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Threatened Plant, Animal, and Fungus Species in Swedish Forests: Distribution and Habitat Associations

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Abstract: *Swedish forestry is among the most technically developed in the world; a large part of all forest is used for commercial forestry, which has had a large impact on the structure and function of forest ecosystems. We have compiled present knowledge on the distribution and habitat associations of 1487 threatened forest species in Sweden, made an attempt to identify structures and elements that are critical for their occurrence, and suggest guidelines for the*

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Especies de plantas, animales, y hongos en peligro en bosques Suecos: distribución y asociacines de hábitats

Resumen: *La silvicultura sueca es una de las más avanzadas en el mundo técnicamente. La mayor parte de los bosques en Suecia son utilizados en forma comercial, lo cual influye en forma significativa sobre su estructura y su funcionamiento. En el presente trabajo hemos reunido la información disponible en la actualidad sobre la distribución y los hábitats de 1487 especies en peligro que habitan en los bosques suecos. Además, hemos hecho una primera identificación de las estructuras y los elementos del bosque críticos para la existencia de estas especies y finalmente, hemos* *maintenance of threatened forest species. Habitat associations and distribution patterns of the threatened species were roughly the same for all organism groups. A significantly higher proportion of the 1487 species in all organism groups (cryptogams, vascular plants, invertebrates, and vertebrates) were found in the south (temperate/hemiboreal region) than in the north (hemiarctic/boreal region) of Sweden. For each organism group, the southern deciduous forest contained the most threatened species. Coniferous forests and other deciduous forests were also relatively species-rich, while deforested areas and scrub areas were the least species-rich habitats for the studied species. Most groups were dependent on specific elements in the habitat, which all were characteristic of old forests. Old living trees (especially deciduous trees) were critical for vertebrates, invertebrates, and cryptogams. Logs were critical for invertebrates and cryptogams. Snags were especially important for invertebrates and to some extent for vertebrates and cryptogams. Vascular plants were more dependent on abiotic factors and stand/site-related factors, such as forest density and forest age, than were the other groups. All groups, however, were largely dependent on old forests or habitat elements associated with old forests. The threatened populations of forest species of international importance (supposed endemics to Scandinavia or with more than 10% of the European population in Sweden) were found to a relatively large extent in coniferous forests in the north of Sweden, while the other threatened species were more restricted to deciduous forests in the south.*

algunas recomendaciones para la conservación de aquéllas especies amenazadas de extinción. En general, las preferencias de hábitat y los patrones de distribución de las especies amenazadas fueron los mismos para todos los grupos de organismos considerados (criptógamas, plantas vasculares, vertebrados e invertebrados). Una mayor proporción de las especies estudiadas estuvieron distribuidas en el sur, en la región templada/semiboreal que en el norte (región semiártica/boreal) y, para todos los grupos de organismos, el bosque caducifolio del sur fue el hábitat con la mayor cantidad de especies amenazadas. La riqueza específica fue también relativamente alta en el bosque de coníferas y en otros bosques caducifolios, mientras que las áreas deforestadas y con matorral fueron los hábitats con menos riqueza. La mayoría de los grupos dependieron, para su presencia, de elementos específicos del hábitat, los que fueron en todos los casos, aquéllos característicos del bosque maduro. Los árboles añosos, con vida (en particular los de hojas caducas) resultaron críticos para los vertebrados, los invertebrados y las criptógamas; mientras que los troncos caídos lo fueron para los invertebrados y las criptógamas. A su vez, los tocones fueron particularmente importantes para los invertebrados y, en menor medida, para los vertebrados y las criptógamas. Las plantas vasculares dependieron más que los otros grupos de los factores abióticos y de aquéllos relacionados con un sitio en particular (densidad y edad del bosque). En general, todos los grupos de organismos fueron significativamente dependientes del bosque maduro. Las especies del bosque amenazadas y con poblaciones con importancia internacional (las especies consideradas endémicas de Escandinavia y aquéllas con más del 10% del total de la población europea, en Suecia) fueron encontradas, en su mayoría, en el bosque de coníferas del norte de Suecia; mientras que el resto de las especies amenazadas estuvieron más restringidas al bosque caducifolio del sur.

Introduction

Interest in conservation biology and threatened species has been growing during recent years, but the biology of rare organisms has long attracted the attention of biologists (see Griggs 1940; Preston 1948). Recent studies have focused on the spatial distribution of rare species (see Schoener 1987; Hanski 1982; Brown 1984) and factors important for determining risk of extinction (see Terborgh & Winter 1980; Goodman 1987; Pimm et al. 1988; Laurance 1991). Studies of biological characteristics, habitat associations, and distribution of threatened species have usually considered only a few organism groups (see Laurila & Järvinen 1989; Lahti et al. 1991) and have been restricted to small areas (see Hodgson 1986). General studies of the biology and distribution of all threatened organism groups in larger areas, which are important for nature conservation, are lacking (see, however, Rassi & Väisänen 1987).

The "Red lists" of threatened animals and plants, in which species are classified into different threat categories as defined by the International Union for the Conservation of Nature (1988), are important tools for the conservation of threatened species, even if the current classification system is under debate (Mace & Lande 1991). In most countries, these lists are incomplete, and knowledge about small organisms (such as fungi, bryophytes, lichens, and invertebrates) is often lacking, because these groups have largely been neglected by biologists (Synge 1981; Wilson 1987). In Sweden, however, knowledge of the fauna and flora is relatively good, and there is a relatively long tradition of compiling red lists, starting with Ahlén (1975). Swedish red lists include most macro-organism groups (except algae) and are relatively well documented, even if detailed knowledge of many invertebrates and cryptogams is still lacking.

Forests are the main terrestrial habitats in Sweden, and Swedish forestry is among the most efficient and technically developed in the world (Gamlin 1988); 95% of Swedish forests are being used for commercial purposes. This has resulted in a decrease of many populations of forest species, and forest habitats are therefore of great interest in discussions of how to maintain high biodiversity in Sweden. It is important to find general guidelines for the conservation of threatened species, and Swedish red lists could be useful for this purpose. We have therefore compiled present knowledge of all forest plant, animal, and fungal species included in the Swedish red lists. This knowledge is relatively poor for some species, and our data are based on the opinions of experts when specific investigations are lacking. The aim of this study was to investigate the habitat associations and distribution of the 1487 threatened forest plant, animal, and fungal species (all threatened species found mainly in forests were included) and to identify structures and elements that are critical for their occurrence in Sweden. We also suggest some guidelines for the future protection of forest areas and modifications of forest management that are important for maintaining populations of threatened forest species in Sweden.

Methods

Sweden—A Brief Description

Sweden, with a total land area of about 411,000 km^2, is dominated by forests that cover 59% of the total land area. Mires (11.4%) and alpine habitats (9.3%) cover a relatively large part of the country. Farmland, covering 8.9% of total land area, is also a relatively important habitat, especially in the south of Sweden (Official Statistics of Sweden 1991; see also Nilsson & Götmark 1992 for details). Sweden crosses a wide range of vegetation zones, from the temperate zone in the south to the hemiarctic zone in the northwest, including the hemiboreal and the southern, middle, and northern boreal zones (Ahti et al. 1968). There is a pronounced biogeographical borderline (Limes Norrlandicus) between boreal forests in the north and mixed agricultural land and hemiboreal/temperate forests in the south (Fransson 1965). A large part of the country is now dominated by boreal coniferous forests, but other types have dominated during periods after the latest glaciation about 10,000 years ago (Sjörs 1965). Thus Swedish landscapes are relatively young, and the number of endemic species is low. Species are still invading (see Järvinen & Ulfstrand 1980), perhaps due to habitat changes.

