Saproxylic and non-saproxylic beetle assemblages in boreal spruce forests of different age and forestry intensity

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Abstract. Current clear-cutting forestry practices affect many boreal organisms negatively, and those dependent on dead wood (saproxylics) are considered as particularly vulnerable. The succession of species assemblages in managed forest habitats regenerating after clear-cutting is, however, poorly known. We compared beetle assemblages in three successional stages of managed boreal spruce forests established after clear-cutting and two types of older spruce forests that had not been clear-cut. We also assessed whether saproxylic and non-saproxylic beetle assemblages show similar biodiversity patterns among these forest types. Beetles were collected in window traps in nine study areas, each encompassing a protected old-growth forest (mean forest age ~160 years, mean dead wood volume 34 m³/ha), an unprotected mature forest (~120 years old, 15 m³/ha), a middle-aged commercially thinned forest (53 years old, 3 m³/ha), a young unthinned forest (30 years old, 4 m³/ha), and a clearcut (5–7 years after harvest, 11 m³/ha). Saproxylic beetles, in particular red-listed species, were more abundant and more species rich in older forest types, whereas no significant differences among forest types in these variables were detected for non-saproxylics. The saproxylic assemblages were clearly differentiated; with increasing forest age, assemblage compositions gradually became more similar to those of protected old-growth forests, but the assemblage composition in thinned forests could not be statistically distinguished from those of the two oldest forest types. Many saproxylic beetles adapted to late-successional stages were present in thinned middle-aged forests but absent from younger unthinned forests. In contrast, non-saproxylics were generally more evenly distributed among the five forest types, and the assemblages were mainly differentiated between clearcuts and forested habitats. The saproxylic beetle assemblages of unprotected mature forests were very similar to those of protected old-growth forests. This indicates a relatively high conservation value of mature boreal forests currently subjected to clear-cutting and raises the question of whether future mature forests will have the same qualities. Our results suggest a high beetle conservation potential of developing managed forests, provided that sufficient amounts and qualities of dead wood are made available (e.g., during thinning operations). Confirming studies of beetle reproduction in dead wood introduced during thinning are, however, lacking.

Key words: biodiversity; clear-cutting; Coleoptera; *conservation; dead wood; forest management; old-growth reserves; red-listed; saproxylic beetles; thinning.*

INTRODUCTION

Globally, intensive forest management and deforestation of natural forests have resulted in severe and long-lasting effects on forest ecosystems and natural biodiversity (Esseen et al. 1997, Siitonen 2001, Grove 2002a, Millennium Ecosystem Assessment 2005). Boreal areas are no exceptions, where clear-cutting forestry, including establishment of even-aged plantations, has dominated for decades. Although we know that clear-felling has dramatic effects on assemblages of species adapted to

old-growth conditions (Berg et al. 1995, Niemelä 1997, Grove 2002a), our knowledge of the recovery of these species in ageing forest plantations is still very limited (but see Grove 2002a, Buddle et al. 2006, Dynesius and Hylander 2007, Caruso et al. 2008, Dynesius et al. 2009). Effective conservation management of boreal forests requires such knowledge. In this study, we focus on boreal beetle assemblages of managed young to middle-aged forests (the oldest available) established after clear-cutting, and compare them with assemblages of older forests that have regenerated naturally and contain more dead wood. The results may be used to assess the need for mitigation measures to secure the persistence of the beetle fauna in managed boreal forests.

In some boreal regions (e.g., Fennoscandia) almost all forests are used for timber production. However, modern high-intensive management is relatively recent (50–60 years), and earlier management was often less

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invasive. For example, mature unprotected forests, earlier only subjected to selective loggings, often still contain species usually associated with old-growth forests (Gustafsson et al. 2004, Gibb et al. 2006c, Johansson et al. 2007b). Many of these seminatural forests have now been clear felled and replaced by managed, even-aged forests, impoverishing the living conditions for many organisms (Larsson and Danell 2001, Siitonen 2001). The percentage of such managed forests in the production landscape is increasing steadily. For example, 37% of the unprotected productive forestland in Sweden is covered by 20–60 year-old forests, and an additional 22% consist of even younger forests or recent clearcuts (Institutionen för skoglig resurshushållning 2009). It is therefore important to assess the biodiversity of these forests, which are presumed to hold low conservation value and lack continuity of important structures like dead wood (Siitonen 2001, Jonsson et al. 2005).

Dead wood and its characteristics are recognized as being one of the most important factors for forest biodiversity (e.g., Berg et al. 1994, 1995, Økland et al. 1996, Jonsell et al. 1998, Siitonen 2001, Grove 2002a, b). Forestry has, however, considerably reduced the amount and quality range of dead wood (Fridman and Walheim 2000, Siitonen 2001, Gibb et al. 2005). In Sweden, for example, the mean dead wood volume is only 7.5 m^3/ha on managed forest land (Institutionen för skoglig resurshushållning 2009) compared to the 50–120 m^3/ha generally found in boreal old-growth forests (see Siitonen 2001 and references therein). Further, the amount and input of dead wood in forests regenerating after clear-cutting is very low (Sippola et al. 1998, Ranius et al. 2003, Jonsson et al. 2005). It is therefore reasonable to believe that these forests are poor in saproxylic species, (i.e., species dependent on dead wood; Speight 1989), and that they need active measures to increase dead wood quantity, connectivity, and continuity to avoid further landscape-level species losses.

Beetles (order Coleoptera) are one of the most species-rich groups of organisms in the world (Gaston 1991), and they are also a dominant component of the saproxylic fauna both generally and in the boreal forests studied here (Siitonen 2001, Dahlberg and Stokland 2004). Their abundance, species richness, and species composition in boreal areas varies most strongly with amount and quality of dead wood (Jonsell et al. 1998, Martikainen et al. 2000, Siitonen 2001, Jonsell and Weslien 2003, Dahlberg and Stokland 2004, Gibb et al. 2006a, c, Jacobs et al. 2007a). Beetles are therefore a highly suitable group to study in relation to anthropogenic disturbances.

