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Biodiversity benefits for saproxylic beetles with uneven-aged silviculture

Joakim Hjältén[a,*], Klara Joelsson[a], Heloise Gibb[d], Timothy Work[b,c], Therese Löfroth[a], Jean-Michel Roberge[a,e]

[a] Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, Sweden
[b] University of Quebec at Montreal, Canada
[c] Center for Forest Studies and Chair in Sustainable Forest Management, Canada
[d] Department of Ecology, Evolution and Environment, La Trobe University, Melbourne, Australia
[e] National Inventory of Landscapes in Sweden (NILS), Department of Forest Resource Management, Swedish University of Agricultural Sciences (SLU), Umeå, Sweden

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ABSTRACT

Large scale use of even-aged silviculture (clear-cutting) commencing in the mid-20th century has had negative impacts on forest biodiversity. As a consequence, uneven-aged silviculture is currently being considered to help meet the ecological and social criteria required for sustainable forest management. Uneven-aged silviculture (e.g. selective felling) involves selective removal of some older trees in a stand which may to some extent mimics natural small scale stand dynamics and thus potentially benefit species associated with old forests. Here we test whether selective felling benefits beetle biodiversity by producing beetle assemblages that better resemble those of old growth stands than those found in uncut production stands. We conducted a field study in northern Sweden, comparing beetles assemblages collected with window traps in three spruce dominated stand types: (1) Stands recently (on average 7 years prior to the study) subjected to selective felling (*Selective felling*), (2) mature uneven-aged stands without recent history of management, resembling selective felling stands prior to management (*Uncut*), and (3) old-growth stands with high conservation values (*Old growth*). As predicted, we found that assemblage composition was similar in selective felling and old growth stands, and that assemblages of cambivores and obligate saproxylics (marginally significant) differed between these two stand types and uncut stands. The differences were largely explained by a higher abundance of saproxylic species presumably associated with old growth conditions and large volumes of deadwood. Thus, although overall assemblage composition did not differ between stand types, part of the beetle community seemingly benefited from selective felling. We therefore recommend that selective felling is considered as an alternative to clear-felling to maintain biodiversity values.

1. Introduction

Anthropogenic disturbance has altered ecosystems worldwide, resulting in habitat loss and species extinctions over a wide range of biomes (Butchart et al., 2010; FAO, 2010). Forest ecosystems are no exception and extraction of forest resources has led to changes in ecosystem structures and processes, and to biodiversity loss (FAO, 2010; Ceballos et al., 2015). Historically, boreal forests have been structured by both large scale stand replacing disturbances, e.g. fire and storms, but also small scale disturbances, e.g. gap dynamics (Zackrisson, 1977; Siitonen, 2001; Saint-Germain et al., 2008; Kuuluvainen and Aakala, 2011). This has created a mosaic landscape with both between- and within-stand variability, thus yielding a multitude of ecological niches and living conditions for many different organisms.

The large scale introduction of even-aged silviculture (e.g. clear-cutting) in the mid-20th century has led to rapid changes in many boreal forest landscapes. Even-aged silviculture results in stands with a simplified forest structure (e.g. tree species and age composition, tree size and spatial configuration of trees), reduced volumes of dead wood, and breaks in forest continuity, which fragments habitats (Östlund et al., 1997; Linder and Östlund, 1998; Pommerening and Murphy, 2004; Kuuluvainen et al., 2012). Although even-aged silviculture has increased timber production, it has had negative impacts on forest biodiversity (Paillet et al.,

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* Corresponding author at: Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, 90183 Umeå, Sweden.

E-mail address: joakim.hjalten@slu.se (J. Hjältén).

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2010), especially on old-growth and deadwood associated forest species (Siitonen, 2001; Tikkanen et al., 2006). Many species disappear from a forest stand during the clear-felling phase (Stenbacka et al., 2010; Rudolphi et al., 2011).

When even-aged silviculture is applied there is a break in the deadwood profile: some deadwood is typically produced or retained at clear-cutting, but after that very little input of deadwood will occur until self-thinning resumes ca. 40–70 years after clear-cutting. During this time, the availability of deadwood will be low (Stenbacka et al., 2010). Dead and dying trees support a high diversity of associated organisms, including insects, wood fungi, lichens and bryophytes (Berg et al., 1995; Esseen et al., 1997; Siitonen, 2001; Grove, 2002; Stokland et al., 2012). These organisms play an important role in forest food webs and in ecosystem processes such as decomposition (Stokland et al., 2012). However, due to their often high degree of specialisation, they are sensitive to habitat change caused by even-aged silviculture (Berg et al., 1994, 1995; Esseen et al., 1997; Siitonen, 2001; Grove, 2002; Stenbacka et al., 2010; Stokland et al., 2012). Increasing deadwood availability is therefore of high priority in forest biodiversity management (Siitonen, 2001; Lindenmayer et al., 2006; Stokland et al., 2012; Ulyshen, 2013).

To mitigate the negative impacts of even-aged silviculture on biodiversity, conservation measures have been introduced, imposed through changes in legislation or certification demand (Johansson et al., 2013). These environmental considerations during clear-felling include leaving buffer zones close to streams, retention of dead trees and small patches of living trees, and active production of high stumps. These measures are likely to improve the situation for biodiversity but are most likely insufficient to maintain biodiversity in the longer term (Gustafsson et al., 2010; Johansson et al., 2013; Roberge et al., 2015) as the protected forest area in many countries may not be sufficient to maintain viable populations of old-growth associated species (Johansson et al., 2013).

Additional measures are therefore needed to maintain biodiversity in managed boreal landscapes and uneven-aged silviculture systems (e.g. selective felling) are under consideration to help satisfy ecological demands and social criteria related to sustainable forest management (Kuuluvainen, 2009; Axelsson and Angelstam, 2011). In contrast to even-aged silviculture, uneven-aged silviculture largely maintains late successional species assemblages (Kuuluvainen et al., 2012; Joelsson et al., 2017). Uneven-aged silviculture involves selectively removing a portion of the older trees in a stand, thus creating small scale variation in light conditions and temperature that may mimic conditions in natural forests subject to gap dynamics (Kuuluvainen, 2009). Such conditions may benefit species adapted to the slightly more open conditions in natural forest compared with denser managed forests. This may be important for these species as stand-level volumes of timber have increased by 40–80% since the 1950s when even-aged silviculture became a standard (SLU, 2012). This suggests that there could be benefits for biodiversity resulting from uneven-aged silviculture. However, even if uneven-aged silviculture generally is widely considered to be more favorable for biodiversity than even-aged silviculture, we lack empirical evidence to support this assumption. There is therefore an urgent need to test the ecological implications of uneven-aged silviculture (Kuuluvainen et al., 2012).

The aim of this study was to test if selective felling benefits beetle biodiversity by producing beetle assemblages that better resemble those of old growth stands than those found in uncut production stands. We thus set out to test the following hypotheses.

