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REVIEW ARTICLE

Tree retention as a conservation measure in clear-cut forests of northern Europe: a review of ecological consequences

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Abstract

Since the mid-1990s, it has been common practice to leave trees for biodiversity purposes when clear-cutting in Finland, Norway and Sweden, and regulations for such tree retention are today included in national legislation and certification standards. Peer-reviewed research publications on tree retention from studies performed in the three countries were analyzed and about 50 relevant biodiversity studies were found, with the first published in 1994. Most studies were directed towards beetles and dead wood, especially high stumps. General conclusions were that retention trees (1) provide some of the substrate types required by early-successional species, (2) alleviate the most serious consequences of clear-cutting on biota, and (3) cannot maintain characteristics of intact mature forests. Larger volumes and more trees tend to maintain diversity better. There is a particular lack of studies on dispersal, landscape effects and long-term dynamics. There is a need to study further the relationship between the biota and the amount of trees, as well as their spatial arrangement. Retention trees should preferably be evaluated in relation to other components in multiscaled conservation, including woodland key habitats and larger protected areas.

Keywords: *biodiversity, conservation concern, dead wood, green-tree retention, high stump, multiscaled, variable retention.*

Introduction

The most common way to preserve forest has been to set aside land as national parks and nature reserves. According to a recent global analysis, 7.7% of the global forest area is designated to conservation in the International Union for Conservation of Nature (IUCN) classes I–IV (Schmitt et al., 2009). This is considered to be insufficient to protect forest biodiversity, and especially so in regions that fall below the global average. In many countries, complementary conservation methods have been introduced recently. A few decades ago, a new direction was taken, with integration of conservation measures into production forests with the main aim to promote biodiversity, and is practised today in North America, Australia and northern Europe (Lindenmayer & Franklin, 2003).

A fundamental component of this activity, which is foremost associated with clear-cutting forestry, is to leave trees of importance to flora and fauna at logging. Such "tree retention" (synonyms include green tree retention, variable retention and retention felling) aims to reduce the intensity of timber harvest during the clear-cutting, by leaving single trees, tree groups, buffer zones bordering lakes, watercourses and mires, and also by saving and creating dead wood. Three important functions of tree retention are: (1) "lifeboating" of species over the regeneration phase; (2) increasing structural variation in the developing stand; and (3) enhancing connectivity in the forest landscape (Franklin et al., 1997). Two additional functions are (4) promoting species linked to dead wood and live trees in early successional environments; and (5) sustaining ecosystem functions (herbivory, nitrogen retention, productivity, etc.). Today, integration of different ecosystem services on the same land, including biodiversity, is a recommended strategy for sustainable land use (Millennium Ecosystem Assessment, 2005).

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Finland, Norway and Sweden are forest-dominated countries, with 58% of the total land area of 1.02 million km^2 covered with forests (FAO, 2006), situated mainly within the boreal and hemiboreal forest biomes (Ahti et al., 1968), between latitudes 55 and 70°N, in northern Europe. Ownership is 76% private and 24% public. Since the 1950s, large-scale, mechanized logging operations have been practised, and today more than 90% of all productive forestland in Finland and Sweden is intensively managed using the single-cohort stands and clear-cutting harvest system. Forest use is more moderate in Norway, which is reflected in a smaller proportion of the annual increment felled, approximately 45%, compared with about 70% and 85%, respectively, for Finland and Sweden (MCPFE, 2007). The area of plantations with exotic tree species is very small, and forests are regenerated instead mainly with the indigenous *Picea abies* (L.) Karst. and *Pinus sylvestris* L., with rotation times between 60 and 100 years. Soil scarification is carried out in most regeneration sites in Finland, in more than 40% in Sweden but in less than 15% of the regeneration sites in Norway (Stokland et al., 2003). Overall, Finland, Norway and Sweden are the countries in boreal and hemiboreal regions in the most advanced stage of forest transition (*sensu* Mather, 1992), with only small remnants of natural forest left (Bryant et al., 1997).

The current intensive management has been applied in Finland, Norway and Sweden only for the past 50–100 years, but it has quickly resulted in structurally simplified production forests, with almost even age-class distribution and a lack of old, dead and deciduous trees compared with intact forests (Esseen et al., 1997; Kouki et al., 2001; Siitonen, 2001). This has contributed to species decline, and today about 2100 forest species are on the red list in Sweden and about 1200 in both Finland and Norway (Rassi et al., 2001; Kålås et al., 2006; Gärdenfors et al., 2010).

Only a small proportion of the forest area (5% at most) is protected in these countries, with set-asides often located in low productive sites in the northern and middle boreal zones (Fridman, 2000; Virkkala & Rajasärkkä, 2007).

In Finland, Norway and Sweden, efforts to integrate biodiversity concern with forest management can be traced back to the late 1970s (e.g. Eckerberg, 1986). In all three countries, legislation and forest management guidelines were revised during the 1980s and 1990s, and forest certification systems were developed in the 1990s, including guidelines on set-asides (Norway, Sweden) and tree retention (all three countries). Today, both legislation and forest certification systems regulate biodiversity actions. All three countries have Forestry Acts focusing on sustainable management of forest resources, promoting both economic development and considerations for biological diversity, although details vary (Table I).

