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Uneven-aged silviculture can reduce negative effects of forest management on beetles

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ABSTRACT

Decline in biodiversity have increased the interest in alternative forest management approaches. Uneven-aged silviculture has been proposed as a mean to maintain continuity of forest canopy cover, mimic small-scale disturbances and provide a stratified forest structure similar to that of old-growth forests and therefore better maintain species associated with unmanaged forest. We used a large-scale chronosequence study spanning 50 years to study beetle diversity in uneven-aged silviculture compared with both short-term impacts and the longer-term legacy of even-aged silviculture. We compared: (1) even-aged recently clear-felled stand, (2) even-aged recently thinned stand, (3) uneven-aged stands subjected to selective felling with (4) uneven-aged reference stands to evaluate whether abundance, species richness and composition of beetles (Coleoptera) were affected differently by even-aged than by uneven-aged management. We collected 15,147 beetles from 461 species using flight interception traps in 30 stands. Beetle composition was maintained in uneven-aged managed stands; composition did not differ from unmanaged reference stands, the exception being cambium consumers. Both even-aged silviculture treatments (clear-felling and thinning) had different beetle composition compared to the reference stands, indicating that assemblages had yet to recover even 50 years into the rotation. However, beetle composition did not differ between uneven-aged managed and thinned stands. The result supports our prediction that uneven-aged silviculture better maintains beetles assemblages associated with semi-natural mature forest than even-aged silviculture. The greater temporal continuity in selectively felled stands could benefit species dependent of mature or old growth forest since some of the needed habitat qualities are continuously available. Uneven-aged silviculture could therefore serve as an important tool for landscape planning to benefit biodiversity and thus help fulfil environmental commitments. However, uneven-aged silviculture may still alter the forest and should therefore be viewed as an alternative to even-aged silviculture, rather than to set-asides.

1. Introduction

Foresters around the world are struggling to maintain or increase wood production while simultaneously preventing loss of biodiversity (CPF, 2012; Mori and Kitagawa, 2014; Kalonga et al., 2016). Intensive wood production often relies on even-aged silviculture (e.g. clear-felling). However, even-aged silviculture has been linked to severe negative effects on forest biodiversity through a simplification and homogenization of forest structure (Berg et al., 1994; Östlund et al., 1997; Butchart et al., 2010; Paillet et al., 2010; Bernes, 2011). To meet environmental challenges and prevent further loss of biodiversity, alternative forest management approaches based on natural disturbance regimes have been proposed (Pommerening and Murphy, 2004; Drever et al., 2006; Axelsson and Angelstam, 2011).

The underlying hypothesis of natural disturbance-based management (NDBM) is that many aspects of biodiversity can be protected and ecosystem resilience secured if forest management maintains habitats and habitat structure consistent with those found in landscapes dominated by natural disturbances (Drever et al., 2006; Shorohova et al., 2011; Kuuluvainen and Grenfell,

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2012). Unmanaged forest landscapes were formed by disturbances ranging from large stand-replacing fires to small scale disturbances; and were thus often structurally diverse (Kuuluvainen, 2002; Shorohova et al., 2011). High-severity fires, insect outbreaks and storm events have historically created highly variable landscapes where patches of mature forests are interspersed with early successional habitats, with large quantities of standing and downed deadwood. In boreal Fennoscandia, stand-replacing disturbances have been historically less widespread compared to boreal North America (Franklin, 2007). In this region, smaller-scale disturbances that cause single-tree or localized mortality may also have played a large role in forming the forest (Ohlson and Tryterud, 1999; Kuuluvainen, 2002). These smaller-scale disturbances maintained stratified old-growth uneven-aged forests with a continuous forest cover and high deadwood volumes.

With increasing conversion to even-aged forests, forest species associated with older, heterogeneous forest habitats are often restricted to smaller remnants of uneven-aged forest. Semi-natural forests that have eluded clear-felling are important refuges for those old-growth favoured species as well as a source of biodiversity for more intensively managed surrounding stands (Berg et al., 1994; Gustafsson et al., 2004; Stenbacka et al., 2010; Hjälten et al., 2012; Johansson et al., 2016). Biological legacies such as dead wood, old trees and microclimatic conditions remaining within those semi-natural forests yield a structure resembling that found in natural small scale disturbance forest. The rationale for uneven-aged silviculture is that, by mimicking small-scale disturbance, a continuously forested stand with uneven-aged tree structure, stratified canopy and stable microclimate would be retained. Retention of these habitat qualities within the managed stand is expected to maintain associated biodiversity (Kuuluvainen et al., 2012). Uneven-aged silviculture may therefore provide an opportunity to combine biodiversity and production, and preserve temporal continuity of forests within the managed landscape by avoiding clear-felling. However, maintaining structures and processes important for biodiversity while meeting timber management goals is an act of balance (Franklin, 2007) and it is crucial to evaluate how uneven-aged silviculture methods affect forest species assemblages.

Beetles constitute a significant portion of forest biodiversity and perform important ecological functions, including dead wood decomposition and nutrient cycling (Grove, 2002). Beetles are also sensitive to silviculture and can thus be good indicators of forest habitat quality (Siitonen, 2001; Martikainen and Kouki, 2003; Paillet et al., 2010; Stenbacka et al., 2010; Boucher et al., 2012). Approximately 20% of the Swedish beetles are red-listed, and forest harvesting has been reported to be one of the main negative influencing factors (Westling, 2015), indicating vulnerability to current management practice. Saproxylic beetles, i.e. beetles that are associated with deadwood for part or all of their life cycle, are among the most sensitive to the impacts of even-aged silviculture (Siitonen et al., 2000). Beetle diversity is known to increase with increasing structural complexity of the stand, such as numbers of microhabitats, higher tree species diversity and deadwood diversity (Esseen et al., 1997; Siitonen, 2001; Bouget et al., 2013; Gibb et al., 2013). Forests with historically limited management support a higher abundance of species preferring natural substrates such as large spruce logs in shaded conditions than managed forests (Martikainen et al., 1996). The differences between unmanaged and managed forest are most pronounced immediately following clear-felling, when a large proportion of the natural substrates have been removed (Niemela, 1997; Gibb et al., 2006a; Paillet et al., 2010). Uneven-aged silviculture has potential to maintain some of those important substrates and is therefore likely to benefit the associated beetles.