Forests in southern Sweden have been used for commercial purposes during the last 400 years (Mattson & Stridsberg 1980), but utilization of forest resources started long before that (Tenow 1974). Of the 23.5 million ha of forest in Sweden, only 2% are virgin forest, the main part of which occur in northern Sweden (Official Statistics of Sweden 1990). Modern forestry practice has created monospecific, even-aged stands with short rotation periods, and clear-cutting regimes have dominated forest management during recent decades. Forest management has had large effects on the Swedish flora and fauna, and many species have declined in number (Ehnström & Waldén 1986; Ingelög et al. 1987; Ahlén & Tjernberg 1992).

Selection of Species and Data Collection

Information was collected on the biology and distribution of 1487 threatened species, including some subspecies and varieties, occurring in Swedish forests (also species that have vanished during the last century). Of these species, 636 were cryptogams (437 macrofungi, 137 lichens, and 62 bryophytes), 739 invertebrates (507 beetles, 120 moths and butterflies, 45 flies, 27 wasps and ants, 18 bugs, 14 snails, 2 lacewings, 1 spider, 4 pseudo-scorpions, and 1 wood lice), 59 vascular plants (53 phanerogams and 6 vascular cryptogams), and 53 vertebrates (35 birds, 12 mammals, 4 frogs, and 2 reptiles). These species have been classified into threat categories by the Swedish Threatened Species Unit at the Swedish University of Agricultural Sciences in Uppsala as follows: Ex (extinct), E (endangered), V (vulnerable), R (rare), as defined by International Union for the Conservation of Nature (1988). However, a fifth category Cd (care-demanding) was also included (Table 1). Species categorized as care-demanding are relatively common, but they are declining in number and therefore require attention, for instance in forestry or farming.

Information on the threatened species was collected from literature, from interviews with experts on different organism groups (a total of about 40 experts), and from data stored at the Swedish Threatened Species Unit at the Swedish University of Agricultural Sciences in Uppsala. Ahlén and Tjernberg (1992) was a valuable data source for vertebrates, Ingelög et al. (1987) for vascular plants and cryptogams, and Ehnström and Waldén (1986) for invertebrates. For many species there are no detailed investigations of habitat associations,

Table 1. Number of species in different threat groups.

Organism Group	*Threat Group*					
	Ex	*E*	*V*	*R*	*Cd*	*All*
Cryptogams	31	128	133	230	114	636
Vascular plants	3	5	13	20	18	59
Invertebrates	30	100	223	110	277	739
Vertebrates	3	4	8	11	27	53
Total	67	237	377	371	436	1487

Ex = extinct species, E = endangered, V = vulnerable, R = rare, and Cd = care-demanding species.

current distribution and population size, and so forth. Thus, our data to a large extent are based on the opinions of experts on different organism groups. Some organism groups are better known than others, and therefore valuable information might be lacking for some groups. Because conservation of biodiversity is an urgent task, however, it is also important at this stage to identify factors crucial for the conservation of threatened species.

Distribution in Sweden

Sweden was divided into six main regions (Fig. 1), and the species were classified as occurring in a region when at least 5% of the Swedish population was estimated to be found in that region. This restriction was used to exclude small, isolated populations from the analyses of distribution. These six regions were grouped into the hemiarctic/boreal zone (regions 1–3, north of Limes Norrlandicus) and the temperate/hemiboreal zone (regions 4–6, south of Limes Norrlandicus). To separate species for which the occurrence in Sweden was of international importance, they were divided into three groups. These were (1) species from which less than 10% of the European population is in Sweden, (2) species for which more than 10% is in Sweden, and (3) species supposed to be endemic to Scandinavia. This was mainly estimated from range data, because density data are lacking for most of the studied species. The last two groups were classified as having populations of international importance in Sweden. Ideally, internationally important Swedish populations should have been defined in relation to the species' occurrence in biomes, but due to lack of data this was not possible.

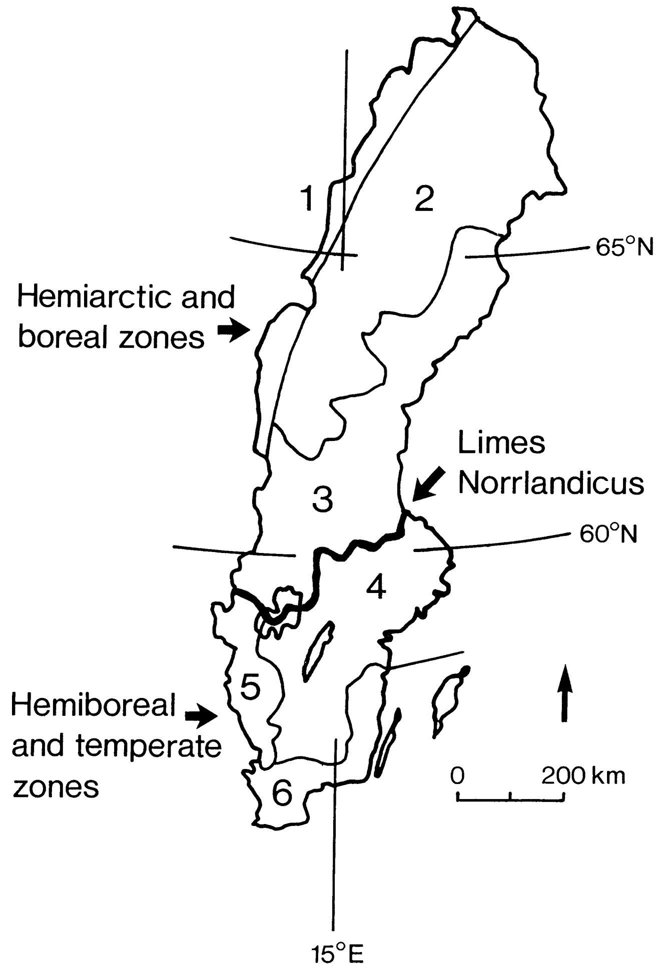

Figure 1. The division of Sweden into six main regions: (1) the alpine zone, (2) Norrbotten and Västerbotten administrative provinces (inland parts) and Jämtland administrative province, (3) Västerbotten (coastal parts), Västernorrland, Kopparberg, Gävleborg, and Värmland administrative provinces, (4) Stockholm, Uppsala, Västmanland, Örebro, Södermanland, Östergötland, Jönköping, Skaraborg, and Kronoberg administrative provinces, (5) Halland, Älvsborg, Göteborg, and Bohus administrative provinces, (6) Malmöhus, Kristianstad, Kalmar, Gotland, and Blekinge administrative provinces. Regions 1–3 are grouped to the hemiarctic/boreal region north of Limes Norrlandicus, and regions 4–6 are grouped to the temperate/hemiboreal region south of Limes Norrlandicus.

Water and Light Conditions

Each species was categorized as associated with dry, mesic, damp, or wet ground. Unsaturated lateral water flow in the upper soil layers was categorized as occurring never/seldom, during short periods, or during long periods at sites where a species occurred. All species were categorized as associated to open-sunny sites, semi-shade, or shade. The species could also be categorized as indifferent to or with unknown preferences for water and light conditions.

Habitat Associations

The occurrence of the studied species in different habitats was first recorded in a detailed hierarchical system of about 125 habitat categories (only categories of higher levels, listed in the Appendix, are used here), comprising mainly forest habitats but also scrub, bogs, farmland, and so forth. Deciduous forests were divided into two main categories. Southern deciduous forests included oak (*Quercus robur* and *Q. petraea*), elms (*Ulmus glabra*), ash (*Fraxinus excelsior*), lime (*Tilia cordata*), maple (*Acer platanoides*), and beech (*Fagus sylvatica*). Other deciduous forests (found throughout Sweden) included birch (*Betula pubescens* and *Betula pendula*), aspen (*Populus tremula*), and alder (*Alnus glutinosa* and *Alnus incana*). The forest categories used were compatible with the ones used by the Swedish National Forest Inventory, which made it possible to use data of areas of different forest habitats. Each species could be categorized as occurring in a maximum of three habitats, and habitat generalists were usually categorized as occurring in habitats of a higher level in the hierarchical system.

