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Biodiversity and its Assessment in Boreal and Nemoral Forests

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We review species richness in major organism groups, mainly using examples from northern Europe. A high proportion of these species is forest living, and large numbers are dependent on decaying wood. Biodiversity can be assessed at various scales using two different principles. One is to use features, such as ancient and dead trees, known to be important for a large number of species. The other method is to choose species or groups of species known to indicate high biodiversity or presence of many red-listed species. We argue that any serious biodiversity assessment method should include the most species rich organism groups, for example insects. In the present paper we point out the most important features for high biodiversity (old trees and large dead trees), and review the quantities of these features in near-virgin forests. The natural disturbance regime of a region should be the basis for defining a suitable scale and the appropriate features for biodiversity assessment. Possible indicator species for high biodiversity in northern Europe are suggested, based on previous investigations. Among epiphytic lichens and wood-living beetles there are many potentially useful species in addition to vascular plants in the nemoral forest. Among vertebrates, woodpeckers and grouses seem to be the most useful. Validation tests for indicator structures and species are largely lacking but urgently needed. The implications of possible delayed local extinctions are important to bear in mind when managing for sustainable forestry. The knowledge of forest history is useful when developing cost-efficient measures. *Key words: ancient trees, beetles, dead trees, disturbance regime, epiphytic lichens, forest fire, forest structure, indicator species, red-listed species, species richness.*

INTRODUCTION

One of the major goals in sustainable forestry should be restoration and preservation of a high biodiversity. In this paper we define biodiversity as the variation within species, species richness, and variation of forest types, with an emphasis on species richness. Whereas genetic variation within species and among microorganisms is an important component of biodiversity, it is beyond the scope of this paper.

To survey all species (total biodiversity) in a landscape is an almost impossible task. Therefore, assessment methods have been used, mostly using indicator structures and/or species that are supposed to represent total biodiversity. In general, vertebrates have been the organism group most used as indicators of a maintained biodiversity in forests (e.g. several papers in Hunter 1999). Recently in Sweden various forest structures and cryptogams (lichens, mosses and fungi) have been used to find stands presumably harbouring red-listed species (Nitare & Norén 1992, Hansson 2001). However, it is still an untested assumption that vertebrates or cryptogams indicate total biodiversity. Instead, it is logical that the most diverse groups of organisms (especially insects, but also macro-fungi and lichens in northern ecosystems) should play a significant role in biodiversity assessment. Unfortunately, they have so far been largly ignored (Colwell & Coddington 1995).

The aim of this paper is to suggest possible principles for assessing the total biodiversity of boreal and temperate forests. By biodiversity assessment we mean the estimation of species richness of the native species and the number of forest types. In some cases, estimation of the number of red-listed species is also covered. Examples will mainly be taken from northern Europe because relatively many studies have recently been performed in this area. The technical aspects of assessing biodiversity (e.g. Hammond 1994, Gaston 1996) are beyond the scope of the paper.

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SPECIES RICHNESS OF MACRO-ORGANISMS

A recent survey in Sweden, a country with forests in the boreal, boreonemoral (= hemiboreal), and nemoral zones (map with regions in Esseen et al. 1997), show that species richness is highest among wasps and allied species (Hymenoptera), flies (Diptera), beetles (Coleoptera), and fungi. About half of all species of macro-organisms are forest living, including species living in glades (Table 1). Vascular plants and mosses constitute the smallest proportion of forest-dwelling species and fungi the largest proportion within the taxonomic groups. In Fennoscandia, species richness of insects is highest in southeast Sweden and decreases to the northwest (Väisänen & Heliövaara 1994) in accordance with the species-energy theory, which states that species richness increases along with available energy (Wright 1983). Similar patterns occur for vascular plants and to a lesser extent for mammals and breeding birds (Gustafsson & Ahlén 1996).

There are few larger forest areas where species diversity has been studied and divided according to habitat requirements. However, several detailed studies have examined the species richness of beetles in northern Europe (Table 2). The greatest richness occurs in the boreonemoral zone, probably due to the many tree species with their associated species. In this transition zone between boreal and nemoral forest types they coexist in a heterogeneous and patchy pattern, which explains some of the richness (Nilsson 1997*a*). Possibly the greatest richness in Europe occurs in the large natural forest of Bialowieza in eastern Poland. For example, up to now about 2,000 species of beetles have been found (J. Gutowski, unpubl. data), of which 37% are wood-living beetles (744 species according to an estimate by R. Baranowski). Wood-beetles are species dependent on wood, bark or associated fungi. We also include species living inside hollow trees, e.g., in wood mould, and predators on other wood-living species. The proportion of wood-dependent beetle species is 25–34% of all beetles in various natural forests in northern Europe (Table 2). About the same ratio is likely to apply for fungi, since more than 1,000 species of at least 4,000 macro-fungi recorded in Sweden are considered to be wood-living (Hallingbäck & Aronsson 1998). The species-rich groups of wasps and ants (Hymenoptera) and flies (Diptera) also contain many wood-dependent species (e.g. Albrecht 1991, Ssymank 1994, Økland 1996, Hammond 1997), but detailed studies are lacking.

