available at www.sciencedirect.com

SCIENCE DIRECT®

journal homepage: www.elsevier.com/locate/biocon

Cost-effectiveness of silvicultural measures to increase substrate availability for red-listed wood-living organisms in Norway spruce forests

Mattias Jonsson [a,*], *Thomas Ranius* [a], *Hans Ekvall* [b], *Göran Bostedt* [b], *Anders Dahlberg* [c], *Bengt Ehnström* [d], *Björn Nordén* [e], *Jogeir N. Stokland* [f]

[a]*Department of Entomology, P.O. Box 7044, Swedish University of Agricultural Sciences, SE-750 07 Uppsala, Sweden*
[b]*Department of Forest Economics, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden*
[c]*Swedish Species Information Centre, P.O. Box 7007, Swedish University of Agricultural Sciences, SE-750 07 Uppsala, Sweden*
[d]*Stationsområdet 224, SE-780 53 Nås, Sweden*
[e]*Botanical Institute, Systematic Botany, Göteborg University, P.O. Box 461, SE-405 30 Göteborg, Sweden*
[f]*Norwegian Institute of Land Inventory, P.O. Box 115, 1431 Ås, Norway*

ARTICLE INFO

Article history:
Received 3 May 2005
Received in revised form
2 September 2005
Accepted 6 September 2005
Available online 19 October 2005

Keywords:
CWD
Forestry
FSC
Picea abies
Saproxylic

ABSTRACT

It is important that measures to maintain biodiversity are taken in a way that is cost-effective for the landowner. We analyzed the cost-effectiveness of silvicultural measures that aim at increasing the substrate availability for red-listed (species that are threatened, near threatened or where species probably are threatened but data is deficient) saproxylic (wood-inhabiting) organisms. We modelled stands of Norway spruce (*Picea abies*) in three regions of Sweden by using computer simulations and a database with substrate requirements of saproxylic beetles and cryptogams on the Swedish Red-List. Conclusions concerning cost-effectiveness of silvicultural measures depend on the extinction thresholds of the species they are intended to conserve; measures that generate only small amounts of coarse woody debris (CWD) may provide too little substrate to be useful for species with high extinction thresholds. In northern Sweden, forestland is relatively inexpensive, so a cost-effective strategy to increase the amount of spruce CWD was to set aside more forests as reserves. In central and southern Sweden, more emphasis should instead be given to increasing the amount of CWD in the managed forest. The regulations by the Forest Stewardship Council (FSC) could be made more cost-effective by prescribing creation of more high stumps and retention of larger amounts of naturally dying trees. Large-sized CWD, CWD from slow-growing trees, and CWD in late decay stages are substrate types that were particularly rare in managed forest in relation to unmanaged forests. Manual soil scarification and retention of living trees are measures that can increase the proportion of these underrepresented CWD types.

* *Corresponding author*: Present address. National Centre for Advanced Bio-Protection Technologies, Lincoln University, P.O. Box 84, Canterbury, New zealand. Tel.: +64 3 325 3696; fax: +64 3 325 3864.
E-mail address: jonssom2@lincoln.ac.nz (M. Jonsson).
0006-3207/$ - see front matter
doi:10.1016/j.biocon.2005.09.004

1. Introduction

Preserving biodiversity may be economically beneficial in a national or a global sense (Balmford et al., 2002), but for private landowners, conservation measures are most often associated with economic costs. Therefore, it is important that measures to maintain biodiversity are chosen so that they are cost-effective for the land owner. Such conservation measures may include setting aside reserves but also altered management of the productive land. In forest ecosystems, biodiversity conservation has long been dominated by setting aside reserves, but especially during the last decade this approach has been combined with changes in silvicultural methods, which aim at increasing habitat quality for species in managed forests (e.g., Larsson and Danell, 2001; Lindenmayer and Franklin, 2002). In Sweden and Finland, the current strategy for preservation of forest biodiversity is, to a large extent, based on improvement of forest habitats in managed forests through altered silvicultural methods (Raivio et al., 2001). These changes have been brought about by adaptations to the forest certification standards (e.g. from the Forest Stewardship Council, FSC). As only a minor part of the forest area is protected in these countries, consideration of managed forest land is probably essential for successful conservation of forest biodiversity.

Dead wood is a key feature for the presence of biodiversity in boreal forests (e.g., Berg et al., 1994; Jonsell et al., 1998; Siitonen, 2001). A large proportion of the species in boreal forests are saproxylic (Hanski and Hammond, 1995; Siitonen, 2001), i.e. they depend directly on dead wood or on other species that require dead wood during some part of their life-cycle (Speight, 1989). In Sweden, at least 6000–7000 species are saproxylic (Dahlberg and Stokland, 2004). Coarse woody debris (CWD, defined as dead wood with a diameter larger than 10 cm) has higher species richness and is more important for red-listed (species that are threatened, near threatened or where species probably are threatened but data is deficient according to the criteria of IUCN (2001)) saproxylic species, than fine woody debris (Jonsell et al., 1998; Grove, 2002; Dahlberg and Stokland, 2004). About 90% of the Swedish red-listed saproxylic species are confined to CWD (Dahlberg and Stokland, 2004), which explains why the efforts to enhance the conditions for them have focused on CWD. Forest management in Fennoscandia has decreased the volume of CWD to 2–30% (normally less than 10%) of the quantity found in old-growth boreal forests (Fridman and Walheim, 2000; Siitonen, 2001). Therefore, many saproxylic species have declined and are now red-listed (Gärdenfors, 2000; Rassi et al., 2000). In Sweden, 1126 saproxylic species are red-listed, which is about 25% of all red-listed species in the country (Dahlberg and Stokland, 2004).

Saproxylic species have different requirements regarding the quality of dead wood (Berg et al., 1994; Jonsell et al., 1998; Stokland et al., 2004). Some factors that have been found to correlate with the richness and composition of saproxylic species are tree species (Lõhmus and Lõhmus, 2001; Lindhe and Lindelöw, 2004; Lindhe et al., 2004), tree diameter (Söderström, 1988; Bader et al., 1995; Ranius and Jansson, 2000; Nordén et al., 2004), stage of decay (Söderström, 1988; Bader et al., 1995; Lundblad, 1998; Lõhmus and Lõhmus, 2001), position, i.e. whether the tree is standing or lying (Jonsell and Weslien, 2003; Lindhe et al., 2004) and light regime (Ranius and Jansson, 2000; Martikainen, 2001; Lindhe et al., 2004; Jonsell et al., 2004). Thus, to maintain saproxylic biodiversity a great diversity of substrate qualities should be secured (Similä et al., 2003).

According to Swedish governmental goals, the amount of hard (less decayed) dead wood should increase by 40% to 2010 (Anon., 2001). A rough estimate suggests that this would cost 4.2 x 10^9 SEK (Anon., 1999). Because large costs are involved, it is important that measures taken to increase the amount of CWD are cost-effective. Several studies have recently analyzed different aspects of cost-effectiveness of biodiversity-oriented forestry in Fennoscandia. Some have analyzed how to select forest reserves in a cost-effective manner (Juutinen and Mönkkönen, 2004; Juutinen et al., 2004), whereas others have focused on cost-effectiveness within managed forests (Carlén et al., 1999; Wikström and Eriksson, 2000; Kruys and Wikström, 2001; Kurttila and Pukkala, 2003; Ranius et al., 2005). Two studies have included analyses on how to increase the amount of substrate for saproxylic species in managed forests. Carlén et al. (1999) estimated effects on biodiversity at final logging by ranking conservation measures according to how they believed that animals were affected. Retention of dead fallen and standing trees was among the measures that had a positive effect on biodiversity but caused no change in net revenue. Kruys and Wikström (2001) modelled dynamics of CWD and population dynamics of the liverwort *Anastrophyllum hellerianum* (Lindenb.) and showed that the occurrence of this particular species can increase considerably at only a small cost. Thus, both studies suggest that it is possible to improve cost-effectiveness of biodiversity-oriented forestry.

In a previous study where Norway spruce stands in Sweden were modelled, it was shown that measures to increase the volumes of CWD differ considerably in terms of their cost-effectiveness (Ranius et al., 2005). Creating high stumps at thinning and clear-cutting, and retaining wind-thrown trees were found to be inexpensive measures, whereas increasing the rotation period was expensive. In that study the response variables were the financial costs for the landowner and the total amount of CWD available if the same management regime prevails over a long time. However, to increase the total amount of CWD is not a goal in itself, but the aim is to decrease the extinction risks of saproxylic species. Because saproxylic species have different requirements regarding the quality of dead wood, and some substrate types are known to host a greater number of species than others (Berg et al., 1994; Jonsell et al., 1998; Stokland et al., 2004), increasing the amount of CWD to a certain extent will affect saproxylic species differently depending on what qualities of dead wood are increased. In analyses of cost-effectiveness of different conservation measures that increase the amount of dead wood it is therefore important to consider the substrate requirements of saproxylic species. However, so far no study has attempted to model financial costs, dead wood dynamics and diversity of saproxylic species using different management scenarios. In this study we build on the results from a previous study of cost-effectiveness of different measures that increase the amount of CWD in Norway spruce forests

(Ranius et al., 2005), but when we estimate the conservation value, we also take the substrate requirements of red-listed saproxylic species into account. We simulated the amount of suitable substrate for red-listed species when different conservation measures are performed and how much these measures cost the land owner. In addition, we ascertained which substrate types were underrepresented in managed forests in relation to unmanaged forests and which, if any, of the conservation measures can make an extra contribution to these substrate types. The analysis was performed for typical spruce stands in three different regions of Sweden.

2. Methods

For each of the management scenarios analyzed, three different kinds of data were obtained as output: economic costs, volumes of different CWD qualities, and the amounts of substrate suitable for different red-listed saproxylic species. We used three models, one that deals with the development of the forest stand, one that deals with the economic outcome and one that deals with CWD (Ranius et al., 2005). To be able to estimate the amount of substrate for red-listed species we compiled a database based on available knowledge about the substrate requirements of the red-listed species. We used two types of estimates of conservation value to compare different conservation measures: a substrate index which is the amount of substrate available multiplied with the number of species that can use it and the number of species finding more substrate than certain threshold amounts. We compared the cost-effectiveness by calculating the economic cost associated with a measure and dividing it with the increase in the conservation value compared with a reference scenario which maximized economic profit. The more cost-effective a conservation measure is, the lower this value becomes. We also compared the proportions of different CWD qualities present under different management scenarios with the proportions present in unmanaged forests to evaluate which substrate qualities that are underrepresented in managed forests and if any measure can decrease this deficit.

2.1. *Forest characteristics and growth*

We compared three model forest stands with 100% Norway spruce in southern (Kronoberg county), central (Gävleborg county) and northern (mountainous part of Västerbotten county) Sweden (Fig. 1). The stands were assigned characteristics (site productivity and different transport distances) close to the average values for each area (see Ranius et al., 2005, for more details).

In scenarios with forest management, forest growth was predicted by using a growth model applied in 'The Stand Method' ('Beståndsmetoden'), which is a flexible growth model for forest valuation developed by the National Land Survey of Sweden (Anon., 1988). The model was parameterized using information from the National Land Survey of Sweden.

In scenarios without management, the number of trees per hectare was predicted by a function from Ranius et al. (2004). The diameters of the trees were described by a negative exponential distribution, which is very near the distribution found empirically (Ranius et al., 2004).