Critical Factors

We also tried to determine the factors that were most critical for the distribution and occurrence of the 1487 species in Sweden. These factors included abiotic factors unrelated to forest management, such as large-scale climate, calciferous soil, and clean air or water. Several biotic factors highly related to forest management, such as the stand/site related factors of forest density and forest age, and the occurrence of specific habitat elements such as logs, snags, and old trees, were also included (see Table 2). A maximum of two factors could be assigned as critical for each species, in order to determine the most important factors for the distribution and occurrence of the studied species.

Results

Taxonomic Groups

It is striking that vascular plants and vertebrates, the taxa that conservationists usually pay attention to, are few in the Swedish red lists compared to cryptogams and invertebrates (Table 1). Among the most important groups (endangered and vulnerable), there are only 18 vascular plants and 12 vertebrates, compared to 584 cryptogams and invertebrates (Table 1).

Table 2. Factors of importance for the occurrence and distribution of the studied species.*

Stand/Site Factors
Forest age
Forest density (dense or open forest)
Burned forest
Grazed or cut farmland within forests
High air moisture
Undisturbed hydrology
No fertilizers
Habitat Elements
Old trees (coniferous or deciduous)
Logs (0–5, 5–50, or >50 years old)
Snags (0–5, 5–50 or >50 years old)
Host/prey species
Others (such as boulders)
Abiotic Factors
Clean air/water
Calciferous soil
Large-scale climate

These factors were divided into three main groups: stand/site factors, habitat elements (both groups influenced by forest management), and abiotic factors (not influenced by forest management).

Distribution of Threatened Species in Sweden

There were large differences in the number of threatened species within different parts of Sweden. More threatened species occurred in the south (the hemiboreal and temperate regions) than in the north (the hemiarctic and boreal regions), despite a lower proportion of the total Swedish forest area being found in the south than in the north of Sweden (Fig. 2). Of the species, 59% occurred only in the hemiboreal/temperate region and 11% only in the hemiarctic/boreal region, while the remaining 30% occurred in both regions. Also, when tested within the four main organism groups (cryptogams, invertebrates, vascular plants, and vertebrates), the proportion of threatened species that occurred in the south was higher than the proportion that occurred in the north of Sweden for all four taxa (Table 3).

The threats to these species seemed to be more severe in the south, because there was a higher proportion of extinct species in the temperate/hemiboreal region (4.2% of threatened species) than in the hemiarctic/boreal region (1.8% of threatened species) ($G = 8.2$, df $= 1$, $p < 0.01$). All organism groups were combined because the proportion of extinct species did not differ between organism groups ($G = 0.7$, df $= 3$, $p > 0.8$). The proportion of the extinct species ($n = 61$) that occurred in the hemiboreal/temperate region (83.6%) was also significantly higher than that in the hemiarctic/boreal region (16.4%, $G = 66.1$, df $= 1$, $p < 0.001$).

The proportion of endangered and vulnerable species (threat categories E + V) was also significantly higher in the temperate/hemiboreal region than in the hemiarctic/boreal region of Sweden for cryptogams and in-

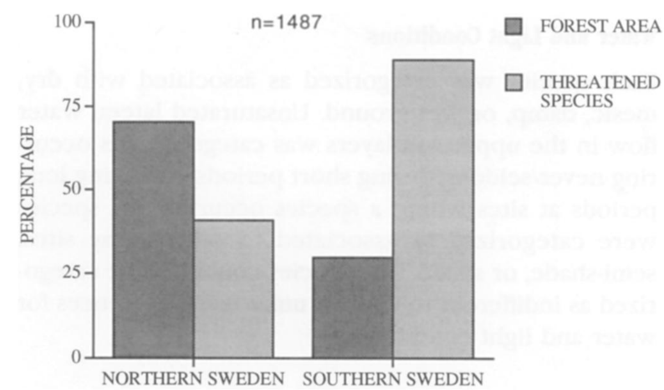

Figure 2. The proportion of the 1487 threatened forest species and percentage of total Swedish forest area in the hemiarctic/boreal (regions 1–3) and temperate/hemiboreal regions (regions 4–6) of Sweden. Significantly more threatened species were found in southern than northern Sweden (log-likelihood ratio chi-square test, G = 807.3, df = 1, p < 0.001), despite that the smaller forest area in the south region was not taken into account.

Table 3. Proportion (%) of threatened cryptogams ($n = 636$), invertebrates ($n = 739$), vascular plants ($n = 59$), and vertebrates ($n = 53$) occurring in the south (temperate/hemiboreal region) and the north (hemiarctic/boreal region) of Sweden.

Group	*South*	*North*	*G-value*	*P-value*
Cryptogams	86.9	43.2	282.9	<0.001
Vascular plants	71.2	44.1	8.9	<0.001
Invertebrates	92.7	37.2	554.5	<0.001
Vertebrates	77.4	58.5	4.2	<0.05

Differences in forest area between regions was not taken into account. G-values from log-likelihood ratio chi-square tests with df = 1.

vertebrates (Fig. 3). The tendency was the same for vertebrates (not significant), while vascular plants showed no clear trend (Fig. 3).

Habitat Associations

The most important habitats for the studied species were, by definition, forest habitats. But a relatively large proportion (30%) of the threatened species was also found in other habitats. There were, however, large differences between organism groups. A high proportion of the vertebrates and of the vascular plants was found in habitats other than forest (Fig. 4). The nonforest habitat with the most threatened species was urban and agricultural land, where 22% of the 1487 species occurred; steep slopes, where 4.8% of the studied species occurred, were also of some importance.

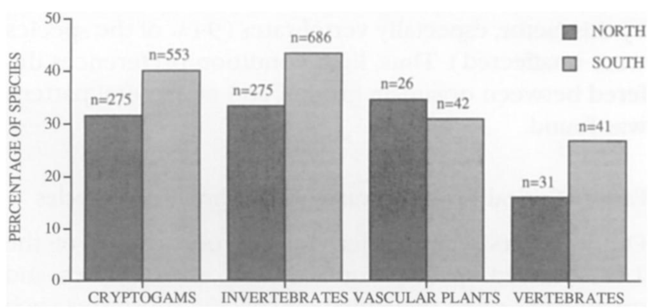

Figure 3. The proportion of threatened species classified as endangered or vulnerable was significantly higher in the temperate/hemiboreal than in the hemiarctic/boreal region of Sweden for cryptogams (log-likelihood ratio chi-square test, $G = 7.3$, $df = 1$, $p < 0.01$) and for invertebrates ($G = 8.1$, $df = 1$, $p < 0.01$). The tendency was the same for vertebrates, but the difference was not significant ($G = 1.2$, $df = 1$, $p > 0.2$), while vascular plants showed no clear trend ($G = 0.1$, $df = 1$, $p > 0.7$). Organism groups were not pooled because the proportion of endangered and vulnerable species differed between groups ($G = 55.7$, $df = 3$, $p < 0.001$).

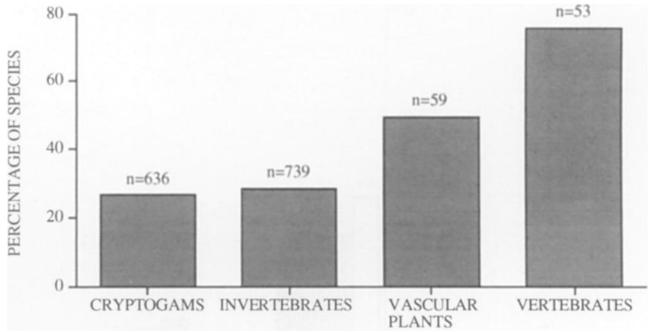

Figure 4. Proportion of threatened species in different organism groups also occurring in main habitats other than forests (urban & agricultural land, steep slopes, wetlands, and bogs). There were significant differences between organism groups in occurrence in nonforest habitats (log-likelihood ratio chi-square test, $G = 66.8$, $df = 3$, $p < 0.001$).

