EFFECTS OF MODERN FORESTRY ON
NORTHWESTERN EUROPEAN FOREST
INVERTEBRATES: A SYNTHESIS

*NYKYAIKAISEN METSÄNKÄSITTELYN VAIKUTUKSET
LUOTEISEUROOPPALAISEN METSÄN
SELKÄRANGATTOMIIN: SYNTEESI*

Kari Heliövaara & Rauno Väisänen

EFFECTS OF MODERN FORESTRY ON NORTHWESTERN EUROPEAN FOREST INVERTEBRATES: A SYNTHESIS

Kari Heliövaara and Rauno Väisänen

Seloste

NYKYAIKAISEN METSÄNKÄSITTELYN VAIKUTUKSET LUOTEISEUROOPPALAISEN METSÄN SELKÄRANGATTOMIIN: SYNTEESI

The effects of modern forestry on northwestern European forest invertebrates are summarized and analyzed mainly on the basis of published literature. The direct influence of different practices including clear-cutting, thinning, burning-over, ploughing, changes in tree species composition of stands, fertilization, insecticides, pheromones and biological control are discussed from a forest zoological point of view. Also the indirect effects of general changes in boreal forest dynamics, loss of primevals, cessation of natural fires and the dominance of young stands are described. The direct effects of different silvicultural practices on the species composition and diversity of forest invertebrates are usually considered to be striking but transient. However, when large areas are treated, the species associated with primevals, especially with the wood composition system in them, as well as the species associated with fires, seem to have drastically declined. In northwestern Europe, efficient forestry has not caused such serious pest problems as is known from tropical countries or North America.

Pääosin kirjallisuuteen perustuvassa yhteenvedossa tarkastellaan ja analysoidaan uudenaikaisten metsänkäsittelymenetelmien vaikutuksia luoteiseurooppalaisen boreaalisen metsän selkärangattomiin. Erilaisten metsänkäsittelyssä käytettävien menetelmien, avohakkuun, harvennuksen, kulotuksen, aurauksen, metsän puulajikoostumuksen muutosten, lannoituksen, hyönteismyrkkyjen, feromonien ja biologisen torjunnan suoria vaikutuksia metsäekosysteemiin tarkastellaan erityisesti metsäeläintieteelliseltä kannalta. Metsien dynamiikassa tapahtuneiden muutosten kuten aarnimetsien vähenemisen, luonnonkulojen harvinaistumisen ja metsiköiden nuorten ikäluokkien lisääntymisen epäsuoria vaikutuksia tarkastellaan myös suhteessa metsien selkärangatonfaunaan. Erilaisten metsänkäsittelyssä käytettyjen menetelmien välittömät vaikutukset metsäselkärangattomien lajikoostumukseen ja diversiteettiin todetaan yleensä jyrkiksi mutta palautuviksi. Luonnontilaisten metsien laajamittainen käsittely näyttää kuitenkin johtaneen erityisesti maatuvissa puunrungoissa elävien lajien selvään vähenemiseen. Myös kuloihin sopeutuneet lajit näyttävät harvinaistuneen. Pohjois-Euroopassa tehokas metsätalous ei ole johtanut läheskään yhtä pahoihin tuholaisongelmiin kuin trooppisten maiden tai Pohjois-Amerikan metsätalous.

CONTENTS

PREFACE

The present joint study was carried out in the Department of Agricultural and Forest Zoology, the Department of Entomology, the Zoological Museum, and the Department of Zoology, University of Helsinki. It is an attempt to summarize and analyse the published literature about northwestern European forest invertebrates in their changing environment, and to connect the present knowledge with our personal observations on the invertebrate fauna in various stages of forest succession. We hope that this piece of work will increase the appreciation and conservation of the rich faunal diversity in boreal forest.

We will express our sincere gratitude to Professors Erkki Annila and Matti Nuorteva for reading the manuscript and making several valuable comments and suggestions, and to Patricia Poussa for revising the English text.

Helsinki November, 1984

Kari Heliövaara and *Rauno Väisänen*

1. INTRODUCTION

Intensive silviculture has often been criticised because of its disturbing effect on the equilibrium in nature. Alterations in the proportional distribution of tree species and the decrease in the area of old virgin forests or primevals have been thought essentially to impoverish the rich native fauna of forests. On the other hand, old forests and primevals have sometimes been regarded as dead, stagnated ecosystems or harmful centres of insect pest dispersal, and thus an increasing threat for the well-managed cultivated forests.

The real effects of modern forestry on the forest invertebrates are still rather poorly understood. The aim of the present synthesis is to summarize both the direct and indirect effects of modern forestry on invertebrates and point out the most conspicuous gaps in our present knowledge. Areally the study is confined to the boreal forests of northwestern European countries, Norway, Sweden, and especially Finland (Fig. 1). Additional data from other countries are included when available.

The invertebrate fauna can possibly be used as an indicative factor giving an accurate picture of the degree to which a primeval forest remains in its original condition, and in a cultivated forest the pest fauna can be regarded as a test of success of the silvicultural practices.

Are the effects of forestry on the forest fauna so striking and irreversible as is sometimes believed? Is the primeval fauna already well conserved within the existing nature reserves or are new reserves needed? Do the protected primevals cause serious pest problems? Are the pest problems, in fact, a feedback effect of the efficient forestry itself? Is such feed-back economically important in a long term perspective? The present state of knowledge does not allow us to answer all these questions directly, but we hope that the literature here reviewed will be useful for further studies.
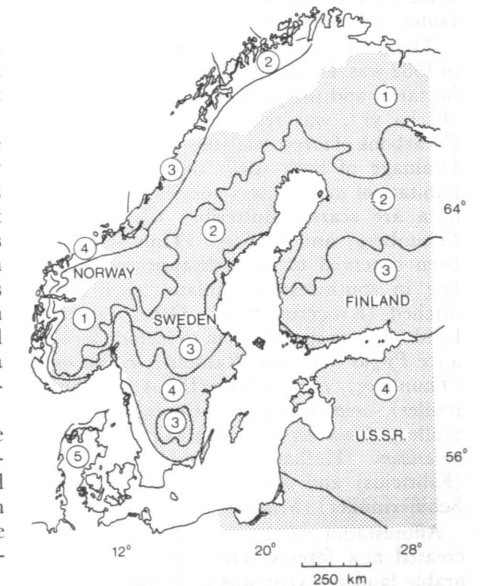
Fig. 1. Boreal subzones in northwestern Europe. 1. N boreal, 2. mid-boreal, 3. S boreal, 4. hemiboreal. (5. atlantic + subatlantic) (according to Ahti et al. 1968). The area of *Picea abies* shaded (simplified from Jalas & Suominen 1973).