In this study we compared beetle assemblages in five boreal spruce-dominated forest habitats in northern Sweden: three habitats created by clear-cutting forestry (clearcuts with seedlings, not yet commercially thinned forests, and commercially thinned forests) and two representing two levels of intensity of previous selective cuttings (old-growth forests in or adjacent to protected areas and unprotected mature forests). Many earlier studies have focused on saproxylic beetle assemblages in clearcuts, mature managed forests, and old-growth forests (e.g., Martikainen et al. 2000, Martikainen 2001, Grove 2002a, Sippola et al. 2002, Gibb et al. 2006c), but studies including also young to middle-aged stands regenerated after clear-cutting are very rare (however, see Similä et al. [2002, 2003], who studied saproxylic beetles in pine forests of both varying age and forestry intensity). We sampled beetles using large flight intercept traps and divided the species into saproxylic and non-saproxylic according to current autecological knowledge. We also surveyed dead wood availability in the different forest types. The following questions were addressed:

(1) Do old, naturally regenerated forests support higher saproxylic beetle abundances and species richness and hold different species assemblages than young to middle-aged managed forests established after clear-cutting?

(2) Do non-saproxylic and saproxylic beetle assemblages vary in a similar way among the five forest types?

MATERIAL AND METHODS

Study areas, design, and trapping methods

The study was conducted in the middle boreal forest zone in northern Sweden (Ahti et al. 1968; Fig. 1). The studied forests were dominated by Norway spruce (*Picea abies* (L.) Karst.) mixed with Scots pine (*Pinus sylvestris* L.), some birch (*Betula pendula* Roth. and *B. pubescens* Ehrh.), and some aspen (*Populus tremula* L.). The understory vegetation was mainly of moist to mesic *Vaccinium myrtillus* L. type (Ebeling 1978), and the altitude ranged from 100 to 550 m above sea level (a.s.l.) The study areas have a long history of forest management and fire suppression, resulting in a current domination of managed forests regenerated after clear-cutting (<60 years old) with relatively large areas of older forest that have been subjected to intensive selective cuttings and minor areas of protected old-growth forests with little trace of forestry.

The study design included nine study areas (Fig. 1), each including five spruce forest types (maximum distance of ~15 km within a study area) representing different age classes and degrees of forestry intensity: an old-growth forest in or in direct association with a nature reserve or national park (mean forest age ~160 yr, mean stand size 249 ha); an unprotected mature forest (mean age ~120 yr, mean size 10 ha); a middle-aged, recently commercially thinned forest (mean age 53 yr [representing the oldest available forests resulting from modern forestry], mean size 8 ha); a young unthinned forest (although in most cases precommercially thinned; mean age 30 yr, mean size 16 ha); and a clearcut area (5–7 yr after harvest, mean size 16 ha). The stand selection procedure started from the few protected
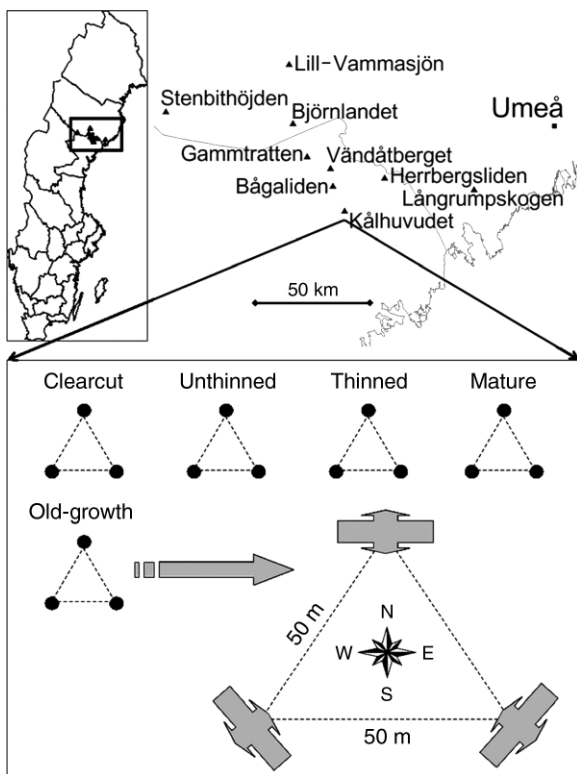
FIG. 1. The nine study areas in northern Sweden containing five forest types each. Three types are results of clear-cutting (clearcuts 5–7 years after logging, ~30-year-old forests before commercial thinning, and ~50-year-old recently thinned forests), and two types have never been clear-cut (~120-year-old unprotected mature forests and ~160-year-old protected old-growth forests). At each site we set up three traps for beetles (50 m apart) with different flight intercept directions. Umeå is at latitude 63°49′ N and longitude 20°15′ E.

old-growth spruce forests in the region. The location and characteristics of these were used as a starting point, and the most appropriate stands for the other successional stages were chosen thereafter in the vicinity of the reserves. The important selection criteria were: spruce domination (>50% spruce), the presence of deciduous trees (mainly birch), the presence of a field layer mainly consisting of dwarf shrubs (*Vaccinium* spp.), and mesic to moist moraine soils. The nonprotected stands were selected from a larger group of stands after visual inspections to ensure that they complied with the selection criteria.

In each site we used a standardized sampling design of three window traps ~50 m apart, with flight direction intercepts of north/south, northeast/southwest, and northwest/southeast, respectively, to minimize differences between sites caused by irrelevant factors such as slope aspect (Fig. 1). Although flight intercept/window traps are not optimal for more detailed studies of specific dead wood substrates (Wikars et al. 2005), they have proven efficient for trapping beetles and are highly suitable for comparisons between different forest envi-

ronments (e.g., Økland 1996, Alinvi et al. 2007, Sverdrup-Thygeson and Birkemoe 2009). Insects were sampled in May–September 2006 with Polish IBL2-traps (CHEMIPAN, Warszawa, Poland; see Pettersson et al. 2007), triangular window traps with semitransparent plastic flight intercepts of ~0.35 m² (Fig. 2). The traps were hung on a polypropylene rope (ø 6–8 mm) strained between two trees, or in some cases on clearcuts between wooden poles (ø 27 mm and ~2.5 m long), and additional cords were strained to the ground to make the traps less wind sensitive. Beetles were collected in 600-mL plastic bottles one-third filled with 50% propylene glycol with a small amount of detergent. A rainwater drainage module was attached between the trap and the bottle to avoid overfilling of the bottle and dilution of the glycol solution. The traps were emptied in late July and late September. All collected beetles were determined to species by experts (except *Acrotrichis* spp.). Nomenclature and systematics of beetles follows Silfverberg (2004). Species were divided into saproxylics and non-saproxylics according to the definition of Speight (1989) and based on The Saproxylic Database (Nordic saproxylic network 2007). Red-listed species classification followed the current Swedish Red List (Gärdenfors 2005): RE = regionally extinct, CR = critically endangered, EN = endangered, VU = vulnerable, NT = near threatened, DD = data deficient.