Habitat associations differed between regions. The proportion of invertebrates found only in forest habitats differed between species restricted to the hemiarctic/boreal region (98% only in forest) and species restricted to the temperate/hemiboreal region (65% only in forest, $G = 35.1$, df $= 1, p < 0.001$), but for the other three organism groups there were no such differences (all $p > 0.5$). Urban and agricultural land were the nonforest habitats with the most threatened species in the south of Sweden (28%), while steep slopes (12%) and wetlands (10%) were the nonforest habitats with the most threatened species in the north of Sweden.

The main forest habitats with most of the 1487 species were, in order of decreasing importance, southern deciduous forest (56%), coniferous forest (31%), other deciduous forest (23%), and mixed forest (12%). The main forest habitats with the fewest species were scrub (3.2%) and deforested areas (2.4%). These main patterns of habitat associations were about the same for all four organism groups (Fig. 5); deciduous forests and mixed forests were especially important if the areas of different forest habitats in Sweden were taken into account (Fig. 5). Among specific southern deciduous forests, forests with oak (where 16% of all species occurred) and beech (9.3%) were important for the threatened species. However, many species in southern deciduous forests occurred in mixed deciduous forests (22%) or in several types of specific southern deciduous forests (26%). The coniferous habitat with the most threatened species was forest with Norwegian spruce (*Picea abies*), where 18% of all species occurred, while 10% of all species occurred in forests with Scots pine (*Pinus sylvestris*). Forests with birch (8.7%), alder (7.7%), or aspen (7.0%) were of about the same importance among other deciduous forests.

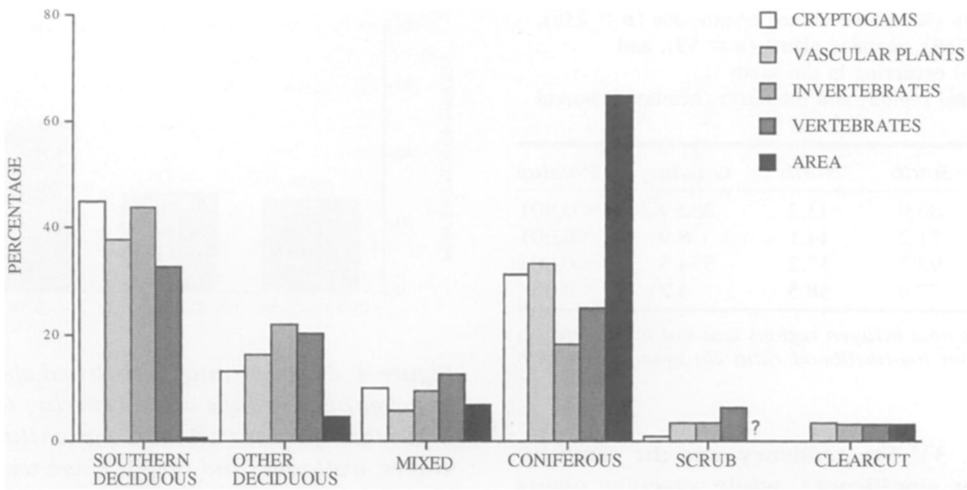

Figure 5. Proportion of threatened forest cryptogams, vascular plants, invertebrates, and vertebrates occurring in different forest habitats in relation to area of forest habitat. There were significant differences between organism groups in occurrence in different habitats (log-likelihood ratio chi-square test, $G = 113.0$, *df = 15,* $p < 0.001$*).*

Water and Light Conditions

Most species preferring specific moisture conditions occurred on mesic ground (32% of all species); the most extreme soil-water conditions, dry (7.5% of all species) and wet ground (8.5% of all species), were less important for the threatened forest species. There were, however, differences between organism groups ($G = 790.6$, df = 15, $p < 0.001$): 24% of the vertebrates preferred wet grounds, which was not important for the other organism groups. Moisture preferences were classified as unknown for 11% of all species. A relatively large proportion of the species (36%) was classified as not affected by soil moisture. This factor seemed to be relatively unimportant, especially for invertebrates (65% of all species unaffected) and vertebrates (57%). Unsaturated lateral water flow in the upper soil layers was unimportant for most of the studied species (55% of all species were unaffected), especially vertebrates (98%) and invertebrates (88%). Organism groups also differed for this factor ($G = 992.2$, df = 12, $p < 0.001$), and 51% of the studied vascular plants preferred sites with short or long periods of unsaturated lateral water flow in the upper soil layers, indicating that this was important for vascular plants. Thus, differences in preference between organism groups were large, and soil-water conditions seemed to be unimportant for a relatively large number of the species. But ground-living species (that are affected by soil water conditions) are less well known than tree-living species, and they therefore might be underrepresented in the present red lists. Soil-water conditions might be more important for some groups than this study suggests.

Light conditions were important for the occurrence of 63% of the 1487 forest species (preferences were classified as unknown for 17% of all species). Shaded habitats were the most frequent, and 28% of all species were found in shade. This was especially important for cryptogam (44% of the species in shaded habitats). Most vascular plants (52% of all species) were found in semishaded habitat. Sun-exposed sites seemed to be the least preferred (14% of all species), but they were of some importance to vascular plants (25% of the species grew at exposed sites) and to invertebrates (22%). A substantial number (20%) of the species was unaffected by this factor, especially vertebrates (94% of the species were unaffected). Thus, light-condition preferences differed between organism groups, and no general pattern was found.

Factors Critical for the Occurrence of Threatened Species

Other factors were critical for the occurrence of the 1487 studied species: for instance, invertebrates and cryptogams often depended on specific substrates such as snags and logs. Critical factors were divided into three main groups: habitat elements, stand/site factors, and abiotic factors (Table 2). Biotic factors (habitat elements and stand/site factors) were more important than abiotic factors. Ninety-six percent of the species in all organism groups combined were classified as being affected by biotic factors, and 19% were classified as being affected by abiotic factors.

Abiotic factors were more important for vascular plants than for the other organism groups (Fig. 6), and more important for cryptogams than for invertebrates and vertebrates ($G = 107.7$, df = 3, $p < 0.001$). Our knowledge of the influence of different abiotic fac-

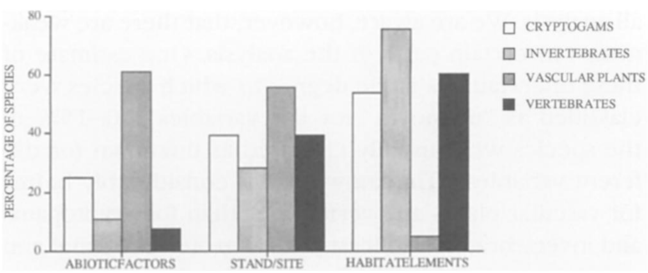

Figure 6. Proportion of 636 cryptogams, 739 invertebrates, 59 vascular plants, and 53 vertebrates for which abiotic factors, stand/site factors, and habitat elements were classified as important for their distribution and occurrence (see Table 2 for list of factors and habitat elements).

tors, however, might be insufficient for some groups of invertebrates. The most important abiotic factors were, in order of decreasing importance, calciferous soil (important for 9.5% of all species), large-scale climate (8.1% of all species), and clean air or water (2.6% of all species).

Biotic factors were important for all groups, but less important for vascular plants than for the other organism groups (Fig. 6). The biotic factors (habitat elements and stand/site factors) are highly related to forest management. The occurrence of specific habitat elements was of great importance for 64% of all species, and stand/site factors for 35% of all species.