Table 1. *Species richness of forest living and all macro-organisms in Sweden, excluding water living groups (data from Cederberg 2001, L. Hedström, unpubl. data)*

Organism group	Forest living	Total	% in forest
Vascular plants	?	1,972	Low
Mosses	300	1,053	24
Lichens	800	2,009	40
Macrofungi	2,700	4,000	68
Vertebrates	180	330	55
Invertebrates	17,000	34,500	49
Hymenoptera	>4,300	>9,100	47
Diptera	>3,200	>7,020	46
Coleoptera	2,384	4,360	55
Lepidoptera	1,421	2,671	53
Chelicerata	?	1,900	?
Homoptera	511	1,102	46
Heteroptera	239	589	41

BIODIVERSITY ASSESSMENTS

An inventory of all the taxa is the only accurate method of assessing biodiversity, but this has never been conducted anywhere in the world. The costs are too great for general use, and furthermore, the availability of experts, especially for Hymenoptera and Diptera, is a severely limiting factor. Therefore, it is obvious that any biodiversity assessment at present can only deal with a fraction of the total species richness. A central question is then: Which groups of species should be selected as indicators of total biodiversity?

Biodiversity can be assessed by two main methods. One is to use features, such as ancient and dead trees, known to be important for a large number of species (e.g. Harding & Rose 1986, Berg et al. 1994, 1995, Peterken 1996, Nilsson & Ericson 1997). The other method is to choose species or groups of species known to indicate a high biodiversity or presence of many red-listed species (Nilsson et al. 1995).

Some woodpeckers and grouse species require special features at the landscape scale. Such features can be measured and monitored, but a more reliable method is to use the species as more direct indicators. Subtle landscape features may be crucial for a high biodiversity, but are difficult to quantify, and may therefore be most easily detected by the presence of

Table 2. *Total number of beetle species (Total), number of species of wood-beetles (Wood-beetles), and proportion of wood-beetles (% wood-beetles) in some naturally regenerated and unmanaged old growth forests in Sweden (S), Norway (N), and Finland (F). Natural forest areas in ha (Area)*

Forest	Area	Total	Wood-beetles	% wood-beetles	Source
Nemoral forests					
Maltesholm, S	100	1,270	320	25	Baranowski 1991, unpubl.
Tromtö, S	200	–	312	–	Baranowski & Nilsson 1994
Boreonemoral forests					
Marsholm, S	60	–	315	–	Nilsson & Baranowski 1993, unpubl.
Fiby, S	60	1,302	353	27	Lundblad 1950
Båtfors, S	1,000	1,385	475	34	Baranowski 1977, 1982, Eriksson 2000
Möckeln, S	900	–	477	–	Nilsson & Baranowski unpubl.
Skultrevassåsen, N	33	–	335	–	Bakke 1999
Boreal forests					
Birtjärnsberget, S	60	–	220	–	Nilsson & Baranowski 1993
Pyhän-Häkki, F	580	–	180	–	Nilsson & Baranowski 1993
Oulanka, F	>10,000	704 [a]	232 [b]	33	Muona & Viramo 1986

[a] True total probably about 870 (J. Muona in Hanski & Hammond 1995).
[b] Reassessed by R. Baranowski using the same criteria as Nilsson & Baranowski (1993).

indicator species. For example, the most valuable tree species for the reproductive success of the lesser spotted woodpecker, *Dendrocopos minor*, differs between years (Olsson et al. 1999). In such cases, long-term persistence may depend on tree species composition in potential habitats. In the prairie habitat the extinction risk of the rodent *Cynomys parvidens* increased dramatically as the number of locally occurring plant species decreased (Ritchie 1999).

The structures used for biodiversity assessments ought to be validated before they are extensively used, which has rarely been done. Recent studies in boreal forests of northern Europe show correlations between densities of dead trees and richness of wood-beetles (Økland et al. 1996, Siitonen et al. 1998, Martikainen et al. 2000), and wood-fungi (Bader et al. 1995, Stokland 1998).

The presence of the beetle *Osmoderma eremita* and pseudoscorpion *Larca lata*, both endangered species living in tree hollows, is dependent on larger groups of ancient hollow oaks (Ranius 2000, Ranius & Wilander 2000). Furthermore, many insects are dependent on sun-exposed ancient and dead trees (Nilsson & Ericson 1997, Kaila et al. 1997, Jonsell et al. 1998, Ranius & Jansson 2000). Thus, apart from density, both aggregation and sun-exposure of important structures may be necessary to measure and monitor.

When species rather than structures are selected for assessment, one can either census selected species in a taxonomic group or census only the red-listed species. The specific aim of a census will dictate what should be used. In the context of sustainable forestry the presence of red-listed species is an important consideration, which does not necessarily indicate total biodiversity. However, in a recent study of epiphytic lichens in forests in southern Sweden, a strong correlation was found between the number of red-listed lichens and overall species richness of epiphytic lichens (Arup et al. 1999). Such correlations may be expected from the nested distributions of species, where the most species-rich sites also harbour the specialised and uncommon species (e.g. Nilsson 1986, Patterson 1987, Wright et al. 1998).

Several studies have revealed only weak or non-existent correlations between the number of red-listed species in different organism groups at the forest stand level (Nilsson et al. 1995, Gustafsson et al. 1999b). In two recent studies a negative correlation was even found between mosses and epiphytic lichens at the stand level (Gould & Walker 1999, Gustafsson et al. 1999*b*). At a regional scale, similarly weak correlations between various groups were found for species richness and endangered species (Pendergast et al. 1993, Dobson et al. 1997, Pendergast & Eversham 1997). These results show that biodiversity assessments must include various groups of organisms

with different general requirements. Otherwise, results may be misleading.

An important aspect is the scale for assessment. For the purpose of sustainable forestry, stand level may be too small a scale and region too large. The scale in between, that of the landscape, may be the most appropriate (see below).