Dead wood survey

We assessed dead wood using four line transects, 100 m long and 5 m wide (i.e., in total 0.2 ha), in each of the 45 sites. The protected old-growth forests, unprotected mature forests, and clearcuts were surveyed in September 2003, and these data were used also in Gibb et al. (2005), while the data for unthinned and
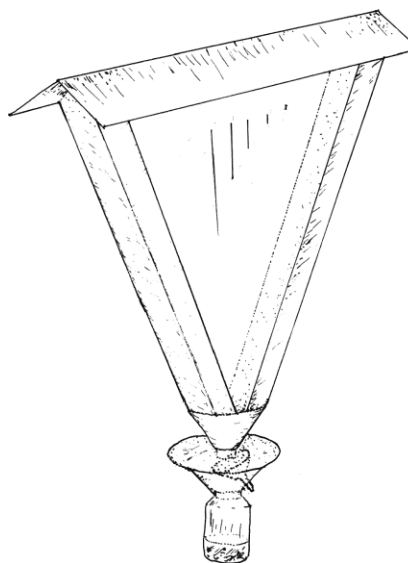

FIG. 2. The flight intercept trap used for beetles (IBL2), with water-removing funnel and collecting bottle.

thinned forests were collected specifically for this study in July–August 2006. The transects in each site headed north, south, east, and west from a midpoint selected between the three traps. Within the transect we recorded lying dead wood (logs) with a minimum diameter of 10 cm and a minimum length of 1.3 m, and standing dead wood (snags and high stumps) with a minimum diameter at breast height (dbh = 1.3 m above ground) of 10 cm. On logs we measured maximum and minimum diameters as well as their length within the transect. For standing dead wood we measured dbh and height. For each dead wood object we recorded the decomposition stage using a simplified classification system with four classes (derived from Söderström [1988]) and tree species. The volume of dead wood objects was calculated using a formula for a truncated circular cone

$$V = (\pi h/3)(r_1^2 + r_1 r_2 + r_2^2)$$

where h = height or length, r_1 = maximum radius, and r_2 = minimum radius. For standing dead wood we calculated maximum and minimum radii (specieswise) using the change in radius per meter derived from logs >3 m long in the transect. For further details on the collection of and calculations on dead wood data, we refer to Gibb et al. (2005), who used the same methods.

Data analysis

All analyses were done separately for saproxylics, red-listed saproxylics, and non-saproxylics. Of all the 135 traps, only five (three on clearcuts and two in mature unprotected forests) were partially broken at the time of collection, which could have resulted in reduced catches. However, excluding these five traps from the analysis did not change the overall results. The exclusion of singleton species (i.e., species represented by a single specimen in the data) is sometimes suggested, because its presence may be a matter of chance. However, the exclusion did not change the qualitative results. Thus both the partially broken traps and the singleton species were included in the analyses to avoid losing any species-specific information. The positioning of the traps (i.e., flight intercept direction) did not show any significant effect on any of the response variables. Therefore we pooled the beetle data from the three traps at each site (i.e., at each forest type and study area) and used forest type as a fixed factor and study area as a random factor. We did not standardize abundances before species richness was calculated, since our completely balanced sampling design with equal-sized sampling areas and sampling periods reduce the need for this. There is also a risk that standardization could lead to errors (e.g., Collins and Simberloff 2009), in our case, overestimations of species richness in clearcuts. To test the effect of forest type, we conducted a randomized block ANOVA on the response variables species richness and abundance. To fulfill the assumptions regarding normality and homogeneity of variances for parametric tests, we log-transformed $(x + 1)$ the data prior to analyses. Even

after transformation, some species groups only marginally fulfilled these requirements, but in large, balanced experiments such as this one, ANOVA is robust to departures from the assumptions (Underwood 1997). When significant differences were detected, we used Tukey's honestly significant difference (hsd) test for pairwise comparisons. We used SYSTAT version 12 (Systat 2007) for the analysis.

For the analysis of species assemblage composition in different forest types, we used PERMANOVA (permutational multivariate analysis of variance; Anderson 2003) in the program PRIMER (PRIMER-E 2007). Nonparametric permutational tests become a useful tool when working with ecological data and using species as variables, as the assumptions of normality and homoscedasticity (as for ANOVA) can be hard to fulfill (Anderson 2001, McArdle and Anderson 2001). PERMANOVA allows investigation of complex models, which also include interactions (Anderson 2001, 2003). We performed the PERMANOVA with forest type as a fixed factor and study area as a random factor. Data were fourth-root transformed in order to reduce the weighting of the most abundant species while still preserving relative abundances (Clarke 1993). For similarity measure we used Bray-Curtis, which is not affected by joint absences (Field et al. 1982); no standardization was used, and we performed 4999 permutations of residuals under a reduced model. For red-listed saproxylics, a dummy variable of one was added to the resemblance matrix due to undefined values between three zero-samples (Clarke et al. 2006). PERMANOVA pairwise comparisons between forest types were conducted when this factor proved significant. To identify species contributing most to observed differences in species assemblages between forest types, we performed SIMPER analysis (similarity percentage analysis; Clarke and Gorley 2006), again on fourth-root transformed data. To graphically illustrate differences in species composition among all the 45 sampled sites, we performed nonmetric multidimensional scaling (nMDS; Clarke and Warwick 2001) and plotted the results in two dimensions.