(1) The assemblage composition of beetles will change following selective felling, becoming similar to that in old growth stands. We thus predict that species associated with old-growth conditions will benefit from selective felling.
(2) Species richness and abundance of beetles will increase following selective felling and become similar to that in old growth stands.

2. Material and methods

2.1. Study sites

Our study was located in the boreal zone of central Sweden, in the counties of Jämtland and Medelpad (Fig. 1). Average monthly temperatures in the region vary from −10 °C in January to 13 °C in July and the annual precipitation averages 600 mm/yr (SMHI, 2013). Our study stands were dominated by multiple cohorts of Norway spruce (*Picea abies*) (>70%) mixed with birch (*Betula pendula* and *B. pubescens*), and smaller proportions of Scots pine (*Pinus sylvestris*), aspen (*Populus tremula*) and *Salix* spp. Stand size varied between 2 and 30 ha, with an average size of 11 ha. Mean elevation was 391 masl (range 247–483 masl). Average tree age of trees forming the top layer of the canopy ranged from 94 to 184 years. Ground vegetation was dominated by bilberry (*Vaccinium myrtillus*) (Table 1).

2.2. Experimental design

Three stand types were included in the study: (1) mature uneven-stands which have recently undergone (2–14 years (average 7 years) prior to the study) uneven-aged silviculture, referred to as *Selective felling* (N = 9); (2) mature uneven-aged stands without recent history of management: *Uncut* (N = 8); and (3) old-growth stands, set aside from commercial forestry due to high conservation values: *Old growth* (N = 8), adding to a total of 25 stands (Fig. 1 and Table 1). Selective felling is rarely used in Sweden but occurs occasionally in the study area. Thus, the stands used were selected from a larger number of candidate stands, based on stand data provided by the forest owner and visual inspection of all stands (Table 1). To reduce between stands variation, stand characteristics were standardized in selected stands and similar variation were obtained within all stand types (Table 1).

Using these criteria, stands in the *Uncut* treatment were very similar to *Selective felling* treatments prior to harvest: both stand types met silvicultural criteria required for selective felling, e.g. they were multilayered. The uncut stands therefore serve as suitable reference stands representing stand conditions in selective felling treatment prior to harvesting. However, no recent (>50 years) management has been carried out in uncut stands and this, together with a low occurrence of natural disturbances, has left these stands denser than natural forest (Table 1). Both selectively cut and uncut stands are part of the production forest with no documented conservation values. In contrast, the old growth stands are set aside due to high conservation values and designated either as key habitats or strict reserves.

Single tree selective felling (selective felling) as applied in this study is the most commonly applied uneven-aged management method in Sweden. During selective felling, approximately 30% of the standing volume is harvested, while 70% is retained. During the first harvest intervention, the timber extraction is mainly concentrated around the 4 m wide harvest trails, placed every 20 m in the stand. In the successive interventions occurring with approximately 25 years intervals, the same harvest trails will be utilized and single trees will be harvested from the strips in between harvest trails. Harvesters drive only in the trails, minimizing damage to understory vegetation and deadwood in the 20 m retention strips in between machine corridors.

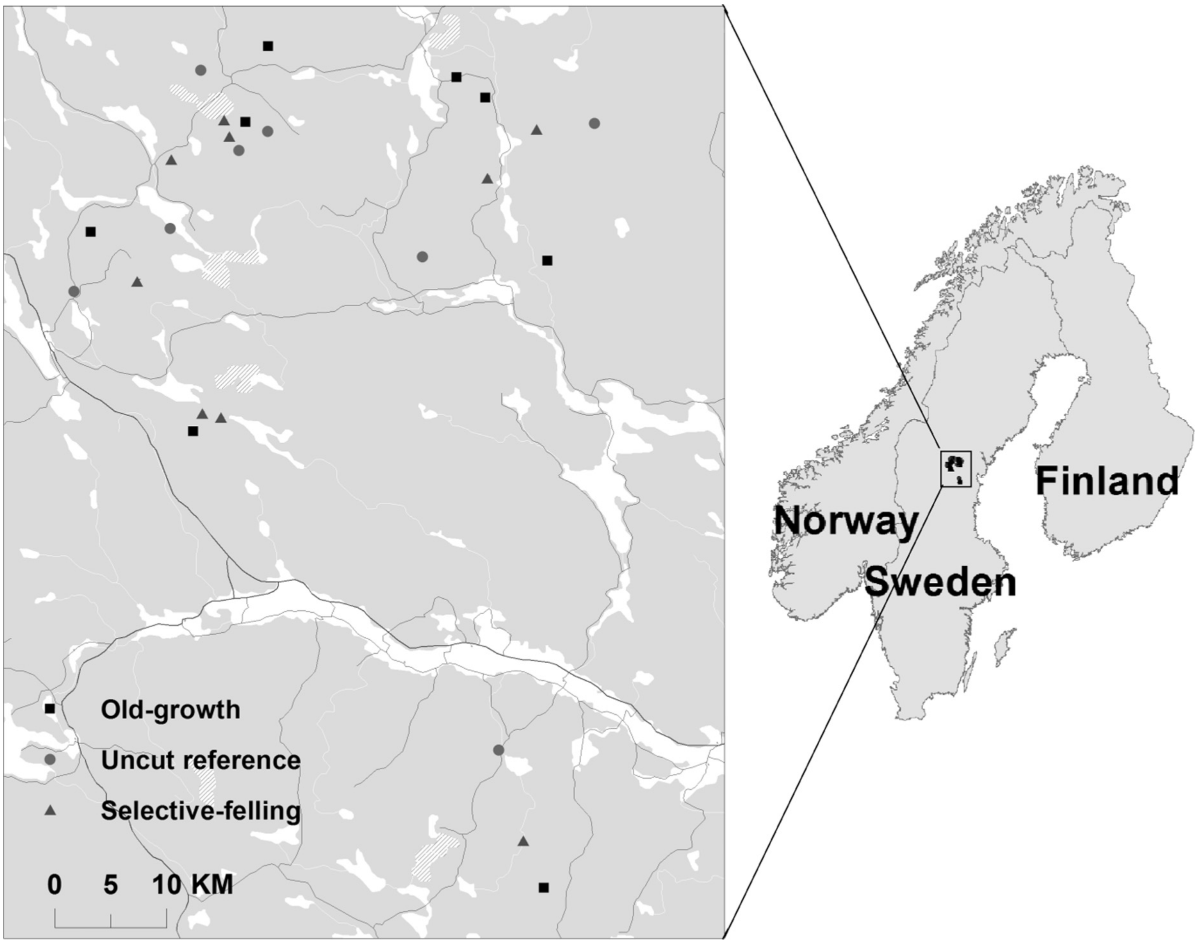

Fig. 1. Maps of the distribution of the forest stands used in the study.

Table 1
Structural characteristics of the experimental forest stands, showing sample mean (±standard error). Note that all stand characteristics except size, age and altitude were measured after selective felling was conducted. GLM analyses were used to test for differences between stand types. Letters after mean values denote significant differences in the post-hoc test ($P < 0.05$).