DISTURBANCE REGIMES AND LANDSCAPE

The scale, type, and frequency of disturbances are important factors to consider when defining a landscape (Spies & Turner 1999). The disturbance regime is a major factor that determines the species assemblage and diversity in a landscape. Tree species composition is defined by the disturbance regime, soil productivity, or ability to grow under low light levels (e.g. Prentice & Helmisaari 1991, Diekmann 1996). In addition, adaptation to and preferences by browsing large herbivores are important, but largely neglected factors (but see Peterken & Tubbs 1965, Falinski 1986, Nilsson 1997*a*, Rackham 1998). High biodiversity requires various types of natural disturbances by wind, fire, water, insects, and large herbivores (e.g. Pickett & White 1985, Nilsson & Ericson 1997, Ulanova 2000). Traditional pasture land use management may simulate some natural disturbances that maintain an open forest (Nilsson et al. 1994, Nilsson & Ericson 1997, Bengtsson et al. 2000, Pykälä 2000).

The life span of trees is important for the number and composition of species (e.g. Palm 1959, Spies & Turner 1999). In boreal forests typically disturbed by large-scale fires, many species like insects, fungi and vascular plants have a high dispersal ability, while in the nemoral region, small-scale gap dynamics (with infrequent large scale disturbances) have favoured species with a lower dispersal ability (Nilsson & Ericson 1997). Landscapes are often complex assemblages of areas with very different disturbance regimes due to differences in climate, hydrology, topography and soil properties (e.g. Zackrisson 1977, Falinski 1986, Granström 1993, Syrjänen et al. 1994). The identification of natural disturbance regime(s) in a landscape is of great importance when choosing appropriate scales for assessing biodiversity, indicator species, or features. Because different species have very different home ranges and occurrence patterns, it could be difficult to assess the presence/absence of species with high dispersal ability if the area assessed is too small. This is probably the case for many fire-dependent insects, for example, the black fire beetle *Melanophila acuminata* that can disperse tens of kilometers.

The past natural disturbance regimes are in most areas very different from the situation of today where disturbances are mainly implemented by forestry (Esseen et al. 1997, Nilsson 1997*a*, Linder et al. 1997, Niklasson & Granström 2000). In areas where fires have been common, but suppressed for a long time, fire-adapted species associated with burnt substrates and dead trees are now rare or extinct (Wikars 1997). We do not know whether or not these species can recolonize if fire regimes are restored. Indicators for presence/absence of fire-related fauna may be highly valuable (Wikars & Ås 1999). Long-term fire suppression has shifted the species composition in many protected and semi-natural, formerly fire disturbed, areas into late-successional dominated assemblages. This fact which is easily overlooked may introduce large biases when assessing the "degree of naturalness" by using indicators found only in late successional stages (Linder et al. 1997). Therefore, the use of indicator species must be placed into the correct historical context and must also encompass the diversity of forest types (Niemelä 1997). Such reasoning is also relevant for other disturbance agents like flooding and wind that used to create features that are now extremely rare due to intensive forestry, water regulations, and the hunting of the beaver *Castor fiber* to extinction in many regions.

Modern forestry creates much denser forests with only a few tree species in contrast to a landscape under a natural disturbance regime. Many peatlands and wet forests have been drained, especially in Europe, and human impact has homogenised the forest landscape (Fuller et al. 1998). In boreal forests, edges along wetlands have high species richness (Sjöberg & Ericson 1997). Large clearcuts can open the forest but the resemblance to the natural openness caused by fire is small (Esseen et al. 1997). Fires kept forests open, uneven, and patchy while wind created openings where grazers were able to maintain glades. Many species are dependent on these openings that are protected from strong winds and provide a warm microclimate. Such species have declined in Sweden and probably in other areas as well (e.g. Nilsson & Baranowski 1996, 1997). In temperate forests, glades and edges of glades are essential habitat for many butterflies

(Warren 1987, Warren & Key 1991, Bergman 1999). Therefore, species dependent on openings and sun-exposed large trees and dead wood are important to include in indicator systems.

Temporal and spatial variation in disturbance regimes influences the dynamics of coarse woody debris. In a region dominated by large-scale disturbances (fire, large windfalls), large amounts of dead wood are created at infrequent intervals. More evenly distributed over time is the death of single trees by disturbance agents like wind, insects, and fungi. Single-tree death is especially important in landscapes with rare large-scale disturbances. However, little data exist on the magnitude and frequency of windfall disturbance. In a French nemoral forest dominated by beech, *Fagus sylvatica*, strong winds created significant gaps about every 25 years (Pontailler et al. 1997). However, these processes have been strongly counteracted by removal of large and recently dead trees. Larger disturbances of a similar interval of 20-30 years have been recorded in temperate oak forests of America (Nowacki & Abrams 1997) where fire may be involved. Fire as a disturbance factor in European temperate forests is not well documented except in a few recent pollen analyses (Lindbladh & Bradshaw 1998). Indicators of an uninterrupted supply of dead wood are important to identify, and probably largely consist of beetle species (Nilsson & Baranowski 1993).

WHAT IS A LANDSCAPE?

Biodiversity should be assessed at appropriate scales, but it is not obvious what these scales are in different types of forests. In a multi-scale study of the diversity of saproxylic beetles correlation with forest structures was best at the largest scale considered, 400 hectares (Økland et al. 1996). One possibility in selecting a landscape scale is to use the size of the home ranges of large specialised vertebrates. For some woodpeckers and one display group (a lek with the surrounding home ranges) of the capercallie *Tetrao urogallos*, this is 200–500 hectares in northern Europe (Wegge & Rolstad 1986, Amcoff & Eriksson 1996, Stenberg 1998, Wiktander et al. 2001). The home range of a female lynx, a female bear, or a wolf pack on the other hand is more than ten times as large. Some big forestry companies now plan for biodiversity preservation in landscapes of 5,000 to 25,000 hectares (e.g. StoraEnso, B. Pettersson, pers. comm.), and Angelstam (1997) suggested 10,000 ha. In temperate forests, with a high resource density and mainly small-scale disturbances, one or a few thousand hectares is probably a useful ''landscape'' for biodiversity assessment.