The forest certification systems are also somewhat different in the three countries. Two main certification systems are in use, either national systems endorsed by the Programme for the Endorsement of Forest Certification (PEFC), or permanent or interim national level standards managed by the Forest Stewardship Council (FSC). Both certification systems aim to promote economic, social and environmental management of forests, but with differences in emphasis. In Sweden, slightly more productive forest land (10 million ha) is certified through the FSC system than the PEFC system (8 million ha). In Finland and Norway, in contrast, national systems endorsed by PEFC dominate, and only small forest areas are certified by FSC (Table I).

Some differences in the regulations that apply to retention can be seen between the countries. In Finland, the minimum number of retention trees to be left in clear-cuts is five per hectare, while in Sweden and Norway it is 10 per hectare. The minimum diameter of possible retention trees is lower in Finland (10 cm diameter at breast height (dbh)) than in Norway (20 cm dbh), while the Swedish standard does not give a minimum diameter. In Finland, retention trees can be either dead or alive, in Norway created high stumps and some dead spruce (maximum 50%) can be counted as retention trees, while in Sweden they should be alive. Creation of high stumps (or girdled trees) is a necessary requirement in Sweden, but is not mentioned or widely applied in the Finnish standard, while in Norway creation of high stumps is only presented as an alternative for trees susceptible to storm felling. In the Swedish system, retention of patches is described specifically, while in the Norwegian system this is not the case. The Swedish and Norwegian standards include retention of buffer zones adjacent to natural water courses and water bodies (riparian zones) as well as on the border of cultural landscapes (default width 10–15 m in Norway). In Finland, protection of stream sites (including a buffer) is part of the Forestry Law rather than certification, where only marginal buffers are required close to water bodies. All three countries have monitoring systems organized by the state and/or by the certification bodies, to follow up the practice of the regulations. Comparing the results between countries is not feasible, as the details of monitoring systems differ. In addition, in Finland and Norway, the monitoring parameters are only qualitative (degree of compliance), not quantitative, while in Sweden they are both qualitative and quantitative (Table I).

Table I. Legislation and certification regulations relating to tree retention in Finland, Norway and Sweden.

Legislation	
Finland	No special requirements for retention trees. Forestry Act lists seven key habitats (mostly <1 ha) where main habitat characteristics must remain; Nature Conservation Act regulates some additional key habitats, including large, solitary trees.
Norway	Leave at least five retention trees per hectare, preferably in groups. Key habitats must be safeguarded. The ecological function of transition zones along waterways, and between forest and other land, must be ensured.
Sweden	Older trees must be left standing on felling sites, preferably in groups. Protective buffer zones must be left adjacent to water, etc. No logging on non-productive forest land. Avoid damaging sensitive habitats and sites with rich flora and fauna.
Certification FSC	
Finland	FSC Working Group in place and a national standard approved with conditions. Only very little (10,000 ha) FSC-certified forest (2008). (www.finland.fsc.org)
Norway	No Norwegian FSC Standard yet (in process), but one group certification unit (71,500 ha) with provisional arrangements[a] (B. M. Eidahl, personal communication). Retention levels follow the Living Forest Standard (see below, under PEFC Norway).
Sweden	10 million ha certified (45% of productive forest land).[a] Retain all snags, windthrows and other trees that have been dead for more than a year plus all such dead wood originating from high biodiversity trees that have been dead for less than a year. Retain retention trees in a way that they will amount to at least 10 old, large, live trees in the next forest generation; prioritize high biodiversity value trees. Create at least three high stumps or girdled trees per hectare. Retain care-demanding patches, edge zones, groups of trees and biodiversity value trees. (www.fsc-sweden.org)
Certification PEFC	
Finland	21.9 million ha is certified (at the end of 2008, mainly group certification) out of 23 million ha. Based on the national Finnish Forest Certification System (FFCS). Leave snags, windfalls and at least five retention trees (minimum 10 cm dbh) per hectare, including trees with high biodiversity value. Leave buffer zone along water, at least 3–5 m (careful logging allowed). (www.pefc.fi)
Norway	7.5 million ha certified (mainly group certification) (www.pefcnorge.org) out of 7.4 million ha productive forest land (12 million ha forested land in total). Based on the national Living Forest Standard (Living Forest 2007), combined with ISO 14001 or EMAS: Leave on average 10 retention trees per hectare (minimum 20 cm dbh), including trees with high biodiversity value. If risk of windthrows, high stumps of spruce and aspen may be created and counted. Leave standing dead deciduous trees, large dead pines and natural high stumps of all tree species. Leave downed coarse woody debris older than 5 years.
Sweden	8 million ha certified (37% of productive forestland).[a] Should be set aside: live conservation trees (deviating, old, large-diameter, deciduous trees, hollow trees, etc.) in a way that they amount to 10 retention trees per hectare, some created high stumps per hectare, some representative logs per hectare, retention patches, and protective zones to sensitive habitats. (www-pefc.se)
Monitoring	
Finland	National Forest Inventory surveys a network of permanent plots every ~10 years, focusing on economically valuable timber. Dead wood and woodland key habitats are included in the recent surveys, but retention trees are not separated. Forest enterprises, Metsähallitus (administrator of the public land) and private forest owners association monitor a sample of clear-cuts annually. Notes on retention trees and other environmental issues are taken. Unprocessed raw data are not usually available.
Norway	The Norwegian National Forest Inventory survey parameters related to productivity and environmental concern on 12,700 permanent plots on a 5-year rotation basis, including occurrence of certain habitats important for biodiversity, retention trees and retention in the form of riparian buffer zones. In addition, the Norwegian Agricultural Authority (SLF) is responsible for an annual county-wise survey of regeneration and environment (retention trees, riparian buffer zones) on a number of randomly selected clear-cuts.
Sweden	The Swedish Forest Agency in its monitoring programme Polytax surveys a number of randomly selected clear-cuts each year regarding compliance with the law regarding environmental concern, including tree retention. This is done qualitatively as well as quantitatively.