	Selective felling	Uncut	Old Growth	GLM (p-value)
Size (ha)	7.99 (±0.76)	7.19 (±1.57)	19.53(±9.00)	0.072
Stand age (years)	120 (±6.33)	132 (±7.11)	136 (±8.24)	0.215
Altitude	391 (±8.65)	364 (±24.7)	418 (±22.8)	0.142
Pine Vol%	6.31 (±3.75)	4.46 (±2.93)	7.76 (±5.07)	0.839
Spruce Vol%	80.0 (±4.16)	80.2 (±3.76)	80.8 (±6.00)	0.985
Birch Vol%	13.4 (±2.07)a	14.1 (±3.44)a	6.12 (±1.66)b	0.025
Aspen & Salix Vol%	0.92 (±0.44)a	0.28 (±0.28)a	5.00 (±2.34)b	0.024
Deadwood (m^3 ha^{-1})	19.8 (±4.09)a	25.0 (±5.45)a	64.7 (±10.2)b	0.001
Basal area (m^2 ha^{-1})	17.9 (±1.00)a	24.5 (±0.98)b	25.7 (±2.92)b	0.006
Stem per hectare	862 (±68.0)	902 (±68.0)	702 (±46.7)	0.063

2.3. Beetle collection and identification

In each stand, we collected beetles using three window traps of the Polish IBL2 model (for description see Stenbacka et al. (2010)) located 25 m from the stand centre and oriented in N, SW and SE directions, respectively. The traps were active from 28 May to 17 September 2014. All beetles were counted and identified to species level, with the exception of the genera *Epuraea*, *Acrotrichi* and *Gabrius*, by the expert taxonomist Bengt Andersson. We classified beetle species as either saproxylic (facultative or obligate) or non-saproxylic according to the definition of Stokland et al. (2012). We further classified beetles by feeding group: predators, fungivores, and cambivores, based on ecological classifications by Koch et al. (1989) and Palm (1959), with the addition of species confined to the northern part of Sweden (Hilszczański, J., Pettersson, R. and Lundberg, S. pers. comm.). Feeding guilds were not exclusive, a species can belong to more than one feeding group. Threat status was based on the Swedish red list (Westling, 2015). Nomenclature and taxonomy of the beetles followthe Swedish taxonomic database (Dyntaxa version 1.1.6102.24188, 2015).

2.4. Characterisation of stand structure

We sampled dead wood (volume, diameter, decay-class and tree species) in three randomly distributed, circular plots of 1000 m^2 per stand. All deadwood with a diameter of $\geq$0.1 m and length ≥1.3 m that originated from within the plot (had their base in the plot) was inventoried. We measured all trees on 500 m^2 plots, using the same three centrum coordinates as above. Based on the measures we calculated tree species composition, stems per hectare, diameter distribution and basal area. We obtained information on stand size, average tree age, altitude, soil fertility and soil moisture from the forest owners' database.

2.5. Statistical analyses

For all statistical analyses on the beetle data, we pooled catches from the three traps within each stand to analyse the richness, abundance and the composition of beetles. We used generalized linear models (GLM) with a negative binomial error distribution from the package "lme4" (Bates et al., 2016) in R, version 3.2.0 (R Core Team, 2012) to test for treatment effects on species richness and abundance. The assemblage composition were analysed using manyGLM from the 'mvabund' package in R (Wang et al., 2012) while controlling for altitude and stand size by including them as co-variates. ManyGLM uses the sum of log-likelihood from many individual GLMs to create a test statistic verified through randomization to evaluate a treatment effect on the assemblage composition. Warton et al. (2012) suggests that this approach provides increased statistical power for detecting differences in communities of less abundant species that may be more poorly represented by distance-based approaches. Statistical significance was evaluated using 999 resampling iterations via PIT-trap resampling (Wang et al., 2012) and all individual univariate GLM models were fitted using negative binomial link functions. We excluded all singleton species from the assemblage composition analyses as rare species has little effect on the statistical outcome but high uncertainty whether they origin from the stand or elsewhere. If the overall test showed significant treatment effects, we performed pairwise comparisons between treatments. The results from the univariate models were retrieved both for the overall test and for all pairwise comparisons. Because the diverse community of beetles, the number of comparisons was high and hence the detectability after adjustment for multiple comparisons very low, making adjustment of p-values less meaningful and questionable (Moran, 2003). Thus, we report unadjusted p-values for all tests but interpret the results with caution.

We also tested for associations between stand treatment and tree species composition, altitude, stand size, and deadwood volume using GLMs with either a normal distribution, a Poisson distribution (with a log link) or exponential distribution (with a reciprocal link) using the software JMP (SAS Institute Inc., 2015). We created rarefied species richness curves, using 100 randomizations in EstimateS (Colwell, 2006) to compare species richness while accounting for differences in abundance.

3. Results

Most stand characteristics, i.e., stand age, size, altitude and the percent pine and spruce of total standing volume, did not differ significantly among stand types. However, basal area was lower in selective felling than in the other stand types (Table 1). Furthermore, tree density was marginally significantly lower in old growth stands, which also had a lower proportion of birch than the other stand types (Table 1). In contrast, the proportion of aspen and *Salix* ssp. was higher in old growth than in selective felling. Similarly, the volume of deadwood was significantly higher in old growth stands than in the other stand types (Table 1).

In total we captured 14,199 beetle individuals belonging to 360 species of which 120 were singleton captures and therefore excluded from the assemblage analyses (see Appendix A for complete species list). The three most abundantly represented feeding guilds were fungivores, predators and cambium consumers. The dominant species were *Dryocoetes autographus* and *Pteryx suturalis* with 3758 and 854 individuals, respectively. We collected 10 red-listed species, totalling 32 individuals. Most of the red-listed species were captured as singletons or doubletons, so sample size was too small to permit statistical analyses (Appendix A).

The assemblage composition (analyses based on the occurrence and abundance of individual species) of obligatory saproxylic beetles and cambivores differed significantly among different stand types (ManyGLM: $p < 0.049$ and $p < 0.032$, respectively, Table 2). For all other feeding groups except non-saproxylic beetles, the effect of stand type on assemblage composition was only marginally significant ($p < 0.10$). The assemblage composition of non-saproxylic beetles did not differ among stand types (Table 2). However, for all feeding groups except cambivores, post-hoc pairwise comparisons were not significant, suggesting that compositional differences among stand-types were relatively minor for these groups. For cambivores, post-hoc pairwise comparisons of stand-types supported our initial hypothesis that composition would differ between selective felling and uncut stands. Also consistent with our predictions, cambivore composition in selective cuts did not differ from old-growth stands but old growth stands differed from uncut stands (Table 2). Altitude explained a significant part of the variation for all beetle groups. Stand size had a significant influence on assemblage composition of obligate saproxylics and cambivores, and a near-significant effect on all beetles and all saproxylic beetles (Table 2).