IMPORTANT FEATURES FOR BIODIVERSITY

Landscape composition

Some species, for example the capercaillie, disappear when the proportion of older forest decreases below 30% (Wegge & Rolstad 1986). The three-toed woodpecker *Picoides tridactylus* requires larger patches with a high density of dead spruce, *Picea abies* (Amcoff & Eriksson 1996). The lesser spotted woodpecker disappears when the proportion of older forest dominated by deciduous trees drop below 20% within an area of at most 200 hectares (Wiktander et al. 1992, 2001). The white-backed woodpecker, *Dendrocopos leucotos*, has similar requirements for deciduous trees, but needs a higher density of snags (Carlson & Stenberg 1995, Virkkala et al. 1993). In the case of the northern spotted owl, *Strix occidentalis*, both survival and reproductive success increase with the proportion of old growth in the landscape (Bart 1995). For other bird species the proportion of old forest and deciduous trees also seems to be important (e.g. Jokimäki & Huhta 1996, Jansson et al. 1999). Among mammals, the flying squirrel *Pteromys volans* disappears when the proportion of old trees drops below a certain threshold (Mönkkonen et al. 1997). Recent research in boreal forests of northern Europe shows that some insect species, especially rare and endangered species, are dependent on a high proportion of old growth or a high density of dead trees (Siitonen & Martikainen 1994, Økland 1996, Økland et al. 1996, Martikainen et al. 2000) (Table 3).

These studies show that a certain minimum proportion of old forest, old deciduous trees, and dead trees are required for maintaining biodiversity in a landscape. These proportions can be monitored directly, but it is unknown what ''old'' forest and trees constitute for unstudied species. Direct monitoring of sensitive species would circumvent this problem.

Forest continuity

Forest continuity is the presence over a long period (two or more tree generations) of features such as high shrub or tree cover (tree continuity), ancient or big trees (ancient tree continuity) or big dead trees (log continuity) (Nilsson & Baranowski 1993,

Nilsson et al. 1995). The importance of forest continuity for species adapted to different disturbance regimes is highly variable, and depends on the dispersal propensity of different species. Habitat predictability has been proposed to govern the evolution of dispersal strategies (Southwood 1977). For species dependent on relatively stable habitats such as bark and tree hollows reaching high ages, we predict a dependence on continuity (Nilsson & Baranowski 1997). Furthermore, species in nemoral forests are expected to be more dependent on continuity than species in boreal forests due to their different disturbance regimes (Nilsson & Ericson 1997). The relevant scale to measure continuity depends on the dispersal ability of species (Nilsson et al. 2000).

The occurrence of recently burnt forest is highly unpredictable. Some fire-dependent forest insects have developed organs that enable them to find fires many kilometres away (Ewans 1966). A buprestid beetle, *Melanophila acuminata*, has been found in many newly burnt forests in Sweden long distances from the nearest previously burned forest (Ehnström 1991, Ehnström et al. 1995). Many of the fire-dependent species only occur in the burned habitat for a few years (Ehnström 1991, Wikars 1992, 1997) and after this they must disperse.

Table 3. *Important features for high biodiversity in boreal and temperate forests at the landscape scale and possible indicator structures and species. Tree diameters (DBH) are minimum values for the most valuable trees for biodiversity preservation in nemoral/boreonemoral and boreal forests (in parentheses), respectively*

Features	Structures	Species
Landscape composition	% deciduous and old stands	Woodpeckers, grouse
Burnt tree history	% deciduous trees with *Daldinia*	Wood beetles
Site history	Tree species composition	Ground flora, epiphytic lichens
Ancient trees (>150 years)	Density of ancient trees >70 (40) cm	Epiphytic lichens, beetles
Hollow trees	Density of hollow trees	Beetles living in hollows
Large dead trees	Density of dead trees >40 (20) cm	Wood beetles, wood fungi

Polypores on dead trees create a habitat of intermediate duration. A relatively common beetle living in such a habitat, *Bolitophagus reticulatus*, seems to be dispersal limited above 30 meters from a source (Rukke & Midtgaard 1998). Several beetle species living in polypores can disperse up to about one kilometer, but their parasites may have lower dispersal propensity (Jonsell et al. 1999). Based on these studies, several beetle species and a species of moth, *Scardia boletella*, have been suggested as indicators of continuity for this habitat (Jonsell 1999).

Tree hollows form a very stable habitat. Studies on the dispersal of insects living in hollow trees are scarce, but a recent study of the scarabaeid beetle, *Osmoderma eremita*, shows a very limited dispersal. Maximum dispersal distances of up to 190 meters have been recorded (Ranius & Hedin 2001) and the vast majority of individuals stay in the same tree throughout their life (Hedin & Ranius, pers. obs.). In a study comparing the beetle fauna of hollow beeches, there was no significant difference in species richness between nearly primeval and previously managed stands. However, the number of red-listed species was higher in living hollow beeches and standing dead hollow beeches in nearly primeval stands than in the previously managed stands. In the dead downed hollow beeches there was no difference in the number of red-listed species between the two stand types (Nilsson & Baranowski 1997). This indicates that some red-listed species have not been able to recolonize hollow trees in previously managed stands.