Kuva 1. Boreaalinen vyöhykejako Luoteis-Euroopassa. 1. pohjoisboreaalinen, 2. keskiboreaalinen, 3. eteläboreaalinen, 4. hemiboreaalinen (5. atlanttinen ja subatlanttinen). Kuusen levinneisyysalue varjostettu.

2. DIRECT EFFECTS OF DIFFERENT PRACTICES

We divide the direct silvicultural effects affecting invertebrates in forest ecosystems provisionally into six groups. Moreover, some other practices in usage of land, such as drainage of bogs and reforestation of agricultural land, which are directed towards establishing a forest in an area, alter the original fauna and create a new one.

The total area of forest drainage to the end of 1982 was, for instance, in Finland 5.4×10^6 hectares, and the peak of this practice, 3.5×10^5 ha yr^{-1}, was reached in the late 1960s (Yearbook of forest statistics 1983: 111—113). Drainage of bogs spells destruction of the habitats of many insect species, but detailed data are scarce. Butterflies *Clossiana freija* (Thunberg) and *C. frigga* (Thunberg) have been observed to have disappeared from a bog in southwestern Finland after it was ditched (Krogerus 1960). Other susceptile lepidopterous species seem to include for instance *Pyrgus centaureae* (Rambur), *Erebia embla* (Thunberg), *Lycaena helle* (Denis & Schiffermüller), *Scopula virgulata* (Denis & Schiffermüller), *Idaea muricata* (Hufnagel), *Mamestra w-latinum* (Hufnagel), *Hypoxystis pluviaria* (Fabricius) and *Aspilates gilvaria* (Denis & Schiffermüller) (Mikkola 1979).

Afforestation of agricultural land has also created new forests. The afforested area of arable land per year was in Finland in 1982 2.6×10^3 hectares and in 1972 as much as 1.3 $\times 10^4$ hectares (Yearbook of forest statistics 1983: 96). In northern Europe the effects of this practice are poorly known (see, however. Hokkanen & Raatikainen 1977). In Poland, for example, usually poor soils formed from loose stands, with a low biological activity and permanent water deficiency, have been reforested. There the communities of soil macrofauna in one to ten-year-old reforestation are dominated by phytophages and zoophages, and are totally different from those in forest plantations on clear-cuttings. Only the soil macrofauna of 60 to 100-year-old stands on arable land soils have the species composition and community structure similar to those in stands of forest soil (Szujecki 1979, see also Szujecki et al. 1983). On the other hand, natural reforestation has decreased the species bound to old agriculture, pastures and meadows abounding in groves (Mikkola 1979, Väisänen 1982; see also Haeggström 1983 for effects on vegetation and flora). The planting of spruce in wooded deciduous meadows has caused declines in invertebrate populations of such habitats, e.g. butterflies *Parnassius mnemosyne* (L.) and *Euphydryas maturna* (L.) in southern Scandinavia (Heath 1981, Svensson 1982). The increased cultivation of spruce in Denmark and southern Sweden has also favoured rapid northward expansion by the geometrid moth *Peribatodes secundaria* (Schiffermüller) (Svensson 1982).

21. Clear-cutting and thinning

The total area of clear-cuttings was, for instance, in Finland 1.9×10^4 hectares in 1982 (Yearbook of forest statistics 1983: 105). The purpose of clear-cutting is to prepare the stand for burning-over, seeding or plantation, and increase wood production. The drastic alteration in the forest naturally removes all insects associated with old trees. Lack of trees directly gives more light to the soil surface, thus increasing vegetation, makes temperature conditions more extreme and changes moisture conditions. Moreover, clear-cutting of trees and subsequent soil management coupled with the modification of microclimatic conditions bring about great changes in the forest soil fauna. Specialized forest and forest-soil invertebrates are eliminated and replaced by eurytopic species with considerable ecological plasticity (Szujecki 1979). As a whole, however, the changes in the soil fauna as a result of clear-cutting are not very conspicuous (Huhta et al. 1967). In spite of the diminution in the number of individuals, the same species seem to dominate. The number of species increases, however, owing to the influx of new ones (Huhta et al. 1967). These new arrivals are present at least in the beginning, in low densities in oribatid mites (Karppinen 1957) and spiders (Huhta 1965). Huhta et al. (1967) have reported four types of reactions in the densities of soil-living animals in consequence of clear-cutting: sudden increase in dipterous larvae and adult Coleoptera, slow increase in Nematoda, Enchytraeidae and Collembola, initial increase' followed by decrease in Oribatidae, other Acarina and larvae of Coleoptera, and, decrease in Lumbricidae and Araneae.

Lenski (1982) did not find any significant difference between forests and clear-cut areas in total species diversity in Carabidae (Coleoptera) in the southern Appalachians in North America. Genus diversity decreased on all clear-cut areas relative to their forest controls, although the difference was not significant. However, after forest cutting there was a reduction in the numerical dominance of one species over its congeners. Coyle (1981) observed with spiders in the southern Appalachians that after cutting, certain functional groups (e.g. web builders) were severely reduced, but within less affected functional groups (e.g. ground hunters) diversity increased. Similar effects on invertebrates may be found in northern Europe.

After clear-cutting the herbs such as *Rubus idaeus*, *Chamaenerium angustifolium*, *Calamagrostis* spp. and *Avenella flexuosa* rapidly cover the area and insects associated with these plants appear, e.g. the geometrid moth *Spargania luctuata* (Denis & Schiffermüller) on *Chamaenerium* (Svensson 1982). The unbinding and mobilization of nutrients turn the clear-cutting area gradually to grassland, with species characteristic of open, sunny field such as many syrphids or butterflies. The faunal composition ot the field layer is heavily affected by the elimination of brushwoods, e.g. *Vaccinium myrtillus*, and replaced by species of open field and meadow. Later on when the released nutrients have been used by pioneer plants, the vegetation becomes monotonous, often dominated by *Avenella flexuosa*, and the fauna seems to become impoverished.

The total area of thinnings of forest land was in Finland in 1982 2.1×10^4 hectares. Effects of thinning on the soil fauna are supposed to be basically the same as those of clear-cutting but much milder (Huhta et al. 1967). The most remarkable change is the decrease of densities of Nematoda, Enchytraeidae and Collembola, quite opposite of the consequence of clear-cutting (Huhta et al. 1967). Mitchell et al. (1983) found that thinnings of lodgepole pine *(Pinus contorta)* stands from below improve the vigor of residual trees and reduced beetle attack in Oregon (see also Knight & Heikkenen 1980).