The manyGLM analysis of cambivores revealed three species that differ significant between selective felling and uncut stands. *Crypturgus hispidulus* and *C. cinereus* were more common ($P = 0.008$, LR (Likelihood ratio) = 8.68 and $P = 0.049$, LR = 5.70, respectively) and *Phloeotribus spinulosus* was less common ($P = 0.008$, LR = 7.74) in selective fellings. Four species, *Crypturgus cinereus, Pissodes harcyniae, Pityogenes chalcographus* and *Polygraphus punctifrons* had higher abundances in old growth than in uncut stands ($P = 0.031$ and LR = 11.33 $P = 0.027$ and LR = 4.16, $P = 0.023$ and LR = 6.59, $P = 0.048$ and LR = 4.99, respectively) (Fig. 2).

The GLM analyses of species richness and abundance of beetles in the different stand types revealed a tendency of higher species richness in selective felling and old growth stands than in uncut stands, but the effects were not significant for any of the functional groups (Table 3 and Fig. 3). The abundance of cambivores was higher in old growth than in uncut stands. Rarefaction curves revealed no difference between stand types in abundance-species richness relationships (Appendix B).

4. Discussion

It has been suggested that management methods mimicking natural disturbances should enhance stand heterogeneity and therefore benefit biodiversity (Kuuluvainen, 2009). We thus predicted that selective felling would alter beetle assemblage composition, making it more similar to that of old-growth stands. We found partial support for our first hypothesis. Although we did not detect differences in overall assemblage composition among stand types, the assemblage composition of both cambivores and obligate saproxylics in selective fellings differed (marginally in the latter case) from those in uncut stands, but were similar to those in old-growth stands. The significant effect on cambivore assemblages, mainly explained by a higher abundance of the bark beetles *Crypturgus hispidulus* and *C. cinereus* in selective fellings than uncut stands, suggests that these species, which are associated with early decay stages of deadwood and semi-open stand

Table 2
Results of the manyGLM analyses exploring the effect of stand type, altitude and stand size on assemblage composition of beetles. Res.Df = Residual degrees of freedom, Dev = deviance, p = p-value. Significant differences are marked in bold numbers to highlight the results.

Overall species composition				Selective/uncut			Selective/Old growth			Old growth/Uncut		
	Res.Df	Dev	p	Res.Df	Dev	p	Res.Df	Dev	p	Res.Df	Dev	p
All beetles												
Stand type	22	2739	0.089	15	366.8	0.123	15	358.4	0.228	14	1364	0.123
Altitude	21	1479	**0.005**	14	440.0	**0.016**	14	416.2	**0.016**	13	1462	**0.007**
Size	20	1364	0.096	13	288.7	0.284	13	384.4	0.055	12	1350	**0.048**
Saproxylic												
Stand type	22	594.9	0.098	15	305.9	0.105	15	277.0	0.221	14	298.5	0.101
Altitude	21	375.6	**0.009**	14	359.8	**0.019**	14	323.0	**0.042**	13	364.3	**0.016**
Size	20	291.6	0.084	13	203.8	0.307	13	308.8	0.062	12	290.8	**0.039**
Obligate saproxylic												
Stand type	22	393.7	**0.049**	15	204.5	0.094	15	177.9	0.184	14	197.3	0.085
Altitude	21	243.9	**0.005**	14	229.6	**0.015**	14	206.6	**0.040**	13	224.7	**0.015**
Size	20	210.6	**0.017**	13	143.2	0.296	13	220.0	**0.018**	12	195.5	**0.034**
Non saproxylic												
Stand type	22	72.8	0.474									
Altitude	21	55.5	0.061		NA			NA			NA	
Size	20	31.1	0.742									
Cambivores												
Stand type	22	100.6	**0.032**	15	50.7	**0.038**	15	39.6	0.183	14	58.4	**0.036**
Altitude	21	48.4	**0.040**	14	65.7	**0.005**	14	37.0	0.167	13	37.8	0.136
Size	20	60.9	**0.010**	13	35.7	0.113	13	56.5	**0.024**	12	58.7	**0.013**
Fungivores												
Stand type	22	339.6	0.091	15	190.1	0.071	15	154.3	0.270	14	152.8	0.190
Altitude	21	202.9	**0.016**	14	178.2	0.069	14	161.4	0.173	13	225.8	**0.009**
Size	20	148.4	0.291	13	133.1	0.303	13	162.5	0.145	12	139.0	0.199
Predators												
Stand type	22	277.2	0.090	15	122.5	0.254	15	155.1	0.110	14	141.3	0.128
Altitude	21	196.3	**0.003**	14	165.5	**0.028**	14	190.0	**0.008**	13	170.3	**0.021**
Size	20	124.3	0.214	13	87.0	0.649	13	132.3	0.154	12	137.5	0.064

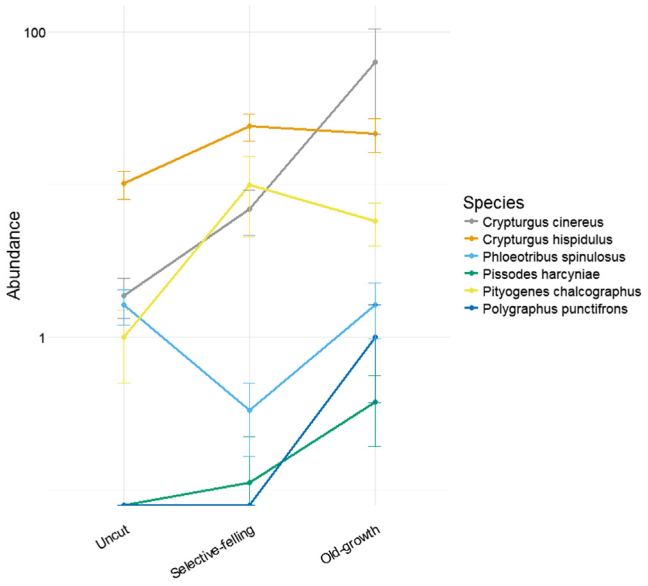

Fig. 2. Mean ± CI abundance per species and stand type for the cambivore species that differed significant ($p < 0.05$) in abundance between uncut stands and selective felling as well as between uncut and old growth stands in the manyGLM analysis. The y-axis is log-transformed.

conditions (Heikkala et al., 2016), were attracted to selective fellings. Both species utilize windthrow areas (Wermelinger et al., 2002) and reach their highest densities in forest reserves (Hjältén et al. 2012). In addition, *C. cinereus* is more abundant on low stumps than on other deadwood substrates (Hjältén et al., 2010), which may explain why they were attracted to selective fellings, where fresh stumps are available. In contrast, *Phloeotribus spinulosus* also had a significant influence on the differences in assemblage composition but this species was negatively affected by selective felling. A previous study suggest that this species is associated with late successional seminatural forests and absent from managed forest in Finland (Simila et al., 2003) and occurs in park landscapes in Sweden, but only where dense undergrowth occurs (Jonsell, 2012). It is thus possible that *P. spinulosus* is disadvantaged by the more open stand conditions created by selective felling. However, it should be noted that by comparison, clear-felling results in profound changes in beetle assemblages composition, disfavoring many old growth associated species (McGeoch et al., 2007; Stenbacka et al., 2010; Hjältén et al. 2012; Joelsson et al., 2017).

