SAPROXYLIC BEETLES IN A SWEDISH BOREAL FOREST LANDSCAPE MANAGED ACCORDING TO 'NEW FORESTRY'

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Abstract—A major threat to biodiversity in Swedish forests is the decline of Coarse Woody Debris (CWD), which is an essential resource for many organisms and plays an essential role for the structure and function of boreal forests. Removal of CWD in commercial forestry has depleted important resources for many rare wood-living (saproxylic) beetles. Replenishment of CWD has been a prominent goal of revised forest management practices (new forestry), through practices such as retention of living trees on clear-cuts, creation of standing dead wood such as snags, and abstinence from removal of wind-felled trees. In an ongoing project in central Sweden the dynamics of CWD as well as beetle species richness and composition are being studied in a landscape where the new forestry has been applied. Our data show that the new management practices have contributed a substantial amount of CWD; new-forestry final cuttings, for example, contained 18 percent of spruce CWD in the landscape. We found a total of 184 saproxylic beetle species in the study landscape. Of these, 16 species are currently included in the Swedish Red List. The highest number (11) of these rare species were found in unmanaged stands, but there were also many (9) species found on new-forestry clear-cuts. We tentatively conclude that the new management practices have improved living conditions for some species of saproxylic beetles, manifested as recruitment of rare species from CWD retained under the new-forestry silviculture.

BIODIVERSITY IN BOREAL FORESTS

The boreal region extends over vast areas and is the second largest forest biome, after the tropical rainforests, comprising 16.6 million km^2. Although the boreal forest is structurally much less diverse than forests at lower latitudes, boreal diversity is still impressive. For example, at least 4,000 species of saproxylic (wood-living) species alone have been recorded from boreal Finland (Siitonen 2001).

The history of management differs radically between boreal Fennoscandia and Russia/Canada, and thus the proportion of pristine habitat that remains is also very different in the two areas. Commercial logging has been practiced in most parts of Fennoscandia for at least one tree generation (>100 years) and for two or three generations in the southern part. The degree to which biological communities have been influenced by this long history of forestry is largely unknown, although an estimated 2,000 species of invertebrates and lower plants are threatened (red-listed) in Swedish boreal habitats (Gärdenfors 2000). Boreal Russia/Canada has a much shorter logging history over most of the area so, conceivably, fewer species have achieved threatened status in these areas.

Because of the very dissimilar logging histories within the boreal region conservation efforts need to be designed and carried out depending on the amount of pristine habitat remaining. In Fennoscandia, with its long history of intensive forestry, considerable focus has been on developing methods to maintain and restore biodiversity in the managed landscape.

Management for biodiversity in Fennoscandia has been in operation since the mid 1990s and was rapidly implemented by integrating conservation measures into silvicultural practices. The basic idea is that commercial forestry can be maintained as long as enough care is taken to preserve and restore features in the managed forest that are of importance for a sustainable diversity of flora and fauna ('New Forestry'; cf. Larsson and Danell 2002). Protected areas (national parks, nature reserves, 'key habitats') do play an important role in Fennoscandian conservation planning. But recently the main focus of conservation efforts has been the management of the matrix, the area interspersed between pieces of protected land (Ehnström 2001, Vanha-Majamaa and Jalonen 2001). Key physical structures that contribute to biodiversity have been identified and management practices designed to enhance them have been developed. Landscape and stand structures considered important include old-growth stands, coarse woody debris, large patches of deciduous trees, burnt forest, and buffer zones along streams. The certification criteria presently in use require actions to be taken in order to preserve and actively restore these elements in the landscape (Anon. 2000).

Although it seems obvious that there is a limit to how much habitat that can be removed before biological diversity starts to decline, it is not at all clear how much habitat is required for the ecosystem to be sustainable and populations to remain viable. The practices introduced in Fennoscandia for matrix management were largely based on informed guesses from biologists with long experience in the natural history of forest organisms. The urgent need to preserve species judged to be threatened by modern forestry justified recommendations that were considered the best available, although recommendations were supported only by meagre scientific data (Larsson and Danell 2001). This approach has increasingly been questioned

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because managing the matrix for preserving biodiversity is not without costs (Raivio and others 2001). Ideally, the methods used should result in as much conservation benefit as possible.