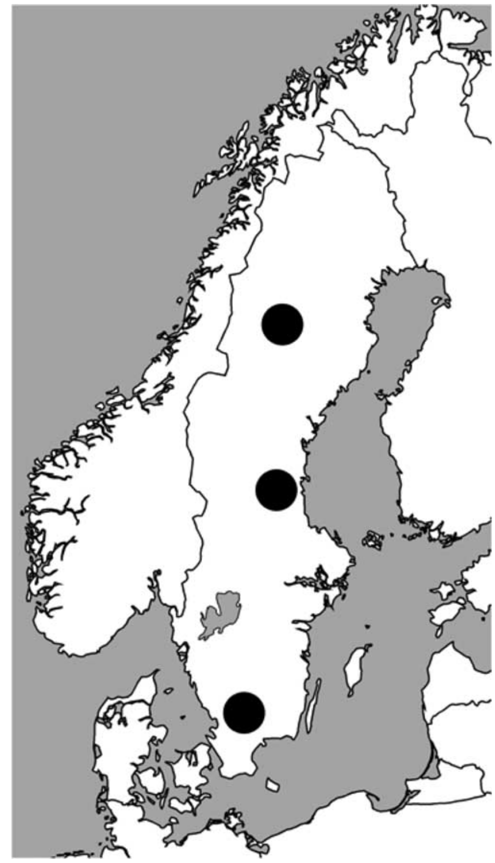

Fig. 1 – Location of the three hypothetical Norway spruce stands that were simulated, from north to south: Västerbotten in northern Sweden, Gävleborg in central Sweden and Kronoberg in southern Sweden.

2.2. *Calculation of CWD amounts*

We simulated the dynamics of CWD in managed stands using a model similar to that presented by Ranius et al. (2003) and in unmanaged stands using the model presented in Ranius et al. (2004). The models predict amounts of CWD that are close to the amounts observed in managed and old-growth forests in Sweden (Ranius et al., 2003, 2004).

To simulate CWD dynamics, we used information on forest growth, data on tree mortality, and a model that describes the decay process of CWD. The output data included the volume of CWD present in the forest, stratified according to decay stage, size, light regime, position (whether standing or lying on the ground), and growth rate of the stem when alive (Table 1). These variables were used when we calculated the amount of substrate for red-listed species.

Tree mortality was assumed to be related to the stand age (Table 2). Among retained trees, especially Norway spruce trees that grow in small groups left on clear-cuts, mortality will often be very high immediately after cutting (Esseen,

Table 1 – Variables reflecting quality of CWD used for categorisation of CWD and substrate associations of red-listed species

Variable	Category
Position	Standing (both whole trees and high stumps)
	Lying
Diameter at breast height (dbh)	10–20 cm
	20–30 cm
	>30 cm
Decay class[a]	(1) Wood hard, bark remaining intact
	(2) Wood hard, bark broken up in patches but more than 50% remaining
	(3) Wood hard, less than 50% bark remaining
	(4) Wood has started to soften, without bark, texture smooth
	(5) Wood soft, with small crevices and small pieces lost
	(6) Wood fragments lost so the outline of the trunk is deformed
	(7) The outer surface of the log is hard to define, possibly with a core of harder wood
	(8) Completely soft without evidence of hard wood, outline indeterminable
Light regime	(1) Sun-exposed (as on a young clear-cutting)
	(2) Partly sun-exposed (as at the edge of a clear-cutting, not directed southwards)
	(3) Partly shaded (as in an open spruce forest)
	(4) Very shaded (as in a dense spruce forest).
Growth rate	(1) Slow grown, i.e. growing on land with a production less than 1 m^3/ha, or with equally slow growth rate, but growing at productive sites
	(2) Moderately slow grown. Trees growing faster than the slow grown, but when they are 100-year-old their dbh is less than 15 cm
	(3) Normal growing. Trees with a dbh of 15–30 cm at an age of 100 years
	(4) Fast growing. Trees with a dbh > 30 cm at an age of 100 years. Such trees are only found on productive land (site index > 30)

a Categories according to Söderström (1988).

Table 2 – Annual tree mortality of Norway spruce in Sweden

Forest type	Mortality (%)
Managed forest of an age equal to 0–50% of cutting age	0.09
Managed forest of an age equal to 50–100% of cutting age	0.21
Unmanaged forest and stands older than recommended cutting age	0.36

Based on data collected by the Swedish National Forest Inventory, presented by Ranius et al. (2003, 2004).

Table 3 – Time a dead tree resides in each decay class (according to Söderström's (1988) classification)

Class	Time (years)	Volume in (%) relation to the tree when alive
1	5.0	100
2	6.4	100
3	8.3	100
4	4.3	80
5	10.1	80
6	12	60
7	12	60
8	12	60

Variability in residence time between trees: log-normal distribution, SD = 0.708. Residence times for class 1–5 from field data (Ranius et al., 2003), other parameter values from own assumptions.

1994) and we assumed this one-time mortality to be 50%, and caused by wind-throw. The volume of the dying trees was calculated as in Ranius et al. (2005).

The average time each stem resided as CWD in central Sweden (Gävleborg) was assumed to be 70 years. This was based on the decay rate estimated by Krankina and Harmon (1995) and the assumption that a log has 'disappeared' when 10% of its weight remains. During the residence time, the logs moved from one decay class (with classes defined according to Söderström, 1988; Table 1) to another (Table 3). Due to differences in climate, we assumed the residence time to be 50 years in southern Sweden (Kronoberg) and 120 years in northern Sweden (Västerbotten) (Ranius et al., 2005). The proportion of the total time an object resided in a certain decay stage was equal in the three model areas. Among dying trees, we assumed that 60% died standing, while 40% were wind-thrown. This was based on a study by Fridman and Ståhl (unpubl.), which showed that in Sweden, on average, about 30% of the dying spruce trees were logs, about 20% were snapped snags and about 50% were intact snags. Based on a study by Storaunet and Rolstad (2002), we assumed the average period a snag remains standing to be 22 years. Simulations based on these two assumptions resulted in standing and lying CWD of similar proportions to what is found on average (of all tree species) in Swedish managed forests in the corresponding regions (Fridman and Walheim, 2000). Artificially created high stumps have a higher durability than full-sized snags, and we assumed that they fell down 10 years later (i.e. after 32 years). The time each snag remained standing

Table 4 – Assumed sun-exposure of CWD objects in even-aged stands of Norway spruce

Stand age[a]	Southern Sweden		Central Sweden		Northern Sweden	
	Snags[b]	Logs[c]	Snags[b]	Logs[c]	Snags[b]	Logs[c]
<7 years (managed forest)	90–10–0–0	70–20–10–0	90–10–0–0	70–20–10–0	90–10–0–0	70–20–10–0
<7 years (at area retained at clear-cutting)	20–40–40–0	20–30–30–20	20–40–40–0	20–30–40–10	20–40–40–0	20–40–30–10
7–14 years (managed and retained part)	50–40–10–0	0–30–40–30	50–40–10–0	30–50–20–0	50–40–10–0	0–40–50–10
15–28 years (managed and retained part)	0–50–50–0	0–20–20–60	0–60–40–0	0–20–40–40	0–70–30–0	0–30–60–10
>28 years (managed and retained part)	0–20–20–60	0–10–10–80	0–20–50–30	0–10–40–50	0–30–60–10	0–20–60–20

Percentages of the CWD in sun-exposure classes (see Table 1) in relation to stand age and geographical location.
a The age (= time since cutting of the managed part) presented here is valid when SI = 24. The age limits is dependent on productivity, with a lower limit in more productive forests.
b Percent of snags that are sun-exposed–partly shaded–very shaded.
c Percent of downed logs that are sun-exposed–partly sun-exposed–partly shaded–very shaded.

was always directly proportional to the total residence time for each object. Consequently, the snags fell after different time periods, however, the decay stage when they fell was always the same; in the model, all naturally generated snags belonged to decay class 4 when they fell, while artificially created high stumps belonged to class 5. Each CWD object was also given a value of growth rate category based on age and diameter at death.

Light regime varied between individual stems. We assumed that the proportion of dead trees in different light regime classes differed between standing trees and downed logs, and that in managed forests it changed with the ageing of the stand (Table 4). We modelled two unmanaged stands differing in their light regime. In one, the light regime of the CWD was, on average, equal to the light regime in 34–82-year-old managed forest, while in the other the light regime of the CWD was equal to the average in the managed forest over the whole rotation period. In this way we emulated one forest with a small gap dynamics (generally more shaded) and another with a large scale disturbance regime (generally more sun-exposed).

The forest stand was simulated over 400–500 years with constant management regime over time, but output data was only taken from the last rotation period (for the unmanaged stand a time period equal to the rotation period of the managed forest). This was done to emulate a situation when the same management regime prevails over such a long time that there is no effect of any former management regime. With all measures except setting aside a stand as a reserve, a large proportion of the increase in CWD takes place immediately after the time of decision. For three methods (manual scarification, retention of snags and retention of naturally dying trees), the whole increase takes place at that time, while for the other measures (creation of high stumps, retention of living trees at harvest and prolongation of the rotation period), the increase takes place over a longer period. The amount of CWD varied over the rotation period, and an average value was calculated. We simulated 500 stands and estimated a mean value, which was a sufficiently large sample size to achieve results that were stable between simulation runs.

2.3. *Database for saproxylic species*

To be able to compare the conservation value of different management scenarios, we first compiled the available knowledge about the substrate requirements of all non-extinct red-listed beetles, mosses, fungi and lichens in Sweden for which spruce CWD is considered an important substrate, into a database. The substrate requirements of all species occurring in the counties of Kronoberg (southern Sweden), Gävleborg (central Sweden) and Västerbotten (northern Sweden) (Gärdenfors, 2000) are summarised in Fig. 2. Beetles, fungi, mosses and lichens together comprise the great majority of red-listed species associated with dead spruce trees in Sweden (Dahlberg and Stokland, 2004). The database includes all species which according to Speight's (1989) definition are saproxylic, i.e. both species living directly from the dead wood, and those depending on other organisms that are living on dead wood. The substrate associations of the red-listed species were categorised according to the variables used in the CWD simulations (Table 1). The classification was carried out by experts associated with the Swedish Species Information Centre and complemented with information from two other databases, one available at the Swedish Species Information Centre and one developed by Dahlberg and Stokland (2004). For some species, knowledge about their associations with certain substrate variables is poorly known. These organisms were classified as generalists for that particular substrate variable, i.e. occurring in all of its categories. An alternative would be to exclude species with unknown associations from the analysis, but as most species only had unknown associations for one or two variables, that would have discarded a lot of information.

2.4. *Modelling conservation value*

For each CWD simulation, we calculated the average volume of CWD that potentially could be used by each red-listed species in the database, V_i, by summing the simulated volumes of CWD with qualities corresponding to the preferences of that species. Only species that have been recorded in the county where the simulated forest was situated (Gärdenfors, 2000) were included in the analysis. We used two types of estimates to compare the conservation value of the different conservation measures: a substrate index, S, and the number of species which have substrate amounts exceeding certain threshold levels. The substrate index for a given simulation was calculated by summing the preferred substrate volumes for all red-listed species included in the database and