Beetle assemblage composition did not differ between selective felling and old growth stands, in agreement with our prediction that these stand types support similar assemblages. Differences in assemblage composition between old growth and uncut stands indicate that selective felling caused beetle assemblages to converge on those in old growth stands. The differences in assemblages between uncut and old growth stands were mainly explained by higher abundances of the cambivores *Crypturgus cinereus, Pissodes harcyniae, Pityogenes chalcographus* and *Polygraphus punctifrons* in old growth stand. Interestingly, these species often occurred in intermediate or high densities in selective felling (Fig. 2), indicating that they benefitted from selective felling. *Pissodes harcyniae* prefer old growth stands whereas *P. chalcographus* emerge in greater numbers from clear-cuts than from reserves (Hjältén et al. 2012). However, *P. chalcographus* is also attracted to areas with large amounts of deadwood, e.g. windrows (Wermelinger et al., 2002). The higher volumes of deadwood, in combination with a lower tree density, and thus potentially more light in old growth stands, might explain the higher abundance of this species in old growth compared to uncut stands.

Table 3
Results of GLM testing the effect of stand type on total abundance and species richness for all beetles and beetle functional groups. Bold p-values highlight significant differences.

	Abundance			Species richness			Posthoc
	Chi^2	Df	p	Chi^2	Df	p	
All species	4.70	2	0.095	2.52	2	0.348	
Saproxylic	4.78	2	0.091	2.11	2	0.348	
Obligate saproxylic	5.73	2	0.057	3.70	2	0.157	
Non saproxylic	0.21	2	0.898	1.67	2	0.432	
Predators	1.99	2	0.369	1.45	2	0.484	
Fungivores	0.43	2	0.805	3.50	2	0.173	
Cambivores	**6.55**	**2**	**0.038**	1.81	2	0.405	**OG > UC**

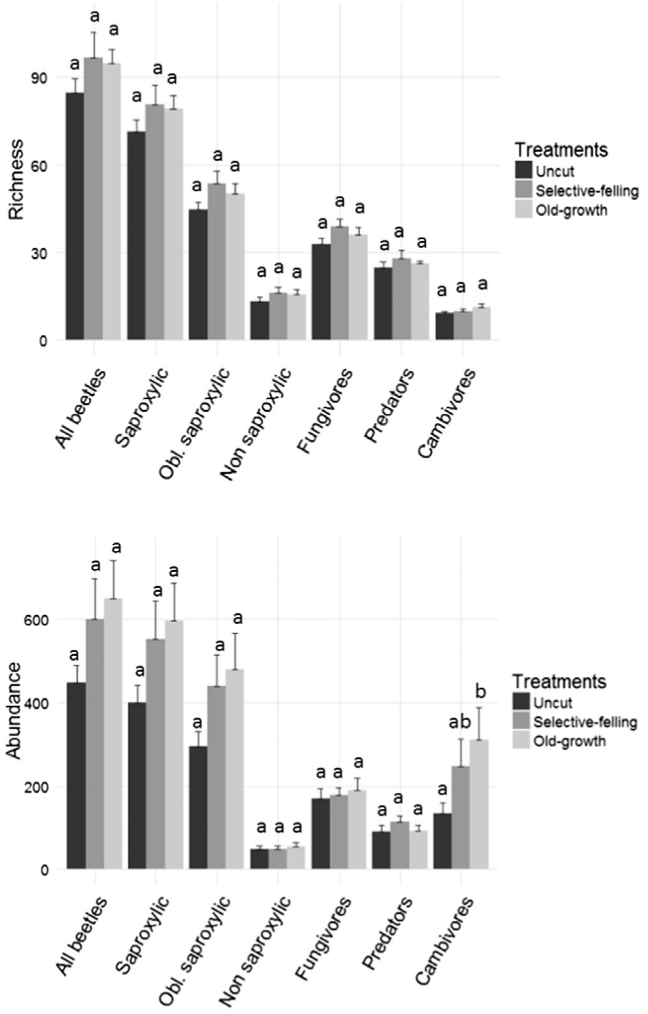

Fig. 3. Mean ± SE of: (a) abundance; and (b) species richness of functional groups of beetles in the different stand types.

Our second hypothesis was only weakly supported by our results. Species richness was not higher in selective felling than in uncut stands, although there was a general trend in this direction. Furthermore, species richness did not differ between old-growth stands and uncut stands. However, abundance of cambium consumers was higher in old-growth than in uncut stands, and the abundance in selective felling did not differ from the abundance observed in old growth stands. This is consistent with the patterns from the assemblage analyses were some cambivore species that had a significant influence on the differences in assemblage composition were more abundant in old growth and selective felling than in uncut stands, probably due to higher abundance of deadwood and a more open canopy.

Stand variables influenced assemblage composition of beetles, with altitude proving particularly influential. Altitude is known to influence species richness and assemblage composition: species richness generally decreases with increasing altitude (McArthur, 1969; Orians, 1969; Terborgh, 1971) although this relationship is sometimes humped (Rahbek, 2005). Previous studies have reported that the species richness of saproxylic beetles decreases and assemblage composition changes with altitude (Tykarski, 2006; Weiss et al., 2016). In this study, altitude ranged from 247 to 483 masl, which corresponds to a differences of approximately 15 day in the length of the vegetation period (daily mean temperature >5 °C) (Morén and Perttu, 1994) which could be sufficient to influence assemblage composition. However, it should be noted that the average altitude did not differ between stand types (Table 1), so this variable could not have confounded the effects of stand type on assemblage composition.

Our finding that assemblages of cambivores and obligate saproxylics (marginally) differed between uncut and selectively felled stands and that this was explained by a higher abundance of some cambivore species in selectively felled stands suggests that selective felling may have benefits for beetle diversity in a short term perspective. At the same time we acknowledge that only a small proportion of the collected species benefitted from selective felling. Thus, we cannot argue that selective felling generally benefit biodiversity in long term perspective. Additional studies of the response of other organism group to selective felling are urgently needed. The species that benefitted from selective felling are associated with semi-open canopy cover or low stumps created by selective felling. This is not that surprising as tree retention at harvest has been shown to benefit species with similar adaptations (Heikkala et al., 2016). On balance, we thus conclude that the ecological benefits might be limited, but that further research is required to better elucidate the long term effects of successive interventions by selective felling. At the same time we did not detect any substantial negative effect of selective felling on species richness, abundance or assemblage composition of beetles and in contrast to clear-felling, selective felling maintains assemblage composition and species richness of beetles within a stand after intervention (Joelsson et al., 2017). We therefore recommend that selective felling is considered as an alternative to clear-felling in areas with production forest where it is especially important to mitigate negative effects of forestry on biodiversity.