Initial evaluations of uneven-aged silviculture have shown that mature or late-successional forest characteristics and species assemblages are better maintained than in even-aged stands (Koivula, 2002a; Kuuluvainen et al., 2012). While informative, most of these studies reflect changes in composition over timescales less than 15 years (Atlegrim and Sjöberg, 1996a,b; Siira-Pietikainen and Haimi, 2009). Here we present a large-scale chronosequence management study that spans over 50 years to compare the long-term impacts of uneven and even-aged silviculture on beetle (Coleoptera) composition. In our study we evaluate how beetle composition differed between uneven-aged silviculture compared to early and late stages of even-aged silviculture, and compared to unmanaged forest.

We expected that uneven-aged silviculture would result in stands which resembled unmanaged forests in terms of species richness, abundance and beetle composition and would therefore from a conservation perspective be an improvement compared to current silviculture. Directly following clear-felling, we expected that compared with unmanaged stands, species richness and abundance of saproxylic beetles would be reduced and beetle composition altered by favouring open-habitat and generalist species. We anticipated that these effects would become less apparent with time, as overstory stand structure is re-established. However we expected that beetle composition in older, even-aged stands that have undergone clear-felling and commercial thinning still differed compared to unmanaged forest and uneven-aged managed forest.

2. Methods

2.1. Study area

Our study area was located in the boreal forest of central Sweden (Fig. 1), in the counties of Jämtland and Medelpad (63.0–62.3 N, 15.2–16.4 W). The forest cover in those counties is about 77% (Nilsson and Cory, 2016). Annual temperature in the region averages 2 °C and yearly precipitation is ~600 mm (SMHI, 2013). Experimental stands were dominated by Norway spruce (*Picea abies* (L.) Karst) (>70% of the volume) mixed with birch (*Betula pendula* Roth. and *B.pubescens* Ehrh) and a smaller component of Scots pine (*Pinus sylvestris* L), aspen *(Populus tremula* L) and willow (*Salix caprea* L). Ground vegetation was mainly composed of bilberry (*Vaccinium myrtillus* L.) and low herbs. Experimental stands varied from 2 to 16 ha in size (mean = 8 ha) and elevation from 247 to 480 m above sea level (mean = 375 masl).

2.2. Experimental design

The study was designed as a randomized incomplete block experiment comparing (1) recently (2–14 year prior to the study) clear-felled stands that were uneven-aged prior to harvesting but became even-aged as a direct consequence of clear-felling (‘Clear-felling’); (2) older, even-aged stands regenerated after clear-felling 50–60 years ago that recently (2–14 year prior to the study) have undergone commercial thinning (‘Thinning’); (3) mature stands originating from uneven-aged, stratified stands which have recently (2–15 year prior to the study) undergone uneven-aged silviculture (‘Selective felling’) and (4) mature stands originating from uneven-aged, stratified stands without recent history (~50 year) of management (‘Reference’). The stands evenly distributed in the landscape and not closer than 1000 m apart (Fig. 1, Table 1).

The most used uneven-aged silviculture method for spruce forests in Sweden is single tree selection felling (hereafter ‘selective felling’), where single large-diameter trees are harvested and a

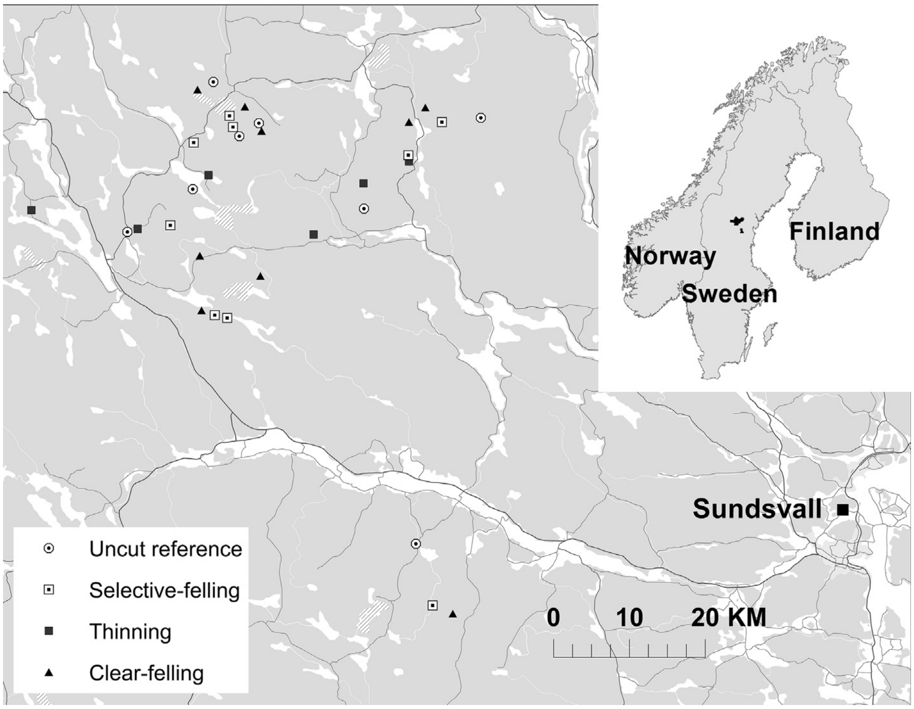

Fig. 1. Field sites are located in central Sweden. Water is displayed in white, roads as black lines.

Table 1
Overview of the 30 experimental stands. Mean ± SE is provided for stand variables. The results from the GLM of stand variables are presented on the right. Bold numbers highlight significance differences at $p < 0.05$.