Timber cutting around the year and stacks of unbarked logs beside roads as well as clear-cutting areas have generated pest problems (see Nuorteva 1964a, 1965). In this article this wide area of forest zoology is only shortly reviewed. Best known cases include *Tomicus* bark beetles in pine (Trägårdh & Butovitsch 1934, Butovitsch & Spaak 1939, Nuorteva 1956, 1957, Långström et al. 1984). In the upper part of the pine wood stacks 20—200 egg galleries m^{-2} of *Tomicus piniperda* (L.) have been observed (Ehnström 1976, Dehlén & Långström 1977, Heikkilä 1978, Juutinen 1978). In Sweden the pest species composition breeding in the pine stacks is usually formed by *T. piniperda*, *Trypodendron lineatum* (Olivier), *Hylurgops palliatus* (Gyllenhal), *Pissodes pini* (L.), *Monochamus sutor* (L.), *Acanthocinus aedilis* (L.), *Orthotomicus laricis* (Fabricius) and *Pityogenes quadridens* (Hartig), and also *Ips acuminatus* (Gyllenhal) in the north (Skogsskyddsutredningen 1977). *Tomicus minor* (Hartig) is seldom met in the pine stacks (Skogsskyddsutredningen 1977, Långström et al. 1984). Concerning the pests breeding in the stacks of spruce, perhaps most attention has been paid to *Ips typographus* (L.). Most of these beetles are also concentrated in the upper parts of the stacks, and they seem to prefer smaller stacks. 1 m^2 of the bark of spruce has been observed to produce up to 1000 new adults (Skogsskyddsutredningen 1977).

Pine stumps created by clear-cutting are also suitable reproducing sites for several insects. *Tomicus piniperda*, *Hylobius abietis* (L.), *Trypodendron lineatum* and possibly *Pissodes pini* of the pest species have perhaps gained the most remarkable advantage (see Wallace 1953, Wiackowski 1957, Elton et al. 1964, Långström 1979, 1982, Hellqvist 1984). Most abundant insect pest species living in the logging waste include the scolytids *Pityogenes chalcographus* (L.), *P. bidentatus* (Herbst) and

P. quadridens. In more heavy slash as in crowns and thick branches also breed *Ips* spp. and *Pissodes* spp. in spruce, and *Tomicus minor*, *Ips acuminatus* and *Pissodes* spp., sometimes also cerambycids in pine.

It is evident that clear-cutting with its consequences as a modern silvicultural practice has increased the abundance of the timber-associated species mentioned in this chapter.

22. Burning-over

Burning is used in practical forestry, especially in places with thick raw humus, in order to improve the quality of the soil and uncover it for seedlings (Huhta et al. 1967). Burning usually destroys the litter and the above-ground parts of vegetation. After burning-over the soil remains still more exposed to fluctuations in temperature and humidity than in clear-cut areas (Huhta et al. 1967). Fire affects the invertebrate fauna of an area in two ways: firstly, there are direct effects of heat and smoke upon the invertebrates living at the time of the fire; secondly, there are indirect effects caused by the fire's modification of the habitat (Lyon et al. 1978, Richardson & Holliday 1982).

The effect of the burning-over procedure itself upon the soil fauna is very destructive to nearly all groups, because of the heat produced. If the environmental conditions in the burnt-over area are favourable for the animals, the fauna, however, soon recovers from the losses caused by burning (Huhta et al. 1967). In the following four years after burning-over, some groups remain permanently at very low levels of density, few if any signs of recovery being observed (Nematoda and Coleoptera with some recovery in the fourth year, oribatid mites and spiders with none). The pH remains permanently unfavourable to the growth of fungi which form an important nutritional resource of these groups. The most sensitive groups seem to be Lumbricidae and Collembola. Enchytraeids and Collembola, however, reproduce quickly after burning, and so possibly do lumbricids, but later on their numbers gradually decline (Huhta et al. 1967). In one study (Huhta et al. 1969) the soil animal populations seemed

to be labile still in the seventh year after burning-over. There had been violent changes in the numbers of animals all the time. Dindal & Metz (1977) have concluded that fire can cause shifts for and against certain species and associations of Collembola, thus modifying their total community structure.

In ground-living spiders, the effect of burning-over seems to be largely the same as that of natural fires. A certain increase in species number has been noticed during the first years after fire in Norway. There also was a qualitative change during these years as some of the 'pioneer species' appeared in the earliest years and then disappeared, being replaced by other species (Hauge & Kvamme 1983, see also Huhta 1971). Schaefer (1980) observed that only 1 % of the spider and harvestman population survived the fire. However, the burned area – as well as the young pine population – were recolonized rapidly. In the second year after the fire the burned pine forest was characterized by number of species, population density, and index of diversity that did not differ very much from the values in the unburned pine forest. Apart from pioneer species, spiders and harvestmen typical of open habitats dominated. Lycosidae, for instance, attained high population densities.

As far as the insects of the ground and field layers are concerned, the burning-over probably has similar effects to natural fires. Pioneer species of open habitats are first favoured, including species living on slime and other fungi which are pioneer stages of 'plant' succession followed by the fire, and zoophagous species of Carabidae and Salpingidae follow the mycetophagous species (Schauermann 1980, Winter 1980, Richardson & Holliday 1982, Szyczko 1984, Lundberg 1984). Some species such as the curculionid weevils *Hylobius abietis*, *H. pinastri* (Gyllenhal) and *H. piceus* (Degeer) are strongly attracted by the smell of smoke, or by the high temperature itself as in the case of *Melanophila acuminata* (Degeer) (Lundberg 1984). Juutinen (1962) even reported burning-over to increase the damage caused by *Hylobius abietis* on the planted pine saplings. Also coniferous trees damaged by the fire may attract some species including the cerambycids *Asemum striatum* (L.), *Acanthocinus*

aedilis and *Monochamus sutor* to burnt-over sites (Forslund 1934, Lundberg 1984). However, the most important difference between the burning-over and natural fires is the fact that in the latter case the damaged trees are left in the burned forest. Several Heteroptera and many Coleoptera are known to be associated just with the burned tree trunks or the rich fungal flora growing on burned trees. Thus, the burning-over does not correspond biologically to the effect of natural fires (see further section 32.).