Acknowledgements

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Appendix A

The abundance of the collected species in different stand types. Species are classified in feeding group (not mutually exclusive) and red-list status is indicated after the species name (NT = near threatened, VU = vulnerable).

Species	Uncut	Old growth	Selective felling	Obl. Saprox.	Predator	Fungivore	Cambivore
Abdera flexuosa	0	0	2	x		x	
Acidota crenata	8	2	11		x		
Acrostiba borealis	3	2	0		x		
Acrotona fungi	1	0	0				
Acrulia inflata	11	5	8			x	
Agathidium badium	0	0	2			x	
Agathidium confusum	22	19	11			x	
Agathidium discoideum (NT)	2	6	4			x	
Agathidium mandibulare	0	1	0			x	
Agathidium nigripenne	2	3	1			x	
Agathidium seminulum	45	59	52			x	
Aleochara fumata	0	1	5		x		
Aleochara moerens	6	1	9		x		
Alosterna tabacicolor	0	0	4	x			
Ampedus nigrinus	9	3	1	x	x		
Ampedus tristis	1	0	3	x	x		
Anaspis bohemica	0	1	0	x	x		
Anaspis rufilabris	1	5	3	x	x		
Anisotoma axillaris	1	1	4	x		x	
Anisotoma castanea	2	1	1	x		x	
Anisotoma glabra	5	8	14	x		x	
Anisotoma humeralis	4	10	8	x		x	
Anisotoma orbicularis	3	1	4	x		x	
Anomognathus cuspidatus	3	3	6	x	x		
Anoplotrupes stercorosus	0	1	0				
Anthophagus omalinus	14	32	31		x		
Aphodius borealis	1	0	0				
Aphodius depressus	4	18	6				
Aphodius fasciatus	0	0	1				
Aphodius lapponum	9	3	7				
Aphodius nemoralis	14	13	19				
Aphodius rufipes	177	160	142				
Arpedium quadrum	2	0	1		x		
Aspidiphorus orbiculatus	19	15	20			x	
Atheta aeneipennis	0	1	0		x	x	
Atheta brunneipennis	1	0	1		x	x	
Atheta castanoptera	5	4	1		x	x	
Atheta corvina	1	0	0		x		
Atheta crassicornis	1	0	4		x	x	
Atheta gagatina	1	0	0		x	x	
Atheta incognita	0	0	14		x	x	
Atheta myrmecobia	1	0	1		x	x	
Atheta paracrassicornis	0	0	1		x	x	
Atheta picipennoides	1	0	0		x	x	
Atheta picipennoides	1	0	0				
Atheta picipes	0	3	0				
Atheta pilicornis	0	0	1				
Atheta sodalis	5	10	0				
Atheta subtilis	0	1	0				
Atheta vaga	0	0	1				
Athous subfuscus	15	5	30		x		
Atomaria atrata	2	0	1			x	
Atomaria bella	17	61	28	x		x	
Atomaria lewisi	0	0	1			x	
Atomaria ornata	8	13	15			x	
Atomaria testacea	0	0	2			x	
Atomaria turgida	0	1	3			x	

(*continued on next page*)

Appendix A (*continued*)

Species	Uncut	Old growth	Selective felling	Obl. Saprox.	Predator	Fungivore	Cambivore
Atomaria vespertina	4	14	0			x	
Atrecus longiceps	14	11	20	x	x		
Atrecus pilicornis	57	25	35	x	x		
Autalia impressa	1	2	1			x	
Bibloporus bicolor	74	48	97	x	x		
Bisnius nigriventris	1	0	0		x		
Bisnius puella	2	9	3		x		
Bolitobius cingulatus	0	0	1		x		
Bolitochara mulsanti	0	3	0	x		x	
Bolitochara pulchra	0	1	0				
Bryaxis bulbifer	0	2	0		x		
Bryophacis rufus punctipennis	8	3	5		x		
Bryoporus cernuus	1	1	1		x		
Byturus tomentosus	1	1	2				
Cacotemnus rufipes	0	1	0	x			
Calodera aethiops	0	0	1			x	
Calodera nigrita	1	0	0				
Calopus serraticornis	1	0	0	x			
Catops coracinus	1	0	0				
Catops longulus	1	1	0				
Catops morio	0	0	1				
Catops nigriclavis	0	2	0				
Catops tristis	1	3	2				
Cercyon borealis	1	3	4		x		
Cercyon convexiusculus	1	0	0			x	
Cercyon impressus	1	0	6		x		
Cercyon lateralis	6	5	7		x		
Cerylon deplanatum	0	0	2	x		x	
Cerylon ferrugineum	137	82	109	x		x	
Cerylon histeroides	110	144	130	x		x	
Cis bidentatus	3	13	6	x		x	
Cis boleti	12	17	26	x		x	
Cis castaneus	1	4	3	x		x	
Cis comptus	4	3	11	x		x	
Cis dentatus	4	17	4	x		x	
Cis fagi	0	0	1			x	
Cis festivus	0	0	2	x		x	
Cis glabratus	0	0	3	x		x	
Cis jacquemartii	12	12	22	x		x	
Cis lineatocribratus	0	0	1	x		x	
Cis micans	1	3	5	x		x	
Cis punctulatus	0	6	10	x		x	
Cis quadridens	0	1	0	x		x	
Cis vestitus	1	5	1	x		x	
Clambus punctulum	0	0	2			x	
Corticaria lapponica	0	0	3	x		x	
Corticaria porochini	0	5	3			x	
Corticaria rubripes	8	10	23			x	
Corticaria serrata	0	0	1			x	
Corticarina minuta	0	1	0			x	
Corticarina similata	0	1	2			x	
Cortinicara gibbosa	0	0	1			x	
Cryphalus saltuarius	0	0	1	x			x
Cryptolestes abietis	1	2	2	x	x		
Cryptolestes ferrugineus	0	2	0				
Cryptophagus lapponicus	118	211	106			x	
Cryptophagus quadrihamatus (NT)	0	1	0	x		x	
Cryptophagus scanicus	8	32	10			x	
Cryptophagus subdepressus	11	5	8			x	
Crypturgus cinereus	15	504	62	x			x
Crypturgus hispidulus	81	173	217	x			x

Appendix A (*continued*)

