# Presence and Abundance of Red-Listed Plant Species in Swedish Forests

LENA GUSTAFSSON*

The Forestry Research Institute of Sweden, Uppsala Science Park, SE-751 83 Uppsala, Sweden

**Abstract:** *This study was performed to obtain information on the presence and abundance of red-listed vascular plants, bryophytes, and lichens of forests in an objective and systematic way and on a large scale. Species were searched for in line transects in three areas in southern Sweden, representing a total of 1350 km$^2$. I investigated 135 ha of production forests and, for comparison, 35 so-called "woodland key habitats" (WKHs) covering 63 ha. It is estimated that there are 70,000 WKHs in Sweden presumed to be important sites for red-listed species. I found 22% of the forest vascular plants, bryophytes, and lichens on the national red list, indicating that most such species are very rare. The red-listed bryophytes and lichens were considerably more common than the vascular plants. Due to a relatively high abundance of a few red-listed species, the average number of records for the three species groups together was 0.9–2.4/ha in the production forest. Extrapolated to the whole hemiboreal region of Sweden, there could be several million occurrences of red-listed plant species within the managed forests. The red-listed species were to a high degree associated with deciduous trees and dead wood and occurred mainly in mature forests. Woodland key habitats had more red-listed species, more species in high categories of threat, and significantly more records per hectare than production forests. Because WKHs constitute only 1% of the productive forest land in Sweden, they cannot alone safeguard the future of red-listed species. The great importance of managed forests, which make up more than 95% of the productive forest land in Sweden, must be acknowledged. Combined conservation planning is recommended, with attention being given to both WKHs and production forests.*

Presencia y Abundancia de Especies de Plantas en Bosques Suecos Incluídas en la Lista Roja

**Resumen:** *Se realizó un estudio para obtener información de la presencia y abundancia de plantas vasculares, briofitas y líquenes de bosques en listas rojas de manera objetiva y sistemática y a amplia escala. Se buscaron especies en transectos lineales en tres áreas del sur de Suecia comprendiendo un total de 1350 km$^2$. Se investigaron 135 ha de bosques en producción y, para comparar, 35 "hábitats boscosos clave" (HBC) que abarcaron 63 Ha. Se estima que en Suecia hay cerca de 70,000 HBC que se consideran ser sitios importantes para especies en la lista roja. Se encontró el veintidós porciento de las plantas vasculares, briofitas y líquenes en la lista roja nacional, indicando que muchas de esas especies son muy raras. Las briofitas y líquenes incluídas en la lista fueron considerablemente más comunes que las plantas vasculares. Debido a que algunas especies incluídas en la lista tenían una abundancia relativamente alta, el promedio de registros para los tres grupos de especies en conjunto fue de 0.9 a 2.4/ha en el bosque en producción. Extrapolado a toda la región hemiboreal de Suecia, podría haber varios millones de ocurrencias de especies incluídas en las listas dentro de los bosques manejados. Las especies enlistadas se asociaron con árboles deciduos y madera muerta y ocurrieron principalmente en bosques maduros. Los hábitats boscosos claves tuvieron más especies enlistadas, más especies en altas categorías de amenaza y significativamente más registros por hectárea que los bosques en producción. Debido a que los HBC constituyen solo el 1% de las tierras forestales productivas en Suecia, por si solos no pueden salvaguardar el futuro de las especies enlistadas. Se debe reconocer la gran importancia de los bosques manejados, que constituyen más del 95% de las tierras forestales productivas en Suecia. Se recomienda la planificación de conservación combinada, brindando atención tanto a HBC como a bosques en producción.*

* *Current address: Swedish University of Agricultural Sciences, Department of Conservation Biology, Box 7002, SE-750 Uppsala, Sweden, email lena.gustafsson@nub.slu.se*
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## Introduction

Biodiversity has been defined in a number of ways, but almost all definitions embrace three major levels: ecosystems, species, and genes. These levels are also fundamental considerations of the Convention on Biological Diversity (Heywood 1995). In the Nordic countries, forest-conservation efforts have been driven by the species aspect of biodiversity because it is well defined, well known, quantifiable, and easily understood. Species that appear on the "red lists" have been the focus of most attention because they represent the decreasing and vanishing fauna and flora most in need of protection and conservation. The ecosystem level is the target of landscape planning and is of increasing importance in forestry (Angelstam & Pettersson 1997). To date, there has been less interest in the conservation of biodiversity at the genetic level.

Despite the interest in red-listed species and great efforts to collect and compile information on their distribution and biology, data on their presence and abundance in the forest landscape are limited. Threats and classification into various categories are usually assessed from a national perspective and are evaluated mainly by experts with field-based knowledge. Little information has been collected systematically and objectively. Data are required on the number of red-listed species present in different types and age classes of forest and on their associations with factors such as soil type, host trees, and other substrates.

Forests cover more than 50% of the land area of Sweden, and more than 95% of the productive forest land in Sweden is used for forestry, mainly for cultivation of the indigenous Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) (National Board of Forestry 2000). Modern forestry, including clearcutting, soil scarification, planting, and thinning, has been practiced for decades. Today, as a result of forestry, the forests have become increasingly homogenous and depauperate of components important to biodiversity, such as deciduous trees, old trees, and dead wood. Fauna and flora have been severely affected (Bernes 1994). Therefore, an important aspect of biodiversity conservation is to find and protect remaining sites with characteristics of natural forest.

At present, sites important for conservation in Sweden and other Nordic countries are being surveyed. In Sweden these sites have been named "woodland key habitats" (WKHs) and are defined as habitats in which red-listed species are likely to occur (Nitare & Norén 1992). Most WKHs are small, only a few hectares, but there is no size limit. Sizes range from solitary, large trees to tens of hectares. They mostly represent remnants of old, natural-like forests, but some WKHs are composed of unmanaged, younger stages (e.g., successional phases after fire, rich in deciduous trees) and may include stands of earlier agricultural use (e.g., abandoned, formerly grazed wooded meadows). The National Board of Forestry carried out an inventory, completed in 1998, of WKHs occurring on the property of small landowners. Land under such ownership amounts to half of all productive Swedish forest land, and more than 40,000 WKHs have been identified on it. The WKHs cover on average 0.8% of productive forest land and have a median area of 1.4 ha (National Board of Forestry 1999). The inventory of the remaining half of the productive forest land (i.e., that mostly owned by forestry companies) will be completed in 2003. These large landowners are responsible for sponsoring, conducting, and reporting their own WKH inventories.