Stand type	Clear-felling	Thinning	Selective felling	Reference	Chi^2	Df	p	Pairwise
Original state	Uneven	Even (Clear-felled ~50 ya)	Uneven	Uneven				
Current state	Even	Even	Uneven	Uneven				
Number of stands	8	5	9	8				
Size (ha)	5.7 ± 1.3	7.7 ± 3.0	8 ± 0.7	7.2 ± 1.6	2.89	3	0.41	
Altitude	376 ± 18	366 ± 34	391 ± 9	365 ± 25	1.22	3	0.75	
Years since treatment	6.7 ± 1.8	6.2 ± 2.2	7.4 ± 1.7	NA	0.31	2	0.85	
Mean tree age (year)	2.6 ± 1.4	51 ± 3.1	120 ± 6.3	132 ± 7.1	418	3	**<0.01**	CF < T < SF = R
Basal area (m^2)	0.3 ± 0.12	18.5 ± 2.3	17.9 ± 1.0	24.5 ± 1.0	294	3	**<0.01**	CF < T = SF < R
Deadwood (m^3)	8.5 ± 3.2	4.6 ± 1.0	13.0 ± 3.5	16.9 ± 4.2	8.96	3	**0.03**	CF, T < R; T < SF; SF = R
Spruce% of basal area	NA	83.2 ± 7.1	80.0 ± 4.1	80.3 ± 3.7	0.22	2	0.90	
Pine% of basal area	NA	6.3 ± 5.1	6.3 ± 3.8	4.5 ± 2.9	0.16	2	0.92	
Birch% of basal area	NA	8.0 ± 3.0	13.4 ± 2.1	14.2 ± 3.4	2.15	2	0.34	

SF = selective felling. CF = clear-felling.
T = thinning. R = reference.

stratified forest is maintained. During selective felling, the majority of the stand is left unharvested and approximately 70% of the standing volume is retained at each felling event. Initial harvest occurs mainly in the harvest trails, spaced approximately 20 m apart. In subsequent interventions, the same harvest trails are used and single trees are extracted from the forest in-between. The harvesters are only driven in the harvest trails, minimizing impacts on vegetation, forest recruitment and deadwood in the 20 m strips separating the machine corridors.

Recovery in species composition as clear-felled stand regrows is expected, and it is therefore important to include later stages of even-aged silviculture as a comparison to uneven-aged silviculture (Franklin, 2007; Stenbacka et al., 2010). The even-aged stands originated from clear-felling. The common practice in even-aged silviculture today is to remove 90–95% of the standing volume followed by planting with improved seedlings. The young even-aged (clear-felled) stands were harvested according to Swedish FSC standards, including approximately 5% retention and creation of deadwood substrate in form of high stumps (FSC, 2010). The older even-aged (thinned) stands were harvested before forest certification was introduced. They have been maintained by thinning, which strives to sustain an even-aged, single layered forest. When reaching suitable age (80–100 years) the even-aged forests will be clear-felled again and enter the next rotation. Clear-felling became common practice in the region around 1950, and the included old even-aged stands (thinning) are among the oldest in the region. Thus the recolonization of species can be expected to be as advanced as possible for available clear-felled stands. Thinning operations extract approximately 30% of standing volume, leaving fresh deadwood material in form of branches and low stumps. Since about 30% of standing volume is harvested in selective felling, the comparison between thinned and selectivefelled stand will be of forest structures and long term legacies from even-aged management under similar decrease in canopy cover.

The reference stands are not natural forests per se, but since no intensive harvesting occurs, they have retained stand structures consistent with natural forests in terms of stratified vertical structure, presence of old trees and deadwood continuity. No recent

(>50 years) management has occurred in these stands. However these forests are not set aside as protected areas and may therefore be managed with either uneven or even-aged silviculture in the future.

All experimental stands were similar in terms of tree species composition, understory vegetation, soil properties and slope prior to management (Table 1). Managed stands (clear-felling, thinning and selective felling) did however vary in the time of harvesting, ranging from 2 to 14 years prior to our study (Table 1).

2.3. Stand characteristics

In each stand, coarse woody material (CWM, diameter $\geqslant 0.1$ m and length $\geqslant 1.3$ m) was sampled in three randomly distributed, circular plots per stand, each covering 1000 m^2. All dead wood for which the centre of the trunk at the root neck was situated within the plot were inventoried (Siitonen et al., 2000). Dead wood was divided into either standing CWM or CWM lying on the ground for each tree species. The volume of individual pieces of deadwood was calculated using the conic-paraboloid formula:

$$V = \frac{L}{12}(5A_b + 5A_u + 2\sqrt{A_bA_u})$$

where L = length (or height of a standing tree), A_b = the cross-sectional area at the base and A_u = the cross-sectional area of the top (Fraver et al., 2007). For the standing deadwood we estimated $A_{u.}$ Decay class for each piece was estimated using classification from McCullough (1948) and Jonsson (2000) ranging from 1 to 6 where 1 is freshly dead and 6 is in a very advanced stage of decomposition.

Diameters of individual trees were measured in 500 m^2 plots using the same centroid as for dead wood sampling. We measured the diameter at breast height (DBH) for all trees $\geqslant$6 cm DBH and tree height for every tenth tree and from that calculated basal area using the standard formula for the area of a circle (πr^2, where r = radius). Tree species composition was calculated as the proportion of basal area per tree species. Stand size (ha) and altitude (masl) were taken from forest owners' databases.

2.4. Beetle sampling

Beetles were collected using three flight-intercept traps (Polish IBL2-traps, CHEMIPAN, Warsawa, Poland) per stand placed at 25 m distance from the centroid in N, SW and SE directions in each stand. The traps were at least 50 m from the stand edge. Traps were active from late May to September 2014. All beetles were identified to the species level by expert taxonomists, with the exception of the genera *Epuraea* (296 individuals), *Acrotrichi* (1887 individuals) and *Gabrius* (116 individuals).

To evaluate the relative impact of treatments on species that require deadwood during their life-cycle, beetle species were classified as either saproxylic or non-saproxylic (Stokland et al., 2012). Beetles were also assigned to feeding guilds. Those functional groups (saproxylic classifications and feeding guilds) were largely based on ecological classifications by Koch et al. (1989) volume 1–3 and Palm (1959). These designations were then expanded to include species found in northern parts of Sweden (Hilszczański, J., Pettersson, R. and Lundberg, S. pers. comm.). Red-list status was determined based on the Swedish red list (Westling, 2015). Nomenclature and taxonomy of the beetles follows the Swedish taxonomic database (Dyntaxa version 1.1.6102.24188, 2015) from the Swedish Species Information Centre.

2.5. Statistical analyses

We used generalized linear models (GLM) to test for treatment effect on average tree age, tree species composition, basal area and log-transformed deadwood volume. We further divided deadwood into tree species and substrate types to compare treatment effect on deadwood diversity. We also used GLM to test if altitude or stand size showed any relationship with treatment.