The importance of different habitat elements (old trees, logs, snags, and host/prey species) varied between organism groups (Fig. 7). The two most important habitat elements were old living trees and logs, which were

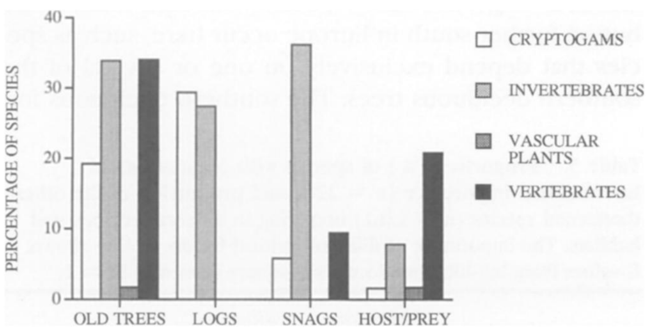

Figure 7. Proportion of 636 cryptogams, 739 invertebrates, 59 vascular plants, and 53 vertebrates for which the occurrences of old trees, logs, snags, and host/prey species were classified as important. The importance of old living trees, logs, snags, and host/prey organisms differed between organism groups (log-likelihood ratio chi-square test, G = 38.6, df = 2, p < 0.001; G = 35.2, df = 2, p < 0.001; G = 190.9, df = 2, p < 0.001; G = 47.3, df = 2, p < 0.001, respectively).

both critical for the occurrence of 26% of all threatened species. Living old deciduous trees (important for 85% of the species requiring old trees) were more important than living old coniferous trees (important for 14% of the species requiring old trees). Old living trees were most important for invertebrates and vertebrates (Fig. 7). Logs were critical only for the occurrence of cryptogams and invertebrates (Fig. 7). Most species (53%) preferred logs of an age after death from 5 to 50 years. Younger logs (0–5 years old) were preferred by 18% of the species requiring logs, while only 2% of the species that required logs preferred old logs (more than 50 years old).

The third most important habitat element was snags, which were important for 21% of all species. Most of the snag-requiring species (53%) preferred snags in the range of 5–50 years after death; a relatively large proportion (31%) preferred young snags (0–5 years old), while old snags (more than 50 years old) were preferred by only 2% of the snag-requiring species. Snags were most important for invertebrates (Fig. 7).

The least important habitat element was host/prey organisms (the occurrence of specific host or prey species), which were critical for the occurrence of 5.4% of all species. Host/prey organisms were most important for vertebrates (Fig. 7), but many invertebrates that are insufficiently known (such as parasitoid insects, mainly *Hymenoptera*), depend on specific host/prey species; this factor is probably more important than suggested by this study.

The most important factors classified as related to stand/site—and influenced by forest management—was forest age (important for 12% of all species). Species that require old or dead trees but not necessarily old forests, however, are not included in this figure. Forest density (important for 12% of all species), undisturbed hydrology (5.6%) and high air moisture (4.2%) were other important stand/site factors. The stand/site factors were more important for vascular plants than for the other organism groups (Fig. 6).

Populations of International Importance

Of the 1487 threatened forest species, 190 (13% of all species) were classified as having more than 10% of the European population in Sweden, and 36 (24% of all species) were classified as endemic to Scandinavia (Table 4). A larger number of species with populations of international importance are found in the temperate/hemiboreal zone than in the hemiarctic/boreal zone. But the proportion of species with populations of international importance is higher than the proportion of other species in the hemiarctic/boreal zone, while it is lower in the temperate/hemiboreal zone (Table 5). Also, a higher proportion of the threatened species in the hemiarctic/boreal zone (24%) than in the temperate/hemiboreal zone (13%) were classified as having

Table 4. Proportion (%) of species in different organism groups classified as endemic to Scandinavia.*

Group	*Endemic*	*>10% of Population*	*<10% of Population*	*Number*
Cryptogams	4.6	22.8	72.6	636
Vascular Plants	0.0	10.2	89.8	59
Invertebrates	1.0	4.6	94.5	739
Vertebrates	0.0	9.4	90.6	53
All Groups	2.4	12.8	84.8	1487

* *Having more than 10% of the European population in Sweden or having less than 10% of the European population in Sweden. The first two groups are classified as having populations of international importance.*

populations of international importance. Occurrence in different forest habitats also differed between these two groups. A higher proportion of the species with internationally important populations occur in coniferous forests, and a smaller proportion occur in southern deciduous forests (Table 5). Also, when compared within regions, the proportion of species associated to coniferous forests was higher for those with populations of international importance than for others, both in the hemiarctic/boreal (77.4% and 48.1%, respectively) and in the temperate/hemiboreal zone (53.3% and 22.4%, respectively).

A lower proportion of the species with populations of international importance was restricted by abiotic factors (Table 5). The species with populations of international importance more often depended on stand/site factors than did other species, while the importance of specific habitat elements did not differ between these two groups (Table 5). These differences, however, might be caused by the large proportion (77%) of cryptogams among the species with populations of international importance.

Discussion

Status of Knowledge of the Flora and Fauna in Sweden

Knowledge of plants, animals, and fungi is better for Europe than in most other parts of the world, and knowledge of Swedish fauna and flora is among the best in Europe. There have been extensive investigations of the distribution and biology of species from the days of Linnaeus and onward, by both professional biologists and a number of skilled amateurs. National floras and faunas have been published for most organism groups, and provincial descriptions and catalogues have been made for several organism groups. Red lists for forest species (vascular plants, cryptogams, vertebrates, and invertebrates) were published early in Sweden (starting with Ahlén 1975); few countries in the world have yet compiled lists of most of these organism groups.

Thus, we consider the knowledge of plants, animals, and fungi in Sweden sufficient for an attempt at an overall analysis. We are aware, however, that there are weaknesses in certain parts of the analysis. One estimate of these uncertainties is the degree to which species were classified as "unknown" for the variables (10–15% of the species were usually classified as unknown for different variables). The knowledge is considerably better for vascular plants and vertebrates than for cryptogams and invertebrates. The least-known groups are fungi and certain groups of invertebrates. Also, the red lists are biased. Among invertebrates, for instance, well-known groups such as *Coleoptera* and *Lepidoptera* were well represented, whereas *Hymenoptera*, for which knowledge is poorer, were scarcely represented. Analysis of Swedish red lists in the future might therefore reveal factors of importance for the conservation of threatened species that were not found in this study. We believe, however, that the common characteristics of the threatened forest species in Sweden found in this study will also be found to be important in future studies.

Common Characteristics of Threatened Forest Species in Sweden

It has been discussed whether the conservation of threatened species is possible without studying individual species, as argued by Gilpin (1987) or whether each species must be studied on a case-by-case basis, as argued by Simberloff (1988). Our results suggest that there indeed are some important general guidelines for the conservation of threatened forest plant, fungi, and animal species in Sweden.

First, southern deciduous forest is the habitat with the most threatened species for all organism groups, especially when the small area of this habitat (Fig. 5) is taken into account. In Sweden this forest type is at its northernmost range, and many species with their main distribution further south in Europe occur here, such as species that depend exclusively on one or several of the southern deciduous trees. The southern deciduous for-

Table 5. Proportion (%) of species with populations of international importance (n = 226) and proportion of the other threatened species (n = 1261) occurring in different regions and habitats. The importance of different critical factors is also shown. G-values from log-likelihood ratio chi-square tests with df = 1.