Although, by definition, WKHs should be occupied by red-listed species, few detailed studies on the species composition of WKHs have been conducted, and no comparisons have been made with the forest matrix (i.e., the surrounding production forests [but see Gustafsson et al. 1999; Gustafsson 2000]). The first step in identifying WKHs is to discern potential stands through studies of aerial photographs and forest maps. These stands are then visited in the field and actual WKHs are identified and delimited through a standardized methodology developed by the National Board of Forestry (National Board of Forestry 1995*a*). To be selected as a WKH, a stand has to fulfil certain structural criteria and usually has to support some indicator species. The structural criteria relate to properties of natural forests and include, for example, the presence of large amounts of dead wood and old trees. More than 300 indicator species (vascular plants, bryophytes, lichens, fungi), as suggested by species' experts, are used to identify the WKHs. It is presumed that these species, most of them less common, indicate the presence of red-listed species.

There is a spatial heterogeneity in species composition on various geographical levels, with some areas being richer in species, endemic species, and rare species than others. Also on a population level there is a subdivision with some subpopulations being more viable than others. Patch theory has dominated many applications in conservation biology, through results from studies of meta-populations and landscape ecology (Wiens 1997). The term "key habitat" is sometimes used for biodiversity-rich areas, but more commonly in autecological studies to denote the critical habitat demands of species (e.g., Karczmarski et al. 2000; Revilla et al. 2000). "Hotspots" is a related term and, although rather undefined, is usually used for areas with high biodiversity values on global (e.g., Myers et al. 2000), continental, regional (Dinerstein & Wickramanayake 1993; Pomeroy 1993), and local (Neitlich & McCune 1997; Hansson 1998) scales.

There is a lack of knowledge not only of the occurrence of red-listed species in production forests but also in habitats identified as especially important for conservation. I report the results of the first detailed survey, conducted at the scale of several hundred square kilometres, of red-listed vascular plants, bryophytes, and lichens in forests. Because rare species are difficult to sample, the investigation was carried out through line-transect analysis and was restricted to three forest areas in southern Sweden ranging in size from 250 to 600 $km^2$.

I detail the number of occurrences of red-listed plant species in Swedish forests and report on differences between production forests and WKHs, sites presumed important for biodiversity. My results give new insights into the variations in population size of red-listed species among vascular plants, bryophytes, and lichens. Such data can be used to evaluate the quality of the red lists. Elucidation of the importance of mature production forest to red-listed species can help assess the need to maintain such age stages in the forest landscape. Collection of data on the substrates of species increases understanding of the importance of various microsites for different species and facilitates the formulation of guidelines for biodiversity conservation in forestry.

## Methods

### Study Areas

The study was conducted in three areas in the hemiboreal vegetation zone (Ahti et al. 1968) in southern Sweden. The Örsundsbro area is situated approximately 70 km northwest of Stockholm, the Roslagen area approximately 80 km north-northeast of Stockholm, and Småland approximately 150 km east of Göteborg. Mean temperatures for February and July vary between $-3°$ and $-5°$ C and $+14$ and $+18°$ C, respectively. Mean annual precipitation ranges between 600 and 800 mm (Table 1). The bedrock in all three areas is Precambrian, with Svecofennian rocks consisting of partly magmatized old granitoids in Örsundsbro and Roslagen. Småland is part of the Transscandinavian granite-porphyry belt and is dominated by Småland-Värmland granite (Fredén 1994). The quaternary deposits are dominated by glacial till, with varying amounts of boulders, stones, gravel, sand, silt, and clay. In Roslagen and Småland there are large areas where the bedrock is covered by only a thin soil layer. All areas are situated below the highest shoreline (i.e., they were covered by the sea shortly after the latest glaciation; Fredén 1994).

The forest canopy in all study areas is dominated by Scots pine and Norway spruce; deciduous trees are less common. Most of the forests (84–92%) are younger than 100 years old (Table 1). Of the productive forest land, 45–80% belongs to small, private forest owners (National Board of Forestry 2000).

The national WKH inventory reports that the proportion of WKHs in productive forest land on the properties of small, private landowners is >4% in the Roslagen area, 1–2% in the Örsundsbro area, and <1% in the Småland area (National Board of Forestry 1999).

### Red-Listed Species

The numbers of nationally red-listed forest vascular plants, bryophytes, and lichens recorded so far from the county of Uppsala (Örsundsbro area) are 19, 21, and 77, respectively; for the county of Stockholm (Roslagen area), 22, 25, and 72; and for the county of Jönköping (Småland area), 17, 29, and 54. These numbers are based on the categories of "present occurrences," "vanished from the province," and "occasionally observed" described by Aronsson et al. (1995). The counties have many species in common. In total, the red list supports 27 vascular plants, 38 bryophytes, and 101 lichens.

### Production Forests

Ten 1000 × 1000 m plots were randomly selected in an area of 10 × 25 km in Örsundsbro, and 20 500 × 500 m plots were randomly selected in areas of 20 × 25 km in Roslagen and 20 × 30 km in Småland. The selection was based on a division of the study areas with the aid of the Swedish National Grid. Line transects 10 m wide were positioned along all four edges of the plots in Roslagen and Småland, amounting to a total of 2 km and 2 ha per plot (Fig. 1). In all, 40 km and 40 ha were included in each of these two study areas. In Örsundsbro, six parallel lines, each measuring 1000 m, were laid out in a north–south orientation starting at one edge of the plot. The transects were 200 m apart, joined by 200-m sections with an east-west orientation. In total, the length of the transects was 7 km and the area covered was 7 ha in each plot (Fig. 1). Therefore, in total, 70 ha were surveyed over 10 plots. A condition for each plot was that the line transects should have a total forest cover of at least 80%. Forest land was defined as having a mean tree production of at least 1 $m^3$/ha at 100 years of age (National Board of Forestry 2000). When species were recorded, unforested land was not searched. The total area of production forest actually surveyed in line transects was 61 ha in Örsundsbro and 37 ha in both Roslagen and Småland (Table 2).