For all statistical analyses on the beetle data, we pooled catches from the three traps within each stand. We compared overall abundance and species richness of beetles between treatments using GLMs. We used a negative binomial error distribution for the models because it proved most suitable given the dispersion of the data (O'Hara and Kotze, 2010; Warton et al., 2012).

To evaluate the effect of treatment on the structure of the beetle composition, we used the manyGLM function from 'mvabund' package in R (Wang et al., 2016). We used manyGLM for the whole dataset and all included functional groups. ManyGLM uses the sum of log-likelihood from many individual GLMs to create a test statistic verified through randomization. Warton et al. (2012) suggest 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. In this test, statistical significance was evaluated using 999 resampling iterations via 'Probability Integral Transform residual bootstrap' (PIT-trap) resampling (Wang et al., 2012) and all individual univariate GLM models were fitted using negative binomial link functions. We excluded all species for which we collected less than three specimens from the composition analyses as including rare species had little effect on the analysis outcome, but considerably slowed processing times. Environmental variables (size of stand and altitude) were tested as covariates. Stand size did not significantly affect the beetle composition and were therefore excluded. The final model included *composition* ~ *treatment + altitude*. We performed pairwise comparisons between treatments. Univariate tests for all species were conducted both for the overall test and for all pairwise comparisons. Unadjusted p-values were used since adjusting would drastically increase the risk of type II errors. However, due to the high number of comparisons, these should be interpreted with caution (Cabin and Mitchell, 2000; García, 2004).

To visualise differences in beetle composition found in manyGLM analyses we compared composition using Non-Metric Multidimensional Scaling (NMDS) plots, created by package Vegan in R (Oksanen et al., 2007). For this analysis, we used Bray-Curtis distances and 20 random starts to find a stable final solution.

3. Results

3.1. Stand characteristics

While stands were selected to be as similar as possible in terms of stand size, vegetation, soil conditions and tree species composition, basal area and deadwood volume differed among treatments. As a consequence of the different management regimes, reference stands had the highest basal area followed by selective-felled, thinned and clear-felled stands. Deadwood volume was greatest in reference and selectively felled stands, followed by clear-felling and finally thinned stands (Table 1).

To evaluate the diversity of the deadwood, we divided total volume into categories based on tree species and substrate type. Spruce contributed most to the total deadwood volume and was highest in reference and selectively felled stands, followed by clear-felling and finally thinned stands. Volume of birch deadwood was lower in thinning than in the other treatments (Fig. 2). Downed deadwood, (including all tree species) occurred in similar

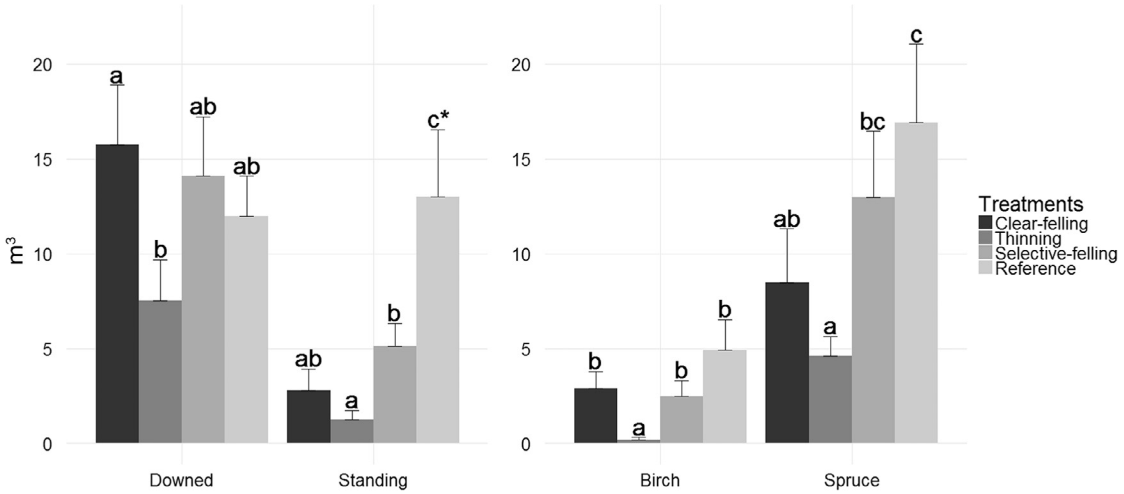

Fig. 2. Mean ± SE deadwood volume (m^3/ha) in the different treatments, divided by tree species (Birch and Spruce, the two dominating tree species) and on substrate type (Downed and Standing for all tree species). Bars with different letter are significantly different ($P < 0.05$) within the category according to the GLM. Overall p-values were 0.05 ($\chi^2 = 7.9$) for substrate type and 0.03 ($\chi^2 = 8.8$) for tree species.

volumes in clear-felled, selectively-felled and reference stands but was lower in thinned stands. Standing deadwood was greatest in reference stands (Fig. 2).

3.2. Species response

We captured 15,147 beetles belonging to 461 species across our 30 study stands. Three hundred and nineteen species (69%) were classified as saproxylic and dominating feeding guilds were predators (180 species), fungivores (177 species) and cambium feeders (44 species). Feeding guilds are not mutually exclusive and species can occur in more than one group. We captured 36 red-listed individuals belonging to 16 species from three red-list categories: vulnerable (1), data deficient (1) and near-threatened (14). *Agathidium discoideum* (Erichson) was the most abundant (7 individuals) and was found mostly in selective fellings. Nine of the red-listed species were only captured as singletons. Sample size for red-listed beetles was so small that statistical analyses for that group would likely have had insufficient power to detect differences among treatments (Appendix A for a complete species list).

Two hundred and seventy-eight species (60% of the captured species) were represented by 3 or more individuals and were therefore included in the many GLM analyses. Nearly 40% of those species occurred in all treatments, suggesting some degree of ecological resilience. Ninety-two percent of the species found in reference stands were also captured in the selective fellings, which was higher than for both thinning and clear-felling (79% and 73% respectively). Only 15 of the species captured in reference stands were absent from selective fellings (Fig. 3). Selective fellings had 65 additional species, absent from reference stands. The majority of those species were common in the more intensively managed landscape. Ninety percent of all beetles captured in thinned stands and 80% of those captured in clear-fellings were also present in selective fellings (Fig. 3).