Factors	*Important species*	*Other species*	*G-value*	*P-value*
Regions				
South	73.9	91.5	116.5	<0.001
North	64.6	36.4	33.9	<0.001
Habitats				
Coniferous	62.4	25.8	73.2	<0.001
Southern dec.	23.4	62.0	158.3	<0.001
Other deciduous	18.6	23.6	8.0	<0.01
Critical factors				
Abiotic factors (all)	9.6	20.0	3.6	<0.05
Stand/site related	46.5	32.4	16.3	<0.001
Habitat elements	53.6	63.4	0.2	>0.6

ests are generally older than most coniferous forests. About 50% of the growing stock of southern deciduous forests is comprised of trees larger than 35 cm in diameter, compared with only 13% for spruce and 14% for the pine (Statistical Yearbook of Forestry 1992). There are only about 100,000 ha of pure stands—in which more than 70% of the basal area consists of southern deciduous trees—of this type in Sweden (Almgren et al. 1986). For biodiversity, remaining old forests should be protected or should have a conservation-oriented management. According to the Swedish Forestry Act, pure stands with southern deciduous forests must, when clear-cut, be regenerated with southern deciduous trees. Plantation with southern deciduous trees (mainly *Fagus sylvatica* and *Quercus robur*), however, can be as impoverishing to the flora and fauna as a coniferous plantation (Almgren et al. 1986). Coniferous-dominated stands with a proportion of southern deciduous trees can also be valuable; in fact several bird species are found in higher densities in mixed than in pure deciduous or coniferous stands (Nilsson 1992). There are about 200,000 ha of coniferous forests with 10–70% basal area of *Fagus sylvatica* or *Quercus robur* in Sweden (Almgren et al. 1986). All such stands are also located south of Limes Norrlandicus and need more attention in the future.

Second, at a habitat-element scale, old and dead trees are important for a majority of the threatened species. Old trees, snags, and logs are all connected with unmanaged forests (see Spies et al. 1988). Long forest continuity has been suggested to be important for species that require a long period to reach reproductive age, for species that depend on particular features of the habitat or on specific microclimatic conditions (Esseen et al. 1992), and for species with poor dispersal abilities (Hansson et al. 1992). The pendent lichen *Usnea longissima* grows on old trees, prefers a microclimate characterized by high and stable air humidity, and does not disperse effectively over long distances. This species has declined drastically in Swedish forests, and sites need to be protected from all kinds of forestry operations (Esseen et al. 1992). Other species, however, such as the golden eagle *Aquila chrysaetos,* build large nests and depend on old trees as nesting trees (mean age 335 years), which do not necessarily have to be located within forests of long continuity (Tjernberg 1983). Logs are important for most animal and plant groups and snags for birds, fungi, and lichens, even when situated in younger forests. Thus, reasons for occurrence in old forests may differ between species, but features of old forests are important for all organism groups.

The occurrence of old and dead trees in Swedish boreal forests has decreased dramatically since the nineteenth century (Linder & Östlund 1992), and the lack of these habitat elements is a severe threat to many forest plant, animal, and fungi species. Today, less than 2% of the total growing stock in Sweden is comprised of dead trees. Most of this dead wood has very small dimensions; only about 10% has a diameter of 35 cm or more (Statistical Yearbook of Forestry 1992). In one area in central Sweden, the amount of dead wood per hectare was estimated to have decreased from 13 m^3/ha around 1890 to 0.1 m^3/ha in 1966, due to the impact of modern forestry (Linder & Östlund 1992).

More old and dead trees must be left and also created in the future if the flora and fauna are to be preserved. Measures that assure a continuous supply of a specific substrate, rather than a high amount, are probably of high value for many insect species. Such a measure could be, for instance, to leave groups of old living trees in which single trees now and then fall down. Storm-fellings and, to some extent, fires can be approximated by leaving large amounts of dead trees on clear-fellings. But in this context there is a conflict between forest protection and fauna-flora conservation. Present regulations in Sweden do not allow unlimited amounts of freshly dead coniferous trees in the forest, because this is the breeding substrates for destructive bark beetle species. Studies are needed to determine in which environments trees are most valuable, and the quantity of old trees and dead wood needed to support viable populations of, for example, invertebrates and cryptogams. Studies on the importance of the spatial distribution of snags for cavity-nesting birds (see Raphael & White 1984) have indicated that groups of snags are more favorable than single individuals. Similar studies for other organism groups, mosses, lichens, and beetles, are lacking.

This analysis and other studies (see Gärdenfors & Baranowski 1992) indicate that the openness of the forest is important for threatened tree-living species. Some species seem adapted to open, sunny conditions, and others are adapted to shady conditions; these preferences differ among species adapted to different tree species. Only a few species (2% of the 1487 threatened species) are directly dependent on fire for colonization and establishment. Examples are the vascular plants *Geranium bohemicum* and *G. lanuginosum.* The seeds of these short-lived species need heat in order to germinate. Many species in the boreal region probably depend on post-fire successional stages, with large amount of deciduous trees and dead wood (Esseen et al. 1992), and the importance of repeated disturbances for many wood-living insects has probably been underestimated (Ahnlund & Lindhe 1992). As a result of fire suppression, only small and scattered sites with post-fire succession remain in Sweden. It might be surprising that factors such as soil moisture and the presence of burned forest areas seem relatively unimportant for the threatened species in Swedish forests. This would imply that forest drainage would not be a major threat to rare species, nor would lack of forest fires be a serious menace.

Such conclusions would be a misinterpretation of our analysis. In fact, forested wetlands are among the most important habitats for dead wood today in the Swedish landscape, because large areas are still left unmanaged, and they have a long stand continuity. Forest-fire areas provide large amounts of dead wood and deciduous trees, and thus they are important for the long-term persistence of many species. In a preliminary analysis of *Coleoptera* in the present study, about 20% of the species were favored by forest fires and/or extensive storm fellings, whereas only 4% were judged to be disfavored. Other species groups are also favored by forest fires. For instance, the White-Backed Woodpecker *Dendrocopus leucotos* occurs in small and isolated populations in Sweden. The low amount of deciduous trees, as in areas that arise after forest fires, in modern forests is probably an important reason for the decline of this species (Aulén 1988).

Third, considerably more threatened forest species were found in the south (89% of all threatened forest species) than in the north (41% of all threatened forest species) of Sweden, and there seems to be a decreasing gradient of threatened species from the temperate zone to the hemiarctic zone. These results coincide with those of a number of earlier studies in different parts of the world showing a correlation between species richness and latitude (see Rohde 1992 for review). The knowledge of different species' distribution and occurrence in northern Sweden is not as good for southern Sweden, but this probably influenced the main distribution patterns found in this study to a minor extent only. Similar distribution patterns have been found in Finland, where a large proportion of the threatened species was found in the southwest of the country (Rassi & Väisänen 1987). But threatened species are only a subset of all species. Comparisons between threatened and nonthreatened vascular plants (Gustafsson 1994) indicate that the higher number of threatened species in the south is due to a higher number of species (threatened and nonthreatened combined) in the south and not to a higher proportion of all species being red listed. Also, among *Coleoptera* (including nonthreatened species) there are considerably more species occurring in the south (4027) than in the north (3030) of Sweden (Lundberg 1986).

The broad classification of taxa might obscure differences between organism groups and perhaps hide factors necessary to consider for taxa that belong to groups containing few species. In our analysis, for example, the large groups fungi and invertebrates dominate, and within the group invertebrates the beetles are predominant. Thus, it might be important to consider factors not shown to be important in this study. Therefore, different organism groups will be analyzed separately: vascular plants (Gustafsson 1994), vertebrates (Berg, in preparation), cryptogams (Hallingbäck, in preparation). However, differences between taxonomic groups at a lower taxonomic level are not reported in this overall analysis. It is evident that important differences will be revealed in these separate analyses. For example, the cryptogams (bryophytes, lichens, fungi) differ considerably regarding critical factors and also to some extent regarding habitats. Long forest continuity and old deciduous trees are very important for lichens and logs for fungi. A large proportion of bryophytes are found in the deciduous forest other than the southern type, mixed forest is especially important for lichens, and so forth (Hallingbäck, in preparation).