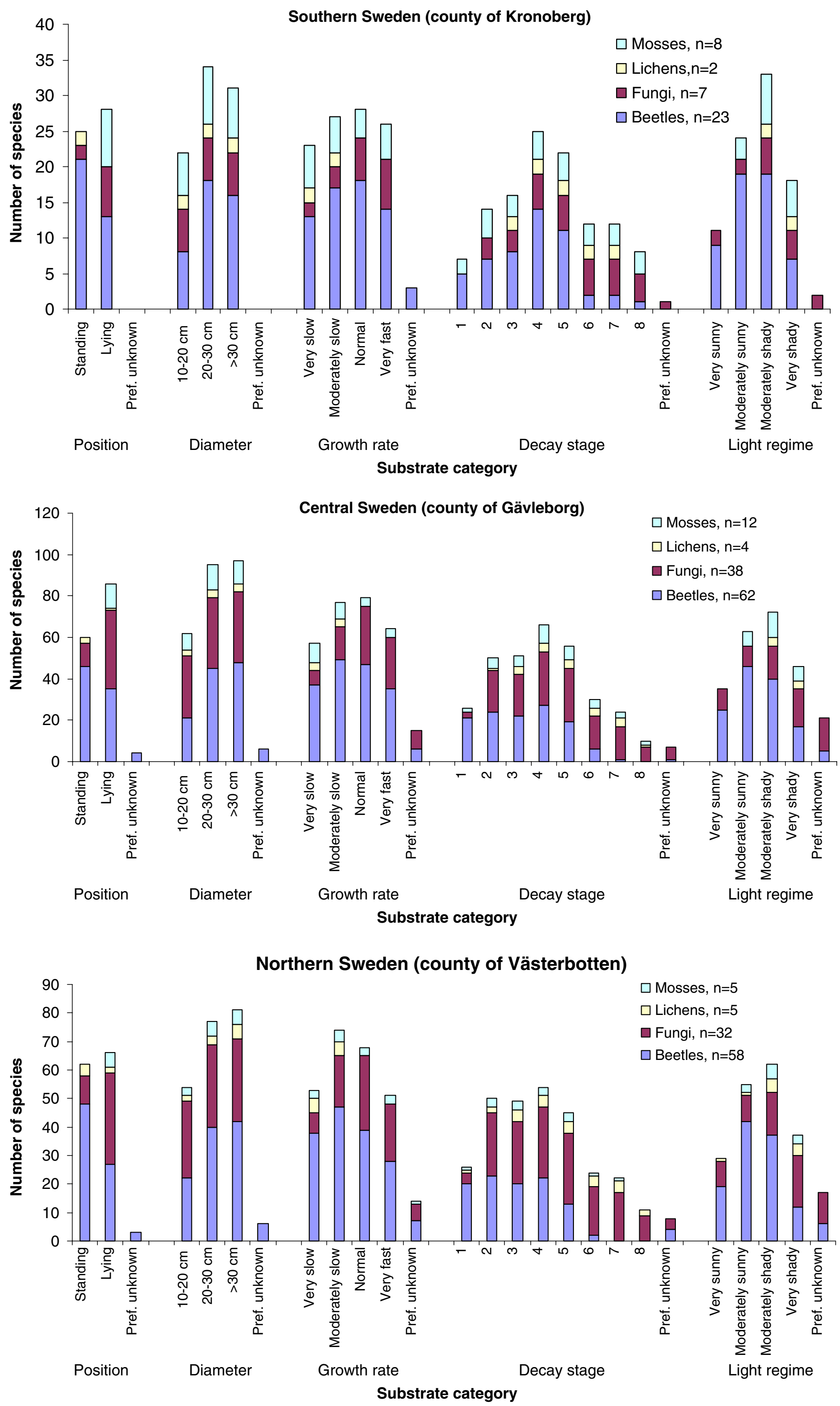

Fig. 2 – Substrate associations of red-listed mosses, lichens, fungi and beetles that utilise dead spruces during some part of their life-cycle and have been recorded from the Swedish counties of Kronoberg (southern Sweden), Gävleborg (central Sweden) or Västerbotten (northern Sweden). *n* Values represent number of species found of a taxonomic group in a region.

occurring in the county (see Eq. (1), where *V* is the substrate volume and *i* counts the red-listed species).

$$S = \sum_{\forall i} V_i. \tag{1}$$

Thus, the size of the substrate index is equal to the predicted volume of each substrate quality multiplied by the number of species that prefer that particular kind of substrate. The substrate index is a relevant measure of conservation value if there is a linear relationship between the substrate amount and the persistence probability for the populations of the red-listed species.

Our second type of estimate of conservation value was achieved by counting the number of species finding more suitable substrate than certain threshold levels at each management scenario. Several theoretical studies agree that extinction thresholds are common, i.e. that the relationship between habitat amount and persistence probability could be described by a sigmoid function (Lande, 1987; Bascompte and Solé, 1996; With and King, 1999; Fahrig, 2001). As knowledge about extinction thresholds of saproxylic species is poor (but see Økland et al., 1996; Ranius, 2002), we arbitrarily selected four different threshold values. The extinction threshold for individual species is not related to the total amount of CWD, but to the amount of CWD suitable for that particular species. To make the extinction thresholds comparable between species associated with different types of CWD, we express this threshold as the percent of suitable substrate in relation to the amount present in unmanaged forests rather than in terms of cubic meters. Therefore, we defined our threshold values as proportions of substrate found in unmanaged forests. Two types of unmanaged forest were simulated, differing in their light regime. We divided the red-listed species into species mainly utilizing the two more sun-exposed substrate classes and those mainly utilizing the two more shaded classes. The threshold values for the more sun demanding species were set to a certain proportion of suitable substrate found in more sun-exposed unmanaged forest and for the more shade demanding species to a certain proportion of the substrate amount found in the more shaded unmanaged forest. Threshold values were set at 10%, 20%, 30% and 50% of the substrate amounts in the two unmanaged forests.

To analyze how well different substrate qualities are represented in managed forests we compared the proportions of CWD belonging to different qualities in the different managed forest scenarios with the proportions of the same qualities in unmanaged forests. For this analysis we pooled substrate qualities so that each variable only had two categories, as equal in size as possible.

2.5. *Modelling economic costs*

We planned the management of the stand and calculated the opportunity costs using 'Plan33', (Ekvall, 2001), in the same way and with the same assumptions as Ranius et al. (2005). The opportunity cost of a measure to increase CWD is defined as the difference between the maximum present value that can be obtained from the stand when no CWD-increasing measure is undertaken and the present value obtained as a result of undertaking a CWD-increasing measure. The costs and revenues were discounted to the point in time when the decision to undertake a CWD-increasing measure was made (Table 5). This way of calculating the present values replicates the decision problem faced by a forest owner expected to increase the total amount of CWD at an estate that consists of many forest stands differing in age. By contrast, using the soil expectation value measure implicitly assumes that all decisions concerning CWD-increasing measures are undertaken in connection to the final cut, which is unrealistic.

Table 5 – Point in time when the decision is made to undertake measures to increase the volume of CWD

Measure	Point in time
Artificial creation of high stumps	First thinning
Retention of living trees	Final felling
Retention of snags	Final felling
Manual scarification	Immediately after final felling
Prolongation of rotation period	Final felling
Setting aside stands as reserves	Final felling
Retention of wind-throw	Halfway between last thinning and final felling

The decision on timing for final clear-cutting and the number, type (e.g. size of felled trees in relation to those retained), timing and intensity of the thinnings was obtained through an iterative search for a global present value maximum. The management regime (rotation period and time and strength of thinnings) was adapted to maximize the present value when no measure to increase the amount of CWD was taken, and was not changed when the measures to increase CWD were analyzed (except when increasing the rotation period was the conservation measure).

All economic calculations were based on the price lists for 2002 from Mellanskog (Ranius et al., 2005). We assumed that the most common methods in Swedish forestry were used. This means that felling, cutting, pruning, and stacking is conducted using a harvester. Transport from the felling site to the logging road is conducted with a forwarder. Manual felling was assumed to be conducted only when the number of trees to be cut was low. At regeneration, soil scarification, planting, re-growth control and pre-commercial thinning was conducted.

What is cost-effective for a small increase in CWD is not necessarily cost-effective for a larger increase. In this study we captured this fact through the use of three levels of intensity for the measures creation of high stumps, retention of living trees and prolongation of the rotation period and two plus two levels for retention of newly formed CWD. The measures retention of snags, manual scarification and setting aside a stand as a reserve are of a dichotomous choice character, i.e. they cannot be conducted in different levels of intensity.

2.6. *Management practices*

Seven different conservation measures were considered: six that involves altered management and one where the whole stand is set aside as a reserve (Table 6). These measures change the amount and quality of CWD, and therefore also persistence probabilities of saproxylic organisms. For each measure we analyzed one to three levels of intensity. If possible, one of the levels corresponds to the FSC regulations (Anon., 2000). For each level, the opportunity cost, CWD volume, substrate index and the number of species above the four different threshold levels were compared with a reference case where forest management was conducted with the sole purpose of maximizing present value.

Table 6 – Management measures taken to increase the amount of CWD, levels of intensity analyzed, and their values when no measure to increase CWD is taken

Management measure	Intensity of management measure	Value when no measure to increase CWD is taken
Retention of area (%) with living trees at harvest	1 5 9	0
Artificial creation of high stumps during thinning operations and at final cutting (no./ha)	3 10 20	0
Scarification of the clear-cutting	Only manually around plants	No restriction
Retention of snags at final cutting (%)	80	0
Prolongation of rotation period (%)	10 25 50	0
Setting aside a stand as a reserve. Two types of unmanaged forests are compared: one with a large scale disturbance regime and on with a small scaled gap dynamics	100%	0%
Retention of newly formed CWD in a year with high natural mortality (volume of newly formed CWD (x) and how much of this that is retained (y) (m^3/ha), always one storm felling per rotation period)	x = 20, y = 20 x = 20, y = 1 x = 5, y = 5 x = 5, y = 1	x = 20, y = 0 x = 5, y = 0

Levels that often occur when FSC prescriptions are followed are underlined.

The seven management measures are described below:

(1) *Retention of living trees at harvest*. When the FSC standard (Anon., 2000) is applied, living trees covering at least 5% of the stand are normally retained at cutting, both as individual trees and in small groups of trees. In retained areas, the volume of standing trees per hectare is lower than the average (Ola Kårén, pers. comm.), and therefore we assumed that the retained area has a productivity and a timber volume per hectare equal to 75% of the average value for the stand. Tree retention at harvest reduces the present value because the standing timber is lost and no timber production will take place on the area in the future.

(2) *Artificial creation of high stumps during thinning operations and at final cutting*. The FSC standard prescribes the creation of high stumps (Anon., 2000). High stumps usually have a height of 3–5 m. In this study, the height was assumed to be 4 m, and the average diameter equal to the cut trees. The CWD volume of a high stump was set to 30% of a whole stem. High stumps are created from trees of all quality classes, but lower classes are overrepresented (Ola Kårén, pers. comm.). We assumed that all high stumps are created from wood of the lowest timber quality class. For harvested trees, the wood at the base of the tree may belong to three different timber quality classes as well as the pulp wood class, and its average value is higher than the value of the lowest timber quality class. Creating high stumps reduces present value because the timber in the stumps is lost, and the harvesting costs increase since high stumps are avoided by the machines.

(3) *Manual scarification of clear-cuts*. Especially at scarification (before plantation), but also at final cutting, machines are used which destroy CWD. In a Finnish study, 58% of the younger CWD, and 88% of the older CWD was destroyed at final cutting if scarification was carried out, while with no scarification the loss was 15% (Hautala et al., 2004). According to the FSC standard, forestry operations should take care to preserve CWD and, if possible, scarification should be avoided (Anon., 2000). We compared two different methods (manual and with machines) of scarification before plantation. We assumed that only 15% of the CWD is lost when manual scarification is used. Manual scarification reduces the present value of forestry since it is more expensive than using machines.

(4) *Retention of snags at final cutting*. If preservation of CWD is not taken into consideration, we assumed that 100% of the snags are actively or incidentally felled at final cutting. These downed logs are then destroyed at scarification to the same extent as CWD that was lying on the ground before final cutting. When care is taken to preserve CWD we assumed that 80% of the snags will remain standing, while 20% fall down accidentally at cutting operations (Ola Kårén, pers. comm.). This conservation measure decreases the present value since machines have to avoid the snags.

(5) *Prolongation of rotation period*. We compared three levels of prolonged rotation time. Prolonged rotation time increases the amount of CWD because the period when the living trees are large enough to possibly generate CWD becomes longer, and destruction of CWD due to cutting occurs at longer intervals. An extension of the rotation time reduces the present value mainly through the discounting effect, i.e. the forest owner must wait longer for the revenues of the harvest.

(6) *Setting aside a stand as nature reserve*. Setting aside the whole stand as a reserve means that it will never be used for forestry, and thus the cost is equal to the present value of the stand.