Species	Uncut	Old growth	Selective felling	Obl. Saprox.	Predator	Fungivore	Cambivore
Curtimorda maculosa	0	0	1	x		x	
Cychramus luteus	17	5	4			x	
Cychramus variegatus	23	6	9			x	
Cyphon coarctatus	0	3	0		x		
Cyphon punctipennis	0	1	0		x		
Cyphon variabilis	0	0	1		x		
Dacne bipustulata	2	1	0	x		x	
Dadobia immersa	1	2	0	x		x	
Dasytes plumbeus	0	1	0	x	x		
Deliphrum tectum	1	0	1		x		
Dendroctonus micans	1	0	1	x			x
Dendrophagus crenatus	23	26	15	x		x	
Dendrophilus pygmaeus	4	3	2		x		
Denticollis linearis	1	1	8	x			
Diacanthous undulatus	1	1	0	x			
Dictyoptera aurora	17	24	23	x	x		
Dinaraea arcana	3	0	4	x		x	
Dinaraea linearis	0	1	0	x		x	
Dolichocis laricinus (NT)	0	2	0	x		x	
Dorcatoma dresdensis	2	1	1	x		x	
Dorcatoma robusta	0	0	1	x		x	
Dromius agilis	0	0	2		x		
Dropephylla linearis	2	7	5	x	x	x	
Dryocoetes alni	1	0	1	x			x
Dryocoetes autographus	793	1392	1573	x			x
Elateroides dermestoides	16	8	29	x		x	
Elmis aenea	0	0	1				
Endomychus coccineus	1	2	4	x		x	
Enicmus apicalis (NT)	3	1	1	x		x	
Enicmus fungicola	111	53	67			x	
Enicmus planipennis (NT)	0	1	0	x		x	
Enicmus rugosus	28	36	57	x		x	
Enicmus testaceus	0	0	1	x		x	
Ennearthron cornutum	1	0	9	x		x	
Episernus angulicollis	1	0	2	x			
Euaesthetus bipunctatus	0	2	0		x		
Euconnus claviger	3	1	1		x		
Euconnus maklinii	0	1	0		x		
Eudectus giraudi	17	5	13	x		x	
Euplectus karstenii	150	183	212		x		
Euplectus piceus	3	5	3		x		
Euplectus punctatus	41	47	48	x	x		
Euplectus sanguineus	1	0	0		x		
Glischrochilus hortensis	1	6	4			x	
Glischrochilus quadripunctatus	2	1	10	x	x	x	
Gyrophaena affinis	0	2	1			x	
Gyrophaena boleti	4	4	3	x		x	
Gyrophaena minima	0	0	1	x		x	
Hadreule elongatula	0	1	1	x		x	
Hadrobregmus pertinax	1	2	1	x			
Hallomenus axillaris	1	3	5	x		x	
Hallomenus binotatus	11	23	20	x		x	
Haploglossa marginalis	1	1	2			x	
Haploglossa picipennis	0	1	0				
Haploglossa villosula	0	4	8			x	
Harpalus laevipes	0	0	1				
Holobus apicatus	2	1	2		x		
Hydrobius fuscipes	0	0	1				
Hylastes brunneus	34	57	74	x			x
Hylastes cunicularius	35	39	41	x			x
Hylobius excavatus	1	0	0	x			x

(*continued on next page*)

Appendix A (*continued*)

Species	Uncut	Old growth	Selective felling	Obl. Saprox.	Predator	Fungivore	Cambivore
Hylobius pinastri	0	0	1	x			x
Hylurgops palliatus	1	0	0	x			x
Ilyobates nigricollis	0	1	0		x		
Ips typographus	2	7	30	x			x
Judolia sexmaculata	0	0	4	x			x
Latridius consimilis	3	1	0			x	
Latridius gemellatus	0	1	1			x	
Latridius hirtus	3	7	5	x		x	
Latridius porcatus	1	0	0			x	
Leiodes ferruginea	1	1	0			x	
Leiodes lucens	0	2	3			x	
Leiodes obesa	1	1	1			x	
Leiodes punctulata	0	0	1			x	
Leiodes silesiaca	3	0	2			x	
Leptophloeus alternans	0	0	1	x	x		
Leptusa pulchella	12	5	7	x		x	
Limnebius truncatellus	0	1	0		x		
Liogluta micans	0	0	1			x	
Liotrichus affinis	6	3	21				
Lordithon exoletus	0	0	1		x		
Lordithon lunulatus	20	13	21		x		
Lordithon speciosus	11	9	7	x	x		
Lordithon thoracicus	4	2	2		x		
Lordithon trimaculatus	1	0	0	x	x		
Lordithon trinotatus	7	9	3		x		
Lypoglossa lateralis	0	2	0		x	x	
Malthinus biguttatus	0	0	1	x			
Malthodes fuscus	0	2	0	x	x		
Malthodes pumilus	5	6	10				
Malthodes spathifer	0	1	3				
Megarthrus denticollis	0	2	0		x		
Megarthrus depressus	4	10	12		x		
Megarthrus fennicus	2	1	3		x		
Megarthrus nitidulus	0	1	1		x		
Megasternum concinnum	10	17	22				
Melanotus castanipes	9	17	33	x			
Melanotus villosus	1	6	10	x			
Meligethes aeneus	1	0	0				
Meotica pallens	0	1	0		x		
Micrambe abietis	3	3	2			x	
Micrambe longitarsis	2	3	0			x	
Microscydmus minimus	9	1	8	x	x		
Molorchus minor	0	0	4	x			x
Monotoma angusticollis	0	0	1				
Monotoma conicicollis	1	0	0		x		
Mycetochara maura	1	0	0	x			
Mycetophagus multipunctatus	0	0	1	x		x	
Mycetophagus populi	0	1	0	x		x	
Mycetoporus eppelsheimianus	0	3	2				
Mycetoporus lepidus	29	29	25		x		
Myrmetes paykulli	7	23	6		x		
Nephanes titan	0	0	2				
Nicrophorus vespilloides	2	4	10				
Octotemnus glabriculus	1	1	4	x		x	
Olisthaerus megacephalus (NT)	0	0	1	x	x		
Olophrum fuscum	0	0	1		x		
Omalium caesum	1	1	3		x		
Omalium rivulare	0	1	0		x		
Omalium strigicolle	0	1	0		x		
Omosita depressa	1	2	1				
Orchesia fasciata (NT)	0	3	4	x		x	

Appendix A (*continued*)