### Woodland Key Habitats

The WKH inventory, carried out by the local forestry boards, was completed in all three study areas, so information on these habitats was available. The WKHs for the present study were chosen randomly from the WKH database, the only criteria being that they should be between 0.5 and 5 ha in size. Ten WKHs each were se-

**Table 1. Description of the three areas in Sweden in which red-listed forest species were surveyed.**

| | *Örsundsbro* | *Roslagen* | *Småland* |
|---|---|---|---|
| Size (ha) | 2500 | 5000 | 6000 |
| Geographic location (central point) (lat., long.) | 59°45′N, 17°15′E | 60°00′N, 18°45′E | 58°00′N, 14°45′E |
| Elevation (m above sea level) | 25–65 | 5–50 | 160–330 |
| Mean annual precipitation (mm)[a] | 600–800 | 600–800 | 600–800 |
| Mean July temperature (°C)[a] | +16–+18 | +16–+18 | +14–+16 |
| Mean February temperature (°C)[a] | −4–−5 | −3–−4 | −3–−4 |
| *Picea abies* (%)[b] | 37 | 39 | 55 |
| *Pinus sylvestris* (%)[b] | 46 | 37 | 31 |
| Deciduous trees (%)[b] | 15 | 22 | 12 |
| Forest area proportion >100 years old (%)[c] | 10 | 16 | 8 |

[a]*For the period 1961–1990 (Raab & Vedin 1995).*
[b]*Proportion of standing stem volume estimated by county: Örsundsbro, County Uppsala; Roslagen, county Stockholm; Småland, county Jönköping (National Board of Forestry 2000).*
[c]*Estimated by county. Counties and reference as in footnote b.*

lected for Örsundsbro and Roslagen, from totals of 56 and 148, respectively. Fifteen WKHs from a total of 50 were selected in Småland (Table 2). More WKHs were surveyed in Småland because their mean size was smaller than those in Örsundsbro and Roslagen. The three study areas were chosen to represent one rich (Roslagen), one average (Örsundsbro), and one poor (Småland) in red-listed forest species, based on advice from the National Board of Forestry.

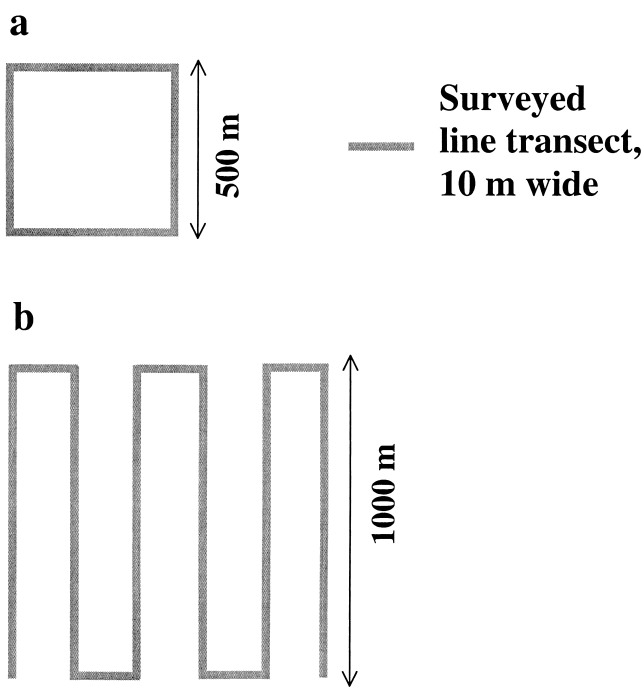


*Figure 1. Sampling design for the study plots in the production forests in the three study areas of Roslagen, Småland, and Örsundsbro, Sweden. A 10 × 10 m section of the transect was regarded as a site (record) for a species: (a) Roslagen and Småland and (b) Örsundsbro.*

The mean size of WKHs surveyed was 1.8 ha in Örsundsbro, 2.7 ha in Roslagen, and 1.2 ha in Småland (Table 2). In Örsundsbro there were four swamp forests, and the rest were stands on mesic-moist soils. Of these, three were dominated by deciduous trees (mainly *Betula* spp., *Alnus glutinosa, Populus tremula*) and one by Norway spruce. Two were dominated by large trees of the southern deciduous species *Acer platanoides*, *Fraxinus excelsior*, *Quercus robur*, and *Tilia cordata.* In Roslagen there were four swamp forests. Two were classified as natural coniferous forests rich in deciduous trees, and three were old, abandoned wooded meadows with large proportions of southern deciduous tree species. Only one of the Roslagen WKHs was described as a pure coniferous forest. In Småland, 8 of the 15 WKHs were coniferous. These were located on shallow soil outcrops of bedrock or on steep mountain slopes and were dominated by Scots pine. The remaining seven WKHs were rich in deciduous trees, mainly *Betula* spp. and *P. tremula*, out of which three were connection with brooks and three were swamp forests. One WKH in Småland was a recently and partially harvested area on which some large oaks (*Quercus robur*) remained.

### Line-Transect Analysis

When a red-listed species was found, its site was regarded as a 10 × 10 m segment of the line transect. Thus, there were 700 potential sites per plot in the production forests of Örsundsbro and 200 in Roslagen and Småland, respectively. The surveyors were instructed to record all nationally red-listed bryophytes, lichens, and vascular plants according to the 1995 Red List (Aronsson et al. 1995). The ground, logs, and living trees, snags, boulders, and other surfaces up to 2 m in height were searched. The surveyors were instructed to put equal emphasis on the different substrates during their search. For each 50-m section of a transect and for each site

**Table 2. Description of the surveyed woodland key habitats and the line transects in the production forests in the three study areas.**

| | *Örsundsbro* | | *Roslagen* | | *Småland* | |
|---|---|---|---|---|---|---|
| | *WKHs*[a] | *production forests* | *WKHs*[a] | *production forests* | *WKHs*[a] | *production forests* |
| *n* | 10 | 10 | 10 | 20 | 15 | 20 |
| Year of survey | 1997 | 1996 | 1997 | 1997 | 1998 | 1998 |
| Size (ha) | | | | | | |
| mean | 1.8 | | 2.7 | | 1.2 | |
| range | 0.5–2.7 | | 0.6–4.7 | | 0.5–3.3 | |
| Transect length per plot (m) | | 7000 | | 2000 | | 2000 |
| Total area WKHs/line transects (ha) | 18.4 | 70 | 27.4 | 40 | 17.2 | 40 |
| Surveyed area (ha) | 18.4 | 61[b] | 27.4 | 37[b] | 17.2 | 37[b] |

[a]*Woodland key habitats.*
[b]*Excluding transects passing through WKHs and unforested land.*

where a record was made (10 × 10 m), the height of the forest, used to estimate age, was classified as in one of four categories: clearcut (mean height <2 m), young forest (≥2–5 m), semimature (≥5–15 m), and mature forest (≥15 m). Old swamp forests and dry pine forests on shallow soils often have a height <15 m but were included in the category of mature forest if they were dominated by old trees. In a 5-m-diameter circle in the center of each site of a species, the dominant tree species was noted, as was the forest density in one of three categories: open (<20% cover of trees and shrubs), semi-open (≥20–70%), or closed (≥70%). Soil wetness was also recorded in one of four categories: dry, mesic, moist, or wet (Hägglund and Lundmark 1982). The substrate was classified into one of five categories: ground, boulder, rock, tree, or other. The condition of trees was recorded as living, partly dead, snag, stump, or log.