Table 7 – Increase of CWD (average over the rotation period assuming that the management has been the same over a long time, m^3/ha), substrate index, the number of species with more substrate than certain threshold levels and financial cost (decrease of predicted present value at the time of decision, SEK/ha) when different measures are taken to increase the volume of CWD at even-aged Norway spruce stands in Sweden

			Number of species above threshold volumes of substrate				
	CWD	Substrate index	10% of unmanaged forest	20% of unmanaged forest	30% of unmanaged forest	50% of unmanaged forest	Cost
Southern Sweden							
Reference case	6.92	29.37	15	5	4	2	0
Retention of area (%)							
1	+1.09	+5.18	+3	+1	0	0	416
5	+5.10	+24.98	+8	+6	+4	+1	2143
9	+9.33	+45.51	+10	+12	+7	+5	3845
High stumps (no./ha)							
3	+0.63	+2.16	+3	+2	+1	+1	44
10	+2.23	+7.48	+9	+4	+2	+1	146
20	+4.32	+14.18	+10	+6	+3	+2	293
Manual soil scarification	+3.69	+19.24	+7	+6	+2	+2	1216
Retention of snags	+1.79	+5.96	+6	+5	+1	+1	53
Rotation period (% prolongation)							
10	+2.25	+9.73	+3	+2	+1	+1	1863
25	+5.87	+25.99	+9	+8	+4	+3	8889
50	+12.93	+58.02	+13	+17	+7	+5	25,979
Setting aside stand as reserve							
Sun-exposed forest	+91.80	+342.42	+25	+35	+36	+38	69,528
Shady forest	+91.58	+351.80	+24	+34	+35	+34	69,528
20 m^3 wind-throw							
Reference case	6.52	27.41	14	6	5	3	0
1 m^3 retained	+0.35	+1.89	0	−1	−1	−1	55
20 m^3 retained	+6.09	+30.25	+7	+6	+3	+1	963
5 m^3 wind-throw							
Reference case	6.70	28.51	13	5	4	2	0
1 m^3 retained	+0.23	+1.10	+1	+1	0	0	53
5 m^3 retained	+1.45	+7.07	+4	+1	0	+1	147
Central Sweden							
Reference case	4.57	81.91	25	7	5	3	0
Retention of area (%)							
1	+0.68	+14.41	+7	+5	0	0	245
5	+3.35	+70.23	+34	+16	+7	+2	1209
9	+5.94	+125.35	+47	+31	+16	+3	2010
High stumps (no./ha)							
3	+0.39	+5.53	+3	+1	0	0	45
10	+1.21	+17.86	+13	+8	0	0	150
20	+2.47	+36.19	+22	+10	+1	0	300
Manual soil scarification	+2.64	+50.04	+22	+12	+7	+1	915
Retention of snags	+1.19	+18.43	+11	+9	−2	0	36
Rotation period (% prolongation)							
10	+1.18	+23.60	+13	+9	0	0	1333
25	+3.14	+62.94	+38	+14	+6	+1	6232
50	+7.84	+160.64	+62	+44	+23	+5	17,099
Setting aside stand as reserve							
Sun-exposed forest	+68.23	+1022.10	+91	+109	+111	+113	43,424
Shady forest	+68.20	+1084.10	+90	+108	+110	+98	43,424
20 m^3 wind-throw							
Reference case	4.50	80.44	25	7	5	3	0
1 m^3 retained	+0.35	+7.46	+4	+3	0	0	−5
20 m^3 retained	+7.10	+143.73	+43	+35	+19	+10	−252

(continued on next page)

Table 7 – Continued

			Number of species above threshold volumes of substrate				
	CWD	Substrate index	10% of unmanaged forest	20% of unmanaged forest	30% of unmanaged forest	50% of unmanaged forest	Cost
5 m^3 wind-throw							
Reference case	4.44	79.68	25	7	5	3	0
1 m^3 retained	+0.40	+7.94	+3	+3	0	0	−8
5 m^3 retained	+1.87	+37.66	+15	+12	+1	+1	−154
Northern Sweden							
Reference case	3.60	64.99	18	6	4	4	0
Retention of area (%)							
1	+0.28	+4.83	+1	0	0	0	194
5	+1.61	+28.53	+11	+4	+2	0	963
9	+3.00	+53.06	+24	+5	+3	0	1731
High stumps (no./ha)							
3	+0.15	+2.48	+1	0	0	0	33
10	+0.49	+7.98	+2	0	0	0	109
20	+0.96	+15.61	+9	+2	+2	0	216
Manual soil scarification	+1.89	+32.91	+7	+6	+2	+1	509
Retention of snags	+0.58	+9.66	+1	0	+2	0	10
Rotation period (% prolongation)							
10	+0.79	+14.33	+9	+2	0	0	618
25	+2.16	+39.43	+16	+6	+3	0	2631
50	+5.14	+95.27	+39	+20	+6	+2	6184
Setting aside stand as reserve							
Sun-exposed forest	+62.61	+991.79	+82	+94	+96	+96	9870
Shady forest	+62.87	+1042.02	+81	+93	+95	+95	9870
20 m^3 wind-throw							
Reference case	3.49	63.17	17	6	4	4	0
1 m^3 retained	+0.37	+6.42	+2	+1	0	0	−75
20 m^3 retained	+7.66	+129.50	+26	+25	+15	+5	−1663
5 m^3 wind-throw							
Reference case	3.52	63.65	17	6	4	4	0
1 m^3 retained	+0.42	+7.30	+3	+2	0	0	−80
5 m^3 retained	+1.94	+32.90	+12	+6	+2	+1	−507

The stands were situated in three different counties, Kronoberg in southern, Gävleborg in central and Västerbotten in northern Sweden. The given values are the difference in CWD (in m^3/ha) and present value (in SEK/ha) in relation to a reference case. When occasions with large amounts of wind-throw occur, the reference cases differ, and imply that all newly formed CWD is taken care of (0 m^3 retained).

(7) *Retention of newly formed CWD in a year with high natural mortality.* If large quantities of spruce CWD are generated by natural mortality, it is usually removed by the forester. This is because the risk for bark beetle outbreaks may increase (Schroeder and Lindelöw, 2002) or because newly dead spruce trees have a commercial value (Törlind, 1998). In our analysis, we assumed that at a particular age (always midway between the last thinning and the final cutting), the mortality is exceptionally high, while for all other scenarios the tree mortality was held constant and no newly formed CWD was removed. Therefore, the results from this conservation measure are not directly comparable to the other measures. In years with exceptional mortality, all trees were wind-thrown and no trees died standing. We compared a scenario with all CWD generated at the year with high mortality retained, with a scenario with CWD from this year removed. Leaving naturally dying trees reduces the present value both because the timber in the trees is lost and because it increases future costs that arise when machines have to avoid the CWD. According to FSC, the forester is not allowed to remove all dead trees generated at a year with high natural mortality; a few representative dead trees per hectare must be retained (Anon., 2000).

3. Results

3.1. *Substrate amounts for red-listed species*

In the simulated unmanaged forests, there was more CWD in the south than in the north; in southern Sweden on average 99 m^3/ha CWD was present, in central Sweden 73 m^3/ha, and in northern Sweden 66 m^3/ha. Also in the reference case where present economic value was optimized more CWD was produced in the south (Table 7).

The substrate index and volume of CWD ranked the different measures in almost the same way (Table 7, Fig. 3). When the increase in number of species above different thresholds was considered, larger differences in relation to the volume of CWD appeared (Table 7, Fig. 3). At some combinations of thresholds and conservation measures, no increase in the number of species above the thresholds was observed (Table 7, Fig. 3). This occurred in all regions, but more often in northern and central Sweden than in southern Sweden (Table 7, Fig. 3). For example, three high stumps created in northern Sweden only resulted in an increase in the number of species above the 10% threshold whereas it gave an increase at all of the threshold levels in southern Sweden (Table 7, Fig. 3).

In all regions, the reference scenario produced a much lower proportion of large-sized (>30 cm) and slow grown CWD than the unmanaged forests, and a somewhat lower proportion of CWD in late decay stages (Fig. 4). In addition, in the reference scenario somewhat lower proportions of CWD in shady positions was present compared with the shady unmanaged forest and in sun-exposed positions compared with the sun-exposed unmanaged forest (Fig. 4). The proportion of CWD that was standing was rather similar to unmanaged forests (Fig. 4). Setting aside whole stands as reserves would obviously in the long run eliminate the under-representation of these substrate types as the stand would become similar to forests that were never managed. Among the conservation measures involving altered management, prolongation of the rotation period was the measure that generated the largest increase of the proportion of CWD of large-size (Fig. 4). In northern Sweden some measures, in particular retaining part of the forest area and increasing the rotation period, significantly increased the proportion of slow-growing trees, whereas no measure did this in southern and central Sweden (Fig. 4). In all regions, manual

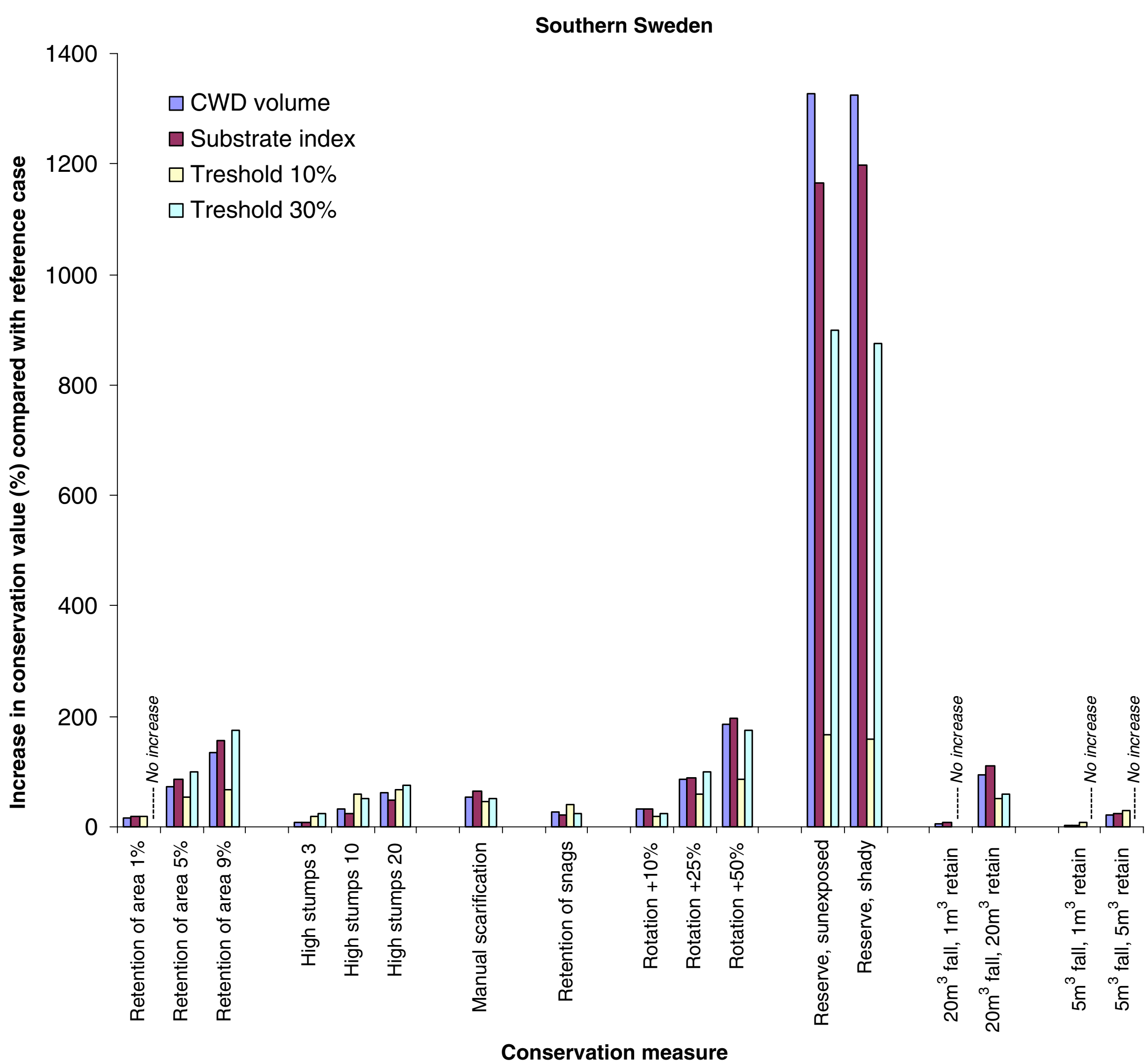

Fig. 3 – Increase in volume of CWD, substrate index and the number of species with more substrate than different threshold levels, following different conservation measures compared with the reference case, i.e. when these measures were not taken. The reference case differs between retention of wind-thrown trees and the other management measures. Measures marked with "No increase" did not lead to any increase in that particular variable. The stands were situated in southern (county of Kronoberg), central (county of Gävleborg) and northern Sweden (county of Västerbotten).