23. Ploughing

In Finland, 5.5×10^4 hectares of forest land were ploughed in 1982 (Yearbook of forest statistics 1983: 92). There are very few observations about the effect of ploughing on the occurrence of forest invertebrates in the literature. Kellomäki (1972) has shown that ploughing increases the amount of flowering herbs and other vegetation. According to Nuorteva et al. (1983) this may be responsible for the recent increase in the population of *Meloe violaceus* Marsham (Coleoptera, Meloidae). Detrimental effects of deep ploughing on forest-soil fauna is reflected in the increase of xerothermophilous and eurytopic species, and in the decrease of hemizoophagous species (Szujecki 1979). This is thought to lead towards delaying faunal succession. Even epigeic carabids, which generally stabilize their communities most rapidly, are affected according to one Polish study (Szujecki 1979).

In northern Finland, the advance of damage in *Pinus sylvestris* plantations on unploughed sites has been observed to be equal to that on ploughed sites, the basic difference being the somewhat milder effect of drought on ploughed sites and evidently the scarcity of vole damage that resulted from the lack of grass cover (Heikkilä 1981). Damage caused by *Hylobius abietis* can be reduced by making 15–20 cm wide zones of mineral around the pine seedlings (Christiansen & Sandvik 1974, Söderström 1976), and it has been observed that the damage has been less serious on ploughed sites, as well (Levula & Heikkilä 1981).

24. Tree species composition of stands

Any study of virgin forests will furnish proof that mixed stands are much safer against insect injury than pure stands. Tree species which tend to form large, homogeneous stands also tend to have a rich and injurious bark beetle fauna (Lekander et al. 1977). In southern Scandinavia the spruce monocultures have also been considered to have partially caused the outbreaks of the nun moth *Lymantria monacha* L. (see e.g. Bejer 1979, 1980, 1981a, 1982). Moreover, the numbers of such predators as Carabidae and parasitoids as Ichneumonidae in forest sites in multispecific stands are higher than in pure stands in the same site (Szujecki 1979, see also Györfi 1952). In fact, it can safely be said that the greater the diversification of tree species, the less frequent insect outbreaks will be (Knight & Heikkenen 1980).

Many human practices in the past have unconsciously encouraged insect outbreaks (Knight & Heikkenen 1980), as well as decreased numbers of other species. Especially species associated with *Populus tremula* (in particular old trees) have decreased (e.g. Väisänen 1982). This tree species has been strongly persecuted because of its low economic value, its tendency to form thickets of sprouts and partially because of its status as a host of *Melampsora pinitorqua*, a serious disease of *Pinus sylvestris*. Also other deciduous trees, e.g. *Salix caprea*, growing among young conifers have been destroyed, either mechanically or by means of herbicides. How this practice affects invertebrates is poorly studied (see e.g. Eijsackers & van der Drift 1976).

The splitting of forests has increased edges of forests with typical bush vegetation associations. The influence of the so-called edge effect has not been studied in forest invertebrates, but this development has surely increased at least species living on young willows etc.

Exotic conifers in the Nordic Countries have mainly been attacked by indigenous pests (e.g. *Pinus contorta*, see Annila et al. 1983; *Larix* spp., see Långström 1981). However, several species are bound to live on *Larix* and have thus been transported to Nordic Countries (Eidmann 1965). Exotic insects associated with seed and small plants have spread best, those associated with bark and

timber have followed the trade routes only (Bejer 1981b).

25. Fertilization

In northern Europe, forest fertilization commenced in the early 1950s. In Finland, 6.6×10^4 hectares mineral land and 4.4×10^4 hectares peatland were fertilized in 1982 (Yearbook of forest statistics 1983: 103). In Norway, the respective areas were in 1981 2.4×10^3 and 1.6×10^3 hectares (Årsmelding for 1981: 43), and in Sweden 1.3×10^5 and 3.0×10^3 hectares in the same year (Skogsstatistisk årsbok 1981–1983: 82). The aim of this practice is to increase the content of nutrients in the soil, and so accelerate the growth of trees. This increase of nutrients unavoidably benefits other vegetation, too, as well as many micro-organisms (Franz 1963, Huhta et al. 1967).

The most important factors in fertilization affecting the soil invertebrates in northern European heath forests are the content of nitrogen and pH value in the soil (Marshall 1977, Lohm et al. 1977, Behan et al. 1978, Abrahamsen & Thomson 1979, Huhta et al. 1984). Microbial activity is quickly accelerated after the application of fertilizer (Franz 1963). This may be due to the decrease in acidity rather than the increase in nutrients (Huhta et al. 1967). The significant role of pH for the soil invertebrates has been recently experimentally demonstrated in several laboratory studies (Bååth et al. 1980, Hågvar & Abrahamsen 1980, Hågvar & Amundsen 1981). The increase of the nematode species feeding on bacteria and the decrease of many typical species of the acid heath forest soils feeding on litter or mycelia (Enchytraeidae, e.g. *Cognettia sphagnetorum*, and several common oribatids) is probably due to the change towards a microbial flora dominated by soil bacteria (Huhta et al. 1984). The impact on Nematoda is transient, lasting only from one to two years. According to Huhta et al. (1967) the numbers of Enchytraeidae, Collembola and dipterous larvae increased in the second or third year after the fertilization treatment. Fertilization seems to decrease the number of Lumbricidae, while it has no effect on macroarthropods of the the soil (Huhta et

al. 1967, Huhta et al. 1984; see also Lohm et al. 1977).

In general, rather little is known about the effect of fertilization on the invertebrate populations of field layer and trees. Forest fertilization has been found to affect the occurrence and harmfulness of many insects (Oldiges 1960, Schwenke 1960, Stark 1965, Hoffmann 1966, Baule 1968, Krauss 1969, Mitscherlich 1975): Fertilization either increases the number of pests, decreases it or has no effect. (1.) Population densities of *Aradus cinnamomeus* Panzer (Heteroptera, Aradidae), a sap sucking insect living on young pines, have been recorded to be greater in fertilized than in unfertilized trees (Heliövaara et al. 1983). It is probably easier for the sucking insects to take sap from host trees which have a high turgor pressure owing to fertilization (Schwenke 1961, Mitscherlich 1975). (2.) Löyttyniemi (1978) reported that nitrogen fertilization with the standard dosage had little effect on pine shoot beetles (*Tomicus* spp., Scolytidae) and caused no essential changes in the level of damage. (3.) An analysis of a recent outbreak of the European pine sawfly (*Neodiprion sertifer* (Fourcroy), Diprionidae) on Scots pine in southern Sweden showed that the damage was less severe in a fertilized stand (Larsson & Tenow 1984). Mortality in the larval stage has been suggested as the main reason for the low number of defoliating insects observed after a fertilization of pine stands (e.g. Schwenke 1960). The better nutritive state of stands probably implies an increase in available resources for allocation to other processes than growth, e.g. for synthesis of defensive chemicals, making fertilized stands less susceptible than non-treated stands (see Larsson & Tenow 1984).