In the WKHs, the 10-m-wide transects were adjacent to one another and thus covered the whole area of each WKH. For each species observed, the same variables as in the production forest were recorded. Six surveyors with expertise in identification of bryophytes, lichens, or vascular plants performed the surveys of production forests and WKHs from September 1996 to September 1998. In total, surveyors examined 35 WKHs covering 63 ha and line transects in production forest covering 135 ha (Table 2). A recommendation of 2 hours per hectare was made for the field survey, but more time was spent in rich areas.

### Data Analysis

The total number of records—a record being one species occurrence in a 10 × 10 m section of the line transect—of red-listed species in production forest and WKHs were compared with a Wilcoxon two-sample test in the SAS statistical package (SAS Institute 1987). Records were square-root transformed and divided by the square root of area to ensure variance homogeneity and to correct for unequal areas. Chi-square analysis of the number of species records in relation to the area of different forest age classes was performed in Proc Freq in SAS.

Cumulative species number curves were constructed in PC-ORD (McCune & Mefford 1997) to assess whether the sample size regarding species number was sufficiently large. In the computer program, subsampling is repeated 500 times to determine the average number of species as a function of size of the subsample. In this program a first-order jackknife estimation of total species richness (Palmer 1990) is also calculated. Most species could be identified in the field, but some specimens needed to be collected for indoor analysis. Nomenclature follows that of Söderström and Hedenäs (1998) for bryophytes, Santesson (1993) for lichens, and Karlsson (1997) for vascular plants.

## Results

### Environmental Factors and Sampling Effort

In production forests, about 63% of all species records were epiphytic, growing on living trees. The proportion of records growing on dead wood was 35%; only 2% were found on the ground. No species were found on boulders or rocks. Considerably more lichen records, 91%, were epiphytic, compared with the bryophyte records, 45%. Affinities with substrates were similar in the WKHs, with 66% found on living trees and 29% on dead wood. The proportion of lichens growing as epiphytes was 70%; of bryophytes, 60%. More than 95% of all epiphytic records in WKHs and production forests were found on deciduous trees.

In the production forest, about equal proportions of species records were found in closed (50%) and semi-open forest (42%). Similar proportions were found in the WKHs (39% of records in closed and 51% in semi-open forest). Most species were found in areas where the soil was classified as mesic: 86% in production forest and 66% in the WKHs. In the production forest, 89% of the lichen records and 84% of the bryophyte records were found in areas with mesic soils; 10% and 16%, respectively, were recorded in areas with moist soils. In the WKHs, 70% of the lichen records and 69% of the bryophyte records were found in mesic stands; 17% and 27%, respectively, were recorded in stands on moist soils.

The cumulative species curves indicate that the sampling effort in the production forests, especially of Roslagen and Småland, was sufficient in number of species because the curves are asymptotic in shape (Fig. 2). The steeper curves of the WKHs suggest that it may have been desirable to increase the sample size in them.

### Species Number and Abundance

In WKHs and production forests, 37 red-listed species were found, among which there was 1 vascular plant, 12 bryophytes, and 24 lichens. Two of the species are classified as "endangered," 6 as "vulnerable," 1 as "rare," and 28 as "care-demanding" on the Swedish Red List (Aronsson et al. 1995) (Table 3). The recorded species represent 22% of the nationally red-listed forest species of vascular plants, bryophytes, and lichens reported from the counties of Uppsala, Stockholm, and Jönköping in which the study areas are located. They represent 4% of the red-listed forest species of vascular plants, 32% of the bryophytes, and 24% of the lichens. The number of species varied slightly between study areas. Roslagen had 1 vascular plant, 9 bryophytes, and 12 lichens; Örsundsbro had 1 vascular plant, 5 bryophytes, and 13 lichens; and Småland had 1 vascular plant, 6 bryophytes, and 10 lichens.

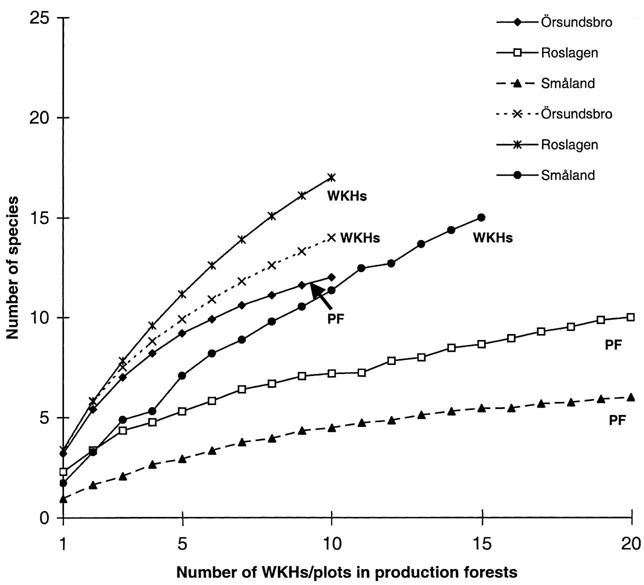


*Figure 2. Cumulative curves for the number of red-listed vascular plants, bryophytes, and lichens in woodland key habitats (WKHs) and plots in production forests (PF) in the study areas of Örsundsbro, Roslagen, and Småland, Sweden. The curves were constructed in PC-ORD (McCune & Mefford 1997), in which 500 subsamples are generated to estimate the average number of species as a function of the subsample. The total area of WKHs and plots varied between the study areas (Table 2).*

Overall, red-listed species were found in 94% of the WKHs and 86% of the plots in the production forests. The proportion of WKHs and production-forest plots in which red-listed species were found was high in all areas and most pronounced in Roslagen, where it was 100%. Among the species groups, the vascular plants had a low frequency, occurring in 6% of WKHs and 2% of production plots. Bryophytes occurred in 63% of WKHs and 66% of production plots, and lichens in 77% of WKHs and 60% of production plots. Relatively low frequencies of occurrence were recorded for bryophytes in Småland WKHs (33%) and for lichens in Småland production forests (15%).