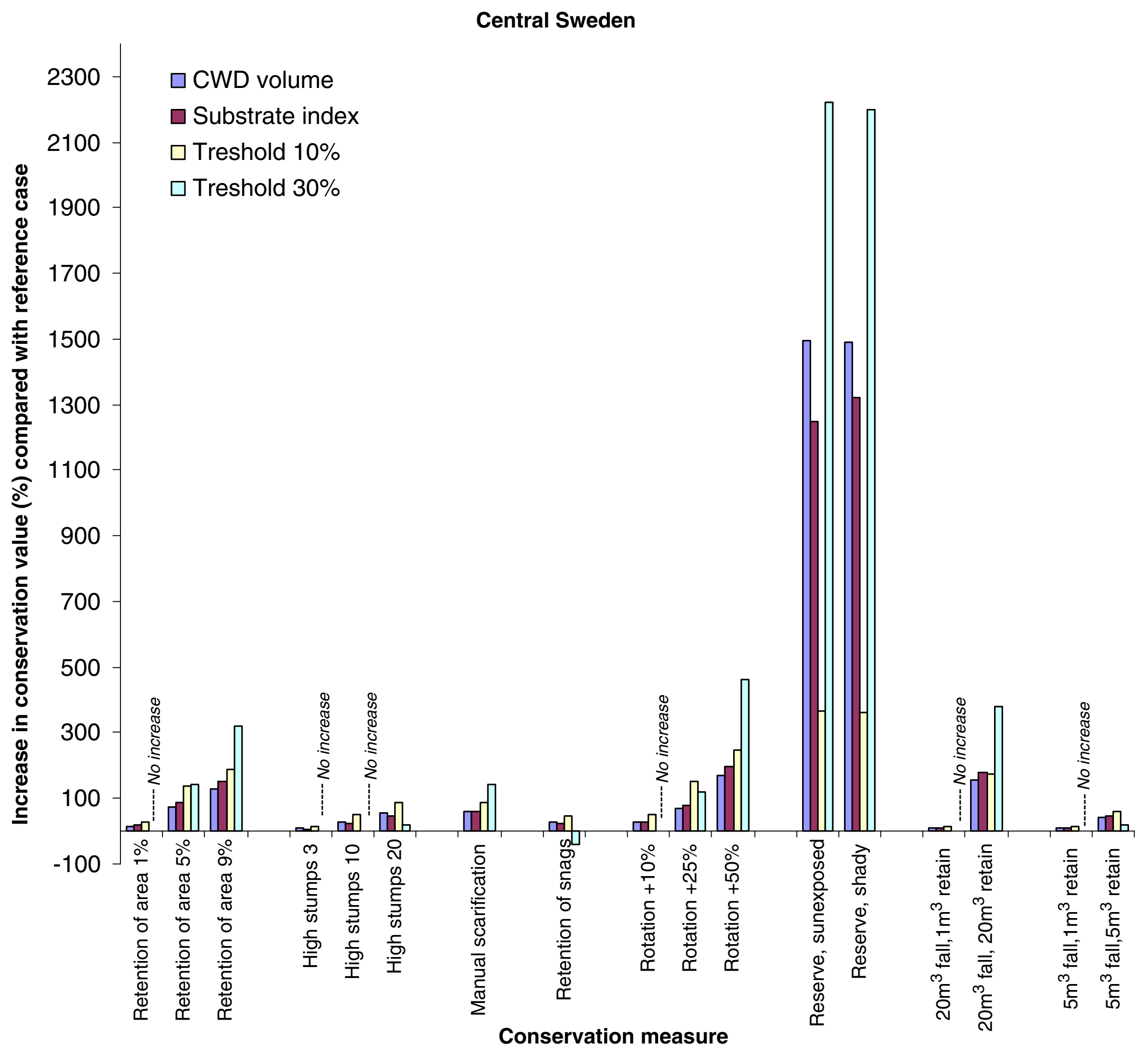

Fig. 3 – *continued*

soil scarification increased the proportion of CWD in late decay stages the most, prolongation of the rotation period increased the proportion of shady CWD the most, and retention of snags increased the proportion of sun-exposed CWD the most (Fig. 4).

3.2. *Cost-effectivity*

The volume of CWD and the substrate index generally ranked the different conservation measures in the same way in terms of cost efficiency. In all regions, the volume of CWD and the substrate index agreed that, in the absence of wind-thrown trees, retention of snags was the most cost-effective measure for biodiversity conservation and that increasing the rotation period was the least cost-effective measure (Fig. 5). Another cost-effective measure in all regions was creation of high stumps (Fig. 5). In northern Sweden, manual soil scarification was almost as cost-effective as creating high stumps whereas it was less cost-effective in the other regions (Fig. 5). Setting aside a reserve was cost-effective in northern Sweden but more expensive towards the south (Fig. 5). Retention of wind-thrown trees when they were available was a cost-effective conservation measure in all regions. In central and northern Sweden this measure resulted in a negative cost, implying that it was cheaper to retain wind-thrown trees than to remove them. In southern Sweden, retention of wind-thrown trees entailed a small cost, but it was still a comparatively cost-effective measure.

Results are partly different for the number of species above certain threshold amounts of suitable substrate compared with volume of CWD and the substrate index. The largest differences were found in central and northern Sweden at the highest threshold levels. Measures only increasing the amount of CWD to a small extent such as retention of snags and creation of a few high stumps did not lead to any, or only a very small, increase in the number of species above the thresholds, making these measures less cost-effective. Instead, measures increasing the amount of CWD to a larger extent such as retaining a large percentage of the forest area and setting aside whole stands as reserves were relatively more cost-effective measures at higher extinction thresholds (Fig. 5, Table 7). In southern Sweden,

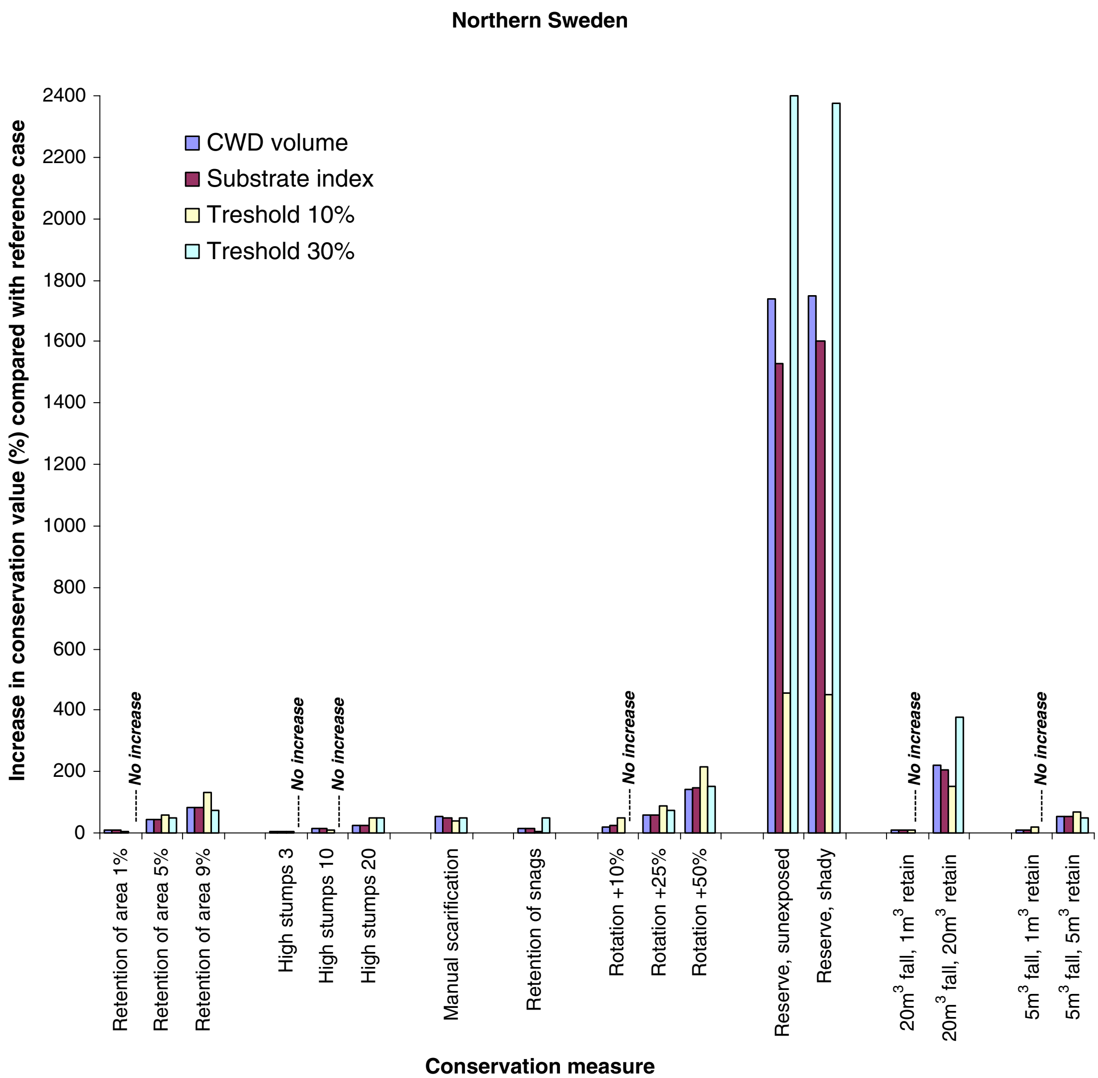

Fig. 3 – *continued*

the difference between the number of species above thresholds and volume CWD and the substrate index was smaller, e.g. retention of snags and creation of high stumps were cost-effective measures and prolongation of the rotation period was relatively expensive (Fig. 5, Table 7). In all regions, different thresholds ranked setting aside the whole stand as a reserve differently. For low threshold levels this measure was rather costly whereas it was more cost-effective at higher threshold levels.

4. Discussion

4.1. *Cost-effectivity*

Our study shows that conclusions concerning cost-effectiveness of different conservation measures depend on the amount of substrate that is needed for the persistence of the species that the measures are intended to conserve. The main reason for this is that several conservation measures do not increase CWD enough to increase the number of species above certain thresholds. In central and northern Sweden, for example, retention of snags and creation of a few high stumps are cost-effective measures when no or low thresholds are considered, but at high thresholds they give no increase in the number of species above the thresholds. Instead, measures resulting in a larger amount of CWD, such as retention of living trees at harvest and setting aside whole stands as reserves become relatively more cost-effective alternatives. This pinpoints the risk that the current conservation strategy in Fennoscandia to spread conservation measures thinly, but evenly over the managed forest area may be inefficient because it produces too little substrate to preserve more demanding red-listed species (Hanski, 2000).