26. Insecticides, pheromones and biological control

As a mean of forest protection, direct control has both special merits and certain disadvantages. Some disadvantages are inherent in some of the methods of direct control because of the damage to the forms of life other than noxious insects, and even the strategic objective of forest protection may be partially defe-

ated by improper use of commonly used tactics. Insecticidal applications are the chief target for criticism in these respects. The undesired effects of insecticides may include damage to beneficial predaceous insects and mites, as well as to birds, fish and other aquatic life (see Gustafsson 1960, Graham 1963, Eidmann et al. 1979).

Various insecticides including DDT, lindane, malathion and dimethoate are used in forestry against harmful insects in northwestern Europe (see Bakke et al. 1984). DDT has been used in Finland from 1945 until September 1971, when its legal use was restricted in treating saplings in nurseries (see Rautapää et al. 1976), but the use of lindane has been wider (e.g. Markkula 1974). In Sweden the use of DDT and lindane has not been permitted since 1975. In the period 1970–1974 treatment of conifer seedlings was the only use of DDT permitted in Sweden. During this period 10.3 tons of DDT were annually used for treating 2.71×10^8 seedlings, amounting to 38 mg DDT per seedling (Eidmann et al. 1979). Instead of DDT, synthetic pyrethroids are nowadays used in Sweden. In 1981, every third pine plant was treated by pyrethroids in central and southern Sweden (Skogsstatistisk årsbok 1981–1983: 71). In Finland there were, for instance, in 1973 two preparates for the control of insects in forest nurseries and two for the protection of unbarked timber. The quantity of these insecticides used in forestry totalled 17.7 tons, and contained 90 kilos of DDT and 3453 kilos of lindane (Markkula 1974). In Norway, 1.5 tons DDT preparate is yearly used against *Hylobius* (Bakke et al. 1984); the accurate amount of lindane used is not available. In Denmark during outbreaks of *Lymantria monacha*, insecticides, especially phenithrothion and endosulphan, and biological control have been used (Bejer-Petersen 1974, Zethner 1976). In Poland, large areas have been treated against *Lymantria* with pyrethroids dispersed from the air (Król 1983).

When planting a new pine stand, protection of seedlings against *Hylobius abietis* with lindane or other means of combatting is usually considered necessary (see Annila 1982a). Treatment with lindane essentially decreases the amount of injuries caused by this serious pest and gives a sufficient shelter for the seedlings for the first period of growth (Eid-

mann 1972, 1974). Though the treatment with lindane kills a proportion of the weevils, we can hardly say that it has decreased the population of *H. abietis*. *Hylobius* specimens are sometimes eaten in great quantities by some birds such as *Larus canus* (Pulkkinen 1983). Thus, transfer of insecticides through this insect species to higher trophic levels is probable.

Chemical control against other forest pests has not been applied very widely in northwestern European forests. In Sweden, DDT has been used in practical forestry against several forest pests, including *Lymantria monacha*, *Panolis flammea* (Denis & Schiffermüller), *Operophthera brumata* (L.), *O. fagata* (Scharfenberg), *Erannis defoliaria* (Clerck), *Cephalcia abietis* (L.), and *Neodiprion sertifer* (Lekander 1954). *Bupalus piniarius* (L.) has been controlled in an area of 6300 hectares with DDT in southeastern Finland (Simolinna et al. 1959), and with Dimilin in 1984 in eastern Finland (unpubl. data). In 1963 a forest area of several hundred hectares in southwestern Häme was sprayed with a thiodan preparation by airplane (Köppä 1964). Other treatments have been in Finland more or less experimental (see Annila 1973, 1977). Tests of chemical methods for protecting stacks of pine pulp wood especially against *Tomicus piniperda* have been made, but they have not been applied very much in practical forestry (see Butovitsh & Eidmann 1962, Rummukainen 1964, Heikkilä 1978, Juutinen 1978).

According to the investigations made by Huhta et al. (1967) the mean density of the soil fauna including all groups of animals except oribatids, was considerably lower in the area treated with insecticides (lindane preparate) than in the untreated control locality. The losses varied from 22 to 35 % in different groups, and in chilopods up to 68 %. The species living mainly on the soil surface and among litter, and especially the predatory ones (beetles, spiders, chilopods), seemed to suffer most (more than 30 %), while the true soil fauna was less affected. Zoebelein (1960) reported that Psocoptera, Arachnida and to some extent Collembola, Carabidae and Chalcididae are particularly threatened by DDT treatment. According to Sheals (1955) BHC (benzene hexachloride) is deleterious to mites and springtails, but DDT

indirectly increases the number of springtails twofold by suppressing predatory mites. Edwards & Heath (1963) also report that the density of springtails is increased by DDT, but decreased by aldrine. Richter (1953) has stated that BHC powder has only a slight influence in forest soil, but that if the same poison is given as an emulsion or suspension, a sharp decline in springtail and mite populations is observed. In Denmark, Dahl & Beier Petersen (1960) have studied the influence of control experiments on the remaining part of the arthropod fauna during a control of *Lygaenomatus abietinus* (Christ). It was estimated that about 3.5×10^6 insects per hectare were killed by the treatment by parathion, but only a few days after the treatment the arthropod fauna again seemed to be of normal size. The groups most seriously affected were Diptera, Hymenoptera and Psocoptera. According to Bracher & Bider (1981), in Canada the lepidopterous and arachnid activity decreased significantly right after the aerial spray of aminocarb. In Germany, DDT treatment caused apparent injury to parasitoid insects, syrphids, coccinellids, spiders etc. during only four days (in some places even up to twenty days) (Zoebelein 1958). Large scale control measures against *Elkneria pudipunda* (L.), using less than 1 kg DDT-active ingredient per hectare reduced the parasitoids of these moths only slightly (Zoebelein 1960). At nearly 100 % kill of *Lymantria* larvae there was a 99 % reduction in injurious insects, and a 45 % reduction in other insects (Zoebelein 1957). The recolonization and replenishment of the fauna of treated areas takes place relatively quickly (Zoebelein 1960).