RESULTS

In total, we trapped 42 457 beetles of 657 species, of which 429 species (65%) were classified as saproxylic, with a total abundance of 35 024 (82%). On clearcuts a total of 360 species were trapped (of which 244, or 68%, were saproxylics); in unthinned forests, 369 (259, or 70%); in thinned forests, 380 (278, or 73%); in unprotected mature forests, 362 (274, or 76%); and in protected old-growth forests, 396 (301, or 76%) species. Among the trapped beetles, 466 specimens (1%) and 34 species (5%) were nationally red-listed (Appendix A). The only red-listed non-saproxylic was also the most abundant red-listed species (*Tachinus elegans*, a species associated with moist spruce forests; 65 individuals). Overall, most species were trapped in low numbers; 23%
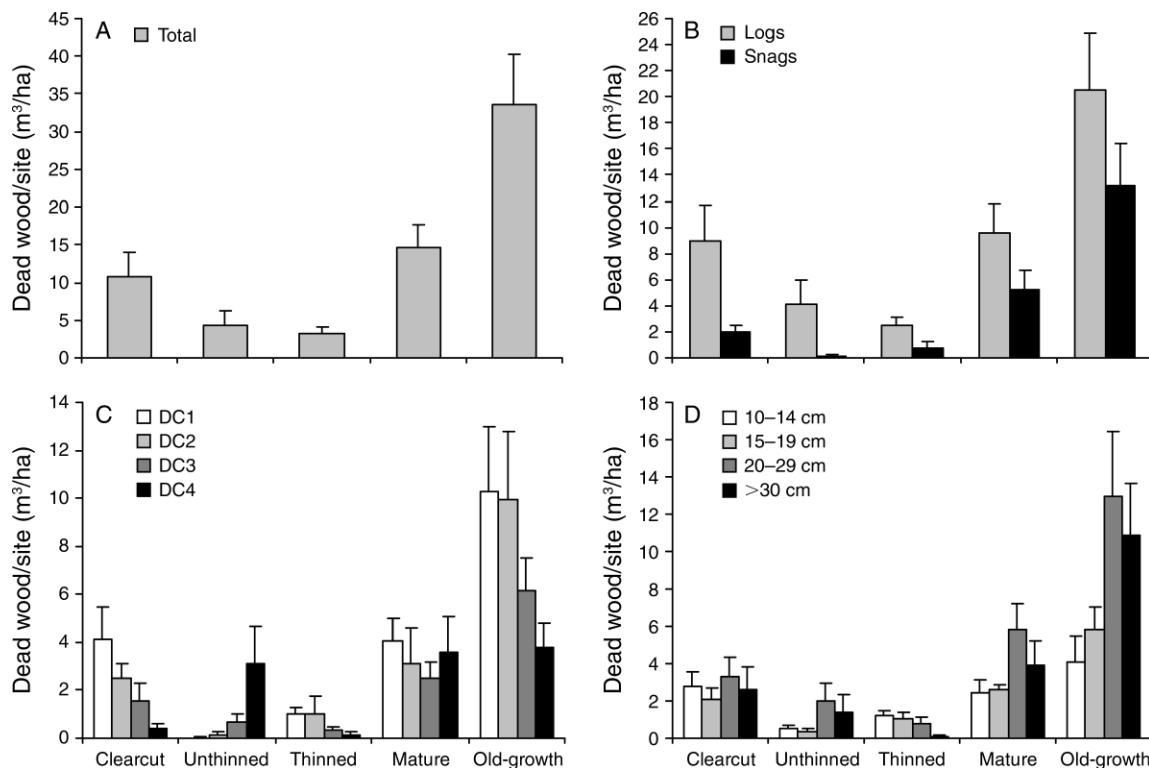
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FIG. 3. Dead wood volumes (mean + SE) in different forest types: (A) total amount; (B) dead wood type (downed logs and standing snags); (C) decomposition classes, DC (1, undecomposed; 4, much decomposed; birch excluded); and (D) stem diameter size classes.

of all species were represented by only one specimen, and for more than half (51%), we trapped five or fewer individuals. In contrast, for each of the eight most abundant species there were >1000 individuals. These were common species and showed a variable response to forest type; e.g., *Cryptophagus lapponicus* and *Dryocoetes autographus* became more abundant with increased successional age, while *Ampedus nigrinus* showed the opposite pattern.

Dead wood volumes were highest in protected old-growth forests and lowest in thinned and unthinned forests (Fig. 3A). Downed logs dominated over snags in all forest types (Fig. 3B). Highly decomposed dead wood constituted a minor proportion in clearcuts and in thinned forests but dominated in unthinned forests (Fig. 3C). In the two oldest forest types (old-growth and mature forests) and in unthinned forests, large-diameter wood dominated (Fig. 3D).

Abundance and species richness in different forest types

The abundance ($P = 0.0001$, $R^2 = 0.57$) and species richness ($P < 0.0001$, $R^2 = 0.62$) of saproxylic beetles increased with forest age (Fig. 4A, B; Appendix B). Both abundance and species richness were significantly higher in protected old-growth forests than in clearcuts and unthinned forests. The unprotected mature forests were also significantly separated from clearcuts, but only

marginally different from unthinned forests ($P = 0.065$ for abundance and 0.060 for richness). No significant differences in abundance and richness of saproxylics were detected between the three oldest forest types, although a positive trend with forest age was seen also here.