Note: FSC = Forest Stewardship Council; PEFC = Programme for the Endorsement of Forest Certification; dbh = diameter at breast height.
[a] Several properties are certified according to FSC and PEFC, i.e. it is not possible to sum area information from FSC and PEFC.

When tree retention was introduced, its effects in alleviating negative ecological consequences of clear-cutting were rather speculative. Since its introduction, research has accumulated quickly, especially during the past few years. This article summarizes the research conducted so far on tree retention in Finland, Norway and Sweden, targeting terrestrial habitats. The focus is on biodiversity and structural habitats, with less emphasis given to aspects of cost-efficiency and ecosystem functions. Important future research directions are also identified.

Materials and methods

Literature was retrieved through searches in Web of Knowledge using search strings 1. (tree retention)

AND (Sweden OR Norway OR Finland), 2. (high stump*) AND (Sweden OR Norway OR Finland), February 12, 2010. Additional references were identified through cross-references and the authors' own knowledge. Only publications in peer-reviewed journals were included. The total number of analyzed biodiversity studies was 52 (Table II). Although less emphasized and not systematically retrieved, 20 studies on cost-efficiency, riparian buffer zones and ecosystem function were also included (Table II).

Results

General

The first study relating to tree retention in Norway, Finland and Sweden appeared in 1994. From 1999 onwards there has been a continuous growth of new studies (Figure 1). The studies are based on very heterogeneous characteristics, and their ecological contexts and methodological frameworks vary considerably. The main sources of variation are related to the following factors:

- geographical location and coverage: most studies are restricted to a specific region
- forest type: pine, spruce and deciduous
- characteristics of the retention trees: whole trees or high stumps, solitary or grouped, alive or dead
- spatial scale: log, stand or landscape
- temporal scale: immediate effects and effects usually during a few years (although one study includes a stand with pines retained 90 years earlier: Jakobsson & Elfving, 2004)
- methodological approach: descriptive, experimental, modelling
- response variable: any of several taxa or structural characteristics of trees.

The studies differ in details, too. For example, the number of replicates and intensity of sampling vary considerably. On a general level, studies seem to set research questions in two different ways: how well retention trees maintain the characteristics found in mature, preharvest forest, or how much retention trees change ecological conditions compared with clear-cuts without retention trees. Most of the studies focus on specific ecological patterns, such as coarse woody debris, species richness, assemblage composition or the occurrence of red-listed species. Sixty-five per cent of the studies were conducted in Sweden, 30% in Finland and 5% in Norway. About 55% of the studies were on beetles while lichens were the second most studied group (10% of the studies). Dead trees were the main focus in about 50% of the studies. Studies on retention groups were considerably more common (covered in 40% of the studies) than studies on single, live trees (15%) (Table II). Only a few studies analyzed the effects of retention trees on timber production and ecosystem function characteristics.

General conclusions from almost all the studies were that retention trees have noticeable effects on forest characteristics, including biodiversity patterns. They tend to maintain at least some species in the harvested stands. However, their value for the