The success of pheromone traps in catching bark beetles gave rise to the idea that traps scattered throughout a pest's environment could be used to control population levels. The most ambitious trap-out programme was undoubtedly that launched in Norway and Sweden in 1979. In Sweden, from 1971 to 1980, the bark beetles have killed $1.2-3.4 \times 10^5$ cubic meters spruce wood every year, and 2.3×10^6 in total (Skogsstatistisk årsbok 1981−1983: 70, 76). Following a population explosion of *Ips typographus*, and the threat of more catastrophic tree losses, pheromone-baited traps (600 000 in Norway and 200 000 in Sweden), were distributed throughout infested forests. Some 2.9

$\times 10^9$ beetles were trapped in 1979 and 4.9×10^9 in 1980. Synthetic pheromones of *Ips typographus* have also been observed to act as kairomones. For instance in 1970s in Norway one predaceous clerid specimen *(Thanasimus formicarius* (L.), *T. femoralis* (Zetterstedt)) was trapped for approximately every fourth *I. typographus* (Bakke & Kvamme 1978, 1980). In new trap models used in the 1980s their proportion was only about 0.2 % (Bakke et al. 1983, 1984). In Finland also *Epuraea* species, predators of bark beetles were trapped (Selander & Nuorteva 1980). Pheromone traps are not used in practical forestry in Finland. Whether the removal of several billion beetles has had any effect on averting even more catastrophic losses remains open to conjecture (see Birch & Haynes 1982).

As regards biological control in the northern European forests, only nuclear polyhedrosis virus against *Neodiprion sertifer* has been applied in practical forestry (see Nuorteva 1972, Bakke et al. 1984). Though the effects in the mortality of its target are indisputable, the application of nuclear polyhedrosis virus has hardly had any permanent influence in the abundance of *N. sertifer*. This is because the latent stage of the polyhedrosis disease is naturally present, especially in areas where these diprionid sawflies have been abundant for several years (Nuorteva 1964b, 1972). In experiments, the nuclear polyhedrosis virus disease of certain other insects has had no effect on other insect species, or on mammals (Ignoffo & Heimpel 1965, Heimpel 1966, 1967, Meinecke et al. 1970). In Denmark and southern Sweden, *Lymantria monacha* has been controlled by aerial spraying of insecticides, NPV-virus and *Bacillus thuringiensis* (Bejer-Petersen 1974, Zethner 1976, Austarå et al. 1983).

We may summarize that the application of insecticides, pheromones, and biological control agents in practical forestry has been used on such a small scale in the Nordic Countries that hardly any irreversible effects on the forest invertebrates are visible. It must be noted that pesticides used especially in agriculture have caused well-known cases of permanent population declines in several vertebrates. The slight usage of chemical control agents in forests can also be seen as a sign of success in silvicultural practices used in northwestern Europe.

3. GENERAL CHANGES IN FOREST DYNAMICS

Untouched boreal forests include both a series of successive age-class stages in a single site and the mosaic-like complex of these sites in different stages. The different forest types (dry heath forest, moist heath forest etc.) can be recognized with the aid of the vegetation of field and bottom layers, although the dominance relations of plant species vary during the succession (see Cajander 1926, 1949, West et al. 1981).

Finegan (1984) has recently reviewed the theories of forest succession. According to the holistic theory of forest succession, successional change is often considered to occur in stages through wave-like invasions by groups of species, and it is thought to be controlled by the vegetation itself. Thus autogenic change caused by the presence of a particular species or a group of species makes the environment suitable for the next group of species and so facilitates successional change. Successional change is usually held to be predictable and therefore deterministic, converging to forest from various different starting points. According to the reductionist theory the plant community is interpreted to be a fortuitous assemblage of species populations, each with unique behaviour. The fundamental stochasticism of this view is supported by evidence of several alternative successional pathways within a given vegetation type. Succession is merely regarded as the sequential physiognomic dominance of the site by species with different life histories, growth rates and sizes at maturity, and, as especially emphasized, all the species participating in a succession become established at or very shortly after initiation (initial floristic composition model). The theoretical background of forest succession is thus controversial and not yet fully understood (see further Finegan 1984). However, it would be valuable to notice the different interpretation possibilities of the succession also when considering the successional changes in invertebrates.

Modern forestry strongly affects any forest just under treatment, as shown in the section 2. The vegetation and presumably also the invertebrate community have a good capability to return to the original composition within a few years after treatment, at least in most cases. However, the detrimental effects become more apparent when larger geographical areas are treated. The large-scale ecological changes in the backwoods and untouched forests are mainly due to the efficient silviculture, since other factors in land usage have had only a minor role in reducing the area of old forest during recent years.

Man's effect on northern European forests dates back to several thousand years before the present day. Woodland burning and tar burning modified the age-class and species composition in the forests over several centuries up to the beginning of the 1900s (e.g. Heikinheimo 1915, Äyräpää 1946). However, old backwoods and remote virgin forests were left untouched by man until the recent years of efficient forestry.

31. Loss of primevals

In virgin forests relatively old age-classes dominate. Two examples of the age-class distribution in boreal forests are given in Fig. 2. These two nature reserve areas have been practically unaffected by human practices at least during this century, either by silviculture or by the prevention of natural fires. In some extreme cases the climax stage can be reached in moist forest types only after 500−600 years from a fire (Heikinheimo 1915, Kalliola 1973). Because fires have usually occurred more often, the real climax stages in boreal forests seem to have been relatively rare even in natural conditions. The present data show, however, the conspicuous fact that even the middle-aged stages are nowadays rarities and areally small in Sweden, Finland and elsewhere in northern Europe (Tables 1, 2, Figs. 3, 4).

The loss of primeval forests has most distinctly influenced the specialized species of the decomposition system associated with de-
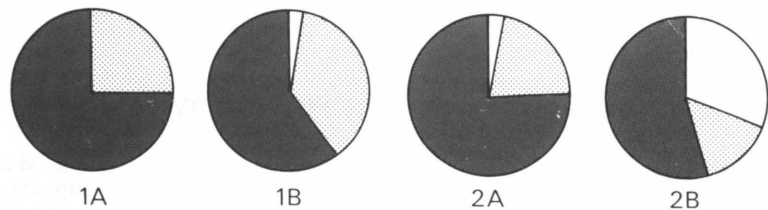
1A 1B 2A 2B

Fig. 2. The age-class distribution of moist and dry heath forests (*Vaccinium myrtillus* and *V. vitis-idaea* site types) in two untouched boreal forest areas. 1. Ulvinsalo, a. moist heath forest (1067 ha), b. dry heath forest (254 ha). 2. Pyhä-Häkki, a. moist heath forest (249 ha), b. dry heath forest (217 ha) (data from Salonen et al. 1980). White – 0–100 years, shaded – 101–150 years (note the difference from Figs. 3–4), black – more than 150 years.