As little is known about the relationship between amount of substrate and extinction risks of saproxylic species it is difficult to say which of our estimates of conservation value is the most appropriate. However, certain patterns of cost-effectiveness are common for many of the estimates. In all regions, creation of high stumps and retention of snags were among the most cost-effective measures, except at high extinction thresholds in central and northern Sweden, where they gave a too small an increase in substrate to increase the number of species above the thresholds. We have only analyzed these measures taken singly but if they are combined with other measures they may contribute also to persistence of species with higher thresholds. We therefore suggest that a cost-effective management program within a managed forest to preserve saproxylic diversity should include retention of snags and creation of high stumps. Creation of high stumps should be conducted at a

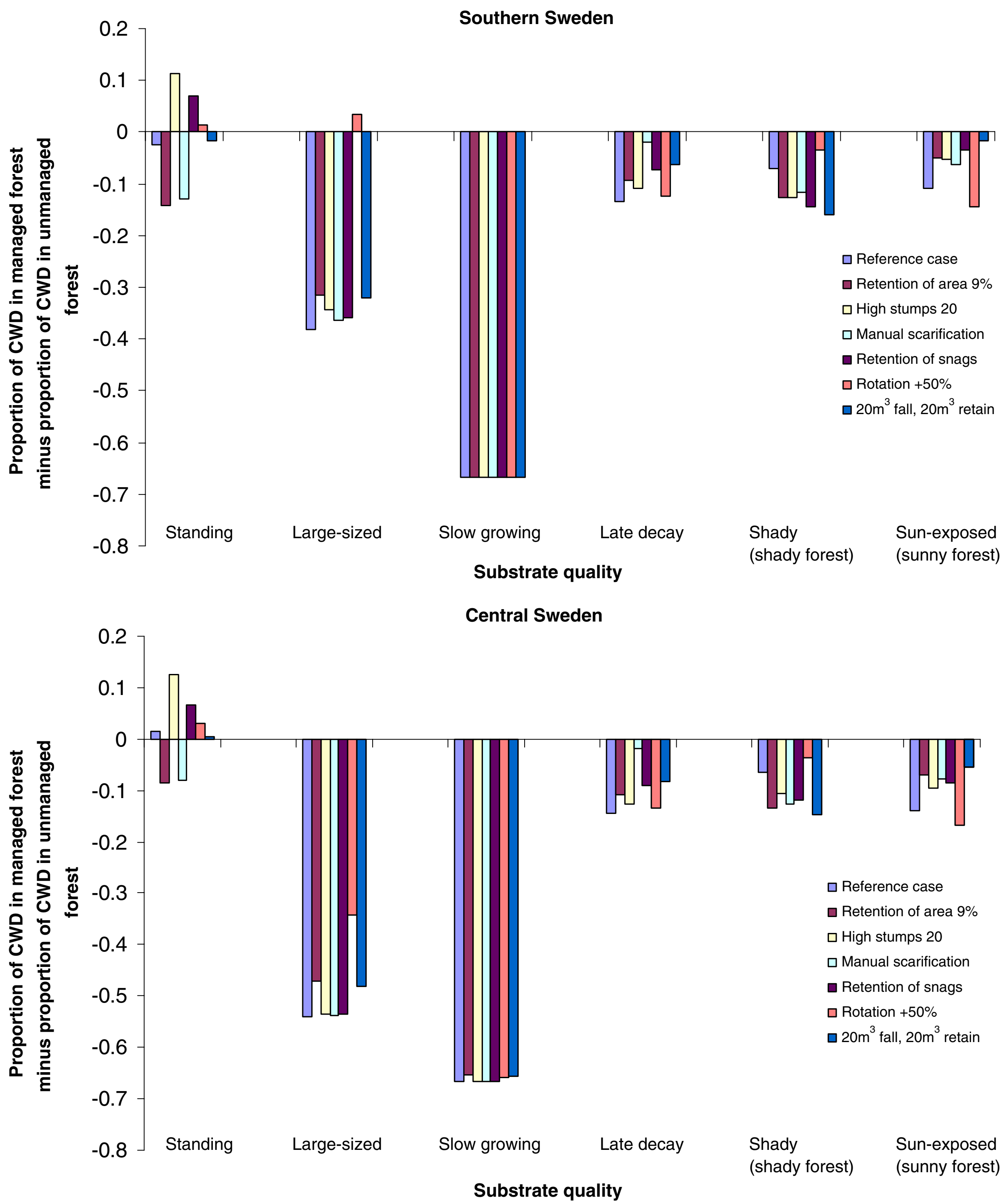

Fig. 4 – Deviation between the proportion of CWD of different substrate qualities at various management scenarios and the proportion of substrate in the same qualities in unmanaged forests. All variables are divided into two categories (small-sized = 10–30 cm, large-sized = >30 cm; slow grown = categories 1–2, fast growing = categories 3–4; early decay = stages 1–4, late decay = stages 5–8; sun-exposed = categories 1–2, shady = categories 3–4) with the deviation in proportions shown for one of them. For light regime, the proportions are compared with two types of unmanaged forests: one more sun-exposed (large scaled disturbance regime) and one shady (small scaled disturbance regime). For the other measures comparisons are with average proportions of the two forest types. The stands were situated in southern (county of Kronoberg), central (county of Gävleborg) and northern Sweden (county of Västerbotten).

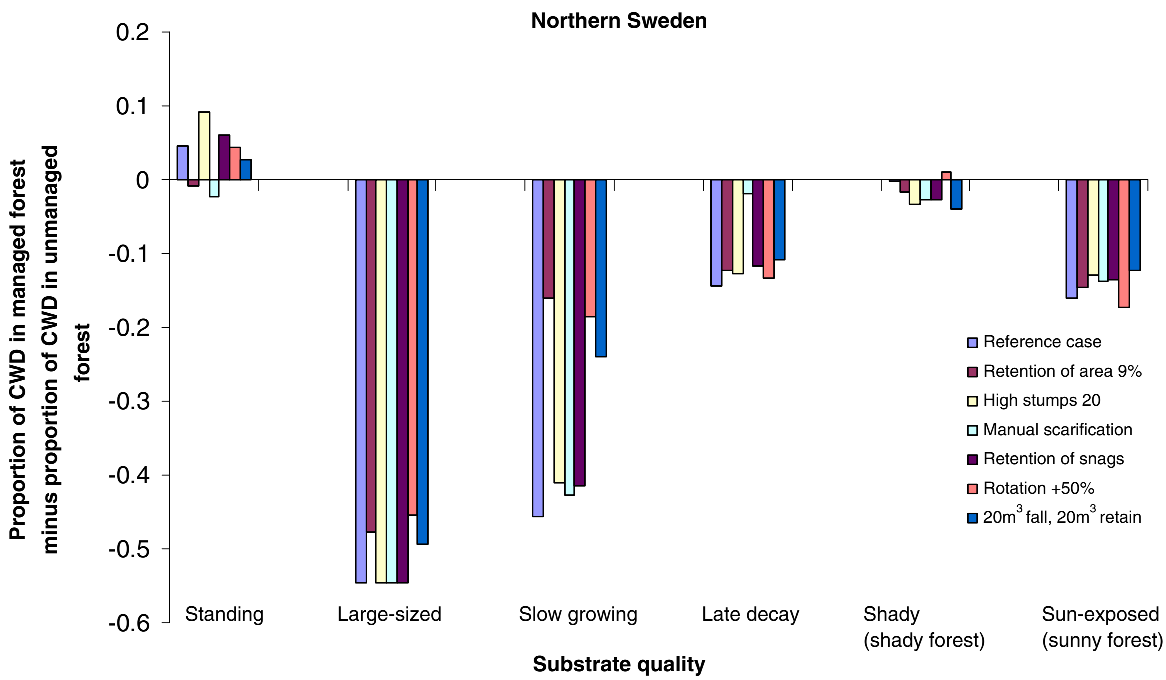

Fig. 4 – *continued*

high intensity (Ranius et al., 2005), however creation of more than 20 high stumps/ha may entail new costs as accessibility for forest machines may decrease.

At occasions with high tree mortality it is cost-effective to retain trees that have fallen, particularly in central and northern Sweden, where such a measure even entails a small benefit (Ranius et al., 2005). According to our calculations it would be most cost-effective to retain as many as possible of the trees that have fallen. However, we have not taken into account any cost associated with increased risks of attacks by bark beetles, mainly *Ips typographus* (L.), that develop in newly dead spruce trees. For volumes of newly formed conifer CWD up to 5 m^3/ha the risk of bark beetle attack is not expected to increase much (Hedgren et al., 2003), but no studies have been conducted using higher volumes of CWD. Thus, we do not know to what extent our conclusion that retention of newly formed CWD after occasions of high natural mortality is cost-effective is valid when more than 5 m^3/ha of conifer CWD is left in the forest.

In managed forests large diameter trees are rare (Siitonen, 2001), CWD from slow grown trees are virtually absent (Ehnström, 2001), and a somewhat lower proportion of the CWD belongs to late decay stages in managed forests compared with in unmanaged ones. Thus, species specialised on these types of substrate will be particularly vulnerable in managed forests, and may need special efforts to avoid extinction. Some of the conservation measures that were analyzed increased the proportion of these substrate types. Manual soil scarification increased CWD in late decay stages and retention of living trees at harvest slightly increased the proportion of large diameter CWD and gave more slow grown trees in northern Sweden. Consequently, these measures should be included in a management program that aims to preserve species associated with substrates that are particularly rare in managed forests. Another measure increasing the amount of otherwise scarce substrate types is prolongation of the rotation period. This measure increased the amount of large diameter CWD, particularly in southern Sweden, and it also increased the amount of slow-growing CWD in northern Sweden. In addition, prolongation of the rotation period will benefit species requiring a shady environment. Thus, our study supports the view that increased rotation will benefit species associated with late successional stages that may find little substrate in managed forests (Martikainen et al., 2000). However, in all regions creation of reserves was a more cost-effective measure than increasing the rotation period. Thus preservation of species associated with late successional stages is probably more cost-effectively performed within reserves.

Our study revealed significant differences in cost-effectiveness among conservation measures between geographic regions. The cost of setting aside reserves is rather low in northern Sweden, mainly because low productivity makes land inexpensive. Therefore, setting aside stands as reserves is a cost-effective measure in this region. This is also reflected in the current distribution of protected forestland in Sweden, which is skewed towards Norway spruce forests in northwestern Sweden (Fridman, 2000). In central and southern Sweden on the other hand, productivity and thus also land prices are higher, which makes setting aside reserves a more costly alternative. It is worth noting however, that here we predict the amount of CWD present in forests that have been managed in the same way for a long time, and we do not take into account any transition states between management regimes, for volume and quality of CWD. For most of the measures taken within managed forests this time period will be rather short, whereas transition from a mature managed