3.2.1. Abundance

Abundance of predators and fungivores did not differ among treatments (Table 2). Cambium feeders, however, were most prevalent in thinned and selectively felled stands, represented largely by *Dryocoetes autographus* (Ratz.), a common secondary bark beetle that primarily attacks the underside of lying spruce and stump roots (Lekander et al., 1977). In contrast, cambium feeders were less abundant in clear-felled stands (Fig. 4).

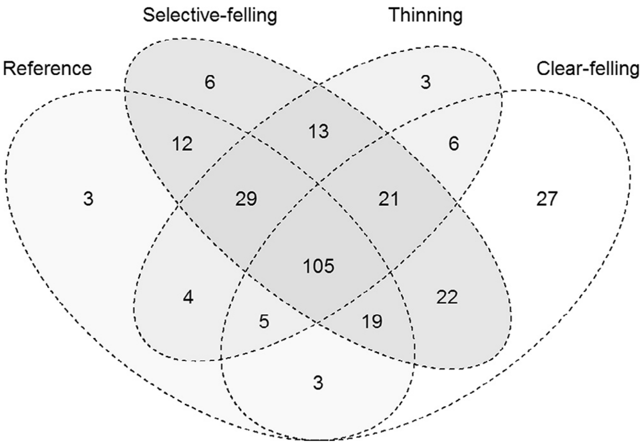

Fig. 3. Number of unique and shared species between the four treatments. The size of areas does not reflect the given numbers. Single and doubleton species are not included.

3.2.2. Species richness

Species richness of saproxylic beetles or individual feeding guilds did not differ among treatments (Table 2). However, we found more non-saproxylic species in clear-felled stands than in reference stands (Fig. 4).

3.2.3. Beetle composition

Selective felling had minimal impacts on beetle composition: ManyGLM did not reveal any differences between reference stands and selective felling. Saproxylics, non-saproxylics and predators were not significantly different, and no species differed significantly in the univariate tests. Composition of cambium feeders however, differed significantly between selective felling and reference stands. Two cambium consumers explained most of the difference between treatments according to the univariate test. *Crypturgus hispidulus* (Thomson) was three times more common in selective felling than in the reference stands and *Phloeotribus spinulosus* (Rey) were four times more abundant in reference stands. Fungivores showed a similar trend to cambium feeders (Table 3).

Immediately following clear-felling, beetle composition differed from all other treatments for all groups of beetles. As even-aged stands regrew and were thinned, overall composition and

Table 2
Results from GLM testing the effect of treatment on total abundance and species richness for the species groups studied. Bold p-values highlight significance differences.

	Abundance			Species richness		
	Chi^2	Df	p	Chi^2	Df	p
All species	3.53	3	0.31	3.35	3	0.34
Saproxylic	3.95	3	0.27	3.83	3	0.28
Non saproxylic	0.86	3	0.83	13.29	3	**0.004**
Fungivores	0.21	3	0.98	5.28	3	0.15
Predators	3.10	3	0.38	1.86	3	0.60
Cambivores	9.57	3	**0.02**	1.13	3	0.77

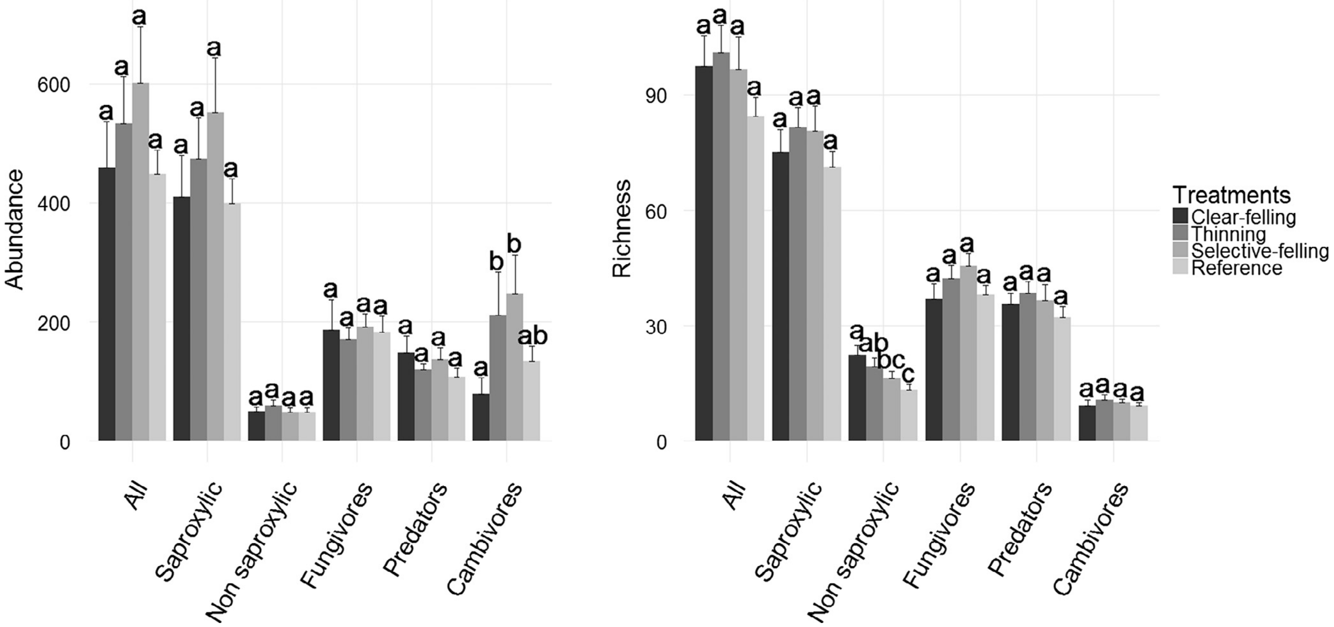

Fig. 4. Mean ± SE species richness and abundance divided in treatments. Bars with different letters are significantly different according to the post hoc contrasts.

Table 3
ManyGLM analyses testing differences among stand types for all species and for functional groups. The overall results from manyGLM are presented at followed by the treatment effect from the pairwise comparisons. SF = selective felling. CF = clear-felling T = thinning. R = reference. Bold numbers highlight significance differences.