Estimation of species richness by the jackknife method indicated that the real total species number would be considerably higher than that observed. Estimates for production forest were as follows (with observed number of species in parentheses): Örsundsbro, 16 (12) species; Roslagen, 15 (10); Småland, 8 (6). Estimates for WKHs were as follows: Örsundsbro, 20 (14); Roslagen, 25 (17); Småland, 24 (15).

In total, 218 species records were found in the production forests and 294 in the WKHs. The most common species were the bryophyte *Orthotrichum gymnostomum*, with 131 records, and the lichen *Acrocordia cavata*, with 117 records. The only vascular plant species found, *Dryopteris cristata*, had only 4 records but was found in all three study areas. Among all species, 14% had more than 25 records and 73% had fewer than 10. The three most common species in the production forest, *Acrocordia cavata*, *Orthotrichum gymnostomum*, and *Buxbaumia viridis* (in order of decreasing abundance), constituted 67% of all records. In the WKHs, 55% of the records were accounted for by *Orthotrichum gymnostomum*, *Acrocordia cavata*, and *Herzogiella turfacea* (Table 3).

The observed mean total number of species records per hectare was higher in WKHs than in production forests: 4.7 compared to 1.6. The range for the three study areas was 2.5–6.0 for WKHs and 0.9–2.4 for production forest (Table 3). In mature production forests (stands with a mean height of 15 m or more), the mean number of species records per hectare was 2.4, with a range of 1.1–4.2 between study areas.

### Floristic Differences between WKHs and Production Forests

Thirty-two species were recorded in WKHs and 21 in production forests. Fifteen species were unique to WKHs

**Table 3. Complete list of red-listed vascular plants, bryophytes, and lichens recorded in woodland key habitats and production forests in the three study areas.[a]**

| *Species* | *Red-list category* | *Total no. of records in production forest* | | | *Total no. of records in WKHs[b]* | | | *Mean no. of records ha$^{-1}$ in production forest* | | | *Mean no. of records ha$^{-1}$ in WKHs[c]* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *O* | *R* | *S* | *O* | *R* | *S* | *O* | *R* | *S* | *O* | *R* | *S* |
| Vascular plant | | | | | | | | | | | | | |
| *Dryopteris cristata* | cd | 1 | | | | 2 | 1 | <0.01 | | | | 0.1 | 0.1 |
| subtotal | | 1 | | | | 2 | 1 | <0.01 | | | | 0.1 | 0.1 |
| Bryophytes | | | | | | | | | | | | | |
| *Amblystegium saxatile* | cd | | | 1 | | | | | | <0.01 | | | |
| *Anastrophyllum hellerianum* | cd | 14 | | | 6 | 5 | 1 | 0.2 | | | | 0.2 | 0.1 |
| *Buxbaumia viridis* | cd | 12 | 2 | 21 | 5 | 2 | 3 | 0.2 | 0.1 | 0.6 | | 0.1 | 0.2 |
| *Calypogeia suecica* | cd | | | | | 2 | | | | | | 0.1 | |
| *Hamatocaulis vernicosus* | cd | | | | | 6 | | | | | | 0.2 | |
| *Herzogiella turfacea* | cd | 5 | 1 | | 4 | 14 | 7 | 0.1 | <0.01 | | | 0.5 | 0.4 |
| *Lophozia ascendens* | cd | 4 | | | | 1 | | 0.1 | | | | <0.01 | |
| *Neckera pennata* | vul | | 1 | | | | | | <0.01 | | | | |
| *Orthotrichum gymnostomum* | cd | 28 | 16 | 3 | 18 | 66 | | 0.5 | 0.4 | 0.1 | | 2.4 | |
| *O. pallens* | cd | | | | | 8 | | | | | | 0.3 | |
| *Plagiothecium latebricola* | cd | | | 3 | | | | | | 0.1 | | | |
| *Trichocolea tomentella* | cd | | | | | | 1 | | | | | | 0.1 |
| subtotal | | 63 | 20 | 28 | 33 | 104 | 12 | 1.0 | 0.5 | 0.8 | 1.8 | 3.8 | 0.7 |
| Lichens | | | | | | | | | | | | | |
| *Acrocordia cavata* | vul | 15 | 43 | 5 | 18 | 30 | 6 | 0.2 | 1.2 | 0.1 | 1.0 | 1.1 | 0.3 |
| *Arthonia cinereopruinosa* | end | | | | | | 1 | | | | | | 0.1 |
| *Biatorella monasteriensis* | cd | | | | 1 | 2 | | | | | 0.1 | 0.1 | |
| *Bryoria nadvornikiana* | cd | 1 | | | 1 | | | <0.01 | | | 0.1 | | |
| *Calicium abietinum* | vul | | | | 1 | | | | | | 0.1 | | |
| *Chaenotheca chlorella* | cd | 3 | | 1 | 9 | 2 | 5 | 0.1 | | <0.01 | 0.5 | 0.1 | 0.3 |
| *C. gracillima* | cd | 1 | | | 1 | | | <0.01 | | | 0.1 | | |
| *C. phaeocephala* | cd | | | | | | 2 | | | | | | 0.1 |
| *Cladonia parasitica* | cd | | | | 1 | | 1 | | | | 0.1 | | 0.1 |
| *Collema nigrescens* | cd | | 1 | | | | | | <0.01 | | | | |
| *C. occultatum* | vul | 1 | | | 1 | | | <0.01 | | | 0.1 | | |
| *C. subnigrescens* | cd | | 13 | | | 8 | | | 0.4 | | | 0.3 | |
| *Cybebe gracilenta* | vul | | | | | | 1 | | | | | | 0.1 |
| *Eopyrenula leucoplaca* | end | | | | | 2 | | | | | | 0.1 | |
| *Gyalecta flotowii* | cd | | | | | | 1 | | | | | | 0.1 |
| *Menegazzia terebrata* | rare | | | | | | 1 | | | | | | 0.1 |
| *Microcalicium ahlneri* | cd | 5 | | | 1 | 1 | 9 | 0.1 | | | 0.1 | <0.01 | 0.5 |
| *Nephroma laevigatum* | cd | 5 | 1 | | 16 | | | 0.1 | <0.01 | | 0.9 | | |
| *Phaeocalicium praecedens* | cd | 1 | 7 | | | 11 | | <0.01 | 0.2 | | | 0.4 | |
| *Phaeophyscia endophoenicea* | cd | | | | | 1 | | | | | | <0.01 | |
| *Phlyctis agelaea* | cd | | 2 | | | 2 | | | 0.0 | | | 0.1 | |
| *Schismatomma pericleum* | vul | | | | | | 2 | | | | 0.1 | | |
| *Sclerophora coniophaea* | cd | | 1 | | 2 | | | | <0.1 | | 0.1 | | |
| *S. peronella* | cd | | | | 2 | | | | | | 0.1 | | |
| subtotal | | 32 | 68 | 6 | 54 | 59 | 29 | 0.5 | 1.8 | 0.2 | 2.9 | 2.2 | 1.7 |
| Total | | 96 | 88 | 34 | 87 | 165 | 42 | 1.6 | 2.4 | 0.9 | 4.7 | 6.0 | 2.5 |