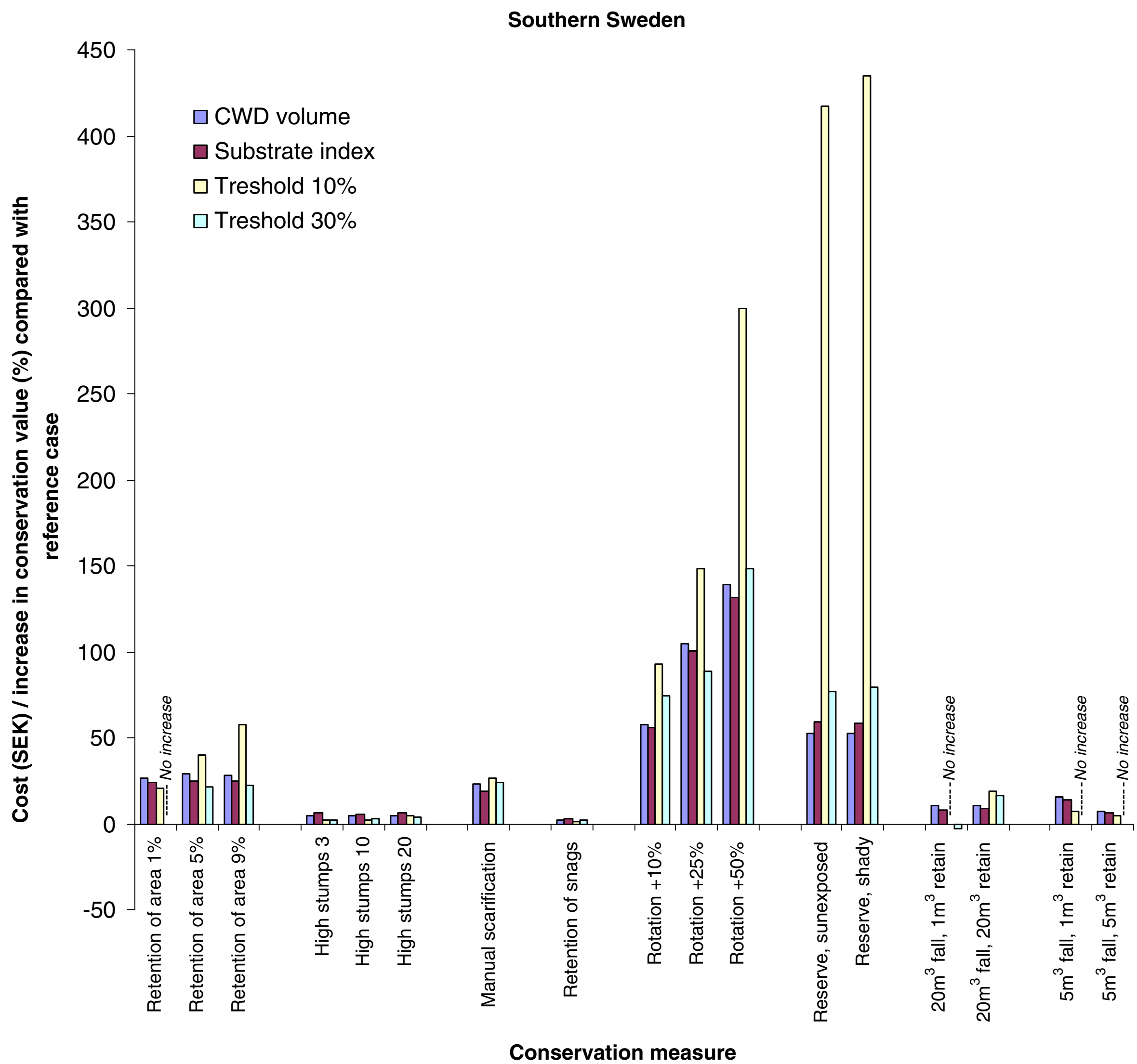

Fig. 5 – Inverted cost-effectiveness of different measures to increase the amount of substrate for red-listed saproxylic species in Sweden. Cost (i.e. decrease in present value at the time of decision, SEK/ha, assuming a discount rate of 3%) divided by the increase in the volume of CWD, substrate index or the number of species with more substrate than different threshold levels. Measures marked with "No increase" did not lead to any increase in that particular variable. The stands were situated in southern (county of Kronoberg), central (county of Gävleborg) and northern Sweden (county of Västerbotten).

forest to an unmanaged forest will take a considerably longer time as long as CWD is not actively generated in them, which would generate costs we have not taken into consideration. This tends to generate an overestimate of the cost-effectiveness of setting aside forest stands as reserves compared with the other measures. The selection of stands to set aside as reserves is important for cost-effectiveness (Juutinen et al., 2004; Juutinen and Mönkkönen, 2004); to choose stands that already host populations of red-listed species (Huxel and Hastings, 1999) or are located close enough to such populations to allow colonisation will make it more effective. In contrast, there are small possibilities to apply conservation measures close to red-listed species when the conservation measures comprise changes in silvicultural measures that are supposed to be applied at a similar intensity throughout the forest land, as they are in Sweden in Finland. Because we do not take the spatial distribution of red-listed species into account in this study, we will tend to underestimate the cost-effectiveness of setting aside forest stands as reserves compared with the other measures.

4.2. *Conclusions and limitations of the study*

Our study shows that a conservation strategy based on a few standard rules applied in the same way over all Swedish managed forests is ineffective from an economic point of view. To be cost-effective, the focus should be on different types of conservation measures in different parts of Sweden. In northern Sweden it is more cost-effective to concentrate on setting aside forest instead of biodiversity-oriented forest management, whereas in central and southern Sweden measures to preserve biodiversity within production stands

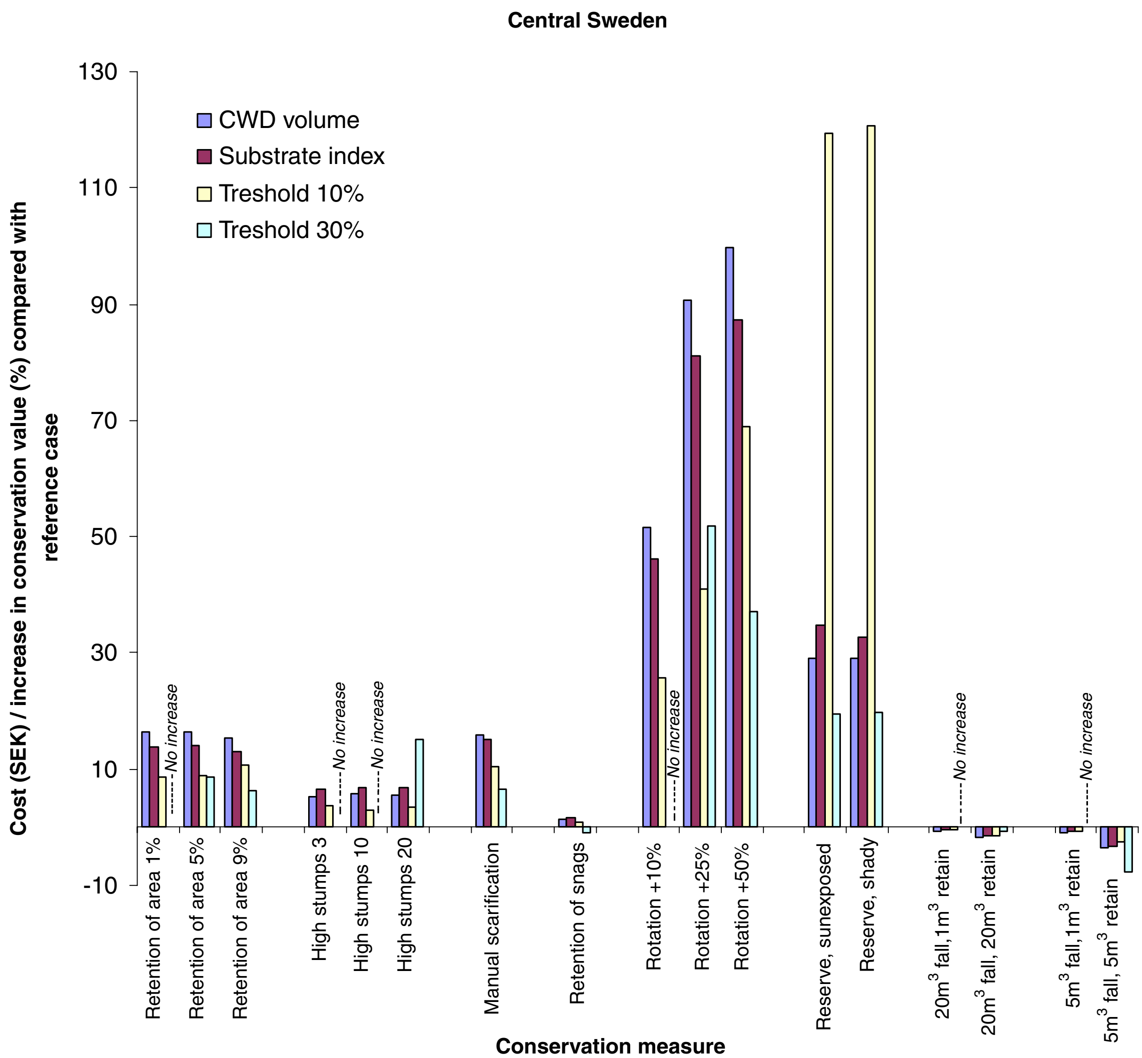

Fig. 5 – *continued*

are cost-effective alternatives. When applied, the recommendations by FSC can also be made more cost-effective. Above all, creation of around 3 high stumps/ha, which is now the norm in forest certified by FSC, is too little (Ranius et al., 2005). This is a cost-effective measure that could be applied at a much higher intensity than today. Retention of newly dead CWD after occasions of high tree mortality is another measure that could be applied to a larger extent than prescribed by FSC today (Ranius et al., 2005). Manual soil scarification and retention of living trees at harvest are also relevant measures because they increase the amount of certain substrate types that are underrepresented in managed forests.

We have only analyzed one forest stand typical for each region. In a real forest landscape, there may be a large variability between stands for factors influencing cost-effectiveness, e.g. tree species composition, site index and distance to the forest road. Therefore, conservation strategies in forest landscapes may need a small-scale, site-specific approach where varying measures are applied in different stands.

The quality of the output from models always relies on the quality of the input data. Little or no quantitative data exists for some parameters that are used in our models, e.g. degree of sun-exposure at different forest ages and geographic locations, natural mortality in relation to forest management and duration of snags. This will affect the reliability of our results. However, we consider the limited knowledge about the demands of the red-listed species as the main source of uncertainty in the present study. Present knowledge is still mainly based on the experience of experts and only to a minor degree on quantitative data. There is, for example, virtually no quantitative data available on species preferences for dead wood resulting from trees with different growth rates. Furthermore, we here assume that the substrate preferences for each species are the same between regions although in reality they may differ geographically. Our conclusions concerning cost-effectiveness depend on our assumptions about the level of the extinction thresholds for which no empirical data are available. The spatial scale at which thresholds occur is also important. We assume here that extinction thresholds are operating at a large scale

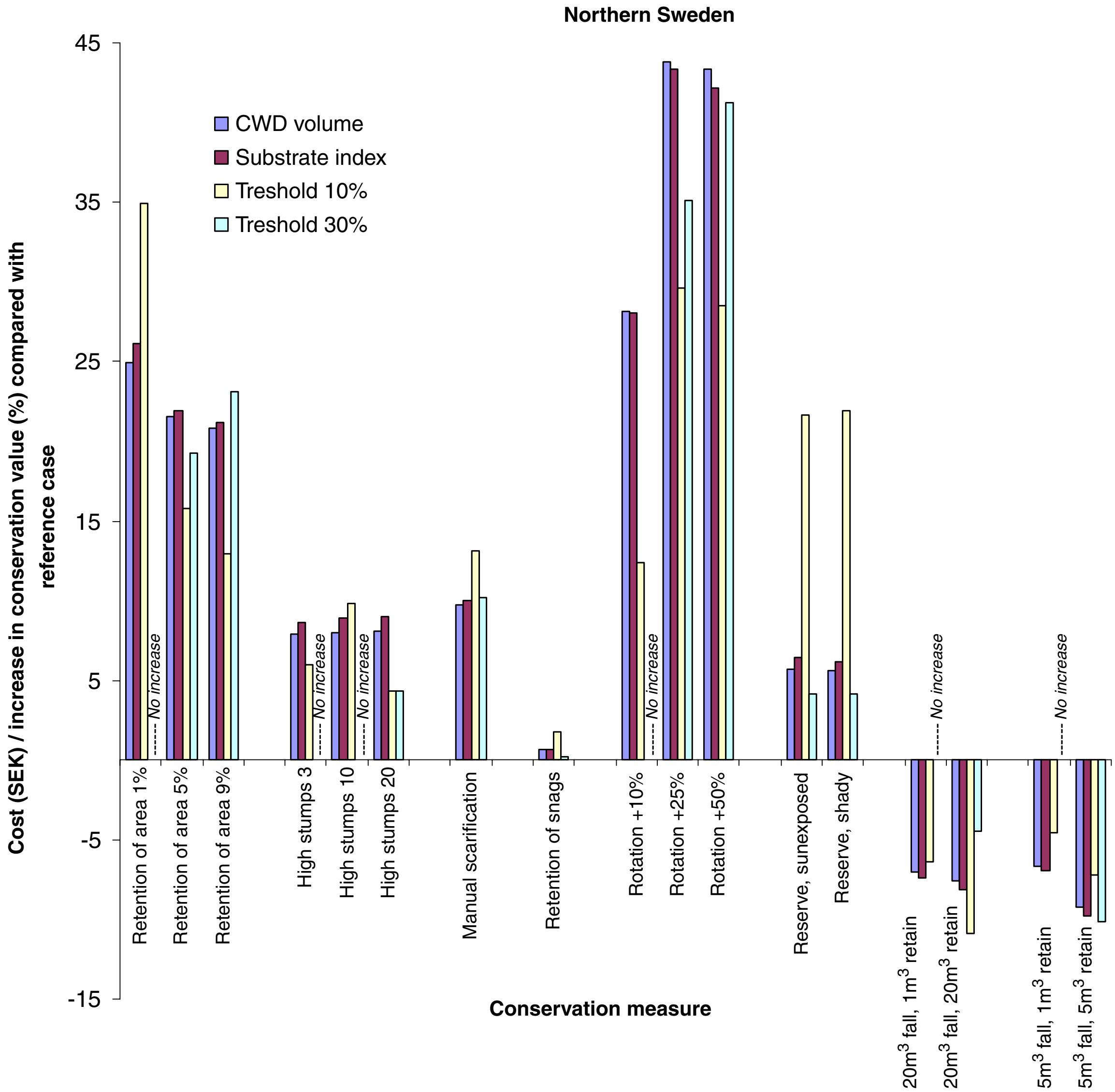

Fig. 5 – *continued*

where several forest stands in different ages are present. Only then do our average values of substrate amounts for whole rotation periods make any sense. If thresholds are operating at a smaller scale, the temporal variation in CWD amounts must be considered.