			All species		Saproxylic		Non saproxylic		Fungivore		Predator		Cambivore	
	Res DF	DF	Deviance	p	Deviance	p	Deviance	p	Deviance	p	Deviance	p	Deviance	p
Treatment	26	3	2161	**<0.01**	1755	**<0.01**	407	**<0.01**	943	**<0.01**	787	**<0.01**	199	**<0.01**
Altitude	25	1	423	**0.018**	354	**0.017**	69	0.195	195	**0.011**	146	0.052	43	0.058
SF -R	15	1	457	0.115	301	0.125	50	0.361	188	*0.082·*	118	0.249	51	**0.038**
SF-T	12	1	307	0.287	305	0.252	59	0.252	112	0.520	120	0.214	37	0.150
R-T	11	1	416	**0.05**	328	*0.067·*	88	**0.02**	174	*0.087·*	148	**0.048**	42	*0.098·*
R-CF	14	1	1348	**<0.01**	871	**<0.01**	210	**<0.01**	498	**<0.01**	393	**<0.01**	99	**<0.01**
SF-CF	15	1	1338	**<0.01**	908	**<0.01**	205	**<0.01**	457	**<0.01**	409	**<0.01**	95	**<0.01**
T-CF	11	1	1057	**<0.01**	671	**<0.01**	179	**<0.01**	352	**<0.01**	324	**<0.01**	76	**<0.01**

composition of non-saproxylics and predators continued to differ from reference stands, but was not different from selectively felled stands (Table 3 and Fig. 5). Saproxylics, cambium feeders and fungivores did not differ significantly between thinned and reference stands, but p-values were all <0.10, suggesting that differences may have become significant with a greater sample size (p = 0.067, p = 0.087 and 0.098 respectively (Table 3).

No significant differences for occurred between selective felling and thinning. This indicates that impacts of even-aged silviculture on beetle composition were initially greater than selective felling, but become less so with time. However, the low number of thinned stands makes the prediction uncertain (Table 3 and Fig. 5).

The manyGLM analysis revealed that 93 species were significantly affected by treatment (Appendix B). These species belonged to different taxonomic groups and functional groups. 43 of the 93 species were more abundant in clear-felled stands and 12 more abundant in reference stands; half of those had second highest abundance in selective fellings. 10 species were more abundant in selective fellings, and 6 more abundant in thinned stands. The last 22 species had similar abundance in reference, selective-felled and thinned stand but low abundance in clear-felling. The general pattern we saw were that species with a high abundance in reference stands tend to decline in selective felling, thinning and are lowest in abundance in clear-fellings. Species with a high

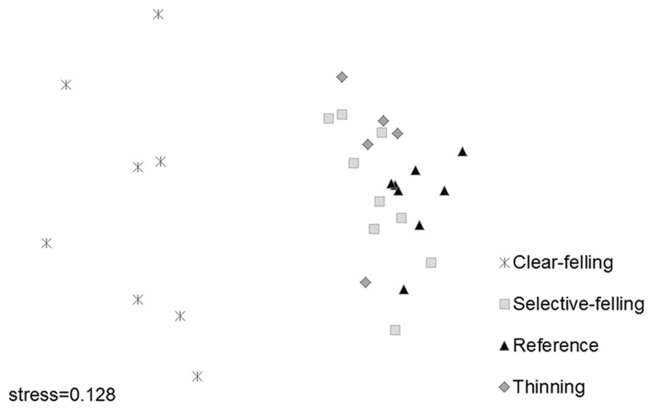

Fig. 5. NMDS plot visualizing the differences in beetle composition structure among treatments. The axes are dimensionless and points closer together represent more similar compositions.

abundance in clear-fellings have a low abundance in reference, selective felling and thinning (Fig. 6, graph a and b).

The same trend appears in the pairwise comparisons. Reference and thinning differed significantly and the species associated with reference occurs in higher abundances in selective fellings; 72% of the species had higher abundance in thinned stands than in reference stands. Species associated with thinning occurs in similar or higher abundance in clear-fellings and in similar or lower abundance in selective fellings (Fig. 6, graph c and d).

4. Discussion

With an increased pressure on forests to produce both timber and biodiversity, management methods that than meet both environmental and production goals are needed. Uneven-aged silviculture has been suggested as a tool to better maintain biodiversity within the managed forest landscape. In accordance with our predictions our results suggest that uneven-aged silviculture has the capacity to maintain similar beetle composition as an unmanaged forest or at least maintain composition better than even-aged silvicultural approaches. Selective felling maintained beetle abundance, richness and composition consistent with reference stands, suggesting that uneven-aged approaches to silviculture may indeed be a feasible compromise for conservation in managed forests. Selective felling performed better than even aged approaches in maintaining species normally found in forests with old growth characteristics, such as *Triplax scutellaris* (Charpentier), *Xylechinus pilosus* (Ratzenburg) and *Eudectus giraudi* (Redtenbacher) (Peltonen and Heliövaara, 1998; Gibb et al., 2006b; Olsson et al., 2012; Westling, 2015). We saw a trend for species associated with unmanaged forest to persist in greater abundance in selective fellings than in thinned and clear-felled stands. Species associated with clear-fellings had low abundance or were absent from the other treatments, as has been extensively documented in previous studies comparing clear-fellings with closed canopy forests (Grove, 2002; McGeoch et al., 2007; Stenbacka et al., 2010; Hjälten et al., 2012).

That selective felling maintains species assemblages similar to unmanaged forest have previously been shown, both for beetles and other taxa. In two Finnish studies of Koivula (2002a, 2002b) carabid beetles associated with open habitat were more abundant and forest species tended to decline on clear-fellings compared with selective fellings and unmanaged forests. We only captured 30 carabids in our study and comparing species response was therefore impossible. However, our study confirms the trend observed by Koivula (2002a, 2002b) that forest species decrease after clear-felling but are maintained within the uneven-aged managed forest with 70% retention. Similarly, the abundance of herbivorous insects and the composition of macro-arthropods were maintained when tree density decreased less than 30% but decreased/changed if the canopy was reduced further (Atlegrim and Sjöberg, 1996a; Siira-Pietikainen et al., 2003; Siira-Pietikainen and Haimi, 2009). Work et al. (2010) propose that more than 50% retention is needed in order to maintain carabid compositions similar to unmanaged stands.