In temperate forests the presence of many species of vascular plants are dependent on stand history (e.g. Peterken & Game 1984, Whitney & Foster 1988, Dzwonko & Loster 1989, Foster 1992, Brunet 1993, 1994, Matlack 1994), and many species are dispersal limited (Ehrlén & Eriksson 2000). These species differ from species with high dispersal capacity, and they mainly live in deciduous forests (Hermy et al. 1999). Some epiphytic lichens (Rose 1976, Fritz & Larsson 1996), molluscs (Boycott 1934, Paul 1978) and beetles (Azmann 1994, Nilsson & Baranowski 1997, Alexander 1998) are also dependent on forest continuity. It is striking that all these studies were from the nemoral and boreonemoral forests of Europe, with their small-scale disturbance regimes.

Many forest-living vascular plants have a very low dispersal rate in current temperate forests. For example Tack & Hermy (1998) found that the number of forest plant species in different parts of Belgium

correlated with the extent of forest cover 700 years ago, but not 200 years ago. In the boreonemoral forests in southern Sweden, Brunet & Oheimb (1998) recorded a mean colonization rate of 0.3 meter per year for 37 forest-living plants in old fields in the process of reverting to forest. When these plants colonized northern Europe after the last ice age, rates must have been considerably higher. The same conclusion is drawn in a North American study of the seed dispersal and migration of *Asarum canadense* (Cain et al. 1998), an ant-dispersed understorey herb in deciduous forests. It was found that this plant should have travelled only 10-11 kilometers from their glacial refugia since 16,000 years before present if ants were its only dispersers. Instead, it has migrated 1,000–2,000 km, implying that occasional events of long-distance dispersal must have played a major role for the Holocene colonization of northern temperate forests. One reason for the difference could be unconstrained movements of large herbivores after the ice age. Fences now prevent long-distance movements of cattle and horses and restrict dispersal of propagules.

The importance of forest continuity for high biodiversity has been questioned for boreal forests (Ohlsson et al. 1997). On theoretical grounds, based on different disturbance regimes, we expect that species in nemoral forests have a lower dispersal propensity than in boreal forests (Nilsson & Ericson 1997). This hypothesis predicts that forest continuity is more important in nemoral forests than in boreal forests. In fact, numerous studies have found evidence for the importance of forest continuity for vascular plants in nemoral forests (review in Hermy et al. 1999) in contrast to boreal forests (Esseen et al. 1997). However, some epiphytic lichens seem to be dispersal limited in managed boreal forests (Dettki 1998, Dettki et al. 2000, Sillett et al. 2000). Furthermore, a beetle, *Pytho kolwensis*, living in recently wind-fallen spruce trees in boreal forests seems to be dependent on a continuous supply of such trees (Siitonen & Saaristo 2000).

It is important to realise that natural disturbances do not necessarily break continuity. For example, a continuously high density of ancient pine trees, *Pinus sylvestris*, may be dependent on high fire frequencies that maintain their habitat open. Also other species such as oaks, *Quercus* spp., birches, *Betula* spp., and aspens, *Populus* spp., may survive fires and carry epiphytic lichens, for example *Pulmonaria* spp., to the next tree generation (Sillett & Goslin 1999).

Ancient and hollow trees

In all types of forests many species are dependent on very old trees (>150 years), called ancient trees. In boreal and boreonemoral forests in northern Europe, trees are cut down before they reach less than half their life span (Esseen et al. 1997, Nilsson 1997a). Few oaks and beeches younger than 150 years old develop large hollows (Therrell & Stahle 1998, Nilsson & Ranius pers. obs., and P. Thorén, unpubl. data, respectively), which means they are generally absent from intensively managed forests. Oak and beech are the most important tree species for endangered species dependent on hollow trees in northern Europe (Harding & Rose 1986, Martin 1989, Nilsson & Baranowski 1994).

Many epiphytic lichens and wood-beetles are dependent on ancient trees. These species are now restricted to small stands with old trees that are many kilometers from other old and suitable stands (e.g. Martin 1989, Speight 1989, McLean & Speight 1993, Nilsson & Baranowski 1994). The sizes of these isolated populations are often less than one thousand individuals (Nilsson & Baranowski 1995, Nilsson 1997b, Ranius 2000), which means they have a high risk of regional extinction. Since there are often no nearby sources for recolonization, the loss may be permanent.

The fauna dependent on hollow trees is much richer in nemoral and boreonemoral forests than in boreal forests (cf. Palm 1951, 1959). One reason could be that cavities are a more common and predictable feature in the tree species that dominate in southern forests. We have found no measurements of the density of hollow trees in boreal forests, but our general observations indicate that there are few cavities even in virgin stands.

Densities of large living trees

Many vertebrates prefer or are dependent on large living trees (e.g. Bunell et al. 1999). Reference densities for large living trees in near-natural forests of different types ought to be established for different regions. In the boreal forest, at a site characterised by a natural fire regime, the original density of living pine trees with DBH (diameter at a height of 1.3 m above ground) above 42 cm was 14 per hectare. Similar or higher densities are recorded in other near natural pine-dominated boreal forests (Linder & Östlund 1998, Wirth et al. 1999).

In nemoral forests, trees are generally larger than in boreal forests and trees with DBH above 70 cm

may be considered to be large, as is the case for tropical forests (Clark & Clark 1996). Some measurements in boreonemoral forests in southern Sweden, eastern Poland, and Slovakia indicate densities of 10–20 such large trees per hectare in old growth forests with a mixture of deciduous and coniferous trees (Nilsson et al., 2001). In the same forests, the densities of trees with large hollows were 10-30 per ha. Smaller hollows, which are important to small birds, occur in many other trees (Wesolowski 1989, Carlson et al. 1998). Trees with such small hollows are difficult to detect from the ground and therefore not suitable for monitoring.

