	1	2	3	
Ciidae	<i>Cis vestitus</i>		1	1	
Ciidae	<i>Orthocis alni</i>	1		1	
Cleridae	<i>Thanasimus femoralis</i>	15	7	22	
Coccinellidae	<i>Propylea quatuordecimpunctata</i>	1	1	2	Near-threatened
Corticariidae	<i>Cartodere constricta</i>	3	3	6	
Corticariidae	<i>Corticaria elongata</i>	3		3	
Corticariidae	<i>Corticaria ferruginea</i>	1	2	3	
Corticariidae	<i>Corticaria lapponica</i>		1	1	
Corticariidae	<i>Corticaria longicollis</i>	3	4	7	
Corticariidae	<i>Corticaria longicornis</i>	45	52	97	
Corticariidae	<i>Corticaria orbicollis</i>		1	1	
Corticariidae	<i>Corticaria rubripes</i>	22	39	61	
Corticariidae	<i>Corticaria serrata</i>	17	8	25	
Corticariidae	<i>Corticarina minuta</i>	12	6	18	Near-threatened
Corticariidae	<i>Corticarina parvula</i>	6	6	12	
Corticariidae	<i>Corticarina similata</i>	2		2	
Corticariidae	<i>Corticaria gibbosa</i>	9	6	15	
Corticariidae	<i>Enicmus rugosus</i>	58	44	102	
Corticariidae	<i>Latridius gemellatus</i>		2	2	
Corticariidae	<i>Latridius minutus</i>		1	1	
Corticariidae	<i>Stephostethus rugicollis</i>		1	1	
Corylophidae	<i>Orthoperus atomus</i>	3		3	
Cryptophagidae	<i>Atomaria affinis</i>		1	1	Near-threatened
Cryptophagidae	<i>Atomaria apicalis</i>	1	3	4	
Cryptophagidae	<i>Atomaria atrata</i>		1	1	
Cryptophagidae	<i>Atomaria bella</i>	47	26	73	
Cryptophagidae	<i>Atomaria fuscata</i>	1	2	3	
Cryptophagidae	<i>Atomaria lapponica</i>	1	5	6	
Cryptophagidae	<i>Atomaria longicornis</i>	2	5	7	
Cryptophagidae	<i>Atomaria peltata</i>	2	1	3	