However the influence on beetle composition may be driven by more than just reductions in stand basal area, and could rather reflect cumulative impacts from prior stand management. Thinned and selective felled stands had similar mean stand basal-area, yet thinning differed from reference in terms of beetle composition, while selective felling did not. The low amount of deadwood in the thinned stand is probably one explanation. On the contrary, the selective fellings maintains at least some important microhabitats comparable to what can be found in reference stands. Uneven-aged silviculture also preserves habitat qualities over time in the form of remaining old trees and undisturbed field vegetation (Jalonen and Vanha-Majamaa, 2001; Atlegrim and Sjöberg, 2004). The high level of tree retention in selective felling can preserve microclimate typical of unmanaged forest (Jacobs and Work, 2012; Lee et al., 2015). Many saproxylic fungivorous beetle prefer shaded condition and moist deadwood (Hjälten et al., 2007; Stokland et al., 2012) and might therefore persist only in forests with high tree retention. The maintained microclimate can also enhance quality in other important microhabitat such as deadwood.

Deadwood is known as a key habitat in boreal forest ecosystem with strong links to beetle abundance and species richness (Siitonen, 2001; Stokland et al., 2012). Consistent with previous studies (Jalonen and Vanha-Majamaa, 2001; Atlegrim and Sjöberg, 2004), reference and selective felled stands had similar deadwood volumes, although lower than expected for a natural forest (Siitonen, 2001; Stenbacka et al., 2010). Selective-felled stands included in our study had undergone one, or in some cases, two harvest events. The harvest has so far had little impact on the strips of forest between harvest trails, which might explain the relatively high levels of dead wood found in these stands. As the management proceeds, a larger area of forest strips will be impacted by harvesting, likely leading to a decrease in dead wood volumes. Nonetheless, damage to deadwood from harvest operation and following soil scarification in clear-felled stands is considerably greater than that expected from forest machines during selective logging. With old trees present at all time in selective fellings, deadwood can be produced continuously, and greater diversity is possible. Reference and selectively-felled stands had higher deadwood diversity, in terms of tree species and substrate types than other stand types. Diversity of deadwood is at least as important as the total volumes as many saproxylic species are habitat specific, for example to tree species or substrate size, type and surrounding microclimate (Gibb et al., 2006b; Stokland et al., 2012; Seibold et al., 2016). The high volume, together with the deadwood diversity and a stable microclimate in selective fellings might explain the maintained beetle composition.

While most beetle groups were found in similar abundances in selectively felled and reference stands, the composition of cambium feeders differed between these stand types. Cambium feeders depend on fresh dead wood, and typically colonize immediately after tree death (Stokland et al., 2012). During selective felling, low stumps and other fresh dead wood debris are generated and could potentially attract cambivores and function as breeding material (Hjälten et al., 2010), explaining the greater abundance of this group in selectively felled stands. Deadwood in selective felling might host background populations of cambivores that can respond fast to increased food availability.