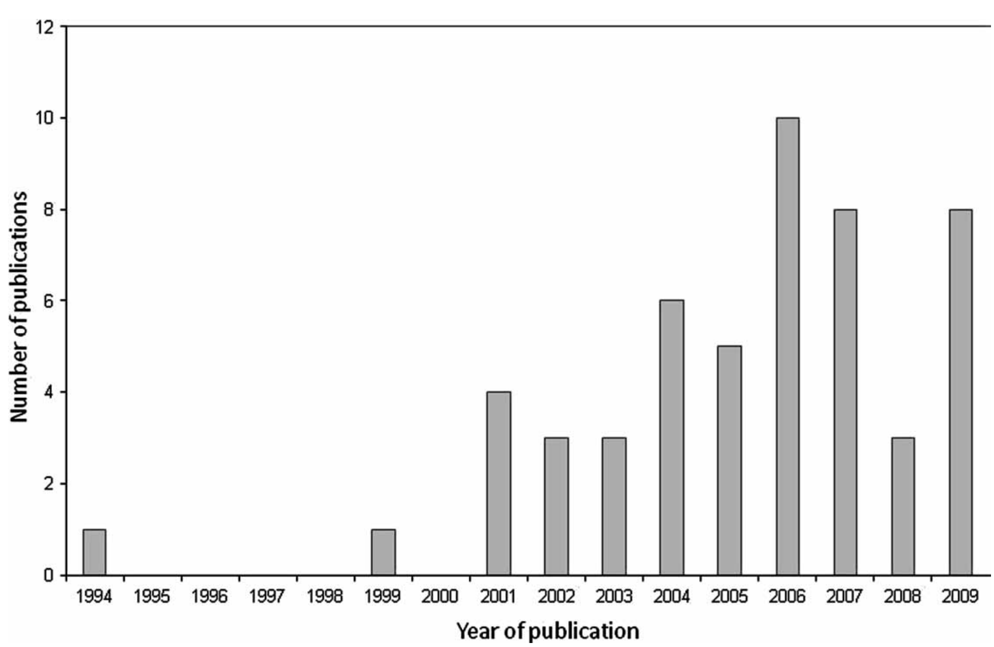

Figure 1. Publications in peer-reviewed journals on biodiversity related to tree retention, in Finland, Norway and Sweden.

red-listed and rare species is often questioned or concluded to depend on the levels of tree retention.

Solitary live trees

Studies on individual, live trees have been largely directed towards the lichen flora on aspen *Populus tremula* L. in boreal Sweden. Hedenås and Hedström (2007) found that two studied crustose, green-algae lichens were more abundant on stems in forests than in clear-cuts, and were especially uncommon on the south side of retained trees. The highest cover of three studied cyanolichens was found on the north side of retained trees, and at sites 24 years after logging they were just as abundant as in the mature forest. The same species were studied in a logging experiment where 50% of the volume was extracted. The two crustose species were severely damaged while two cyanolichens were largely unaffected, and one showed an intermediate response (Hedenås & Ericson, 2003). The importance for epiphytes of the north, shaded side of retained trees has been stressed by Hedenås et al. (2007), who claim that this side offers suitable sites for lichen colonization, since free-living photobionts are available. In a transplantation study of the lichen *Lobaria pulmonaria* and the bryophyte *Antitrichia curtipendula* on retained aspens, Hazell and Gustafsson (1999) found that both had higher survival and vitality on the north than on the south side. The lichen, but not the bryophyte, was even more vigorous on clear-cuts than in forest. In a stand with pines retained 90 years earlier, ground-dwelling lichens were found to be more common close to than farther away from individual trees (Elfving & Jakobsson, 2006).

Retention patches

Group retention, i.e. retention in patches (Figure 2), is often considered in the management recommendations as a preferred way to leave retention trees (Table I), but direct ecological evidence supporting this view is rather scarce. Several studies include retention patches in their design but only a few studies have assessed the role that retention patch size has on ecological phenomena. Retention patches are sometimes thought to preserve mature forest conditions better than solitary trees (lifeboats) and they may also provide a longer term supply of dead wood to a regeneration area (Djupström et al., 2008). Esseen (1994) and Jönsson et al. (2007) followed the dynamics of trees in retention patches of differing sizes during an 18-year period in a wind-exposed, high-altitude site. The retention patches showed considerably higher tree mortality than corresponding mature forests, and thus maintained unnaturally high dead-wood volumes. The smaller the patches (the range was 1/16 to 1 ha), the higher the recorded mortality. Hautala et al. (2006) monitored tree dynamics on spruce-dominated patches in southern Finland. In their study area, the size of the retention patches affected tree uprooting only slightly. More important for the uprooting and tree dynamics was the biotope: in the paludified site spruce trees were uprooted more often than in upland sites. This pattern was interpreted as a result of different soil characteristics. Peat-covered and stony soils in paludified sites seem to increase uprooting of trees.

Retention patches tend to maintain species richness better than solitary trees (Hyvärinen et al., 2006), but there are no studies that control both grouping and retention level at the same time. In the studies, grouping is typically confounded with higher retention level. Perhans et al. (2009) observed that for groups with an average size of 0.12 ha richness and abundance of bryophytes, but not lichens, decreased significantly over a 6-year period. In one study, retention patches sized 0.01–0.02 ha did not mitigate the vegetation response to clear-cutting (Jalonen & Vanha-Majamaa, 2001), while in an experiment with sparse groups of shelterwood trees, vegetation changes were smaller than on clear-cuts (Hannerz & Hånell, 1997). Size of the retention group also seems to be important for soil macrofauna (Siira-Pietikäinen & Haimi, 2009), but short-term effects are weak or not present (Siira-Pietikäinen et al., 2001, 2003). Beetles tend to survive better in group retentions, possibly because of the higher heterogeneity of dead-wood substrates in these groups (Hyvärinen et al., 2005, 2006; Martikainen et al., 2006*a*). However, even very high retention amounts or large groups cannot maintain the forest interior species that are typical in mature and old-growth forests (Koivula, 2002; Martikainen et al., 2006*a*; Matveinen-Huju et al., 2009). The type of trees that are included in the retention groups may have a strong effect on species composition. Lie et al. (2009) recommend that to maintain epiphytic flora, trees in retention groups should be large and old.