CWD—A RESOURCE IN SHORT SUPPLY

Coarse woody debris (CWD) is commonly considered to be a resource in short supply in commercially managed forests (Siitonen 2001). Many organisms depend on CWD and, because of the shortage of it in today's managed forests, many wood-dependent species have become rare. The Swedish red list, for example, has 501 species of beetles, 33 species of lichens, 55 species of mosses, and 382 species of fungi considered to be dependent on CWD (Dahlberg and Stokland 2004).

The amount of CWD in the undisturbed landscape is one to two orders of magnitude higher than in managed Fennoscandian boreal forest (Siitonen 2001). In the natural landscape CWD is created by natural disturbances such as fires, insect and disease outbreaks, and windstorms (Angelstam 1997, Kuuluvainen 2002). In the commercial forest landscape clear-cuts have sometimes been considered comparable to natural disturbances. At harvest, however, CWD is commonly destroyed (Hautala and others 2004). Biodiversity-oriented forestry aims to minimize destruction of existing CWD and to produce new CWD.

The degree to which CWD-dependent organisms respond to the increase in CWD following biodiversity-friendly harvesting is essentially unknown. It is also largely unknown how the spatial distribution of CWD in the landscape influences putative positive effects of the new management practices. Because CWD in Fennoscandian boreal landscapes is likely to be very aggregated, we expect organisms with dissimilar dispersal capacities to respond differently to retention of CWD at clear-cutting.

It is clearly a challenge to design research programs that can assess the benefit of the new forestry in terms of long-term maintenance of biodiversity. Most likely, organisms with different life histories (reproduction, dispersal capacity, territoriality) will show different temporal and spatial responses to management practices, and thus, the scale of study will be important. Further, the suite of forestry practices in use are likely to be of variable importance for different types of organisms, e.g., CWD for organisms dependent on dead wood and burnt habitats for fire-dependent organisms. Thus, in order for research to be operational, efforts will need to focus on a subset of organisms, a subset of forestry practices, and ideally, for the majority of organisms, be executed at the landscape level.

Currently a number of research projects are underway in Sweden and Finland aiming to elucidate how certified forest management contributes to preservation of biodiversity. The present paper focuses on results from an on-going landscape-wide project in the south boreal region of Sweden, aimed at quantifying the efforts to manage CWD. Assemblages of saproxylic beetles, a species-rich group of organisms of great concern in Swedish nature conservation (Ehnström 2001), are studied. The aim of this project is to estimate, at the landscape level, the amount of CWD that results from the new forestry, and to determine the degree to which saproxylic beetles are affected by this relative increase in CWD.

Study Site

The study landscape, a management unit of Holmen Skog AB (www.holmenskog.com), is located close to Delsbo in central Sweden (62°N, 16°E) and consists of stands that typically have been managed for at least one rotation period. The size of the landscape is 24549 ha of which 20294 ha is productive forest land; small lakes, low productive forest land, and bogs make up the remaining 4155 ha. The landscape is typical for the middle-boreal region (Sjörs 1999) with Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) the dominate tree species. Birch (*Betula pendula, B. pubescens*) and aspen (*Populus tremula*) are the most common deciduous tree species, but they rarely constitute more than a small proportion of the managed forest.

The landscape consists of 2,173 management blocks (stands), and in addition, three legally protected nature reserves (table 1). Of the company-managed area, 375 stands (1920 ha) have been designated 'set-asides', i.e., they will not be commercially managed but do not have legal protection (see below). The 17723 ha forest that is commercially managed is dominated by stands harvested in the 1960s and the 1970s; more than half of the area (9459 ha) is in the age class 15-59 years. This age class holds a significant number of stands planted with the exotic lodgepole pine (*Pinus contorta*); stands with >50 percent lodgepole pine cover an area of 5787 ha. There are 853 mature stands (>60 yrs) covering an area of 5511 ha, corresponding to 31 percent of the commercially managed area, or 22 percent of the entire landscape. Most of the mature stands are dominated by Scots pine, or a mix of Scots pine and Norway spruce. Spruce-dominated mature stands (>40 percent spruce) cover an area of 1841 ha (33 percent). Only a small fraction of the area of mature stands (2 percent) has a substantial (>40 percent) amount of deciduous trees.