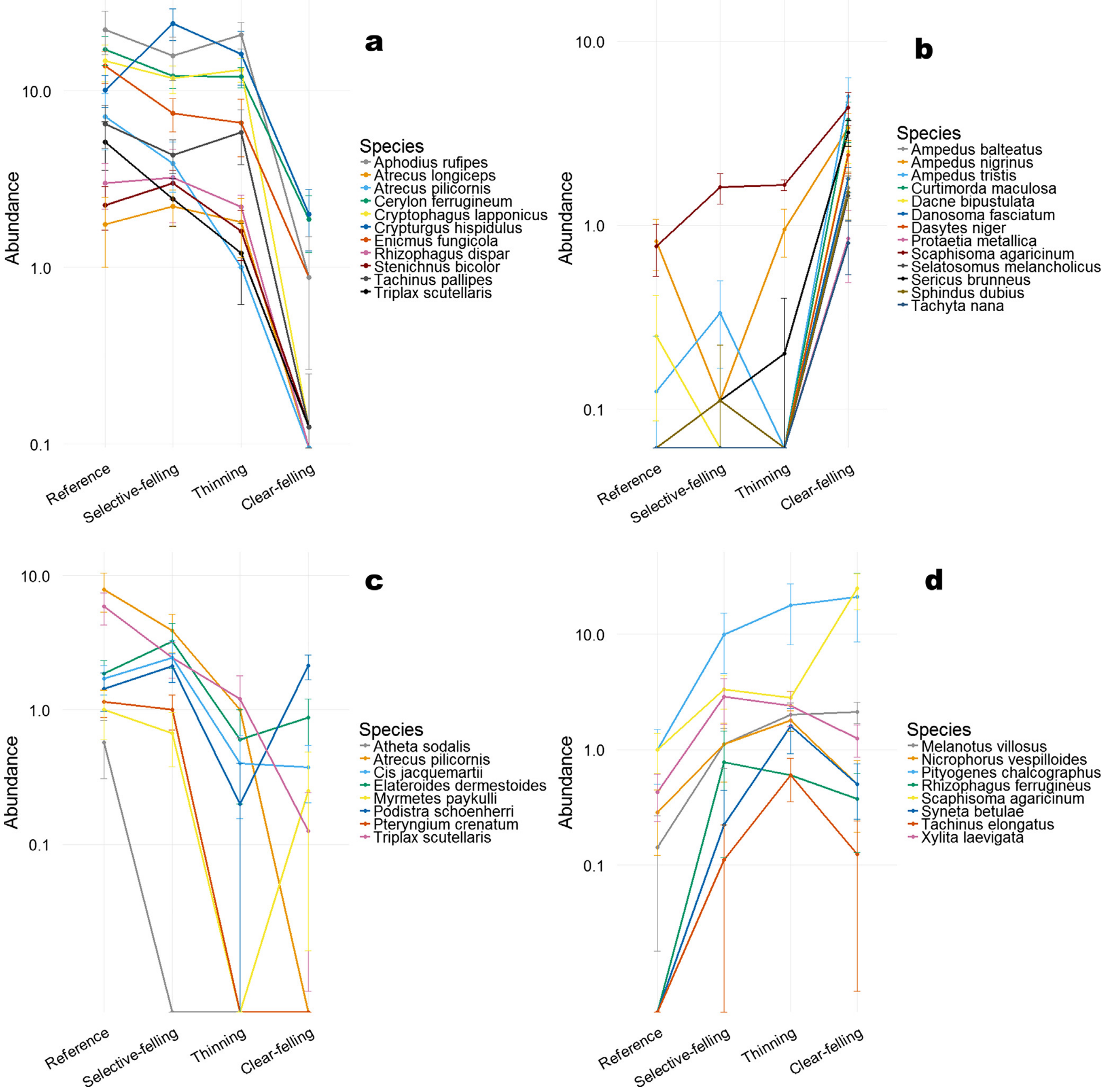

Fig. 6. Mean ± SE abundance per species and treatment: (a and b) show the species for which p = 0.001 in the manyGLM analysis, divided based on preference for older forests (a) and clear-fellings (b); (c and d) show species that differed most between reference and thinned stands, respectively. The y-axis is log-transformed. A complete list over significantly affected species is available in Appendix B.

As predicted, even–aged silviculture had greater effects on beetle diversity than uneven-aged management following clear-felling. Clear-felling had beetle compositions characterized by high abundance of species that were missing or occurring in low abundance in the other treatments, seven out of the ten species with highest abundance in clear-fellings seven had lower population sizes in the regrown forest. Several saproxylic species prefer sun-exposed deadwood and will thus benefit from clear-felling (Lindhe et al., 2005). This can explain the clear difference in species composition between clear-felling compared to the stands with a more closed canopy. For example, *Dasytes niger* (L), *Danosoma fasciatum* (L), and *Ampedus balteatus* (L) was exclusive to clear-fellings and occurred in all our clear-felled plots.

Consistent with our prediction, the effect of clear-felling on composition of beetles decreased with time; composition in thinned stands was more similar than clear-cuts to reference stands. This suggests recovery of beetle composition once the forest canopy returns. Similar trends have been reported elsewhere (Stenbacka et al., 2010; Johansson et al., 2016). Recovery over time indicates landscape resilience and capacity to buffer change induced by clear-felling (Drever et al., 2006). Yet stands that had originated from clear-felling showed differences in beetle composition compared to the reference, suggesting that the effects of even-aged harvesting persist at least 50 years into the rotation. Species known to prefer old growth forest, such as *Xylechinus pilosus* (Ratzenburg) and *Eudectus giraudi* (Redtenbacher), were absent from thinned stands (Peltonen and Heliövaara, 1998; Westling, 2015). Fifty years after clear-felling, differences between habitats in even-aged and reference stands persist: even-aged stands have younger trees and much lower volumes of deadwood, the latter most likely resulting in a much lower production per hectare of saproxylic beetles in thinned compared to reference stands (Hjälten et al., 2012). Flight interception traps used in this study capture species flying around in the stands but do not provide information about whether species reproduce successfully in these stands or are merely transients. This must be taken into consideration when interpreting the results since it can mean an overestimation of the species richness and abundance in a stand type that lacks suitable breeding habitat. However Sverdrup-Thygeson and Birkemoe (2008) demonstrated that flight intercept traps clearly respond to the immediate surroundings.

Species found in thinned, but absent or in low abundances in reference stands tended to be highly abundant on clear-fellings, such as *Anisotoma glabra* (Kugelann), *Scaphisoma agaricinum* (L), *Xylita laevigata* (Hellenius) and *Pityogenes chalcographus* (L). All above mentioned species benefits from clear-felling (Hjälten et al., 2012). This may suggest these species have persisted from earlier stages in even aged silviculture. However, several of those clear-felled associated species (for example *Xylita laevigata* (Hellenius) and *Pityogenes chalcographus* (L)) were captured in similar abundance in selective fellings, indicating that those species also might benefit from disturbance caused by selective felling. After disturbance, a change in species composition can be expected. The question is however, how large the change is and for how long it will persist. Change induced by clear-felling is likely to have much longer lasting effects then selective-felling.

Selective felling and thinning differed in habitat characteristics, such as deadwood volume. Thinning has significant lower levels of deadwood, and the deadwood that occurred was less diverse. The very low volumes of dead wood in thinned stands can the explained by the lingering clear-felling affects and the lack of self-thinning in these relatively young stands (Stenbacka et al., 2010). Most of the deadwood was fresh, and old coarse wood and continuity of deadwood substrate was missing. Despite the difference in deadwood availability and forest structure, we did not find significant differences between thinning and selective felling in terms of beetle composition. However the low sample size of thinned stand reduced power in our analyses and could have left differences between thinning and selective felling undetected.

Nonetheless, difference between uneven-aged and even aged silviculture in terms of beetle composition was only pronounced for the early stage of even-aged management: clear-felling differed from both selective felling and thinning. However, in order for assemblage structure in thinned stands to recover from clear-felling, species need to recolonize the stand. A major benefit of selective felling is that species are less dependent on recolonization since a stand maintains species even after harvest. Based on our study, we cannot conclude how long it takes before the beetle compositions is restored after clear-felling have taken place, but Stenbacka et al. (2010) found that effect of even aged silviculture remained in stands 30–50 years after clear-felling. Thus, during the recovery time there will be less suitable habitat in the landscape for forest preferring species. Forest managed with uneven-aged silviculture might therefore also act as an important source of biodiversity to surrounding forest stands, provided that beetle composition fully recovers between harvests.

4.1. Management implications

As predicted we found that uneven-aged silviculture maintains beetle assemblages better than even aged silviculture. However, the recovery of beetle composition in even-aged stands was high, 50 years after clear-felling it was closer to reference stands, although they still differed significantly. Uneven-aged silviculture on the other hand appears to maintain the structures and the species found in semi-natural spruce forests with old-growth qualities, while providing additional resources for cambium consumers. The greater temporal continuity in selectively felled stands could benefit species dependent of mature or old growth forest since some of the habitat qualities needed are continuously available, contrasting the abrupt habitat change caused by clear-felling in even aged silviculture. The forest is nonetheless affected by uneven-aged silviculture, thus it should be viewed as an alternative to even-aged silviculture, rather than to set asides for conservation. Uneven-aged silviculture could be an important tool for landscape planning to benefit biodiversity and thus help fulfil environmental commitments.

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Appendix A and B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.02.006.

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