High stumps

Several studies have compared beetles in high stumps (Figure 3) under different sun exposure, e.g. in clear-cuts versus forested sites. One common conclusion is that high stumps in clear-cuts host a large number of both common and red-listed species dependent on warm, sun-exposed environments, often not found in closed forest. This has been shown in studies of beetles in aspen (e.g. Martikainen, 2001; Sverdrup-Thygeson & Ims, 2002; Jonsell et al., 2004; Lindhe &

Table II. Studies on different types of tree retention and organism groups in Finland, Norway and Sweden: studies on cost-efficiency, riparian buffer zones (biodiversity aspects) and ecosystem function are also listed, although they were less emphasized in the review.

	Natural high stumps/logs	Created high stumps/logs	Single live trees	Retention groups
Structures	Ranius & Kindvall (2004), Ekbom et al. (2006)	Ranius & Kindvall (2004), Schroeder et al. (2006)		Esseen (1994), Hautala et al. (2004), Hautala & Vanha-Majamaa (2006), Jönsson et al. (2007)
Beetles and other invertebrates	Kaila et al. (1997), Martikainen (2001), Sippola et al. (2002), Sverdrup-Thygeson & Ims (2002), Brunet & Isacsson (2009*a*, *b*)	Jonsell & Weslien, (2003), Jonsell et al. (2004, 2005), Lindhe & Lindelöw (2004), Lindhe et al. (2005), Wikars et al. (2005), Abrahamsson & Lindbladh (2006), Gibb et al. (2006), Johansson et al. (2006), Schroeder et al. (2006), Hedgren, (2007), Hjältén et al. (2007), Lindbladh et al. (2007), Abrahamsson et al. (2008), Fossestøl & Sverdrup-Thygeson (2009), Sverdrup-Thygeson & Birkemoe (2009)	Sverdrup-Thygeson & Birkemoe (2009)	Siira-Pietikäinen et al. (2001, 2003), Koivula (2002), Hyvärinen et al. (2005, 2006), Pitkänen et al. (2005, 2008), Martikainen et al. (2006*a*), Matveinen-Huju et al. (2006, 2009), McGeoch et al. (2007), Djupström et al. (2008), Siira-Pietikäinen & Haimi (2009)
Birds				Söderström (2009)
Bryophytes			Hazell & Gustafsson (1999)	Jalonen & Vanha-Majamaa (2001), Vanha-Majamaa & Jalonen (2001), Perhans et al. (2007, 2009)
Lichens			Hazell & Gustafsson, (1999), Hedenås & Ericson (2003), Hedenås et al. (2007), Hedenås & Hedström (2007), Elfving & Jakobsson (2006)	Perhans et al. (2007, 2009)
Macrofungi	Junninen et al. (2007)	Lindhe et al. (2004)		
Vascular plants			Jakobsson & Elfving (2004), Elfving & Jakobsson (2006)	Jalonen & Vanha-Majamaa (2001), Vanha-Majamaa & Jalonen (2001)
Cost-efficiency	Ranius et al. (2005), Jonsson et al. (2006, 2010), Wikberg et al. (2009)			
Riparian buffer zones	Hylander et al. (2002, 2004, 2005), Mönkkönen & Mutanen (2003), Hågvar et al. (2004), Hylander (2005), Hylander & Dynesius (2006)			
Ecosystem function	Jacks & Norrström (2004), Jakobsson & Elfving (2004), Lauren et al. (2005), Pitkänen et al. (2005, 2008), Elfving & Jakobsson (2006), Martikainen et al (2006*b*), den Herder et al. (2009), Löfgren et al. (2009)			

Lindelöw, 2004; Sahlin & Ranius, 2009), spruce (e.g. Gibb et al., 2006; Fossestol & Sverdrup-Thygeson, 2009) and beech (Brunet & Isacsson, 2009*a*). In studies of fungi, high stumps have also been found to be important, although less so than logs (Lindhe et al., 2004).

Natural high stumps represent a more heterogeneous substrate and therefore host a more diverse species assemblage of beetles (Schroeder et al., 1999; Jonsell et al., 2004) or fungi (Lindhe et al., 2004) than artificially created stumps, but no fundamental differences have been found. Studies of stumps of different heights showed that species composition differed in vertical subsections of high stumps (Abrahamsson & Lindbladh, 2006). This study also suggested that high stumps constitute a better substrate than low stumps for parasitic Hymenoptera, which are important enemies of pest species (Hedgren, 2007). Two studies of spruce stumps in Sweden showed that the presence of certain common wood-rotting fungi affects the species composition of beetles (Jonsell et al., 2005; Abrahamsson et al., 2008).