## Appendix A (continued)

Family	Species	Control	Stumped	Total	IUCN Red-Listed Category
Cryptophagidae	<i>Caenoscelis ferruginea</i>	1		1	
Cryptophagidae	<i>Cryptophagus acutangulus</i>		1	1	
Cryptophagidae	<i>Cryptophagus dentatus</i>	1	2	3	
Cryptophagidae	<i>Cryptophagus dorsalis</i>	1	2	3	
Cryptophagidae	<i>Cryptophagus punctipennis</i>		1	1	
Cryptophagidae	<i>Cryptophagus saginatus</i>	3	5	8	
Cryptophagidae	<i>Cryptophagus setulosus</i>	4		4	
Cryptophagidae	<i>Cryptophagus subdepressus</i>		3	3	
Cryptophagidae	<i>Henoticus serratus</i>	2	1	3	
Cucujidae	<i>Pediacus fuscus</i>	21	25	46	
Curculionidae	<i>Brachyderes incanus</i>		1	1	
Curculionidae	<i>Crypturgus pusillus</i>	1198	2020	3218	
Curculionidae	<i>Crypturgus subcribrosus</i>		21	21	
Curculionidae	<i>Dendroctonus micans</i>		1	1	
Curculionidae	<i>Dryocoetes autographus</i>	650	633	1283	
Curculionidae	<i>Hylastes brunneus</i>	50	30	80	
Curculionidae	<i>Hylastes cunicularius</i>	89	72	161	
Curculionidae	<i>Hylastes opacus</i>	1		1	
Curculionidae	<i>Hylobius abietis</i>	185	112	297	
Curculionidae	<i>Hylobius pinastri</i>	18	10	28	
Curculionidae	<i>Hylurgops palliatus</i>	3	2	5	
Curculionidae	<i>Magdalis frontalis</i>		1	1	
Curculionidae	<i>Orthotomicus suturalis</i>	4	19	23	
Curculionidae	<i>Phloeotribus spinulosus</i>	2	2	4	
Curculionidae	<i>Pissodes harcyniae</i>	1	2	3	
Curculionidae	<i>Pissodes pini</i>	1		1	
Curculionidae	<i>Pissodes piniphilus</i>	2	1	3	
Curculionidae	<i>Pityogenes bidentatus</i>	2		2	
Curculionidae	<i>Pityogenes chalcographus</i>	6	3	9	
Curculionidae	<i>Pityogenes quadridens</i>	1		1	
Curculionidae	<i>Rhyncolus ater</i>	4	1	5	
Curculionidae	<i>Rhyncolus sculpturatus</i>	4	12	16	
Curculionidae	<i>Scolytus ratzeburgi</i>	1		1	
Dermestidae	<i>Anthrenus museorum</i>	1		1	
Dermestidae	<i>Globicornis emarginata</i>	1	2	3	
Elateridae	<i>Ampedus balteatus</i>	29	31	60	
Elateridae	<i>Ampedus nigrinus</i>	20	17	37	
Elateridae	<i>Ampedus pomonae</i>	2	5	7	
Elateridae	<i>Ampedus tristis</i>	46	51	97	
Elateridae	<i>Athous subfuscus</i>	115	92	207	
Elateridae	<i>Cardiophorus ruficollis</i>	3		3	
Elateridae	<i>Danosoma conspersum</i>	1	1	2	Near-threatened
Elateridae	<i>Denticollis linearis</i>	5	7	12	
Elateridae	<i>Liotrichus affinis</i>	3	4	7	
Elateridae	<i>Melanotus castanipes</i>	40	27	67	
Elateridae	<i>Paraphotistus impressus</i>	14	8	22	
Elateridae	<i>Paraphotistus nigricornis</i>	7	3	10	
Elateridae	<i>Selatosomus aeneus</i>	3	2	5	
Endomychidae	<i>Endomychus coccineus</i>	5	22	27	
Erotylidae	<i>Dacne bipustulata</i>	6	6	12	
Histeridae	<i>Eblisia minor</i>	2	5	7	Near-threatened
Histeridae	<i>Platysoma angustatum</i>	1	3	4	
Histeridae	<i>Plegaderus vulneratus</i>	7	8	15	
Laemophloeidae	<i>Laemophloeus muticus</i>		1	1	Vulnerable
Latridiidae	<i>Corticaria fulva</i>		1	1	
Leiodidae	<i>Agathidium arcticum</i>		1	1	
Leiodidae	<i>Agathidium badium</i>		1	1	
Leiodidae	<i>Agathidium laevigatum</i>		1	1	
Leiodidae	<i>Agathidium mandibulare</i>	3	1	4	Near-threatened
Leiodidae	<i>Agathidium nigrinum</i>		1	1	Near-threatened
Leiodidae	<i>Agathidium pisanum</i>	10	8	18	

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## Appendix A (continued)