Species with Populations of International Importance

A larger number of species with populations of international importance are found in the south than in the north of Sweden, although a higher proportion of threatened species in the hemiarctic/boreal zone (24%) than in the temperate/hemiboreal zone (13%) was classified as having populations of international importance. The classification of the internationally important species was the most difficult part of the study. The knowledge of distribution of species is fairly good for northern and middle Europe, but there are large gaps in our knowledge of the flora and fauna in regions such as the boreal parts of European Russia. Thus, the importance of the Swedish taiga for many boreal species might be overestimated, and a reevaluation of which populations are of international importance might be necessary in the future. The tendency for coniferous forests to be important is so strong, however, that we think the main differences presented here are real. Thus, if the main goal is to maintain large populations of species of international importance, conservation must focus on different habitats and to some extent on different regions of Sweden than when conservation is focused on nationally threatened species. In our opinion, the first priority must be to maintain the populations of internationally important species, whereas the protection of internationally common but nationally rare species must be a second priority. In addition, populations of several species not classified as threatened in Sweden are of international importance (Gustafsson 1994). The maintenance of these populations is also of great importance and should be considered in the future.

Forest Reserves or Modified Forest Management?

A primary goal of biological conservation is to preserve the natural diversity of plants and animals in communities where natural processes are working (Soulé 1986; Esseen et al. 1992). Forest reserves are important for many forest plants and animals in Sweden, where 95% of the forests are used for commercial purposes and commercial forestry is more developed than in most other countries. A forest reserve system that is representative for the total Swedish forest landscape is therefore important. But the present system of forest reserves is probably not comprehensive enough for the long-term survival of many forest plants and animals in Sweden (Esseen et al. 1992; Nilsson & Götmark 1992). The total protected area in Sweden was 5.9% of the total area in 1990 (Swedish Environmental Protection Agency 1990), but nearly 70% of this area consisted of alpine landscapes (Nilsson & Götmark 1992). Thus, the total protected forest area is probably too small; most reserves are small and are probably insufficient for plants and animals requiring large areas. Furthermore, many areas are protected for human-oriented recreational reasons (Götmark & Nilsson 1992). Timber harvest is often allowed in these areas, especially in the south (Nilsson & Götmark 1992); the truly protected areas are less extensive than suggested above. Several specific types of forest ecosystems are also underrepresented in the existing system of forest reserves (Esseen et al. 1992; Nilsson & Götmark 1992), especially forest habitats on productive soils in nonmountain counties in central and southern Sweden. Only 1% of the total area of deciduous forests and 1.2% of the coniferous forests in nonmountain counties are protected (Nilsson & Götmark 1992). Our results suggest that larger areas of coniferous forests in the nonmountain areas in middle and southern Sweden must be protected, because the number of species with populations of international importance and the total number of threatened species are large in these habitats and regions. Protection of larger areas of deciduous forests in southern Sweden should be given priority, due to the large number of species in these habitats and the small protected area. Some organism groups (vascular plants and especially vertebrates) are also found to a relatively large extent in habitats other than forests, which makes the conservation of these species more complex. The protection of whole landscapes (including nonforest habitats such as open wetlands and farmland) is probably important for many of these species.

Several studies have predicted loss of species in nature reserves (Willis 1974; Soulé et al. 1979; Glenn & Nudds 1989), despite the reserves being large in some cases. It is therefore important to modify forest management in the surrounding areas to increase the change of maintaining populations of many forest species. This is especially important for those species requiring large areas of a specific habitat or a natural disturbance regime (Angelstam 1992). Forest reserves might work as core areas (Harris 1984), and it is probably important to coordinate the management of protected areas with their surrounding (Mott 1988).

In Sweden forestry operations must, according to the Swedish Forestry Act, be performed in a way that "considers the flora and fauna." This implies that sites with rare or threatened species up to the size of about one hectare should be left unmanaged or should be managed with respect to the preservation of the species. The Forestry Act also states that certain important habitats, such as screes, ravines, small islands, and edge zones to agricultural land, should have a conservation-oriented management or should be left without forestry operations. Biodiversity should also be considered in the performance of ordinary forestry measures, such as clear-cutting (snags and logs should be left, although their number is not defined), thinnings and clearings (residuals should not be left in brooks or at biological important sites), and so forth. Although this act has been valid for more than 15 years, it is very weak and is rarely enforced (Skogsstyrelsen 1991).

The ideas behind this law are biologically sound and it should be strengthened. If this is done, sites with rare species and important habitats will be distributed on commercial forest land in all parts of Sweden, creating a network of "biological islands" that could serve as bases for the preservation and dispersal of species. Such a system, combined with protected areas (nature reserves and national parks), would be most beneficial for biodiversity. If in addition to this the amount of old trees and dead wood is increased through increased retaining of logs, snags, and old trees on clear cuts and in thinning operations, the situation for many forest species in temperate and boreal forests in Sweden most certainly would improve considerably.

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Literature Cited

Ahlén, I. 1975. Hotade ryggradsdjur (exkl. fiskar) i Sverige. [Threatened vertebrates (excluding fish) in Sweden.] Sveriges Natur. Årsbok **1975**:126–129. In Swedish.

Ahlén, I., and M. Tjernberg. 1992. Artfakta. Sveriges hotade och sällsynta vertebrater 1992. [Threatened and rare vertebrates in Sweden 1992.] The Swedish University of Agricultural Sciences, Uppsala, Sweden. In Swedish.

Ahnlund, H., and A. Lindhe. 1992. Hotade vedinsekter i barrskogslandskapet—några synpunkter utifrån studier av sörmländska brandfält, hällmarker och hyggen. [Endangered wood-living insects in coniferous forests—some thoughts from studies of fire sites, outcrops and clearcuttings in the province of Sörmland, Sweden.] Entomologisk Tidskrift **113**:13–23. In Swedish, with English summary.

Ahti, T., L. Hämet-Ahti, and J. Jalas. 1968. Vegetation zones and their sections in northwestern Europe. Annales Botanicí Fennici **5**:169–211.

Almgren, G., T. Ingelög, B. Ehnström, and A. Mörtnäs. 1986. Ädellövskog: Ekologi och skötsel. [Southern deciduous forests: Ecology and management.] Skogsstyrelsen, Jönköping, Sweden. In Swedish.

Angelstam, P. 1992. Conservation of communities: The importance of edges, surroundings and landscape mosaic structure. Pages 9–70 in L. Hansson, editor. Ecological principles of nature conservation. Elsevier Applied Science, London, England.

Aulén, G. 1988. Ecology and distribution history of the White-Backed Woodpecker (*Dendrocopus leucotos*) in Sweden. Dissertation from Department of Wildlife Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden.

Brown, J. H. 1984. On the relationship between abundance and distribution. American Naturalist **124**:255–279.

Ehnström, B., and H. W. Waldén. 1986. Faunavård i Skogsbruket, del 2. Den lägre faunan. [Fauna conservation in forestry. Vol. 2. Invertebrates.] Skogsstyrelsen, Jönköping, Sweden. In Swedish.

Esseen, P.-A., B. Ehnström, L. Ericsson, and K. Sjöberg. 1992. Boreal forests: The focal habitats of Fennoscandia. Pages 252–325 in L. Hansson, editor. Ecological principles of nature conservation. Elsevier Applied Science, London, England.

Fransson, S. 1965. The borderland. In: The plant cover of Sweden. Acta Phytogeographica Suecica **50**:167–175.

Gamlin, L. 1988. Sweden's factory forests. New Scientist **1597**:41–44.

Gärdenfors, U., and R. Baranowski. 1992. Skalbaggar anpassade till öppna respektive slutna ädellövskogar föredrar olika trädslag. [Beetles living in open deciduous forests prefer different tree species than those living in dense forests.] Entomologisk Tidskrift **113**:1–11. In Swedish, with English summary.

Gilpin, M. 1987. Theory vs. practice. Trends in Ecology and Evolution **2**:16.

Glenn, S. M., and T. M. Nudds. 1989. Insular biogeography of mammals in Canadian parks. Journal of Biogeography **16**:261–268.