Densities of large dead trees

Forestry reduces densities of large dead trees relatively much more than thinner trunks (e.g. Green & Peterken 1997, Kirby et al. 1998, Spetich et al. 1999). Cavity nesting birds often prefer dead trees with large diameters (e.g. Raphael & White 1984, Hågvar et al. 1990, Bunell et al. 1999). Some of the more specialised wood-dependent beetles only live in large trunks, which are often totally lacking in managed forests. Few data exist, but the beetle *Grynocharis oblonga* has only been found in standing trunks with a diameter above 40 cm in the boreonemoral forest (Nilsson 1997*b*). The stag beetle *Lucanus cervus* lives in decaying wood, mainly of oak. It can survive in higher cut stumps, but their diameter must be at least 40 cm (Klausnitzer 1995). Two virgin forest relicts, the beetles *Rhysodes sulcatus* and *Lacon lepidopterus*, which are regionally extinct in most of Europe (Horion 1953, Palm 1959, Speight 1989), are still relatively common in the large natural forest of Bialowieza, eastern Poland (J. Gutowski, pers. comm., S.G. Nilsson pers. obs.). There, we have only found these species in logs above 40 cm in diameter. Many insects have lower demands, but logs of 20 cm have been identified as a minimum diameter for many wood-beetles in boreal forests (Palm 1951, Siitonen & Saaristo 2000). Red-listed cryptogams in boreal forests also show strong preferences for large diameter coarse woody debris, with the most demanding species restricted to trunks over 20 cm (Kruys et al. 1999). Thus, dead trees with diameters over 20 and 40 cm seem to be critical for more demanding species in boreal and nemoral forests, respectively.

The volume of dead trees is often reported in different types of forests. However, for maintaining biodiversity the number of large dead trees above certain diameters may be crucial rather than the total volume of dead wood. Furthermore, big trunks remain standing for a longer time than smaller trunks (e.g. Raphael & White 1984, Lindenmayer et al. 1997) and decomposition takes longer (Harmon et al. 1986, Stone et al. 1998). Many wood-beetles are dependent on standing dead trees and cannot develop in downed logs (e.g. Palm 1959, Nilsson 1997*b*). Even after long droughts, big trunks will remain moist in their centre thus preventing sensitive species from drying out. From these various considerations we suggest that for a given volume of dead wood, big trees can host more species than the same volume of thinner trees. Therefore, we argue that the diameter distributions and density of large trees are important data that should be recorded when surveying the volume of dead wood.

In near-virgin beech-dominated forests in Sweden, the diameter distribution of dead trunks was approximately normally distributed with very few trunks above 100 cm DBH (Nilsson & Baranowski 1997). In beech stands that were previously managed but are now in old growth, there were both relatively more thinner and larger dead trunks. In old growth in midwestern U.S.A. the highest volumes of dead wood occurred in the diameter interval of 25–85 cm, with total volumes increasing with site productivity (Spetich et al. 1999). We have found the same pattern in boreonemoral forests of Europe (Nilson et al., 2001).

Some measurements in boreonemoral forests in southern Sweden, eastern Poland, and Slovakia indicate densities around 30 dead trees with DBH above 40 cm per hectare in old-growth forests with a mixture of deciduous and coniferous trees (Nilsson et al., 2001). About half of these large dead trees were standing, but only 14% among trunks with diameters between 20 and 40 cm. Other studies including smaller trunks found that only one fourth of the dead wood volume is standing (Linder et al. 1997, Kuuluvainen et al. 1998, Spetich et al. 1999). This pattern is expected because trees of large dimensions will remain standing for a longer time.

In 13 near-virgin boreal forests of northern Sweden, the densities of dead trees with diameters above 20 cm were about 190 per hectare (data in Linder & Elfving 1996). Nearly half of these trunks were standing. In the same plots there were 19 standing dead trunks with 40–60 cm DBH per hectare, about half

of them pine and the rest spruce. These studies show that large dead trees were common in the landscapes where forest-living species evolved. Therefore, because of the former abundance and special conditions in large-diameter logs many species may have adapted to these dimensions of dead wood.

Burnt forest

In northern Europe at least 70 species, mainly insects and fungi, are directly dependent on burnt forests (Wikars & Ås 1999). The number of specialists in a burnt forest is apparently dependent on fire history in the landscape and the richness of insects can be predicted from the proportion of deciduous trunks with the fungi *Daldinia concentrica* (Wikars & Ås 1999). Many more species in the boreal forests are dependent on the events following fire, e.g. a high density of dying and dead trees and deciduous successions with birch and aspen (Heliövaara & Väisänen 1984, Wikars 1992, Esseen et al. 1997).

Minimum habitat amount and dispersion

Results from extinction models and some empirical data for vertebrates indicate that regional species extinction starts to accelerate when the original habitat area drops below 20–30% (e.g. Lande 1987, Lamberson et al. 1992, Andrén 1994, 1997). Therefore, we suggest that at least 20% of original densities of ancient/hollow trees and large dead trees are needed at the landscape level for biodiversity preservation. In spruce-dominated forests in southeastern Norway some threatened species of beetles were only present where the density of dead trees with diameters above 40 cm DBH was higher than four to seven per hectare (Økland et al. 1996). This is about 20% of the density recorded in several old-growth forests in Europe (Nilsson et al., unpubl. data). A lower proportion of burnt forest in relation to original amounts may be enough to maintain the fire-dependent species in the landscape due the high dispersal rate of such species. However, we must be aware that 20% of the original amounts of old growth and structures will not prevent local extinction of the most sensitive species (Økland 1996, Soulé & Sanjayan 1998). These species must therefore be preserved in large forest reserves.