Red-listed saproxylic abundance ($P < 0.0001$, $R^2 = 0.57$) and species richness ($P = 0.0002$, $R^2 = 0.55$) also showed a strong positive relationship to forest age (Fig. 4C, D; Appendix B). In clearcuts and unthinned forests, we trapped significantly fewer individuals of saproxylic red-listed species than in the two oldest forest types. Although the mean abundance was also much lower in thinned forests than in the older forest types (Fig. 4C), the differences were only marginally significant between thinned and protected old-growth forests ($P = 0.058$). The species richness of red-listed saproxylics (Fig. 4D) showed a somewhat weaker pattern, with unthinned forests only marginally separated from mature unprotected forests ($P = 0.058$) and thinned forests marginally separated from protected old-growth forests ($P = 0.093$). Again, no difference was detected between protected old-growth and unprotected mature forests. In the 40% of the traps situated in these two oldest forest types unaffected by clear-cutting, we trapped 71% of all red-listed specimens and 74% of all red-listed species found in the study (see Appendix A).
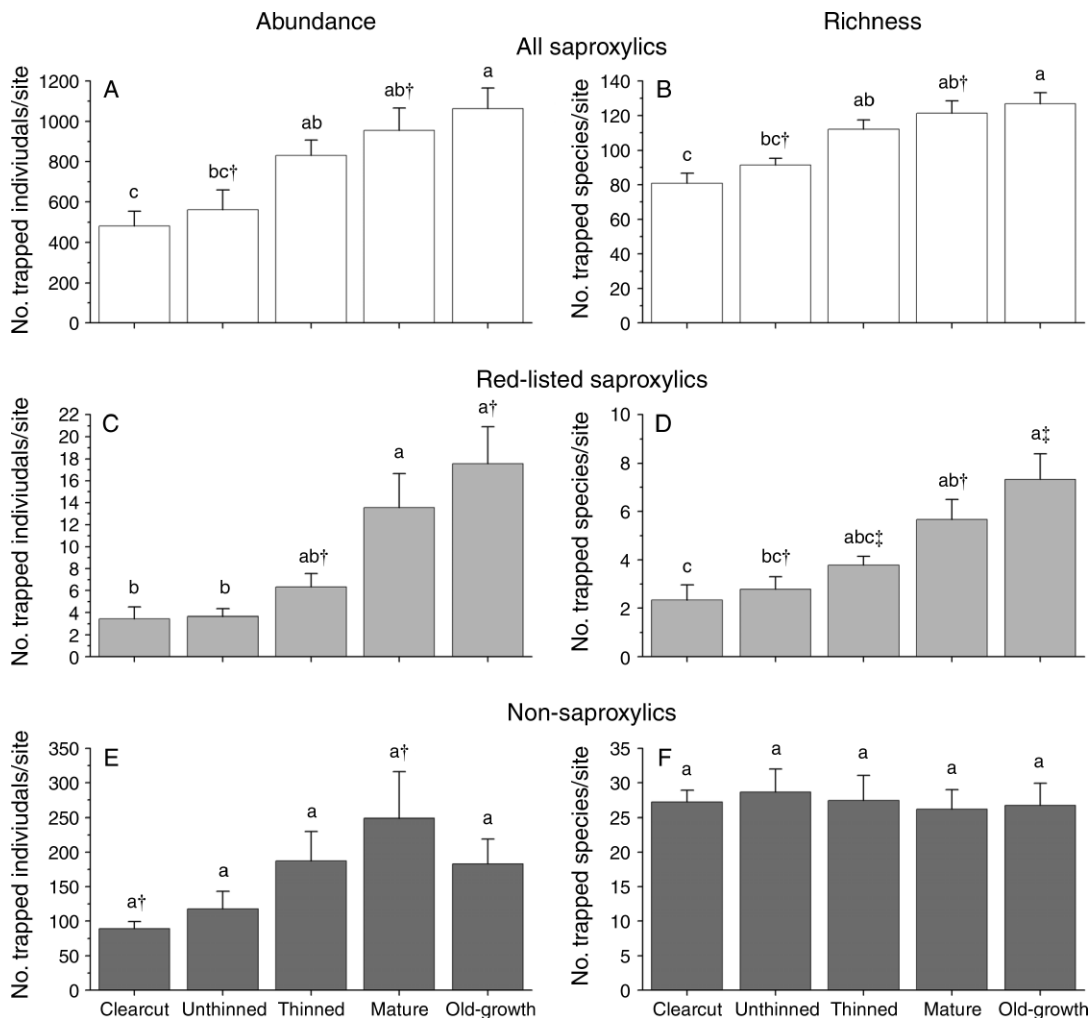
FIG. 4. Abundance (left-hand panels) and species richness (right-hand panels) in different forest types for (A, B) all saproxylic beetles; (C, D) red-listed saproxylics; and (E, F) non-saproxylics. Values are means + SE. Forest types not sharing the same letter are significantly different ($P \leq 0.05$) according to Tukey tests. Forest types that differ marginally significantly are denoted by † or ‡ ($P \leq 0.065$ and $P = 0.093$, respectively).

In sharp contrast, non-saproxylic species richness did not respond significantly to forest type ($P = 0.996$, $R^2 = 0.22$, Fig. 4F; Appendix B). Abundance of this group was, however, significantly affected ($P = 0.034$, $R^2 = 0.44$), with low numbers trapped in clearcuts and unthinned forests and the highest abundance in unprotected mature forests (Fig. 4E). Tukey tests could, however, only detect one marginally significant difference (i.e., between clearcuts and unprotected mature forests; $P = 0.063$).

No effect of the identity of the study area could be detected for any of the three groups of beetles (Appendix B).

Assemblage composition in different forest types

The species composition of saproxylic beetles clearly differed between forest types (Table 1, Fig. 5A). Saproxylic assemblages in both clearcuts and unthinned forests were significantly different from assemblages in all four other forest types. In contrast, species composition in the three oldest forest types did not differ significantly, although thinned forests differed marginally. The beetle species that contributed most to the differences in saproxylic assemblage composition detected among the forest types (Appendix C: Table C1, section 1) were mainly species known to be associated with open areas or with old forests (e.g., *Dacne bipustulata* and *Xylechinus pilosus*, respectively).

The red-listed saproxylic assemblage composition was also affected by forest type (Table 1, Fig. 5B). Clearcuts significantly differed from all other forest types except thinned forests, for which the difference was only marginally significant. Further, the assemblages in unthinned forests were also clearly separated from those of the two oldest forest types, while again, the three oldest forest types did not differ from each other. A few

TABLE 1. PERMANOVA and pairwise a posteriori comparisons of saproxylic, red-listed saproxylic, and non-saproxylic beetle assemblages in different forest types.