NEW FORESTRY

Because Holmen Skog AB is certified according to FSC (Forest Stewardship Council, see www.fsc-sweden.org) their land has been managed for almost ten years using silvicultural methods developed for preservation and restoration of biodiversity. At present, there are a number of silvicultural practices performed at final harvest stipulated by FSC standards. It is required that a certain number of living trees be retained on clear-cuts, at present ten trees (DBH>15 cm) per ha must be left. These retained patches, small in size (<<1 ha), most likely contribute future CWD because there is a high probability that trees in these wind-exposed habitat islands will be blown down during heavy storms (Esseen 1994). It is further stipulated by current certification that naturally fallen trees, frequently from stands along clear-cut edges, should be left unless the volume exceeds 3 m^3/ha, in which case there might be an increased risk for bark beetle infestation. According to FSC it is recommended that a few artificial snags should be created per ha at final harvest. These snags are usually cut at a height of 3-5 meters and should be representative of the harvested stand with respect to tree species and diameter. In the study landscape artificial snags were systematically introduced around 1995 and are presently supposed to be created at a density of three per ha. According to the FSC

Table 1—Composition of the study landscape at Delsbo, central Sweden, and sampling efforts in the different stand categories

Stand category	Stands	Area	No. of sampled stands: CWD	No. of sampled stands: Beetles	No. of sampled objects: Beetles
	number	*ha*			
Managed forest					
0 – 2 years	20	343	0	0	0
3 – 7 years	47	666	20	19	115
8 – 14 years	82	1,744	10	0	2
15 – 59 years	796	9,459	11	2	0
≥ 60 years spruce	331	1,841	14	13	103
≥ 60 years pine	493	3,447	9	5	35
≥ 60 years deciduous	29	123	5	5	9
Unmanaged forest					
Set-asides	375	1,920	11	9	74
Reserves	3 (6 + 6 + 2)[a]	751	14	14	139
Sum forest	2,176	20,294	94	67	477
Nonforest		4,155			
Entire landscape		24,449			

CWD = coarse woody debris.
[a] The reserves were larger than the managed stands. Therefore, the reserves were divided into subareas, six for the larger ones (427 and 242 ha) and two subareas for the small one (82 ha).

protocol prescribed burning, aimed at creating suitable resources for fire-dependent organisms, is required on dry mesic sites on an area corresponding to 5 percent of the final harvest area. In addition to creating habitats for fire-specialists, burns also result in the creation of CWD, the amount being dependent on substrate availability and fire intensity. Of course, if burning is carried out on a clear-cut, with substrate mainly consisting of slash, only small amounts of CWD will be created. Prescribed fires for conservation purposes in the study landscape occurred in 1997 (40 ha), 1999 (32 ha), and in 2002 (15 ha). In addition, a wildfire occurred in 2002 on about 10 ha.

The 375 areas classified as set-asides constitute about 9 percent of the forest area in the landscape. The small areas retained at clear-cut could, in principle, be regarded as set-asides, but they are not formally included in this category. A more substantial contribution to set-asides comes from so-called 'key objects'. These are generally small stands (in the study landscape: mean area 5.1 ha, range 0.3-94 ha) of unusually high conservation value that have been identified using the same criteria as for 'key-habitats' (Hansson 2001). A second category of set-asides includes habitats that do not meet the criteria for key habitats but for other reasons are considered valuable for biodiversity. For example, deciduous tree species are considered to be present in much lower proportions (often <5 percent) in the managed boreal landscape compared to the unmanaged landscape (Angelstam and Andersson 2001). For this reason it has been stipulated that the proportion of deciduous trees should increase to 5-20 percent.

Silvicultural methods motivated by concerns about biodiversity, as described above, were gradually introduced into forest management from around 1995 and eventually formalized in the FSC regulation beginning in 2000. From a CWD point of view management practices in connection with final harvest can be assumed to be of particular interest. In the study landscape, 67 stands have been harvested during the period 1995-2002, totalling an area of 1009 ha (5 percent of the forested area). The majority of these stands should have been exposed to the new-forestry principles. Older clear-cuts, 8 years and older and harvested before the new forestry was introduced, are expected to have much less, if any, intentionally preserved or created CWD.