Kuva 2. Metsän ikäluokkajakauma tuoreella ja kuivahkolla kankaalla (MT ja VT) kahdella koskemattomalla metsäalueella. 1. Ulvinsalo, a. MT (1067 ha), b. VT (254 ha). 2. Pyhä-Häkki, a. MT (249 ha), VT (217 ha). Valkea – 0–100 vuotta, varjostettu – 101–150 vuotta (huomaa ero kuviin 3–4), musta – yli 150 vuotta.

caying logs and wood-rotting fungi, and species with strict microclimatic requirements (stable moisture and shade). Many such invertebrate species have drastically declined and some of them seem to have vanished from northern Europe. Often the evidence of faunal changes is very weak due to the scarcity of old reference studies and the present rarity of the declined species. No abundant invertebrate species strictly restricted to primeval forests is known to the authors. More abundant primeval species such as geometrid moth *Eupithecia conterminata* (Zeller), noctuid moth *Xestia sincera* (Herrich-Schäffer), or beetles *Ostoma ferruginea* (L.) and *Dendrophagus crenatus* (Paykull) can be met in cultivated forests, too, although in lesser numbers. The tendencies in the population declines of different species have, however, usually been observed over large geographical areas. Species commonly collected by students of the previous centuries are rare or have disappeared today in spite of the many more collectors, and seem to be evident cases of declines or even local extinctions. Invertebrate species associated with primeval forests in northern Europe are listed in Table 3. The data is based mainly on literature such as Saalas 1932, 1939, Krogerus 1943, Kangas & Kangas 1944, Kangas 1947, 1961, 1971, 1979, 1983, Lundblad 1950, Kaisila 1960, Linnavuori 1967, Lindroth 1973, Mikkola 1974, 1979, Baranowski 1977, Lundberg 1977a, b, 1978, Biström 1978, Imby & Palm-

qvist 1978, Muona 1978, 1984a, b, Rutanen 1980, Helve 1981, Bilý 1982, Clayhills 1982, Palm 1982, Väisänen 1982, Heliövaara & Väisänen 1983.

At present many important invertebrate groups of northern European forest ecosystems which have possibly suffered from the large-scale forest management are still taxonomically very poorly known or even cannot be identified at all (e.g. Diptera, Mycetophiloidea and several parasitoids). Thus, the available data are restricted to large and conspicuous species and the above list of declined primeval species must be seen only as a collection of examples.

The invertebrate species in the decomposition system of timber seem to be the ecological group which has most seriously suffered from the loss of primevals. Fresh wood can be attacked by scolytid, curculionid, buprestid and cerambycid beetles or sawfly larvae and later by Diptera such as Tipulidae, Mycetophilidae, Cecidomyiidae and Sciaridae. Some beetles carry ambrosia fungi which proliferate in the tunnels and provide food for their larvae. Moisture is important and soaking for long periods makes the woody tissues more susceptible to attack by micro-organisms. Fungal mycelia ramify through cracks and soften tissues, and then many invertebrates, especially scarabaeids, millipedes and isopods begin to invade the moist tissues. Often mosses may begin to grow on the outside of the wood and provide a moist habitat

Table 1. Age structure of the stands on forest land in 1978–1982 by forestry boards districts in Sweden (see Fig. 3). All tree species (data from Skogsdata 83, 1983).

Taulukko 1. Metsien ikärakenne metsämaalla vuosina 1978–1982 piirimetsälautakuntien alueilla Ruotsissa (katso kuva 3). Kaikki puulajit.

| District	Age classes/per cent of total area 0–100	101–140	141–	Total area of forest land/ 1000 hectares
1	95.0	5.0	0.0	84
2	96.6	3.4	0.0	288
3	98.5	1.4	0.1	190
4	97.6	2.3	0.1	295
5	95.2	4.5	0.3	194
6	67.8	28.3	3.9	138
7	92.8	6.7	0.5	723
8	95.9	4.0	0.1	628
9	92.9	6.3	0.8	693
10	90.5	9.1	0.4	705
11	93.1	6.2	0.7	382
12	91.0	8.3	0.7	607
13	92.0	6.9	1.1	329
14	13.7	12.3	1.4	286
15	90.6	8.8	0.6	421
16	91.3	8.2	0.5	386
17	89.4	9.8	0.8	569
18	83.7	14.1	2.2	1325
19	66.9	26.8	6.3	2048
20	82.6	15.5	1.9	1469
21	76.4	20.9	2.7	1715
22	56.0	32.3	11.7	2804
23	64.8	26.1	9.1	3300
24	62.0	24.7	13.3	3924
1–12	92.9	6.6	0.5	4925
13–19	79.6	17.1	3.3	5364
20–22	68.4	24.9	6.7	5988
23–24	63.2	25.4	11.4	7224
1–24	74.5	19.4	6.1	23501
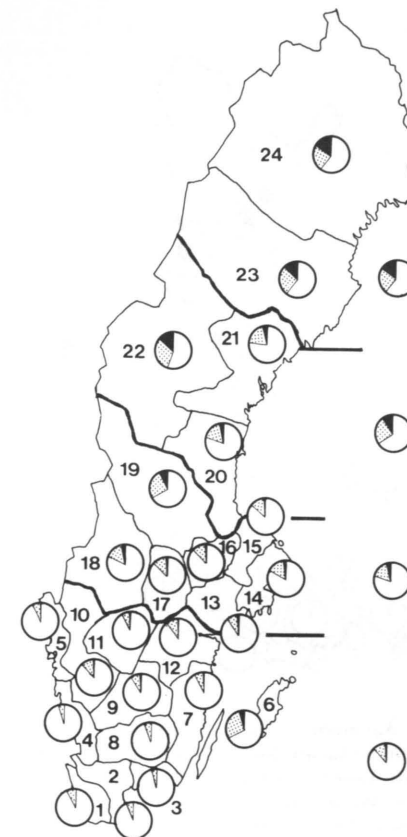
Fig. 3. Age structure of the stands on forest land in 1978–1982 by forestry boards districts in Sweden (data from Table 1). White – 0–100 years, shaded 101–140 years, black more than 140 years.