Although it is important to understand the connections between landscape features and fire frequency, the link is rather loose (Granström 2001). In our view, the ASIO model of forest management of boreal forests (Angelstam 1997) will solve few of the most urgent problems with biodiversity preservation. Instead, we stress the importance of sufficient amounts of burnt, ancient and large dead trees with different degrees of sun exposure in the landscape. In southern Sweden, wet and productive sites have often been treeless meadows while dry and stony sites have better tree continuity (Nilsson 1997*c*), quite the opposite of the assumption of the ASIO model. Fire suppression has been practised about a century longer in the south (Niklasson & Drakenberg, 2001), further erasing the original differences in forest structure due to soil wetness in the boreonemoral forest. The actual tree and ancient tree continuity of a forest stand, as indicated by vascular plants and epiphytic lichens, respectively, is crucial in biodiversity conservation planning. The remaining sites with dispersal-restricted red-listed species are important to identify, preserve, and expand.

The spatial dispersion of hollow trees is important, and they should occur in groups to be of the highest value for biodiversity preservation (Ranius 2000, Ranius & Wilander 2000). The same goes for groups of old trees for the preservation of cryptogams in managed forests (Hazell & Gustafsson 1999) and dead trees used by insects (Sverdrup-Thygeson & Midtgaard 1998, Kehler & Bondrup-Nielsen 1999, Schiegg 2000, Thunes et al. 2000). Thus, when investigating the presence of indicator species, it is important to know the location of the largest concentrations of important substrates.

INDICATOR SPECIES

We need preliminary lists of indicator species for a high biodiversity or many red-listed species. Here, we propose some potentially useful species (Table 4) based on previous attempts to identify such species (Rundlöf & Nilsson 1995, Nilsson et al. 1995, Kuusinen 1996, Esseen et al. 1999). The suggested species, or their feeding traces, are relatively easy to identify due to their size and distinctiveness. Most of the species are now rare. It has been argued that indicator species should not be rare, but landscapes with continuity of ancient trees and large dead trees are so rare in many regions that indicators must be sets of rare species (Nilsson & Baranowski 1994, 1995). However, in near-virgin forests these species have a high frequency in suitable substrates (e.g. Nilsson et al. 2000, Siitonen & Saaristo 2000).

We have argued that most vertebrates are not suitable as indicators, mainly due to their generalised requirements. However, evidence is accumulating that

Table 4. *Important features for biodiversity preservation and examples of possible indicator species of a high biodiversity or many red-listed species in northern Europe. Revised and expanded from Rundlöf & Nilsson (1995)*

Feature	Species
Landscape composition	The birds *Picoides tridactulus*, *Dendrocopos minor*, *D. leucotos*, *Tetrao urogallus*, *Bonasia bonasia*, *Parus cinctus*
Burnt trees	The beetles *Melanophila acuminata*, *Platyrhinus resinosus*, *Dicerca furcata*, *Upis ceramboides*, *Denticollis borealis*, *Stephanopachys* spp.
Site history	The plants *Actaea spicata*, *Lathyrus vernus*, *Tilia cordata*, *Galium odoratum*, *Festuca altissima*; the lichens *Lobaria* spp.
Ancient trees	The lichens *Lobaria* spp., *Alectoria sarmentosa*, *Usnea longissima*, *Collema* spp., *Basidia rosella*, *Gyalecta ulmi*; the beetles *Poecilonota variolosa*, *Microbregma emarginata*, *Corticeus fasciatus*, *Nothorhina punctata*
Hollow trees	The beetles *Elater ferrugineus*, *Liocola marmorata*, *Osmoderma eremita*, *Gnorimus* spp., *Ischnomera* spp., *Tenebrio opacus*, *Allecula* spp, *Prionychus* spp.
Large dead trees	The beetles *Ceruchus chrysomelinus*, *Platycerus* spp., *Lucanus cervus*, *Dorcus parallelepipedus*, *Danosoma* spp., *Harminius undulatus*, *Ampedus sanguinolentus*, *Ampedus nigroflavus*, *Xylophilus corticalis*, *Dicerca* spp., *Buprestis novemmaculata*, *Bostrichus capucinus*, *Lymexylon navale*, *Thymalus limbatus*, *Calitys scabra*, *Peltis grossa*, *Ostoma ferruginea*, *Grynocharis oblonga*, *Cucujus cinnaberinus*, *Mycetina cruciata*, *Pytho kolwensis*, *Oplocephala haemorrhoidalis*, *Upis ceramboides*, *Corticeus unicolor*, *Corticeus bicolor*, *Hypulus quercinus*, *Saperda perforata*, *Tragosoma depsarium*, *Anoplodera scutellata*, *Necydalis major*, *Monochamus urussovi*, *Callidium coriaceum*, *Semanotus undatus*, *Acanthoderes clavipes*

large carnivores are important for a high biodiversity because they depress populations of smaller carnivores and herbivores (Soulé & Terborgh 1999). Therefore, the presence of large predators, e.g. wolf, lynx, and bears in the landscape may be one component of a sustainable use of forests. However, they are hardly suitable as indicator species (Linnell et al. 2000).