Source	df	MS	F	P	A posteriori comparisons
Saproxylics					
Forest type	4	4979.6	5.5	0.0002	CC $\neq$ U, T, M, OG; U $\neq$ T, M, OG; (T $\neq$ M, OG)†
Study area	8	1312.2	1.5	0.0002	
Residual	32	902.22			
Total	44				
Red-listed saproxylics					
Forest type	4	5131	2.9	0.0002	CC $\neq$ U, M, OG; U $\neq$ M, OG; (CC $\neq$ T)‡
Study area	8	2456.3	1.4	0.038	
Residual	32	1784.4			
Total	44				
Non-saproxylics					
Forest type	4	5310.3	3.2	0.0002	CC $\neq$ U, T, M, OG; U $\neq$ M, OG§
Study area	8	2336.7	1.4	0.0008	
Residual	32	1648.3			
Total	44				

Notes: Fourth-root-transformed abundance data of individual species were used. Abbreviations are: CC, clearcut; U, unthinned; T, thinned; M, unprotected mature; and OG, protected old-growth forest.

† CC $\neq$ U, $P = 0.003$; CC $\neq$ T, $P = 0.0018$; CC $\neq$ M, $P = 0.0002$; CC $\neq$ OG, $P = 0.001$; U $\neq$ T, $P = 0.0124$; U $\neq$ M, $P = 0.0042$; U $\neq$ OG, $P = 0.0016$; (T $\neq$ M, $P = 0.083$); (T $\neq$ OG; $P = 0.0608$).

‡ CC $\neq$ U, $P = 0.0236$; (CC $\neq$ T, $P = 0.0732$); CC $\neq$ M, $P = 0.0036$; CC $\neq$ OG, $P = 0.0036$; U $\neq$ M, $P = 0.04$; U $\neq$ OG, $P = 0.0056$.

§ CC $\neq$ U, $P = 0.0022$; CC $\neq$ T, $P = 0.0028$; CC $\neq$ M, $P = 0.0014$; CC $\neq$ OG, $P = 0.0016$; U $\neq$ M, $P = 0.0288$; U $\neq$ OG, $P = 0.0442$.

red-listed species were more abundant on clearcuts (e.g., *Denticollis borealis*), but the more abundant red-listed species typical of older forests (e.g., *Atomaria alpina*, *Cis dentatus*, *Enicmus apicalis*, and *Epuraea deubeli*) contributed most to assemblage differences (Appendix A, Appendix C: Table C1, section 2).

For non-saproxylic species, assemblage composition on clearcuts was different from those of all other forest types (Table 1, Fig. 5C). In addition, assemblage composition of unthinned forests differed from that of the two oldest forest types. Again, no difference could be detected between the three oldest forest types. In contrast to saproxylics, species connected to clearcuts were the most important for the assemblage differences between forest types for non-saproxylics (e.g., *Sericus brunneus*; Appendix C: Table C1, section 3).

Not only forest type, but also the identity of the study area significantly affected assemblage compositions of all three groups of beetles (Table 1), which might be an effect of varying site characteristics (e.g., location, altitude, slope, and management history).

DISCUSSION

Most studies of forestry impact on the saproxylic beetle fauna have compared the situation in clear-felled areas with that in old-growth forests, or have evaluated different methods (tree retention, burning, etc.) aimed at reducing negative forestry impacts (e.g., Martikainen et al. 2000, Grove 2002*a*, Jonsell and Weslien 2003, Hyvärinen et al. 2006, Jacobs et al. 2007*b*, Toivanen and Kotiaho 2007). Our study included also relatively young stands established after clear-cutting with little or no attention to conservation. We compared three young

successional stages heavily affected by forestry practices (clear-cutting, regeneration measures, thinning) with two old-successional stages that have been much less intensively managed (no initial clear-cutting). This design implies, however, that we could not draw firm conclusions about the influence of forest age and forestry impact separately. What we did show is that beetle assemblages in recently thinned middle-aged forests regenerated after clear-cutting approached those found in the seminatural mature forests currently exposed to clear-cutting. Note, however, that the flight intercept traps used in this study showed the occurrence of saproxylic beetles in different forest types, but not if the forest type was a source or sink habitat (i.e., if the beetles originated from dead wood within a particular stand). Potential input of "tourist species" in the samples must thus be considered.

Saproxylic beetles

The low saproxylic beetle abundance and species richness (Fig. 4A–D) and distinct assemblage composition (Fig. 5A, B) on clearcuts compared to mature and old-growth forests were most likely due to the reduced amount of dead wood (Fig. 3) and changed habitat/microclimatic conditions. In general, saproxylic beetle assemblages, particularly assemblages of fungivores and predators, are known to be less species rich on clear-felled areas (Gibb et al. 2006*c*, Johansson et al. 2007*b*). Still, many boreal species are adapted to the conditions after a stand-replacing disturbance, such as thermophilic species dependent on sun-exposed wood, cambium consumers that can initially benefit from the input of fresh dead wood, and fire-favored species that may be

adapted to open, disturbed habitats in general (Kaila et al. 1997, Ehnström 2001, Martikainen 2001, Wikars 2002, Lindhe et al. 2005, Gibb et al. 2006c, Hjältén et al. 2007). For example, the red-listed *Denticollis borealis*, which we found exclusively on clearcuts (Appendix A), is known to be attracted to sun-exposed standing birch wood and to burnt areas (Kaila et al. 1997, Wikars 2002). Many aspen-associated saproxylic species can utilize retained aspens on clearcuts (Martikainen 2001, Sverdrup-Thygeson and Birkemoe 2009), for example, the red-listed *Mycetophagus fulvicollis* that we trapped in all forest types except unthinned forests (Dahlberg and Stokland 2004). Thus clearcuts may be beneficial even for some red-listed saproxylics as long as suitable substrate is available, and dead wood management on clearcuts is therefore of great importance.