Schroeder et al. (2006) studied the relative importance of spruce high stumps for beetles on a landscape level. They found that out of the 29 most frequent beetle species in their study, high stumps were the major source of recruitment at the

Figure 2. A retention patch, Norway. (Photographer: Anne Sverdrup-Thygeson.)

Figure 3. An artificial (left) and a natural (right) high stump. Sweden. (Photographer: Lena Gustafsson.)

landscape level for only one beetle species (the Ciidae *Hadreule elongatula* (Gyllenhal, 1827)). For the remaining 28 beetle species, less than 1% of the landscape's population occurred in high stumps on clear-cuts. In another study, it was estimated that all eight aspen-associated species studied had higher habitat availability on clear-cuts (Sahlin & Ranius, 2009). For four of these species, more than 20% of the population occurred in this environment.

Brunet and Isacsson (2009*b*) studied the influence of spatial location and density of beech (*Fagus sylvatica* L.) snags for beetle diversity and distribution. They found that retention of snags close to existing populations of red-listed species was more beneficial than an even, dispersed distribution. In another study, however, no detectable effect of hotspot landscapes with a documented rich fauna of red-listed beetles was found on the beetle fauna in high stumps (Lindbladh et al., 2007). In a follow-up study using window traps instead of bark sampling, a certain effect of hotspot surroundings could be seen for birch high stumps, but not for spruce high stumps (Abrahamsson et al., 2009).

The associated species and the function of high stumps change with time since creation. Sverdrup-Thygeson and Birkemoe (2009) studied beetle fauna in retention trees cut into high stumps. They documented that the abundance of cambium-living species first increased and then decreased, reaching a maximum in year 2 after high stump creation. The abundance of late-successional species peaked later. For fungi, Lindhe et al. (2004) found that annual diversity peaked 4–7 years after high stump creation.

Other dead wood

Downed dead wood is usually maintained during harvest operations in northern Europe, and certification criteria also require this (Table I). Lying dead wood may significantly contribute to the overall amount of coarse woody debris. However, a major threat to downed wood is caused by silvicultural operations during the regeneration phase. Hautala et al. (2004) showed that up to 60–70% of the downed dead wood may be destroyed when soil scarification and planting is carried out by machines in southern Finland. They observed that also inside retention groups the downed dead wood is reduced (by 20%), probably owing to small size of the groups. In particular, downed birch was destroyed in clear-cut sites.

A few studies have focused on different types of simulated dead wood during the early successional phases. Downed retention trees of tree top boles or logs in early decay stages in clear-cuts have been compared with natural (Sverdrup-Thygeson & Ims, 2002) or artificial high stumps (Jonsell & Weslien, 2003; Gibb et al., 2006; Hjältén et al., 2007; Fossestøl & Sverdrup-Thygeson, 2009). The studies all found that the beetle fauna in logs differ from the fauna in high stumps, and that both should be left when clear-cutting to cater for the variety of habitat preferences among beetles. The biological importance of downed, well-decayed retention trees, in contrast, is rarely studied, as this substrate has not yet been available apart from in the oldest retention sites. Junninen et al. (2007) surveyed the fungi flora on aspens retained at clear-cutting 6 or 13 years ago, which had fallen and started to decay. More species were observed in clear-cut sites than in older forests, but the occurrence of fungi in this case study was probably dependent on the high-quality substrate of retained trees and a rich species pool in the surroundings. In a study that followed fungal succession on artificially created logs in clear-cuts for 9 years, logs hosted more species, higher species diversity and more red-listed species of fungi than high stumps cut at the same time (Lindhe et al., 2004).

Substrate amounts and dynamics

In a 24,000 ha landscape in central boreal Sweden, clearly more coarse woody debris in an early decay stage was found on recent clear-cuts with tree retention than in old managed stands (Ekbom et al., 2006). A simulation study showed that the amount of dead wood will double in 100 years in a hypothetical landscape with spruce, if various restoration measures are taken (Ranius & Kindvall, 2004). The most important measures to achieve this included setting aside of areas, retention of living trees, limiting destruction of coarse woody debris and not removing naturally dying trees. Another study based on simulations showed that retention trees are particularly important to avoid temporal discontinuities in coarse woody debris availability at the stand level (Ranius et al., 2003). In a study of high stumps in boreal forest, Schroeder et al. (2006) found that high stumps yielded only 0.13% of coarse woody debris volume and bark area in the landscape.

Cost-efficiency

Studies from Sweden indicate that there are variations in the cost-efficiency of retaining different structures, and also according to region. For instance, for live trees it is most cost-efficient to save birch and aspen in southern Sweden, and pine and spruce in the north (Jonsson et al., 2010). To create dead wood, it is most efficient to set aside forest in northern Sweden, while in southern Sweden it is better to increase the amounts in managed forests (Jonsson et al., 2006). In general, for the creation of dead wood it is more cost-efficient to save naturally dying trees and to create high stumps than to retain living trees, to scarify the soil manually after logging to avoid harm to logs, and to prolong the rotation period (Ranius et al., 2005). Wikberg et al. (2009) found that key habitats and retention patches were more cost-efficient than nature reserves and old production forests, of mesic spruce type, when total species richness for two species groups was used as a proxy for biodiversity value.