Acknowledgements

Support for this project came from the project "Cost-efficiency of a biodiversity-oriented forestry" financed by The Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS), by the Oscar and Lili Lamm Memorial Foundation, and from the project "Conservation of Biodiversity in Managed Forests" financed by the Faculty of Forestry at the Swedish University of Agricultural Sciences (SLU). Tomas Hallingbäck, Göran Thor, Karl-Henrik Larsson, Malte Edman, and Oskar Kindvall are thanked for invaluable help with the database for red-listed species. Barbara Ekbom and two anonymous reviewers provided valuable comments on the manuscript.

REFERENCES

Anon., 1988. Beståndsmetoden för skogsvärdering. Rapport 1988: 1–3, National Land Survey of Sweden, Gävle, Sweden (in Swedish).
Anon., 1999. Miljökvalitetsmål 8: Levande skogar. National Board of Forestry, Jönköping, Sweden (in Swedish).
Anon., 2000. Svensk FSC-standard för certifiering av skogsbruk. Svenska FSC-rådet, Uppsala, Sweden (in Swedish).
Anon., 2001. Regeringens proposition 2000/01:130. Svenska miljömål – delmål och åtgärdsstrategier. Miljödepartementet Stockholm, Sweden (in Swedish).
Bader, P., Jansson, S., Jonsson, B.G., 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biological Conservation 72, 355–362.
Balmford, A., Bruner, A., Cooper, P., Costanza, R., Farber, S., Green, R.E., Jenkins, M., Jefferiss, P., Jessamy, V., Madden, J., Munro, K., Myers, N., Naeem, S., Paavola, J., Rayment, M., Rosendo, S.,

Roughgarden, Trumper, K., Turner, K., 2002. Economic reasons for conserving wild nature. Science 297, 950–953.
Bascompte, J., Solé, R.V., 1996. Habitat fragmentation and extinction thresholds in spatially explicit models. Journal of Animal Ecology 65, 465–473.
Berg, Å., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M., Weslien, J., 1994. Threatened plant, animal and fungus species in Swedish forests: distribution and habitat associations. Conservation Biology 8, 718–731.
Carlén, O., Mattsson, L., Atlegrim, O., Sjöberg, K., 1999. Cost efficiency in pursuing environmental objectives in forestry. Journal of Environmental Management 55, 111–125.
Dahlberg, A., Stokland, J.N., 2004. Vedlevande arters krav på substrat. Rapport No. 7. Skogsstyrelsen, Jönköping (in Swedish).
Ehnström, B., 2001. Leaving dead wood for insects in boreal forests – suggestions for the future. Scandinavian Journal of Forest Research (Suppl. 3), 91–98.
Ekvall, H., 2001. Plan 33 – Ett verktyg för ekonomisk analys av skogsbruksföretagets virkesproduktion. Licentiate thesis Report No. 123, Dept. of Forest Economics, Swedish University of Agricultural Sciences, Umeå (in Swedish, English abstract).
Esseen, P.A., 1994. Tree mortality patterns after experimental fragmentation of an old-growth conifer forest. Biological Conservation 68, 19–28.
Fahrig, L., 2001. How much habitat is enough? Biological Conservation 100, 65–74.
Fridman, J., 2000. Conservation of forest in Sweden: a strategic ecological analysis. Biological Conservation 96, 95–103.
Fridman, J., Walheim, M., 2000. Amount, structure and dynamics of dead wood on managed forestland in Sweden. Forest Ecology and Management 131, 23–26.
Gärdenfors, U. (Ed.), 2000. The 2000 Red-List of Swedish Species. Artdatabanken, Swedish University of Agricultural Sciences, Uppsala.
Grove, S.J., 2002. Saproxylic insect ecology and the sustainable management of forests. Annual Review of Ecology and Systematics 33, 1–23.
Hanski, I., 2000. Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. Annales Zoologici Fennici 37, 271–280.
Hanski, I., Hammond, P., 1995. Biodiversity in boreal forests. Trends in Ecology and Evolution 10, 5–6.
Hautala, H., Jalonen, J., Laaka-Lindberg, S., Vanha-Majamaa, I., 2004. Impacts of retention felling on coarse woody debris (CWD) in mature boreal spruce forests in Finland. Biodiversity and Conservation 13, 1541–1554.
Hedgren, P.O., Schroeder, L.M., Weslien, J., 2003. Tree killing by *Ips typographus* (Coleoptera: Scolytidae) at stand edges with and without colonized felled spruce trees. Agricultural and Forest Entomology 5, 67–74.
Huxel, G.R., Hastings, A., 1999. Habitat loss, fragmentation, and restoration. Restoration Ecology 7, 309–315.
IUCN, 2001. 2001 IUCN Red List Categories and Criteria version 3.1. IUCN Species Survival Commission. IUCN, Gland, Switzerland, Cambridge, UK.
Jonsell, M., Weslien, J., 2003. Felled or standing retained wood – it makes a difference for saproxylic beetles. Forest Ecology and Management 175, 425–435.
Jonsell, M., Weslien, J., Ehnström, B., 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity and Conservation 7, 749–764.
Jonsell, M., Nittérus, K., Stighäll, K., 2004. Saproxylic beetles in natural and man-made deciduous high stumps retained for conservation. Biological Conservation 118, 163–173.
Juutinen, A., Mönkkönen, M., 2004. Testing alternative indicators for biodiversity conservation in old-growth boreal forests: ecology and economics. Ecological Economics 50, 35–48.
Juutinen, A., Mäntymaa, E., Mönkkönen, M., Salmi, J., 2004. A cost-efficient approach to selecting forest stands for conserving species: a case study from northern Fennoscandia. Forest Science 50, 527–539.
Krankina, O.N., Harmon, M.E., 1995. Dynamics of the dead wood carbon pool in north western Russian boreal forests. Water, Air and Soil Pollution 82, 227–238.
Kruys, N., Wikström, P., 2001. Optimising uneven-aged management for economic efficiency and occurrence of wood-inhabiting species. In: Kruys, N., Bryophytes and Fungi on Dead Spruce: Integrating Conservation with Forest Planning. Dissertation, Department of Ecology and Environmental Science, Umeå University, Umeå.
Kurttila, M., Pukkala, T., 2003. Combining holding-level economic goals with spatial landscape-level goals in the planning of multiple ownership forestry. Landscape Ecology 18, 529–541.
Lande, R., 1987. Extinction thresholds in demographic models of territorial populations. American Naturalist 130, 624–635.
Larsson, S., Danell, K., 2001. Science and the management of boreal forest biodiversity. Scandinavian Journal of Forest Research (Suppl. 3), 5–9.
Lindenmayer, D.B., Franklin, J.F., 2002. Conserving Forest Biodiversity. A Comprehensive Multiscaled Approach. Island press, Washington.
Lindhe, A., Lindelöw, Å., 2004. Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. Forest Ecology and Management 203, 1–20.
Lindhe, A., Åsenblad, N., Toresson, H.-G., 2004. Cut logs and high stumps of spruce, birch, aspen and oak – nine years of saproxylic fungi succession. Biological Conservation 119, 443–454.
Lõhmus, P., Lõhmus, A., 2001. Snags, and their lichen flora in old Estonian peatland forests. Annales Botanici Fennici 38, 265–280.
Lundblad, I., 1998. Wood-inhabiting fungi on fallen logs of Norway spruce: relations to forest management and substrate quality. Nordic Journal of Botany 18, 343–355.
Martikainen, P., 2001. Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clearcut areas. Ecological Bulletins 49, 205–218.
Martikainen, P., Siitonen, J., Punttila, P., Kaila, L., Rauh, J., 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biological Conservation 94, 199–209.
Nordén, B., Ryberg, M., Götmark, F., Olausson, B., 2004. Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. Biological Conservation 117, 1–10.
Økland, B., Bakke, A., Hågvar, S., Kvamme, T., 1996. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodiversity and Conservation 5, 75–100.
Raivio, S., Normark, E., Pettersson, B., Salpakivi-Salomaa, P., 2001. Science and the management of boreal forest biodiversity – a forest industries' view. Scandinavian Journal of Forest Research (Suppl. 3), 99–104.
Ranius, T., 2002. Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. Biological Conservation 103, 85–91.
Ranius, T., Jansson, N., 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. Biological Conservation 95, 85–94.
Ranius, T., Kindvall, O., Kruys, N., Jonsson, B.G., 2003. Modelling dead wood in Norway spruce stands subject to different management regimes. Forest Ecology and Management 182, 13–29.
Ranius, T., Jonsson, B.G., Kruys, N., 2004. Modelling dead wood in Fennoscandian old-growth forests dominated by Norway spruce. Canadian Journal of Forest Research 34, 1025–1034.

Ranius, T., Ekvall, H., Jonsson, M., Bostedt, G., 2005. Cost efficiency of measures to increase the amount of coarse woody debris in managed Norway spruce forests. Forest Ecology and Management 206, 119–133.
Rassi, P., Mannerkoski, I., Peltonen, S.-L., Alanen, A., 2000. 2nd Red Data Book of Finland. Ministry of Environment, Helsinki.
Schroeder, L.M., Lindelöw, Å., 2002. Attacks on living spruce trees by the bark beetle *Ips typographus* (Col.: Scolytidae) following a storm-felling: a comparison between stands with and without removal of wind-felled trees. Agricultural and Forest Entomology 4, 47–56.
Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49, 11–41.
Similä, M., Kouki, J., Martikainen, P., 2003. Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. Forest Ecology and Management 174, 365–381.
Söderström, L., 1988. Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in northern Sweden. Nordic Journal of Botany 8, 89–97.
Speight, M.C.D., 1989. Saproxylic Invertebrates and Their Conservation. Council of Europe, Strasbourg.
Stokland, J.N., Tomter, S., Söderberg, U., 2004. Development of dead wood indicators for biodiversity monitoring: experiences from Scandinavia. In: Marchetti, M. (Ed.), Proceedings of the IUFRO Conference on Monitoring and Indicators of Forest Biodiversity in Europe – From Ideas to Operationality. EFI Proceedings 51, 207–226.
Storaunet, K.O., Rolstad, J., 2002. Time since death and fall of Norway spruce logs in old-growth, selectively cut boreal forest. Canadian Journal of Forest Research 32, 1801–1812.
Törlind, Å., 1998. Markägares hantering av vindfällen I samband med slutavverkning. En studie i Norduppland. Department of Silviculture, Swedish University of Agricultural Sciences, Umeå (in Swedish, English summary).
Wikström, P., Eriksson, L.-O., 2000. Solving the stand management problem under biodiversity-related considerations. Forest Ecology and Management 126, 361–376.
With, K.A., King, A.W., 1999. Extinction thresholds for species in fractal landscapes. Conservation Biology 13, 314–326.