Sampling Program

In order to investigate the effect of new-forestry practices on availability of CWD and associated saproxylic beetle assemblages, we stratified the forest landscape into nine categories based on stand age and type of management using information from the Holmen Skog AB database and additional information about the forest reserves (see table 1). The first two categories, 0-2 years and 3-7 years, represent clear-cuts on which creation of high stumps and green tree retention have been practiced at final cutting. However, CWD occurring on the youngest clear-cuts was not included in the study because this quality of wood is not suitable for the subset of saproxylic beetles that is the focus of this study. Thus, no sampling was performed in this type of stand.

In each stand category, except reserves, a random sample of stands located throughout the landscape was selected (table

1). All three nature reserves within the landscape were sampled. Because reserves were larger than managed stands the two largest were divided into six sub-areas (denoted stands) of approximately equal size and the smallest was divided into two sub-areas. In each chosen stand, amounts of CWD and beetle abundance were estimated. Sampling of logs (downed woody debris) was carried out using a Line Intersect Sampling method (Marshall and others 2000). Four transects of 100 m were sampled in each stand. The same transects were used to delimit sampling plots for snags (standing dead wood). The plot extended 10 m on each side of the transect forming a 20 x 100 m rectangle. The following data were for each piece of CWD: classification as snag or log, intact or broken/cut snag, diameter (at transect line for logs and at DBH for snags), height of snags, tree species, percentage of surface area covered by bark, and decay class. The classification into decay classes (1-6) was based on the hardness of the wood (Siitonen and Saaristo 2000). The volume of snags was estimated using tree-specific functions with diameter at 1.3 m and height as input variables. Bark area on single snags was calculated by using the formula for the surface area of a cone as an approximation. Volume of logs per ha was calculated for each transect using formulae from Marshall and others (2000). Surface area was estimated by modifying the formula for "total projected area" by replacing diameter with circumference. Surface area for each object was multiplied by the proportion of remaining bark. For each stand, an average for each variable was calculated based on the four intersect lines. Further details concerning sampling can be found in Ekbom and others (2006).

Snags and logs in decay classes 2-3 from spruce, pine, and birch were sampled for beetles. Bark was peeled off and broken into small pieces that were sifted through a course net. The resulting fine fraction was placed in Tullgren funnels, where beetles were extracted under a lamp. This method was chosen because we wanted to only sample beetles actually using CWD in different stand categories. Ten objects of CWD were sampled in each stand. In stands where ten suitable objects were not available all appropriate objects were sampled. In some stands no suitable objects were found, and hence the number of stands sampled for beetles is lower than the number of stands sampled for CWD (table 1). Each sample consisted of 0.5-1.0 m^2 bark. All beetle adults were identified to species or genus level.

CWD in the Landscape

The total volume (m^3/ha) of CWD found in nature reserves and set-asides was about twice that of managed stands (Ekbom and others 2006). Bark area (m^2/ha) on CWD in nature reserves and set-asides was not significantly different from that found in managed spruce-dominated stands older than 60 years. The amount of bark found on clear-cuts and other old-managed stands was about half as much as that found in nature reserves, set-asides, and old-managed spruce stands. In young forest stands (8-59 years), bark was a sparse resource; these stands contained 10-20 times less CWD bark area than other stands. Most of the volume of CWD was pine, but the greater portion of bark area was on deciduous and spruce CWD.

The area of new-forestry final cuttings made up 4.9 percent of the landscape but they contained 8.7 percent of total CWD bark and 18.4 percent of spruce CWD bark available in the landscape. If new forestry is practised then the volume of CWD would increase by 4.5 percent at the landscape level when compared to the possibility that no CWD at all is left at final cutting (table 2). All CWD was obviously not removed under the previous management regime because the old clear-cuts (7-14 years) we inventoried were not devoid of CWD. Results from the CWD inventories are in broad agreement with simulations performed to compare past management with management according to new-forestry practices (Ranius and Kindvall 2004). In simulations, the volume of CWD roughly doubled in young stands after only 20 years. Although there is room for improvement, new management practices have increased the availability of resources for saproxylic beetles associated with bark.