In the forests regenerating after clear-cutting, the recruitment of new dead wood was low, as shown by the lower amounts and higher decomposition of dead wood in unthinned forests than on clearcuts (Fig. 3A, C; see also Sippola et al. [1998], Ranius et al. [2003], Similä et al. [2003], Jonsson et al. [2005]). However, the higher availability of dead wood of later decay stages in unthinned forests (Fig. 3C) did not make the saproxylic beetle assemblage composition (Fig. 5A, B), richness, or abundance (Fig. 4A–D) more similar to the two oldest forest types. Persistently unfavorable microclimatic conditions and lack of substrate during the first decades after clear-cutting for saproxylic species adapted to closed-canopy forests and moist conditions (e.g., *Xylechinus pilosus*; Appendix C: Table C1, section 1) are the likely causes (Peltonen et al. 1997, Gibb et al. 2006c, Johansson et al. 2007b). Ironically, for species that could cope with the open habitat during this phase there is a lack of suitable substrate; i.e., early-successional cambium consumers utilizing fresh dead wood, which in turn also affect associated species like natural enemies (e.g., predatory beetles or saproxylic parasitoids [Similä et al. 2003, Hilszczański et al. 2005, Johansson et al. 2007a]). This emphasizes the conservation value of leaving an adequate supply of retention trees at clear-cutting operations to provide a continuous supply of dead wood in managed forests (e.g., Grove 2002a, Similä et al. 2003, Toivanen and Kotiaho 2007).

Thinned forests, on the other hand, with a more developed canopy cover, can provide suitable habitat for shade- and moist-loving saproxylics. Still, the lack of clear differences in saproxylic abundance, species richness (Fig. 4A–D), and assemblage composition (Fig. 5A, B) compared to the two older forest types was somewhat surprising, as the dead wood supply was much sparser and of less diverse composition in thinned forests (Fig. 3). Considerable amounts of slash (fine woody debris <10 cm in diameter) and stumps are, however, created at thinning operations, but we did not survey these fractions as dead wood. On clearcuts, stumps and slash may serve as important substrates even for some saproxylics of conservation concern (Jonsell et
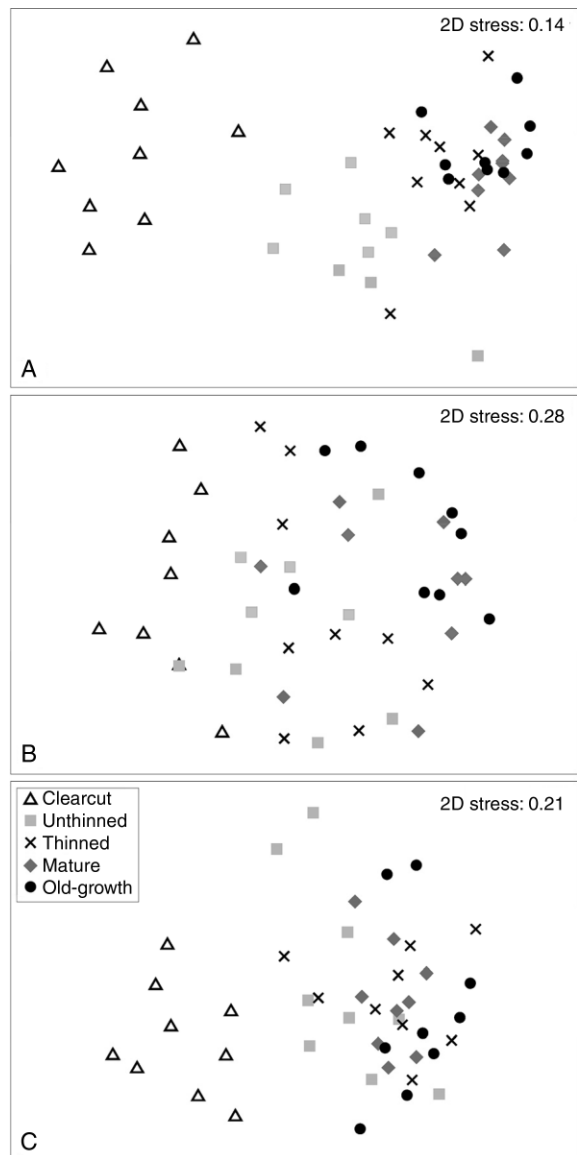

FIG. 5. Nonmetric multidimensional scaling (nMDS) plots of the assemblages of (A) saproxylic, (B) red-listed saproxylic, and (C) non-saproxylic beetles in different forest types. Each symbol denotes one sampling site.

al. 2007), but may particularly attract early-successional saproxylic beetles that are good dispersers and that use fresh substrate (Sippola et al. 2002, Gibb et al. 2006a). The role of these substrates in closed forests is, however, unknown. We found that some common saproxylics associated with closed forest were relatively abundant in thinned forest (e.g., the bark beetle, *Dryocoetes autographus*; Johansson et al. 2007b), suggesting that they find dead wood of the right quality and in the right microclimate in thinned forests. In turn, also species associated with these common closed-forest saproxylics were fairly abundant in thinned forests (e.g., the predator *Epuraea pygmaea*; Johansson et al. 2007a, b).

However, commercially thinned forests with their extremely low amounts of large-diameter and more decomposed dead wood, are unlikely to sustain populations of species specialized on such dead wood qualities. The low abundance of species specialized on characters of old, naturally developed forests could explain the tendency (marginally significant) in saproxylic assemblage differences between thinned forests and the two older stages (Appendix C: Table C1, section 1); e.g., red-listed saproxylic abundance was lower (marginally significant) in thinned than in old-growth forests (Appendix A). The trapped red-listed species were, however, almost exclusively of the category "near threatened." Only four species, representing <1% of the red-listed specimens, were from categories regarded as threatened ("vulnerable" and "endangered"). A larger sampling effort would have made it possible to evaluate patterns for threatened species as well, but this was not feasible. Threatened species are often much more ecologically specialized in their habitat requirements, and it is likely that they would have shown clearer differences among forest types than the near-threatened group. Because forestry rotation periods are short and as long as no active measures to increase dead wood availability are implemented in forests of this age, it is questionable if populations of species associated with old-growth conditions ever will recover in these prospective mature forests. In particular, threatened saproxylic species with poor dispersal capacity (e.g., Ranius and Hedin 2001), which are more dependent on dead wood connectivity (Schiegg 2000) and continuity (Similä et al. 2003), may be at risk.