[a]*Abbreviations: cd, care-demanding; end, endangered; rare, rare; vul, vulnerable (Aronsson et al. 1995); O, Örsundsbro; R, Roslagen; S, Småland.*
[b]*Woodland key habitat.*
[c]*One record = presence in a 10 × 10 m quadrat along the line transect.*

and 4 to production forests. Of the 8 species belonging to the two highest categories of threat—endangered and vulnerable—7 were recorded in WKHs and 3 in production forests (Table 4).

The WKHs had significantly more total records of red-listed species than did production forests in all three study areas ($p = 0.008–0.017$), but there was large variation among species groups. The WKHs were significantly richer in bryophytes than were production forests only in Roslagen ($p = 0.005$). There were significantly more lichens in WKHs than in production forests in Örsundsbro ($p = 0.010$) and Småland ($p < 0.001$).

**Table 4. Number of red-listed species found in production forests and woodland key habitats (WKHs) in the three study areas of Örsundsbro, Roslagen, and Småland, Sweden.[a]**

| | *Production forest* | *WKHs[b]* |
|---|---|---|
| No. of red-listed species (vascular plants, bryophytes, lichens) | 19 | 31 |
| No. of unique species[c] | 5 | 16 |
| No. of species in threat categories of endangered or vulnerable[d] | 1 | 5 |

[a]*The surveyed area was 135 ha for production forest and 63 ha for WKHs.*
[b]*Woodland key habitats.*
[c]*Species occurring in WKHs or production forest only.*
[d]*Threat categories according to Aronsson et al. (1995).*

Because there were only four records of vascular plants in total, statistical testing of this species group was not possible (Table 5).

The differences were less pronounced when only records in mature production forests and in WKHs were compared (Table 5). For total number of species records, the WKHs seemed richer in Örsundsbro ($p = 0.053$) and Småland ($p = 0.057$), but no difference was revealed in Roslagen ($p = 0.533$). No significant differences were observed for bryophytes in any of the three study areas. There was a significant difference between lichens in Örsundsbro and Småland ($p = 0.010$ and $p < 0.001$, respectively).

### Forest Age

In the production forests, the distribution of forest age classes was similar between the three study areas: clearcuts represented 13% (Örsundsbro), 14% (Roslagen), and 11% (Småland); young forest 13%, 19%, and 11%; semimature forest 19%, 25%, and 34%; and mature forest represented 55%, 42%, and 45%. Of all records made in the production forests, 70% were in mature forest, 21% in semimature stands, 5% in young stands, and 3% in clearcuts (Fig. 3). In comparison with the lichens, bryophytes tended to be more confined to the older stands. There was an overrepresentation of species records in the mature forests (df = 3, $\chi^2 = 22.2$, $p = 0.001$). All except one of the WKHs were mature forests, so forest age was of minor importance.

## Discussion

### Rarity of Red-Listed Forest Species

The majority of the red-listed plant species were very rare in production forests and WKHs. Ninety-six percent of the vascular plants, 68% of the bryophytes, and 76% of the lichens belonging to a forest environment—classified as nationally red-listed and earlier reported from the counties in which the three study areas were located—were not found during this study. This suggests that if WKHs and areas of production forest are to be protected to safeguard red-listed species, it is important to concentrate on known sites and to increase the effort in making detailed surveys of rare species. Many populations are probably so small that they will require special management plans for their preservation.

### Red-Listed Plant Species in Production Forests

By implication, red-listed plants are assumed rare, but some species were surprisingly common in this study, with a high average number of records per area. Mean numbers of records per hectare in the production forest

**Table 5. Statistical comparison (Wilcoxon two–sample test) of the number of records of species belonging to different species groups in woodland key habitats (WKHs) and production forests of combined age classes and in woodland key habitats and mature production forests (>15 m mean height) in Sweden.**

| *Comparison and species group* | *Örsundsbro* | | *Roslagen* | | *Småland* | |
|---|---|---|---|---|---|---|
| | z | p | z | p | z | p |
| WKHs vs. combined age-class forest | | | | | | |
| bryophytes | 0.91 | 0.362 | 2.83 | 0.005 | −1.42 | 0.156 |
| lichens | 2.57 | 0.010 | 0.46 | 0.643 | 3.69 | <0.001 |
| vascular plants* | — | — | — | — | — | — |
| Total | 2.39 | 0.017 | 2.64 | 0.008 | 2.60 | 0.009 |
| WKHs vs. mature forest | | | | | | |
| bryophytes | 0 | 1.0 | 1.57 | 0.117 | −1.35 | 0.179 |
| lichens | 2.59 | 0.010 | −0.27 | 0.791 | 3.65 | <0.001 |
| vascular plants* | — | — | — | — | — | — |
| Total | 1.93 | 0.053 | 0.59 | 0.553 | 1.90 | 0.057 |

**Only four records of vascular plants were made, so statistical testing for this species group was not possible, but the data were included in the comparison of total records.*