Ecosystem function

In a Finnish experiment, the damage rate to pine seedlings from pine weevil predation was less on clear-cuts with 50 m^3 retained trees than on those with 10 m^3 and 0 m^3 retained trees (Pitkänen et al., 2005). Higher catches of walking and flying individuals of *Hylobius abietis* L. were made in retention groups than in open areas (Pitkänen et al., 2008). It is possible that canopies of retention trees provide alternative food source for *Hylobius* and, consequently, damage to pine seedlings remains lower in regeneration areas. den Herder et al. (2009) observed that green-tree retention enhanced survival of aspen, rowan and birch during the period of six growing seasons after cuttings, in particular at high retention levels (50 m^3 ha^{-1}). Retention may reduce herbivory effects on deciduous tree seedlings (den Herder et al., 2009). It is sometimes argued that tree retention may enhance the likelihood of pest outbreaks in neighbouring stands. Martikainen et al. (2006*b*) studied the shoot damage caused by pine shoot beetles around traditional and tree retention clear-cuts. They found that retention cuttings seemed to have a similar impact on the surrounding forest stands to traditional clear-cuttings. One forest production aspect of tree retention is that seedling survival and growth may increase owing to a reduced risk for frost damage (Langvall & Ottosson Löfvenius, 2002). Based on two studies in Sweden, one embracing one stand and another 25 stands, both pine-dominated, the loss of production in regenerating stands during a rotation from retaining 10 pines per hectare was estimated to be about 3% (Jakobsson & Elfving, 2004; Elfving & Jakobsson, 2006).

Discussion

Finland, Norway and Sweden were early players in the introduction of tree retention in clear-cut production forests. Today, it is practised or being discussed in, for example, Tasmania (Baker et al., 2009), Canada (Work et al., 2003), the USA (Aubry et al., 2004) and Argentina (Martinez Pastur et al., 2009). Global analyses of studies on retention models applied in different forest biomes would increase the understanding of biodiversity patterns and processes, and give guidance on potential practical developments. It is equally clear, however, that each region has many peculiarities, with implications on how, where and when retention is most efficient ecologically, as well as on the economic and social consequences of this activity.

Consequently, the intention with the current review was not to make an in-depth global evaluation of the relevance and quantitative effectiveness of tree retention, but instead to identify major variables and factors that have been included in the studies conducted so far in northern Europe. Presumably, these factors indicate what ecologists regard as the most relevant in this context. The focus on a single, ecologically rather uniform geographical area, i.e. Finland, Norway and Sweden, facilitates insights that may be difficult to observe in more heterogeneous global data. To proceed towards a more quantitative direction, a systematic review approach (Pullin & Stewart, 2006) including meta-analyses should preferably be applied, although such studies often lose a considerable amount of detail. For example, the only extensive review conducted on tree retention so far was presented a few years ago and included 214 papers, embracing North America and Europe, but then only live trees were targeted (Rosenvald & Lõhmus, 2008). When exposed to meta-analysis, however, only 39 studies could be used.

The practice of leaving retention trees for biodiversity purposes was introduced widely to Finland, Norway and Sweden 15–20 years ago, and since then the issue has generated substantial research interest. The present review of research conducted in this region shows that the number of published studies on biodiversity so far is about 50, but also that every year about 10 new publications appear (Figure 1). New results and new insights into the ecological effects are thus accumulating rapidly, and this trend is naturally not restricted to northern Europe alone. This knowledge was first summarized a decade ago, by Vanha-Majamaa and Jalonen (2001), but at that time fewer than 10 studies on the topic from the region had been published. This early overview also included results from two experimental studies, and discussed contemporary research needs.

Overall, three general patterns can be discerned from the analyzed studies. (1) Tree retention can supply some of the substrate produced in the natural early-successional phase after storm-felling or fire, with sun-exposed weakened or downed trees. Several saproxylic species benefit from this, although the amounts of sun-exposed substrate are low compared to natural landscapes. (2) Tree retention alleviates the dramatic consequences that clear-cutting has on boreal biotas since it maintains assemblages and structures of mature forests to some extent. (3) However, it is equally convincing that tree retention cannot maintain the structures and the microclimate that are important for species living in mature and old-growth forests. In particular, the advantages that retention trees provide to red-listed species have often been questioned. The significance of retention trees for red-listed species thus remains unclear but is probably affected by the level of retention.

In all the studies reviewed here, retention has comprised a minor proportion of the volume of harvestable timber (often 1–10%), which makes it practically impossible to avoid edge effects and random demographic effects. If the aim is to maintain more of the mature forest characteristics in production forests, the harvest intensities should at least in some areas be clearly lower than is currently the case. To mimic truly the exposed or semi-exposed postdisturbance stands, higher dead-wood volumes than today need to be retained and created, at least in some sites. The exact levels that are required to secure long-term viable populations of different species, as well as the most cost-efficient implementation of these conservation measures, remain a major challenge for future research.