Species	Uncut	Old growth	Selective felling	Obl. Saprox.	Predator	Fungivore	Cambivore
Orchesia micans	0	3	2	x		x	
Orithales serraticornis	0	1	0				
Orthocis alni	6	4	9	x		x	
Orthoperus punctatus	5	4	6			x	
Orthotomicus laricis	0	1	1	x			x
Otiorhynchus scaber	1	0	0				
Oxymirus cursor	1	1	0	x			
Oxypoda abdominalis	0	0	1		x		
Oxypoda alternans	10	7	4			x	
Oxypoda spectabilis	0	1	0			x	
Paraphotistus impressus	3	0	0		x		
Pediacus fuscus	0	1	0	x		x	
Peltis ferruginea	1	3	4	x		x	
Philonthus addendus	1	0	1		x		
Philonthus decorus	0	0	2		x		
Philonthus politus	0	0	1		x		
Philonthus succicola	0	0	1		x		
Phloeonomus punctipennis	1	2	6	x	x		
Phloeonomus sjobergi	4	11	10				
Phloeostiba lapponica	2	0	8	x	x		
Phloeotribus spinulosus	13	13	3	x			x
Phratora vitellinae	0	0	1				
Phyllodrepa melanocephala	0	2	0	x	x	x	
Pissodes harcyniae	0	3	1	x			x
Pityogenes bidentatus	1	0	0	x			x
Pityogenes chalcographus	8	46	89	x			x
Pityophagus ferrugineus	1	3	1	x	x		
Pityophthorus micrographus	0	1	0	x			x
Platycerus caprea	0	0	1	x			
Platycis minutus	1	3	3	x	x		
Platydracus fulvipes	1	0	0		x		
Plegaderus vulneratus	0	3	3	x	x		
Pocadius ferrugineus	2	1	0			x	
Podabrus alpinus	0	0	1		x		
Podistra schoenherri	10	3	19	x	x		
Pogonocherus fasciculatus	1	1	1	x			x
Polydrusus pilosus	0	1	0				
Polydrusus tereticollis	1	5	1				
Polygraphus poligraphus	64	116	91	x			x
Polygraphus punctifrons	0	8	0	x			x
Polygraphus subopacus	8	90	14	x			x
Proteinus brachypterus	1	3	0		x		
Proteinus laevigatus	0	1	0		x		
Pteryngium crenatum	8	6	9	x		x	
Pteryx suturalis	256	248	350	x		x	
Ptiliola kunzei	0	1	0			x	
Ptilium modestum	0	0	2			x	
Ptinella johnsoni	0	0	2	x		x	
Ptinella tenella	0	0	2	x		x	
Ptinus subpillosus	3	7	5	x			x
Ptinus villiger	0	1	0				x
Ptomaphagus sericatus	0	1	0				
Pyropterus nigroruber	2	0	4	x	x		
Pytho abieticola (VU)	0	0	1	x	x		
Quedius brevis	2	4	2		x		
Quedius cinctus	0	1	0		x		
Quedius lucidulus	0	3	0		x		
Quedius mesomelinus	5	32	25		x		
Quedius plagiatus	26	20	29	x	x		
Quedius tenellus	11	10	32		x		
Quedius xanthopus	15	19	20		x		

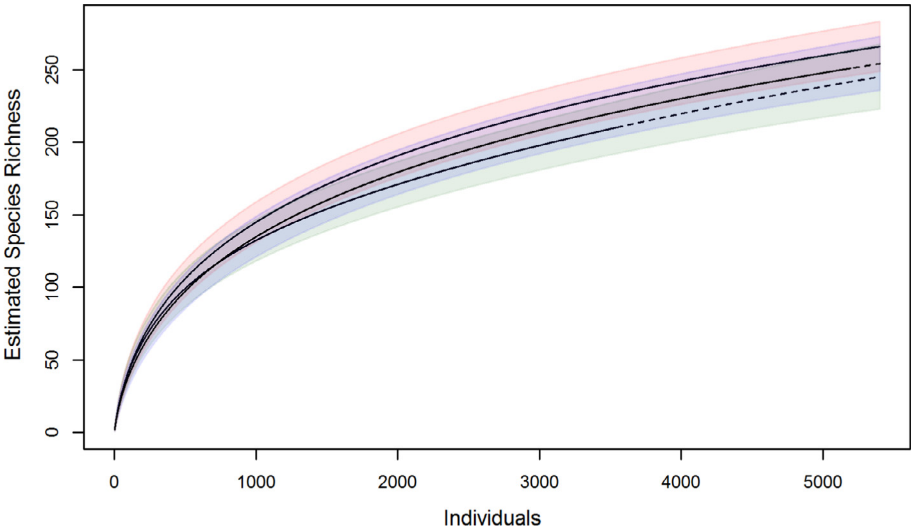
(*continued on next page*)

Appendix A (*continued*)

Species	Uncut	Old growth	Selective felling	Obl. Saprox.	Predator	Fungivore	Cambivore
Rabocerus foveolatus	0	1	1	x	x		
Rhagium inquisitor	0	1	2	x			x
Rhagium mordax	1	1	0	x			x
Rhagonycha atra	11	5	19		x		
Rhizophagus cribratus	0	1	2	x	x		
Rhizophagus depressus	0	1	0	x	x		
Rhizophagus dispar	24	19	29		x		
Rhizophagus fenestralis	47	17	100	x	x		
Rhizophagus ferrugineus	0	17	7	x	x		
Rhizophagus grandis (NT)	1	0	0	x	x		
Rhizophagus nitidulus	14	31	33	x	x		
Rhopalodontus strandi	0	1	3	x		x	
Rhyncolus ater	0	1	1	x			
Rhyncolus sculpturatus	0	0	1	x			
Salpingus ruficollis	11	17	8	x	x		
Scaphisoma agaricinum	8	15	30			x	
Sciodrepoides watsoni	13	11	20				
Selatosomus melancholicus	0	0	1				
Sepedophilus constans	0	1	0			x	
Sepedophilus littoreus	35	19	59			x	
Sepedophilus marshami	0	1	0			x	
Sericus brunneus	0	0	1				
Serropalpus barbatus	0	1	0	x			
Silvanoprus fagi	1	2	3	x	x		
Spavius glaber	1	1	0			x	
Sphaerites glabratus	0	1	2		x		
Sphindus dubius	0	0	1			x	
Stenichnus bicolor	18	12	27		x		
Stenichnus collaris	0	3	3		x		
Stenotrachelus aeneus	0	2	1	x			x
Stephostethus pandellei	1	0	0			x	
Stephostethus rugicollis	5	7	7			x	
Sulcacis nitidus	4	0	0	x		x	
Syneta betulae	0	2	2				
Syntomium aeneum	2	3	4		x		
Tachinus elegans (NT)	0	1	0		x	x	
Tachinus elongatus	0	0	1		x	x	
Tachinus laticollis	7	10	9				
Tachinus pallipes	52	35	39		x	x	
Tachinus rufipes	0	8	0		x	x	
Tachinus subterraneus	0	0	4		x	x	
Tetratoma ancora	1	1	1	x		x	
Tetropium castaneum	1	8	4	x			x
Tetropium fuscum	0	2	0	x			x
Thalycra fervida	1	3	4			x	
Thanasimus femoralis	1	0	1	x	x		
Thiasophila wockii	1	1	1	x	x		
Trichophya pilicornis	0	2	2			x	
Triplax aenea	15	6	11	x		x	
Triplax russica	0	0	3	x		x	
Triplax scutellaris	41	18	22	x		x	
Trixagus carinifrons	0	1	1			x	
Trypodendron domesticum	1	0	3	x		x	
Trypodendron laeve	12	3	7	x		x	
Trypodendron lineatum	115	154	126	x		x	
Tyrus mucronatus	0	0	1			x	
Xantholinus linearis	0	0	1				
Xantholinus longiventris	0	1	0		x		
Xylechinus pilosus	3	5	6	x			x
Xylita laevigata	4	20	26	x		x	

Appendix B

Rarefaction curves (with confidence intervals) showing the relationship between abundance and species richness in different stand types.



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