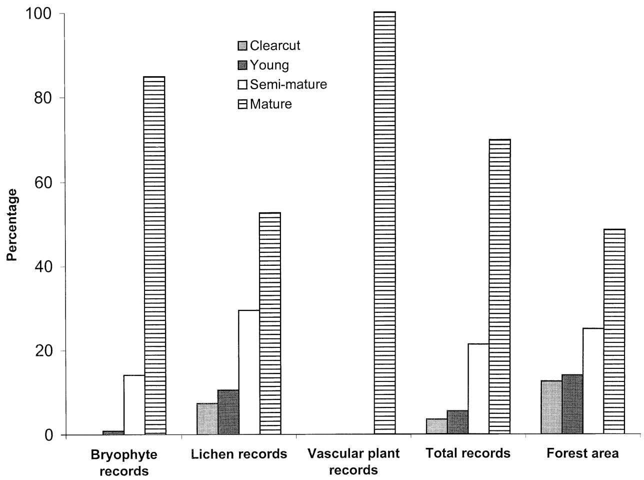


*Figure 3. Percentage of records of red-listed species found in different age classes in the production forest and the percentage of area of the four forest-age classes surveyed. Calculations are based on records of 111 bryophytes, 106 lichens, and 1 vascular plant in 135 ha of forest.*

ranged from 0.9 to 2.4. I did an analysis of running mean (mean number of records per study plot plotted with increasing sample size) (Chapman 1976). For all three study areas together, the curve stabilized at approximately 30 out of a total 50 study plots. This indicates that extrapolation to larger areas should be valid. Such extrapolations suggest that there could be approximately 20,000 occurrences of red-listed plant species in Örsundsbro (250 km$^2$), 30,000 in Småland (600 km$^2$), and more than 70,000 in Roslagen (500 km$^2$), given a proportion of productive forest land of 60% in each area.

As a mathematical exercise, the amount of area considered could be expanded to comprise the three counties, Uppsala, Stockholm, and Jönköping, in which the study areas are located. Calculated in this manner, the number of occurrences of red-listed vascular plants, bryophytes, and lichens could amount to more than 2 million for a forest area of 14,000 km$^2$. Should extrapolation be made to the whole hemiboreal vegetation zone, the number of records would be several million. These calculations should be treated with caution, however. The density of red-listed plants could vary between geographical areas to a larger degree than revealed by my results, although I selected areas to represent a range of densities of red-listed species from high (Roslagen) to moderate (Örsundsbro) to low (Småland).

A few red-listed species accounted for most of the records: 70% of the records in the production forests derived from only three species. The populations of these species seem to be very large in the study areas. The extrapolated number of occurrences in all three study areas (1,350 km$^2$) was 38,000 for the epiphytic lichen *Acrocordia cavata*, 28,000 for the epiphytic bryophyte *Orthotrichum gymnostomum*, and 21,000 for the dead-wood bryophyte *Buxbaumia viridis.* There were large differences between study areas in the abundance of these species, however: *B. viridis* was most common in Småland, for instance, but *O. gymnostomum* seemed unusual in this area.

My study was based on the Swedish Red List of 1995; a new one has since been published (Gärdenfors 2000). In the new list, classification according to threat categories has been done more objectively than before, with estimation of extent of occurrence, population decline, and probability of extinction in different time perspectives (World Conservation Union 1994). In some cases, fulfillment of one criterion can be sufficient for a red-list classification, but often several criteria in combination are used. For example, a species is qualified for the red list if it has a population of less than 1000 individuals. Qualification is also fulfilled if a species has less than 10,000 individuals and at the same time has a decreasing total population. Of the species recorded in this study, the lichens *Acrocordia cavata*, *Chaenotheca chlorella*, *C. phaeocephala*, *Microcalicium ahlneri*, *Phaeocalicium praecedens*, *Phaeophysica endophoenicea*, and *Phlyctis agelaea* have been removed from the new list. Although some species have been removed, the number of red-listed species in forests has increased from 66 to 84 species for vascular plants, 74 to 102 species for bryophytes, and 159 to 209 species for lichens. My results would not change much for the bryophytes or vascular plants if the new red list had been used instead of the former one. But radical changes would occur for the lichens because of the high abundance of *Acrocordia cavata*, which has been removed from the 2000 Red List. The total number of records for the red-listed lichens then would be 77% less for the production forests and 61% less for the WKHs calculated for all three study areas together. One must take into account, however, that this change might have been compensated for by occurrences of new species on the 2000 Red List, not recorded in my study.

Indicator species were used as one tool with which to select the WKHs in the national survey, and a few of these are also red-listed species. Thus, there is a risk that from the beginning the study was biased towards a higher number of red-listed species in the WKHs. But the protocols of the local forestry boards, which conducted the national WKH-survey, show that only three taxa of red-listed species were recorded: the bryophytes *Anastrophyllum hellerianum* and *Buxbaumia viridis* and one lichen, *Collema* sp. (eight occurrences). These occurrences amounted to 3% of all records of red-listed species, so the risk of bias should be minimal.

### Differences in Abundance among Species Groups

Large differences were discovered between the abundance of red-listed vascular plants and that of bryophytes and lichens. For Sweden as a whole, the proportion of all forest species that are red-listed is similar for vascular plants (17%), bryophytes (25%), and lichens (20%). Consequently, my results indicate that there may be different levels of discrimination in the selection of species to be included on the red list. Expert committees on the different species groups compile the lists, and because knowledge of vascular plants is considerably better than that of the bryophytes and lichens, the cryptogam committees might prudently include more species. Another explanation might be that the cryptogams generally seem more threatened by forest operations, because many of them depend on deciduous trees, old trees, and dead wood (Berg et al. 1994). Many red-listed vascular plants apparently can tolerate a certain degree of logging, and some may even be promoted by the opening up of stands (Berg et al. 1994; Gustafsson 1994).

The quality of the red lists is continuously improved through regular revisions and incorporation of new knowledge. Still, there are likely many misjudgements because data on the ecology and distribution of most species are scarce. If large-scale monitoring of rare species in forested landscapes was performed at regular intervals, with methodology similar to that in my study, it would be possible to discern species that ought to be removed from the lists, and species that are qualified to be included.

### WKHs versus Production Forests

The nation-wide survey performed by the National Board of Forestry has identified approximately 40,000 WKHs to date; in total, it is estimated there are about 70,000 in the country (National Board of Forestry 1998, 1999). Although numerous, they cover <1% of the productive forest land. The WKHs have no legal protection but at present usually are set aside voluntarily by both small and large forest owners. The National Board of Forestry has recently received increased governmental funding to protect WKHs, with the restriction that they must not be larger than 5 ha. But because the funding is limited, only a small number of such "biotope protection areas" can be established. Nature reserves and national parks are other instruments of protection but are usually localized to large, continuous tracts of old forests, and here too funding is limited. In all, little forest is protected in Sweden—beneath the mountain region <1% of the productive forest land (National Board of Forestry 2000).