Table 2—Estimates of available substrate (the volume and bark area of CWD of different tree species) in the landscape at Delsbo, central Sweden. The percentage increase in substrate attributable to "new forestry" is calculated by assuming that under earlier management regimes no CWD at all would be left on clear-cuts

		All tree species		Spruce		Pine		Deciduous	
Stand type	Area	Volume	Bark area	Volume	Bark area	Volume	Bark area	Volume	Bark area
	ha	*m^3*	*m^2*	*m^3*	*m^2*	*m^3*	*m^2*	*m^3*	*m^2*
Clear-cut	1,009	13,281	125,974	3,513	47,729	7,015	19,426	2,753	58,819
Managed, excluding clear-cut	16,714	223,007	921,843	16,133	155,146	160,411	284,801	46,463	481,896
Unmanaged	2,753	73,505	525,571	7,878	103,947	54,159	135,317	11,468	286,307
Total area in clear-cut (percent)	4.9								
Increase in CWD in managed forest attributed to "new forestry" (percent)		4.5	8.7	14.6	18.4	3.3	4.6	4.8	7.7

CWD = coarse woody debris.

Beetle Species Richness and Assemblages

A total of 184 species and 10,804 individuals of saproxylic beetle adults were recorded from a total of 67 sampled stands (table 3). Beetle species richness was positively correlated with available bark area on a stand by stand basis ($r = 0.47$, $p<0.0001$, $n = 51$; McGeoch, M.A. and others. Contribution of managed boreal forest stands to the conservation of saproxylic beetle diversity. Manuscript submitted. Author can be reached at Department of Conservation Ecology, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa). For all stand categories increased CWD bark generally resulted in enhanced species richness. Unsurprisingly, the highest number of species (126) was found in reserves, followed by old-managed stands (combined spruce-, pine-, and birch-dominated; 105 species). Clear-cuts were found to have almost as many species (97) as the old-managed stands. The young-managed stands had very little CWD (Ekbom and others 2006), and consequently, had very few saproxylic beetle species. The rather low number of species (81) found in set-asides is difficult to explain; approximately the same number of individuals were collected (table 3). Fewer set-aside stands were sampled, but there were as many beetle individuals sampled in set-asides as in the reserves, and thus rarefaction estimates for the two habitats have roughly the same precision (McGeoch and others. Contribution of managed boreal forest stands to the conservation of saproxylic beetle diversity. Manuscript submitted. Author can be reached at Department of Conservation Ecology, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa).

As expected, beetle assemblage structure, i.e., the combined consideration of species richness, relative abundance, and species composition, varied among stand types. Canonical correspondence analysis (CCA) showed that beetle assemblage on clear-cuts was very different from that in old-managed stands, set-asides and nature reserves (McGeoch and others. Contribution of managed boreal forest stands to the conservation of saproxylic beetle diversity. Manuscript submitted. Author can be reached at Department of Conservation Ecology, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa). It is interesting that the assemblages found in old-managed stands differed from set-asides and reserves. Likewise, Similä and others (2002) found the beetle assemblage of early succession pine forest in Finland to differ from that in mature pine forest stands, and Kaila and others (1997) found distinct birch beetle assemblages associated with clear-cuts and mature forests.

Occurrence of Rare Saproxylic Beetles

For the purpose of this paper we define rare species as those that are currently included on the Swedish Red List (Gärdenfors 2000), although we recognize that rare organisms need not be red-listed, or vice versa. A total of 16 species of rare saproxylic beetles were found in the 67 stands (table 4). The highest number (11) was found in the reserves. But there were also many species (9) found on the clear-cuts. Old-managed stands and set-asides were intermediate with six rare species each.

Data in this study are based on the method of sieving insects from bark samples. Thus, we know that the specimens that were collected have indeed been living under the bark (no 'tourists' included). Determining beetle assemblages from sieving underestimates the true number of saproxylic beetles because the method does not usually extract insects living inside the wood or in fungal fruiting bodies. For example, Wikars and others (2005) concluded that 18 percent of spruce-living saproxylic species collected by emergence traps, an efficient but arduous method, mainly live inside wood; most of these species would not be sampled by sieving.

A great advantage of sieving bark from a particular decay class is that the quality of CWD can be reasonably well defined. Because samples were taken from logs and snags in decay stages 2-3 few beetle species feeding on fresh cambium, e.g., bark beetles, were found. The fraction of CWD that we have studied is characterized by a high density of fungal mycelium in the space between bark and wood. Interactions between fungi and insects are likely to be important in the dynamics of CWD, and of utmost importance in the preservation of the organisms (Jonsell and Weslien 2003, Jonsell and others 2001). The biology of the rare species found in this microhabitat in our study is not known in detail, but it can safely be assumed that the majority of them are associated with fungi (Personal communication. 2004. Lars-Ove Wikars, Scientist, Department of Entomology, Swedish University of Agricultural Sciences, Box 7044, 750 07 Uppsala, Sweden). The click beetle *Harminius undulatus* and the staphylinids are considered mainly to be predators, but even these species may occasionally consume fungal tissue.