Goodman, D. 1987. The demography of chance extinction. Pages 11–34 in M. E. Soulé, editor. Viable populations. Cambridge University Press, Cambridge, England.

Götmark, F., C. Nilsson. 1992. Criteria used for Protection of Natural Areas in Sweden 1909–1986. Conservation Biology **6**:220–231.

Griggs, R. F. 1940. The ecology of rare plants. Bulletin of Torrey Botanical Club **67**:575–594.

Gustafsson, L. 1994. A comparison of biological characteristics and distribution between Swedish threatened and non-threatened forest vascular plants. Ecography 17:39–49.

Hanski I. 1982. Dynamics of the regional distribution: The Core and satellite species hypothesis. Oikos **38**:210–221.

Hansson, L., C. Solbreck, and L. Söderström. 1992. Dispersal in relation to conservation. Pages 162–200 in L. Hansson, editor. Ecological principles of nature conservation. Elsevier Applied Science, London, England.

Harris, L. D. 1984. The fragmented forest. Island biogeography theory and the preservation of biotic diversity. University of Chicago Express, Chicago, Illinois.

Hodgson, J. G. 1986. Commonness and rarity in plants with special references to the Sheffield flora. Part I. The identity, distribution and habitat characteristics of the common and rare species. Biological Conservation **36**:199–252.

Ingelög, T., Thor, G., and Gustafsson, L. 1987. Floravård i skogsbruket. Del 2—Artdel. [Flora conservation in forestry. Vol. 2.] Andra uplagan. Skogsstryrelsen. Jönköping. (In Swedish).

International Union for the Conservation of Nature. 1988. 1988 IUCN red list of threatened animals. Gland, Switzerland.

Järvinen, O, and S. Ulfstrand. 1980. Species turnover of a continental bird fauna: Northern Europe, 1850–1970. Oecologia (Berlin) **46**:186–195.

Lahti, T., E. Kemppainen, A. Kurtto, and P. Uotila. 1991. Distribution and biological characteristics of threatened vascular plants in Finland. Biological Conservation **55**:299–314.

Laurance, W. F. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. Conservation Biology **5**:79–89.

Laurila, T., and O. Järvinen. 1989. Poor predictability of threatened status of waterfowl by life-history traits. Ornis Fennica **66**:165–167.

Linder, P., and L. Östlund. 1992. Förändringar i Sveriges boreala skogar 1870–1991. [Changes in the boreal forests of Sweden 1870–1991.] Svensk Botanisk Tidskrift **86**:199–215. In Swedish, with English summary.

Lundberg, S. 1986. Catalogous Coleopterum Sueciae. Entomologiska Föreningen i Stockholm och Naturhistoriska Riksmuséet, Stockholm. In Swedish.

Mace, G. M., and R. Lande. 1991. Assessing extinction threats: Toward a reevaluation of IUCN threatened species categories. Conservation Biology **5**:148–157.

Mattson, L., and E. Stridsberg. 1980. Skogens roll i Svensk markanvändning. [The importance of forests in Swedish land use.] Department of Forest Economics, Swedish University of Agricultural Sciences, Umeå, Sweden. In Swedish.

Mott, W. P. 1988. Looking beyond national park boundaries. Natural Areas Journal 8:80–82.

Nilsson, S. G. 1992. Forests in the temporal-boreal transition: Natural and man-made features. Pages 373–393 in L. Hansson, editor. Ecological principles of nature conservation. Elsevier Applied Science, London, England.

Nilsson, C., and F. Götmark. 1992. Protected areas in Sweden. Is natural variety adequately represented? Conservation Biology 6:232–242.

Official Statistics of Sweden. 1990. The natural environment in figures. 3rd edition. Stockholm, Sweden.

Official Statistics of Sweden. 1991. National Board of Forestry, Jönköping, Sweden.

Pimm, S. L., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. American Naturalist 132:757–785.

Preston, F. W. 1948. The commonness and rarity of species. Ecology 43:185–215.

Rabinowitz, D. 1981. Seven forms of rarity. Pages 205–217 in H. Synge, editor. The biological aspects of rare plant conservation. John Wiley & Sons, New York.

Raphael, M. G., and M. White. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildlife Monographs 86:1–66.

Rassi, P., and R. Väisänen, editors. 1987. Threatened animals and plants in Finland. English summary of the report of the Committee for the Conservation of Threatened Animals and Plants in Finland. Miljöministeriet, Helsinki, Finland.

Rohde, K. 1992. Latitudinal gradients in species diversity: The search for the primary cause. Oikos 65:514–527.

Schoener, T. W. 1987. The geographical distribution of rarity. Oecologia (Berlin) 74:161–173.

Simberloff, D. S. 1988. The contribution of population and community biology to conservation science. Annual Review of Ecological Systems 19:473–511.

Sjörs, H. 1965. Forest regions. Acta Phytogeographica Suecica 50:48–63.

Skogsstyrelsen. 1991. Tagen hänsyn vid slutavverkningar 1989–91. [Conservation measures taken at final fellings 1989–91.] Meddelande nr 4—1991, Jönköping, Sweden. In Swedish.

Soulé, M. E., editor. 1986. Conservation biology: The science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.

Soulé, M. E., B. A. Wilcox, and C. Holtby. 1979. Benign neglect: A model of faunal collapse in the game reserves of East Africa. Biological Conservation 15:259–272.

Spies, T. A., J. F. Franklin, and T. B. Thomas. 1988. Coarse woody debris in Douglas-fir forest of western Oregon and Washington. Ecology 69:1698–1702.

Statistical Yearbook of Forestry. 1992. Official Statistics of Sweden. National Board of Forestry, Jönköping, Sweden.

Swedish Environmental Protection Agency. 1990. Naturvårdsplan för Sverige. [A plan for nature conservation in Sweden.] Solna, Sweden. In Swedish, with English summary.

Synge, H. 1981. The conservation of lower plants. Reports from a panel discussion. Pages 125–137 in H. Synge, editor. The biological aspects of rare plant conservation. John Wiley & Sons, New York.

Tenow, O. 1974. Det nordiska skogslandskapets och skogsbrukets utveckling fram till 1900-talet—en kort översikt. [The forest landscape in the Nordic countries and the development of forestry until the twentieth century—a brief review.] Swedish Coniferous Forest Project, Internal Report 2. Naturvetenskapliga Forskningsrådet, Stockholm. In Swedish.

Terborgh, J., and B. Winter. 1980. Some causes of extinction. Pages 119–133 in M. E. Soulé and B. A. Wilcox, editors. Conservation biology: An evolutionary ecological perspective. Sinauer, Sunderland, Massachusetts.

Tjernberg, M. 1983. Habitat and nest site features of golden eagle *Aquila chrysaetos* (L.), in Sweden. Swedish Wildlife Research 12:131–163.

Willis, E. O. 1974. Population and local extinctions of birds on Barro Colorado island, Panama. Ecological Monographs 50:111–130.

Wilson, E. O. 1987. The little things that run the world. The importance and conservation of invertebrates. Conservation Biology 1:344–346.

Appendix

System for categorizing habitat preferences of "red listed" forest plants and animals. Each species could be categorized as occurring in a maximum of three habitats.

- Forest or Shrub dominated areas
  - Coniferous forest
    - Spruce forest
    - Pine forest
    - Prealpine coniferous forests
  - Southern deciduous forest
    - Beech forest
    - Oak forest
    - Ash forest
    - Elm forest
    - Mixed deciduous forest
  - Other deciduous forest
    - Alder forests
    - Birch- and aspen forests
  - Mixed forest
    - Coniferous forest with many aspens or willows
    - Other mixture
  - Temporarily deforested areas
    - Clear-cut (tree diameter <10 cm)
    - Burned areas
  - Shrub areas
  - Mirelands
- Alpine areas
- Slopes and rocks
- Agricultural landscapes and urban areas
- Shores of lakes and running water
- Coast