One important problem in biodiversity assessments is the presence of relict populations, which may not be viable in the future. A few remnant ancient trees may still support a small population of an indicator insect or even a single individual of an epiphytic lichen. Among insects and lichens in southern Sweden this situation is common (e.g. Nilsson & Baranowski 1995, Fritz & Larsson 1996, Nilsson 1997*b*, Ranius 2000). In such cases, knowing the frequency of the species in the landscape is more useful than having a simple indication of their presence. Frequencies may be based on tree individuals or on plots of 1, 10, or 100 hectares depending on the biology of the species.

Various considerations are important when selecting indicator species (e.g. Pearson 1995). In the context of sustainable forestry, it is essential that sets of species dependent on all important structures and successional stages in the landscape are represented. This was clearly not the case in the recent survey of ''key habitats'' in Sweden. Some forest types, especially open stands with pine *Pinus* spp., aspen *Populus tremula* and birch *Betula* spp., which often have very rich insect faunas, were not represented at all in that survey. Among the indicator species suggested in Table 4 the following wood-living beetles are dependent on open forests: *Melanophila acuminata*, *Upis ceramboides*, *Denticollis borealis*, *Poecilonota variolosa*, *Microbregma emarginata*, *Nothorhina punctata*, *Tenebrio* spp., *Lucanus cervus*, *Danosoma* spp, *Ampedus nigroflavus*, *Dicerca* spp., *Buprestis novemmaculata*, *Calitys scabra*, *Peltis grossa*, *Grynocharis oblonga*, *Oplocephala haemmorrhoidalis*, *Tragosoma depsarium*, *Anoplodera scutellata* and *Acanthoderes clavipes*. It is likely that other insects such as hoverflies (Diptera, Syrphidae) may also be useful as indicators (Sahlén et al. 1999). On the other hand, tiger beetles (Pearson & Cassola 1992) and butterflies (New 1997), suggested as useful indicators among insects, are less suitable. The reason is that few species in these groups are restricted to high biodiversity habitats in boreal forests. However, further south in temperate forests, butterflies may be more useful as indicators.

The number of indicator species found could be a measure of biodiversity or the number of red-listed species, but efforts must be standardised for useful comparisons between landscapes. The frequencies of some species also may be used as indicators (Esseen

et al. 1999), which is most useful at the landscape scale.

GENERAL DISCUSSION

Reliable biodiversity assessment methods are essential for sustainable forestry. Proposed indicator systems have been applied long before their validation and this unfortunate state of affairs should be rectified. The widespread presumption that retaining and creating important structures for biodiversity in every landscape automatically results in a high biodiversity should be tested. If forest continuity and substrate history are important for retaining a high biodiversity, as suggested in this paper, structures alone may not be appropriate indicators. Furthermore, continuity of ancient and of big dead trees may no longer occur at the same location as some data from southern Sweden indicates (Nilsson et al. 1995). In such cases, the most cost-efficient strategy for retaining a high biodiversity is to put the highest effort into increasing the structure with the best historical continuity in a landscape. Even the tree species involved often have different histories. For example, there has been a drastic decrease of ancient sun-exposed oak in Sweden during the last 200 years (Eliasson & Nilsson 1999), and the dependent fauna may experience delayed extinctions (Nilsson 1997*b*, Ranius 2000). In this case future extinctions may be prevented by a restoration of a high density of ancient oaks near relict populations. Thus, history may be a guide to the future in biodiversity preservation. Delayed extinction is probably a severe and generally neglected problem in biodiversity preservation. Recent studies indicate that it may be important in many situations (Tilman et al. 1994, Hanski 1998, Carlson 2000).

If forest history is an overriding factor for high biodiversity (Peterken 1996, Nilsson & Ericson 1997), species may be better indicators than structures. Evaluation of this idea is costly, because it requires sampling and species identification of diverse groups of forest-living organisms. If appropriate resources are not allocated to validation tests, we risk using unreliable methods. This may cause unnecessary species extinctions. As argued above, the importance of forest history and continuity for a high biodiversity is expected to be higher in nemoral than in boreal forests. Therefore, results of tests may be difficult to generalise between regions. The indicator value of species can differ between regions (Nilsson & Ericson 1997, Hermy et al. 1999). This means that tests must be performed in appropriate regions based on disturbance regimes. As an example, a positive correlation between red-listed lichens and mosses were found in boreal forests stands, but not in nemoral and boreonemoral stands in Sweden (Gustafsson et al. 1999*a*).

The principles discussed and indicators suggested have been developed in the context of sustainable forestry, but they are equally pertinent in selection and management of nature reserves. In northern Europe, little effort has been devoted to the evaluation of management of protected forests. Lack of fire has resulted in more closed forests with an altered tree species composition (e.g. Linder et al. 1997). Unfortunately, the consequences for biodiversity have not been studied.

STRATEGY FOR THE FUTURE

Based on our review we suggest the following measures for the future:

1. Conduct all-taxa inventories in managed and natural forests. Educate taxonomic experts who can conduct inventories on the species-rich insect groups of Coleoptera, Hymenoptera, and Diptera.
2. Develop biodiversity assessment methods that include the most species-rich organism groups, mainly insects. Sets of species dependent on all important structures and successional stages in the landscape must be represented.
3. Validate the efficiency and accuracy of biodiversity assessment methods using both forest structures and indicator species in order to develop practical methods. Such tests must be performed in different regions to avoid spurious generalisations.
4. Develop landscape parameters that reflect the species richness at different scales and incorporate them into land management strategies. Examples may be density and dispersion of ancient and large dead trees.
5. Incorporate the concept of delayed extinctions especially for species with low dispersal ability into biodiversity conservation. It may save more local populations and enhance biodiversity in landscapes.

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