In a hostile matrix of managed forests with little dead wood, many rare saproxylics have become restricted to protected scattered old-growth patches (Penttilä et al. 2004; J. Hjältén, F. Stenbacka, R. B. Pettersson et al., unpublished manuscript; Appendix A). These forests contain a much greater, more diverse, and continuous supply of dead wood substrates (e.g., Sippola et al. 1998, Siitonen 2001, Gibb et al. 2005; Fig. 3) and in our study supported the highest species number and abundance of saproxylic beetles (Fig. 4A–D; see also Siitonen [2001] and references within). They were generally inhabited by species dependent on moist dead wood, species adapted to stable habitats of late-successional stages, and species that require large-diameter and/or well-decomposed wood. These are typical requirements of many red-listed saproxylics (Jonsell et al. 1998, Dahlberg and Stokland 2004, Tikkanen et al. 2006). However, in our study areas, the unprotected mature forests, including their saproxylic beetle assemblages (Fig. 5A, B; Appendix C: Table C1, sections 1 and 2), were relatively similar to the protected old-growth forests. Such resemblances have also been reported earlier (e.g., Gustafsson et al. 2004, Gibb et al. 2006c, Hjältén et al. 2007, Johansson et al. 2007b). Historically, these seminatural forests have been subjected to more selective cuttings, removal of dead trees, killing of deciduous trees, etc., than the currently protected old-growth forests, resulting in a reduction of dead wood. Still, it seems that this past low-intensive management has not considerably reduced present saproxylic richness and abundance, nor significantly changed species assemblage composition. As Similä et al. (2003) argued, the diversity of dead wood substrates, which was similar in old-growth and mature forests (Fig. 3B–D), is more important for beetle assemblage composition than actual dead wood amount (difference between 15 and 34 m³/ha; Fig. 3A). But as seminatural mature forests are continuously harvested, active measures to improve the conditions in managed forests established after clear-cutting (e.g., Hyvärinen et al. 2006, Toivanen and Kotiaho 2007) are needed for a successful long-term conservation of saproxylic beetles.

Non-saproxylic beetles

Non-saproxylic species richness was indifferent to forest type, but their abundance on clearcuts appeared to be lower than in mature unprotected forests (Fig. 4E, F). Non-saproxylic beetles are, however, a broad ecological group, and an overall response to forest management can be hard to detect, as stated by Martikainen et al. (2000). Although species richness and abundance of non-saproxylics were hardly affected by forest type, suggesting that non-saproxylic beetles are less sensitive to forestry, the assemblage composition was affected in a similar way as for saproxylics (Fig. 5C). This indicates that species richness alone is not always the most appropriate variable for biodiversity assessment, especially not in disturbed and fragmented landscapes (Noss et al. 2006, Paquin 2008). Instead, more detailed species assemblage analyses may be preferable for more qualitative habitat comparisons. Our results are in accordance with Sippola et al. (2002), who found distinct differences in beetle assemblage composition (attributed to forest openness) both for saproxylics and non-saproxylics, between clearcut areas and old-growth spruce forests. Compared to saproxylics, a bigger share of non-saproxylics was attracted to clearcuts, and these species also had a great impact on assemblage differences (e.g., Sericus brunneus; Appendix C: Table C1, section 3). Earlier studies have shown that some non-saproxylics (e.g., ground beetles) generally respond positively to clear-cutting because of many open-habitat specialists among this group (Niemelä et al. 1993, Koivula et al. 2002, Buddle 2006). As in Martikainen et al. (2000), we could not find any significant difference in non-saproxylic beetle assemblages between the two oldest forest types, and most forest-associated species were generally also abundant in thinned and unthinned forests. Even the only red-listed species, Tachinus elegans, which usually is associated with older forests (Gibb et al. 2006b), was found in all forested stand types (Appendix A). Further, some of the non-saproxylics seemed to be habitat generalists and were found in all five forest types. To sum up, some non-saproxylics use all forest types, some thrived on

clearcuts, and "forest species" even seem to survive in young unthinned forests.

Conclusions

Dead wood amounts affect the abundance and species richness of saproxylic beetles, but not of non-saproxylics. Assemblage compositions appear, however, to be more influenced by the dichotomy "open/closed habitat" (i.e., clearcut/forest), and microclimatic conditions are probably the dominating factor.

Unprotected mature forests only subjected to selective felling are, to a large extent, inhabited by the same saproxylic setup as protected old-growth forests. We cannot, however, draw this conclusion for red-listed species that qualify as threatened, because we only trapped four specimens of this category. The mature forests studied here will, however, be replaced by homogenous, even-aged forests regenerated after clearcutting (i.e., the current middle-aged forests of our study). Will the late-successional organisms found in today's mature forest also find their habitat in these future mature forests? Our study shows that in unthinned forests, many saproxylic beetles intolerant to clear-cutting are still missing, while thinned forests show potential also for species adapted to later successional stages (relatively similar assemblages), even though dead wood volumes are low (and thus also saproxylic abundances). However, the traps in this study do not distinguish locally reared beetles from immigrating ones, and studies of beetle reproduction in dead wood substrates in thinned forests are needed before their potential can be further evaluated. Nevertheless, as many saproxylic beetle species are present in these forests (and are fairly mobile), improving dead wood availability is most likely an important management tool in maintaining relatively intact saproxylic species pools in managed boreal landscapes. Thus retaining and creating dead wood during thinning operations may become an effective method of counteracting the increasing isolation of saproxylic species confined to protected old-growth forests and should be an important future consideration in management of boreal forest ecosystems.

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APPENDIX A

A table showing all collected red-listed beetles in different forest types (*Ecological Archives* A020-088-A1).

APPENDIX B

Results of ANOVA testing for forest type effect on abundance and species richness on saproxylic, red-listed saproxylic, and non-saproxylic beetles (*Ecological Archives* A020-088-A2).

APPENDIX C

Results of SIMPER analysis showing average dissimilarities and the main contributing species among beetle assemblages [(1) saproxylic, (2) red-listed saproxylic, and (3) non-saproxylic] between different forest types (*Ecological Archives* A020-088-A3).