Table 3—Total number of saproxylic beetle species and individuals recorded as adults from the different stand categories at the study landscape at Delsbo, central Sweden

Stand type	Stands	Total species	Total individuals
	number		
Reserve	14	126	2,366
Set-aside	9	81	2,502
Old managed (total)	23	105	4,233
Old managed (spruce)	13	89	3,327
Old managed (pine)	5	57	679
Old managed (deciduous)	5	30	227
Young managed	2	18	158
Clear-cut	19	97	1,545
Total	67	184	10,804

Table 4—Red-listed saproxylic beetle species recorded as adults in the 482 sieved CWD objects from the study landscape at Delsbo, central Sweden

		Individuals				
Family and species	Red-list category[a]	Clearcut	Old managed	Set-aside	Reserve	Total
		- - - - - - - - - -	- - - - - -	*number*	- - - - - -	- - - - - - - - - -
Scydmaenidae						
Eutheia linearis Mulsant	NT	1	0	0	0	1
Staphylinidae						
Olisthaerus megacephalus (Zetterstedt)	NT	0	1	0	0	1
Olisthaerus substriatus (Paykull)	NT	0	0	1	14	15
Euryusa castanoptera Kraatz	NT	0	0	0	1	1
Elateridae						
Harminius undulatus (De Geer)	NT	0 (21)	0 (51)	0 (13)	1 (6)	1(91)
Silvanidae						
Dendrophagus crenatus (Paykull)	NT	3 (5)	3 (16)	5 (4)	5 (3)	16 (28)
Endomychidae						
Leiestes seminigra (Gyllenhal)	NT	0	0	0	1	1
Corticariidae						
Enicmus planipennis Strand	NT	2	0	2	4	8
Corticaria lapponica (Zetterstedt)	NT	1	5	0	2	8
Corticaria fennica Johnson	VU	0	1	0	0	1
Cisidae						
Ennearthron laricinum (Mellie)	NT	4	4	1	13	22
Mycetophagidae						
Mycetophagus fulvicollis Fabricius	VU	1	0	0	0	1
Tenebrionidae						
Bius thoracicus (Fabricius)	VU	0	0	0	1	1
Upis ceramboides (Linnaeus)	VU	2 (6)	0	0	0	2 (6)
Melandryidae						
Orchesia fasciata (Illiger)	VU	1	0	0	1	2
Zilora ferruginea (Paykull)	NT	0	0	7	7	14
Total		15 (32)	14 (67)	16 (17)	50 (9)	96 (125)

CWD = coarse woody debris; VU = vulnerable; NT = near threatened.
Numbers in parentheses are larvae.
[a] Red-list categories are according to Gärdenfors (2000).

Rare species made up 5-10 percent of the total number of species, with no appreciable differences among stand types. Many species were represented by only one individual (singletons) (table 4), which is so often the case when studying rare organisms. Differences among stand types with regard to proportion of singletons (range 0.33-0.44) were negligible.

As mentioned earlier, many of the new-forestry initiatives aim at increasing the amount of CWD in connection with final harvest. Of the nine rare species on clear-cuts three were exclusively found there (*Upis ceramboides*, *Eutheia linearis*, and *Mycetophagus fulvicollis*). Of these, *E. linearis* and *M. fulvicollis* were found as singletons. Thus, it is difficult to know whether they commonly occur on clear-cuts, although Jonsell and Weslien (2003) reported another *E. linearis* singleton from a clear-cut. *Upis ceramboides* was collected from three clear-cuts. This species is known to colonize early succession habitats, and thus can be presumed to be favoured by increased CWD on clear-cuts.