Family	Species	Control	Stumped	Total	IUCN Red-Listed Category
Leiodidae	<i>Agathidium rotundatum</i>	6	6	12	
Leiodidae	<i>Agathidium seminulum</i>	8	11	19	
Leiodidae	<i>Amphicyllis globus</i>	1	1	2	
Leiodidae	<i>Anisotoma axillaris</i>	105	40	145	
Leiodidae	<i>Anisotoma castanea</i>	15	13	28	
Leiodidae	<i>Anisotoma glabra</i>	90	38	128	
Leiodidae	<i>Anisotoma humeralis</i>	2		2	
Lycidae	<i>Dictyoptera aurora</i>	3		3	
Lycidae	<i>Lygistopterus sanguineus</i>		1	1	
Lycidae	<i>Pyropterus nigroruber</i>	1	4	5	
Lymexylidae	<i>Elateroides dermestoides</i>		2	2	
Melandryidae	<i>Abdera flexuosa</i>	3		3	
Melandryidae	<i>Hallomenus axillaris</i>	1		1	Near-threatened
Melandryidae	<i>Wanachia triguttata</i>	5	1	6	
Melandryidae	<i>Xylita laevigata</i>	2	1	3	
Melyridae	<i>Aplocnemus nigricornis</i>	1		1	
Melyridae	<i>Dasytes niger</i>	45	53	98	
Melyridae	<i>Nepachys cardiaca</i>	9	8	17	
Monotomidae	<i>Rhizophagus bipustulatus</i>	4	1	5	
Monotomidae	<i>Rhizophagus dispar</i>	20	57	77	
Monotomidae	<i>Rhizophagus ferrugineus</i>	3	4	7	
Monotomidae	<i>Rhizophagus grandis</i>		1	1	
Monotomidae	<i>Rhizophagus nitidulus</i>	1	9	10	
Mordellidae	<i>Curtimorda maculosa</i>	2	1	3	
Mycetophagidae	<i>Mycetophagus fulvicollis</i>	1		1	Near-threatened
Nitidulidae	<i>Epuraea aestiva</i>	2	1	3	
Nitidulidae	<i>Epuraea angustula</i>	5	18	23	
Nitidulidae	<i>Epuraea binotata</i>	1		1	
Nitidulidae	<i>Epuraea laeviuscula</i>		1	1	
Nitidulidae	<i>Epuraea marseuli</i>		1	1	
Nitidulidae	<i>Epuraea oblonga</i>		1	1	Near-threatened
Nitidulidae	<i>Epuraea pallescens</i>		1	1	
Nitidulidae	<i>Epuraea pygmaea</i>	5	9	14	
Nitidulidae	<i>Glischrochilus hortensis</i>	1	1	2	
Nitidulidae	<i>Glischrochilus quadripunctatus</i>	1	3	4	
Nitidulidae	<i>Pityophagus ferrugineus</i>	4	5	9	
Oedemeridae	<i>Chrysanthia geniculata</i>	2	3	5	
Oedemeridae	<i>Chrysanthia viridissima</i>	3	1	4	
Ptiliidae	<i>Pteryx splendens</i>	14	59	73	
Ptiliidae	<i>Pteryx suturalis</i>	5	14	19	
Pyrochroidae	<i>Schizotus pectinicornis</i>		1	1	
Scarabaeidae	<i>Protaetia metallica</i>	1	1	2	
Scraptiidae	<i>Anaspis arctica</i>	1		1	
Scraptiidae	<i>Anaspis bohémica</i>	1	7	8	
Scraptiidae	<i>Anaspis marginicollis</i>		5	5	
Scraptiidae	<i>Anaspis rufilabris</i>	85	147	232	
Scydmaenidae	<i>Eutheia linearis</i>	6	16	22	
Scydmaenidae	<i>Microscydus minimus</i>		6	6	
Scydmaenidae	<i>Neuraphes perssoni</i>		1	1	Vulnerable
Scydmaenidae	<i>Stenichnus bicolor</i>	2		2	
Silphidae	<i>Phosphuga atrata</i>	6	2	8	
Silvanidae	<i>Silvanus bidentatus</i>		2	2	
Sphindidae	<i>Aspidiphorus orbiculatus</i>	2	1	3	
Sphindidae	<i>Sphindus dubius</i>	15	17	32	
Staphylinidae	<i>Acidota crenata</i>	43	44	87	
Staphylinidae	<i>Acrulia inflata</i>	1	1	2	
Staphylinidae	<i>Anomognathus cuspidatus</i>	4		4	Vulnerable
Staphylinidae	<i>Anthophagus caraboides</i>	3	5	8	
Staphylinidae	<i>Atheta crassicornis</i>		6	6	
Staphylinidae	<i>Atheta harwoodi</i>	3	3	6	
Staphylinidae	<i>Atheta myrmecobia</i>	2	3	5	