Although knowledge is increasing rapidly, several crucial aspects remain poorly studied. There have been no studies on dispersal from retention structures to surroundings, possibly because such studies are hard to conduct under field conditions. There are also few studies that describe the contribution of tree retention to structures such as old trees and dead wood at large scales like landscapes or regions. The relatively short period for which tree retention has been practised gives few opportunities to show empirically the temporal dynamics at stand and landscape levels. Most of the current studies on these aspects rely on simulations where several simplifying assumptions are necessary (Ranius et al., 2003; Ranius & Kindvall, 2004; Tikkanen et al., 2007). A step forward would be to conduct true landscape studies, i.e. to repeat sampling in different landscapes to assess large-scale effects. Such studies may also give guidance on regional prioritizations of retention measures. The ecosystem function also remains to be further studied, with potential important implications for production aspects such as seed and seedling predation, mycorrhiza interactions and nitrogen retention.

This review has focused on ecological issues, and also touched upon economic aspects, since studies on cost-efficiency were included. The social dimension is essential to explore further, so that implementation of this specific management is feasible. Values and policies relating to conservation are also highly related to tree retention practices. To the authors' knowledge, there are very few social studies that specifically address tree retention (but see Silvennoinen et al., 2002; Uliczka, 2003; Tönnes et al., 2004).

Conceptually, a few issues need attention as the retention measures in different countries are not uniformly classified and terminologies vary. For example, riparian buffer zones adjacent to small lakes and creeks are classified as key habitats in Finland (Timonen et al., 2010), while in Norway and Sweden they are part of the tree retention concept. Owing to this geographical difference, this habitat type was not included in the present overview of the literature. Nevertheless there are studies on the effect on biodiversity (Hylander et al., 2002, 2004, 2005; Mönkkönen & Mutanen, 2003; Hågvar et al., 2004; Hylander, 2005; Hylander & Dynesius, 2006) as well as the impact on water quality, e.g. nitrogen retention (Jacks & Norrström, 2004; Lauren et al., 2005; Löfgren et al., 2009) that could be elaborated in future reviews.

The practice of tree retention needs to be viewed in relation to other conservation measures. In Finland, Norway and Sweden multiscaled conservation models are applied, i.e. areas are set aside at different scale levels (Lindenmayer et al., 2006). Tree retention represents the lowest level with setting aside of individual trees and tree groups. An intermediate level is woodland key habitats, i.e. small areas with high biodiversity values. Woodland key habitats have recently been mapped in large inventories in Finland, Norway, Sweden and the Baltic states, and their mean size varies between 0.7 and 4.6 ha (Timonen et al., 2010). Nature reserves represent the highest scale level, often embracing hundreds of hectares. A future important task for research is to evaluate the efficiency of these three scale levels, and analyze how they overlap and complement each other. Such knowledge may guide future conservation policies and allocation of resources. The task of verifying the contribution of conservation measures at different spatial scales is complicated by temporal issues, as the spatial scale and temporal dynamics of different conservation measures are related. For example, tree dynamics and mortality patterns may be accelerated in retention groups and woodland key habitats (Jönsson et al., 2007, 2009) so that these dynamics barely resemble those of larger tracts of mature forests (Hofgaard, 1993; Kouki et al., 2004; Fraver et al., 2008). These interrelated spatial–temporal dynamics and their assessment in multiscaled conservation are poorly understood.

In the southernmost parts of Finland, Norway and Sweden there are remnants of former cultural landscapes with the presence of old trees of southern tree species such as *Acer platanoides* L., *Fraxinus excelsior* L., *Quercus robur* L. and *Tilia cordata* Mill. Such trees are also often found in suburban and urban environments. Retained trees on clear-cuts of such tree species may complement the existing networks of ancient trees located in more or less open environments, and even increase the amount of such habitat. In forest–farmland mosaics, clear-cuts with retained trees may offer suitable substitution habitats for some declining grassland birds (Söderström, 2009). New studies are needed to analyze further the role of tree retention in biodiversity associated with environments other than strict forests, and how this varies with landscape type.

Although clear-cutting prevails in many boreal countries, selective harvest models are also being practised in northern Europe, especially among small forest owners. Accumulated knowledge on boreal forest dynamics in northern Europe points to less importance of stand-replacing fires than previously assumed (Kuuluvainen, 2009), and thus clear-cutting may be increasingly questioned as a nature-based logging method in the future. Many large industrial forest owners, in contrast, are moving towards higher intensification through the use of propagated material, regeneration with exotics, and in some countries also through the use of nitrogen fertilizers. It will be essential to evaluate the effects on biodiversity of various tree retention measures in such gradients of management intensity. Ideally, retention should be designed to achieve the highest benefit within a given framework. This implies adjustment of levels according to not only the type of stand, but also the landscape configuration.

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