It is interesting that six rare species were found both in reserves and on clear-cuts. These two stand types represent end points in the forest succession, and clearly provide very different environments for beetles. Nevertheless, these stand types shared a considerable number of species. It will be difficult to adequately interpret this observation until the habitat requirements of the species are better known. It is possible that this subset of saproxylic beetles accepts a wide range of stand types, as long as there is CWD of suitable quality. If so, then the new-forestry initiative of creating CWD at final harvest may reduce the risk of local extinction for some species. But it is also possible that the observed rare species on clear-cuts are simply remnants from the harvested stands. Future studies will have to specifically address this question.

CONCLUDING REMARKS

The managed boreal forest landscape contains a small fraction of CWD, compared with the pristine forest (Siitonen 2001). Under natural conditions significant amounts of CWD are produced in maturing stands through ageing and self-thinning, and in the early succession phase following disturbances such as fire, insect and disease outbreaks, and wind storms (Ranius and others 2004). The Fennoscandian attempts to increase CWD in the managed forest landscape have, to a large extent, been linked to operations at final harvests, i.e., mimicking CWD production in early succession habitats. This means that, at the landscape level, most of the additional CWD resulting from the new forestry is to be found on, or in close proximity to, clear-cuts. Less has been achieved with respect to increasing the amount of CWD in mature stands.

The amount of CWD that is retained and produced at final harvest, about 14 m^3/ha at the study landscape, is an improvement compared to the situation in Sweden in the 1960s and 1970s when virtually nothing was left. However, one must bear in mind that the amount of CWD present on today's clear-cuts is only a small fraction of what was produced after natural disturbances in the pristine boreal landscape (cf. Siitonen 2001). The question, then, arises as to whether or not present management of CWD significantly decreases the risk of local extinction for CWD-dependent organisms.

Data collected in this study support the notion that saproxylic beetles benefit from the new silvicultural methods. A considerable number of saproxylic beetle species was found to utilize CWD retained and created on clear-cuts, including species that are considered threatened (red-listed) (also cf. Jonsell and Weslien 2003). Not surprisingly, the beetle assemblage on clear-cuts differed from those in the intact stands. However, it is probably premature to conclude that restoring CWD at final harvest will only benefit saproxylic beetles that are exposed-habitat specialists. Clear-cuts and reserves shared a number of species (e.g., six red-listed). Perhaps such species accept a broad range of habitats, given that the appropriate resource is available (cf. Martikainen 2001).

Coarse woody debris with intact bark is a resource that is crucial for many beetle species, including many red-listed, that are associated with saproxylic fungi. In the present study we restricted sampling to this resource, and thus, any conclusions are limited to this subset of CWD-associated beetles. This is a problem when communicating with forest managers and scientists studying other CWD organisms, because silvicultural practices were developed in order to preserve and restore a multitude of organisms, not only saproxylic beetles living under bark. On the other hand, in order for the scientific method to be successful it is essential that the study object be clearly defined. With respect to CWD, it is obviously of little relevance to consider decay categories not used at all by the study organism. Estimates of total volumes of CWD, including the full range of decay classes, are difficult to relate to specific organisms because few, if any, grow and reproduce in all categories of CWD.

The fact that saproxylic beetles can be found in CWD on clear-cuts is intriguing, but not conclusive evidence that the management practices included in the new forestry have reduced the risk of species disappearance from the boreal landscape. We found some support for the conjecture that saproxylic beetles are limited by the availability of their resource, i.e., beetle species richness correlated positively, on a stand by stand basis, with available bark area. Thus, it is conceivable that an increase in bark area in the landscape could enhance species richness. However, precise predictions are not possible at this stage. One major uncertainty is the form of the relationship between bark area and species richness (or any other response variable, e.g., population density of rare species). There are good theoretical reasons to assume that thresholds are important (Fahrig 2002), and that threshold values differ depending on the species considered. The existence of thresholds calls for more intensive studies of the spatial distribution of CWD in the landscape, in particular the distribution of CWD in relation to the dispersal capacity of the beetles.

Finally, there is an important spatio-temporal aspect as to the value of new-forestry CWD. The category of CWD that we have studied has a turnover of about 10-20 years, depending on tree species and habitat (Kruys and others 2002, Ranius and others 2004). Assuming that, at the landscape level, harvesting occurs with the same intensity over time the input of CWD will roughly equal the disappearance of this category of CWD through decomposition. Each 'cohort' of CWD will then last 10-20 years. The arrangement of this cohort of CWD in the landscape should be designed to facilitate colonization and successful reproduction by target organisms.

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