It is hard, based on this study, to evaluate the significance for the red-listed species of larger protected areas. It is likely that they are a prerequisite for species with large area demands such as certain bird and mammal species. One challenge for future research is to compare the abundance of red-listed species belonging to different species groups in landscapes with different spatial patterns of protected forests (landscapes with a few large set-aside areas and others with numerous small ones in a matrix of managed forests). Balances between values for biodiversity and forest production then could also be assessed.

Because the purpose of WKHs is to secure sites for red-listed species, it is vital to evaluate their role for these species. My results suggest that the abundance of red-listed plant species is significantly higher in WKHs than their average abundance in the different forest age classes of the production forests, and only slightly higher than in the mature stage. Although the area of WKHs investigated was less than half that of production forest, the number of species present was considerably higher, 32 compared with 21. In addition, the number of species in the highest threat categories, endangered and vulnerable, was greater in WKHs (seven) than in production forests (three). Thus, apart from containing higher numbers of red-listed species, the WKHs also seem to host more species classified as more threatened than do the production forests.

Because WKHs cover a very small area, they alone cannot safeguard the future of red-listed species. In conservation planning, the WKHs must be considered in combination with the matrix—the production forest—which in Sweden amounts to more than 95% of all productive forest land. Conservation actions in forestry, such as tree retention, set-aside of small groups of trees, prolonged rotations, and creation and protection of border zones along lakes and watercourses should ideally be planned with the WKHs in mind. Enlargement of WKHs in many cases would be an efficient conservation measure. The surroundings can be rapidly restored in some cases by burning or flooding. The properties and qualities of the matrix are important to consider when WKHs are selected for protection and restoration. It is not unlikely that the best model for the long-term preservation of forest biodiversity would be to have a number of protected WKHs, a few nature reserves large enough to allow a natural disturbance regime, and a matrix with pronounced retention of structures such as old trees and dead wood.

The National Board of Forestry estimates that as many as 50% of the WKHs could have been missed during the national inventory (National Board of Forestry 1995*b*). Thus, there was a risk that such sites would be encountered during the line-transect analysis in the production forests. But species surveyors, who were instructed to note such missed WKHs, found them infrequently. Thus, the risk was small that the abundance of red-listed species in the production forests was overestimated.

### Invertebrates and Fungi

Vascular plants, bryophytes, and lichens constitute only approximately 20% of all red-listed forest species. The largest groups are invertebrates, with approximately

55% of the species, and fungi, with approximately 25% (Gustafsson & Ahlén 1996). To evaluate the quality of WKHs for red-listed species, these large species groups should also be investigated. Many fungal fruiting bodies are annual, and populations fluctuate with seasonal weather conditions. It would be possible, however, to study the long-lived bracket fungi (Polyporaceae in a wide sense) that grow on wood. Collecting invertebrates is time-consuming and poses sampling difficulties. For example, some types of traps capture the invertebrate fauna over a larger area than required for examination of WKHs. The methodology for identifying WKHs seems to be biased toward sites with red-listed plants, because the structural criteria used in the national WKH survey are focused on old-growth conditions, which cryptogams seem to prefer. However, extensive areas in the natural forest landscape were composed of early successional stages. Conservation of the flora and fauna associated with these phases also needs to be addressed.

### Implication for Forestry, Including Certification

The most important implication of my study for production forestry is the significance of managed forests for red-listed species. If the sites of red-listed species are to be preserved, consideration of the habitat requirements of the species is necessary in daily forest operations. Data on the substrates of the red-listed species recorded in my study suggest that the presence of deciduous trees and dead wood is vital for many red-listed plant species. Retention of tree groups and creation of dead wood are new conservation methods, recently introduced into Nordic (e.g., Vanha-Majamaa & Jalonen 2001), North American, and Australian forestry (e.g., Lindenmayer & Franklin 1997). The results support the importance of these measures for red-listed plant species. A central question in conservation-orientated forestry is how natural forest dynamics can best be mimicked (e.g., Niemelä 1997; Seymour & Hunter 1999; Simberloff 2001), and a future challenge for research is to assess the amounts of natural-forest characteristics, at stand and landscape levels, necessary to maintain viable populations of rare forest species.

The fate of present populations of red-listed species also depends, to a large degree, on how successfully these species survive forest thinning and final harvest. Because a large number of the species recorded are found in stands soon to be harvested, clearcutting could dramatically reduce their population size. It is important for conservation biology researchers to investigate the extent to which the species in the old stands can disperse to younger stands, and their potential to survive on retained tree groups.

Thirty to forty percent of Swedish productive forest land has been certified as meeting the national standard set by the Forest Stewardship Council (FSC). The first certification was approved in 1997, so it is too early to expect any positive effects on biodiversity. The paragraph in the Swedish national FSC standard that relates to sites for red-listed species states that such sites should be considered in all forest operations and on all forest land (Forest Stewardship Council 2001). Using my data, I can calculate the area that would be affected by conservation actions for the investigated taxa. If each red-listed species occurrence required a $10 \times 10$ m protective zone, then between 1% and 2% of the forest land would be affected. If a $30 \times 30$ m protective zone is required, the area affected would increase to between 8% and 19%. If only the mature forest is considered, the proportions would be as large as 9% to 36%. However, probably none of the landowners in the study areas were aware of the sites of red-listed species. Bryophytes and lichens are far too difficult for inexpert people to identify.

## Conclusions

Most red-listed forest vascular plants, bryophytes, and lichens are rare, but some species have surprisingly large populations. Red-listed forest lichens and bryophytes are considerably more common than red-listed forest vascular plants. The red-listed species are not homogeneously distributed, being confined largely to mature stands and associated with deciduous trees and dead wood. Production forests are important for the continued existence of red-listed plant species. Extrapolation to large areas indicates that the number of occurrences of red-listed species is high, probably in the range of millions in southern Sweden. Present management systems, including retention of trees and tree groups and other biodiversity considerations, could be critical for the long-term survival of red-listed species. The WKHs are richer than production forests in terms of both the presence and abundance of red-listed plants but, because they cover <1% of the productive forest land, they alone cannot guarantee the long-term preservation of these species. Instead, conservation strategies must consider WKHs and production forests in combination.

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