## Appendix A (continued)

Family	Species	Control	Stumped	Total	IUCN Red-Listed Category
Staphylinidae	<i>Atheta sodalis</i>	8	14	22	
Staphylinidae	<i>Atheta subtilis</i>	1		1	
Staphylinidae	<i>Atheta vaga</i>	3	12	15	
Staphylinidae	<i>Atrecus affinis</i>	2	2	4	
Staphylinidae	<i>Atrecus pilicornis</i>		3	3	
Staphylinidae	<i>Batrisodes venustus</i>	12	6	18	In preparation for listing
Staphylinidae	<i>Bibloporus bicolor</i>	6	13	19	
Staphylinidae	<i>Bolitochara pulchra</i>	10	19	29	
Staphylinidae	<i>Dadobia immersa</i>	4	3	7	
Staphylinidae	<i>Dinaraea aequata</i>		1	1	
Staphylinidae	<i>Dinaraea arcana</i>	4	3	7	
Staphylinidae	<i>Dinaraea linearis</i>		1	1	
Staphylinidae	<i>Dropephylla clavigera</i>	9		9	Near-threatened
Staphylinidae	<i>Dropephylla linearis</i>	4	2	6	
Staphylinidae	<i>Eudectus giraudi</i>	1		1	Near-threatened
Staphylinidae	<i>Euplectus karstenii</i>	24	36	60	
Staphylinidae	<i>Euplectus piceus</i>	2		2	
Staphylinidae	<i>Euplectus punctatus</i>	39	33	72	
Staphylinidae	<i>Gabrius expectatus</i>	9	21	30	
Staphylinidae	<i>Gyrophaena affinis</i>	1		1	
Staphylinidae	<i>Gyrophaena boleti</i>		2	2	
Staphylinidae	<i>Gyrophaena manca</i>		2	2	
Staphylinidae	<i>Haploglossa villosula</i>		1	1	
Staphylinidae	<i>Homalota plana</i>	1		1	
Staphylinidae	<i>Ischnoglossa elegantula</i>	3		3	
Staphylinidae	<i>Leptusa fumida</i>	3	3	6	
Staphylinidae	<i>Leptusa pulchella</i>	3	2	5	
Staphylinidae	<i>Lordithon lunulatus</i>	3		3	
Staphylinidae	<i>Lordithon thoracicus</i>	2		2	
Staphylinidae	<i>Medon apicalis</i>		1	1	
Staphylinidae	<i>Mycetoporus rufescens</i>		3	3	
Staphylinidae	<i>Nudobius lentus</i>	162	174	336	
Staphylinidae	<i>Othius lapidicola</i>	1		1	
Staphylinidae	<i>Othius myrmecophilus</i>	1		1	
Staphylinidae	<i>Oxypoda annularis</i>	1	2	3	
Staphylinidae	<i>Oxypoda soror</i>	2		2	
Staphylinidae	<i>Oxypoda spectabilis</i>	1		1	
Staphylinidae	<i>Pentanota meuseli</i>		1	1	Near-threatened
Staphylinidae	<i>Phloeonomus pusillus</i>	98	151	249	
Staphylinidae	<i>Phloeonomus sjobergi</i>	2	5	7	
Staphylinidae	<i>Phloeopora corticalis</i>	4	1	5	
Staphylinidae	<i>Phloeostiba lapponica</i>	2	2	4	
Staphylinidae	<i>Phyllodrepa melanocephala</i>		1	1	
Staphylinidae	<i>Proteinus brachypterus</i>		1	1	
Staphylinidae	<i>Quedius brevis</i>	7	7	14	
Staphylinidae	<i>Quedius cruentus</i>	1		1	
Staphylinidae	<i>Quedius fuliginosus</i>	1	3	4	
Staphylinidae	<i>Quedius limbatus</i>		1	1	
Staphylinidae	<i>Quedius maurus</i>		1	1	
Staphylinidae	<i>Quedius mesomelinus</i>	4	3	7	
Staphylinidae	<i>Quedius plagiatus</i>	18	32	50	
Staphylinidae	<i>Quedius tenellus</i>	2	7	9	
Staphylinidae	<i>Quedius xanthopus</i>	2	2	4	
Staphylinidae	<i>Scaphisoma agaricinum</i>	311	134	445	
Staphylinidae	<i>Sepedophilus immaculatus</i>	3	2	5	
Staphylinidae	<i>Sepedophilus littoreus</i>	20	48	68	
Staphylinidae	<i>Sepedophilus testaceus</i>	2	4	6	
Staphylinidae	<i>Syntomium aeneum</i>	1	1	2	
Staphylinidae	<i>Trichophya pilicornis</i>	1	1	2	
Staphylinidae	<i>Tyrus mucronatus</i>	3	2	5	
Staphylinidae	<i>Xantholinus tricolor</i>	6	1	7	

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## Appendix A (continued)

Family	Species	Control	Stumped	Total	IUCN Red-Listed Category
Stenotrachelidae	<i>Stenotrachelus aeneus</i>		1	1	Near-threatened
Tenebrionidae	<i>Corticeus linearis</i>	1		1	
Tenebrionidae	<i>Mycetochara flavipes</i>		1	1	
Tenebrionidae	<i>Mycetochara obscura</i>	1		1	
Tenebrionidae	<i>Scaphidema metallicum</i>	1		1	
Total		4548	5273	9821	

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