Kuva 3. Metsien ikärakenne metsämaalla vusina 1978–1982 piirimetsälautakuntien alueilla Ruotsissa. Valkea – 0–100 vuotta, varjostettu – 101–140 vuotta, musta – yli 140 vuotta.

for invasion by arthropods. Eventually the wood becomes soft, fragmented, gradually incorporated into the humus layer, and finally thoroughly distributed through the upper layer of soil (Edwards et al. 1970).

Ehnström (1978, 1979) distinguished four temporal successive phases in the invertebrate community exploiting dead wood (Fig. 5): Phase A – a short-term stage mostly with

species feeding on bark, such as Scolytidae, Cerambycidae and species living in their cavities as well as parasites and predators of them. Phase B – a rather short stage with species mainly living under bark and in the surface layer of timber, and species associated with fungi. Bark becomes loose and falls from the stem. Phase C – a long term stage which can take several decades, mostly with wood-
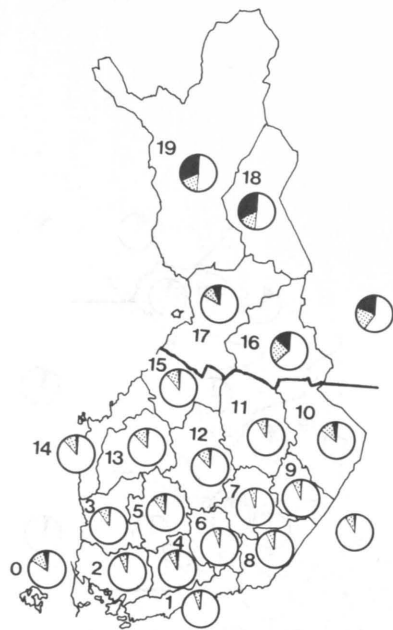
Fig. 4. Age structure of the stands on forest land in 1971–1976 by forestry boards districts in Finland (data from Table 2). Symbols as in Fig. 3.

Kuva 4. Metsien ikärakenne metsämaalla vuosina 1971–1976 piirimetsälautakuntien alueilla Suomessa. Merkkien selitykset kuten kuvassa 3.

Table 2. Age structure of the stands on forest land in 1971–1976 by forestry boards districts in Finland (see Fig. 4). All tree species (data from Yearbook of forest statistics 1983).

Taulukko 2. Metsien ikärakenne metsämaalla vuosina 1971–1976 piirimetsälautakuntien alueilla Suomessa (katso kuva 4). Kaikki puulajit.

District	Age classes/per cent of total area			Total area of forest land/ 1000 hectares
	0–100	101–140	141–	
0	83.1	14.8	2.1	70
1	92.1	7.1	0.8	352
2	91.4	7.4	0.8	459
3	89.9	9.6	0.5	661
4	90.8	8.1	1.1	533
5	89.1	9.7	1.2	782
6	94.8	4.8	0.4	609
7	95.7	4.2	0.1	805
8	93.7	5.8	0.5	621
9	93.7	6.1	0.2	509
10	88.1	9.7	2.2	1368
11	93.0	6.5	0.5	1312
12	89.7	9.5	0.8	1226
13	89.0	10.5	0.5	883
14	87.5	12.0	0.5	445
15	90.5	8.8	0.7	677
16	65.5	23.6	10.9	1627
17	81.3	13.9	4.8	1472
18	51.6	16.3	32.1	1783
19	49.8	16.9	33.3	3544
0–15	91.1	8.1	0.8	11312
16–19	58.6	17.6	23.8	8426
0–19	77.2	12.2	10.6	19738

Table 3. Invertebrate species associated with primeval forests in northern Europe. There is a great variation in the strictness of the association.

Taulukko 3. Harvinaisia, erityisesti vanhoista metsistä Pohjois-Euroopassa tavattuja selkärangatonlajeja.

ARACHNIDA
Pseudoscorpionida
Lamprochernes chyzeri

INSECTA
Heteroptera
Cryptostemmatidae
(?) *Ceratocombus corticalis*
Aradidae
Aradus pictus
Meziridae
Mezira tremulae

Homoptera
Achilidae
Cixidia confinis
Cixidia lapponica

Lepidoptera
Arctidae
Borearctia menetriesii
Noctuidae
Xestia borealis

Diptera
Pachyneuridae
Pachyneura fasciata

Keroplatidae
(?) *Keroplatus sesioides*
Mycetophilidae
(?) several species
Solvidae
Solva interrupta

Hymenoptera
(?) several parasitoid species

Coleoptera
Leiodiidae
Liodopria serricornis
Agathidium pulchellum
Staphylinidae
Tachinus elegans
Eucinetidae
Eucinetus caucasicus
Lucanidae
Ceruchus chrysomelinus
Eucnemidae
Hylochares cruentatus
Buprestidae
(?) *Chalcophora mariana*
Peltidae
Peltis grossa
Thymalus limbatus

Thymalus subtilis
Nitidulidae
Ipidia sexguttata
Cucujidae
Uleiota planata
Cucujus cinnaberinus
Cucujus haematodes
Languriidae
Eicolyctus brunneus
Oedemeridae
Ditylus laevis
Pythidae
Pytho kolwensis
Pytho abieticola
Boridae
Boros schneideri
Mordellidae
Conalia baudii
Melandryidae
Xylita livida
Zilora elongata
Cerambycidae
Tragosoma depsarium
Leptura thoracica
Monochamus urussovi
Scolytidae
Orthotomicus longicollis

inhabiting species. Most of the species declined belong to this stage. Phase D – a very long stage during which many wood-inhabiting species are replaced by species living under the shelter of decaying logs, such as soil insects, molluscs and chilopods. At this stage the stem begins to break.

Although the invertebrate species of the decomposition system of timber seem to be the ecological group which has most seriously suffered from loss of primevals, we can find even there species that have, in fact, became more abundant. The pioneer species, the phase A of this system which occurs in the logs during the first few years after the death of the tree has had the best success, and many of these species are nowadays injurious pests of cultivated stands, although in primevals they had only a minor role (see Franz 1948, Lindberg & Saris 1952, Schimitschek 1952, 1953a, b, 1954). After storms some scolytids of the phase A such as *Tomicus* spp. and *Ips typographus* living in the windthrown conifers in old natural forests may increase in numbers and cause injury also in the nearby cultivated forests (Kolbe 1980, Annila 1982b). Also the last phase D seems to have suffered only little, like the soil fauna in which there are no evident examples of species exclusively associated with primeval forests (see e.g. Huhta & al. 1967, Palmgren & Biström 1979). In herbivorous invertebrates the
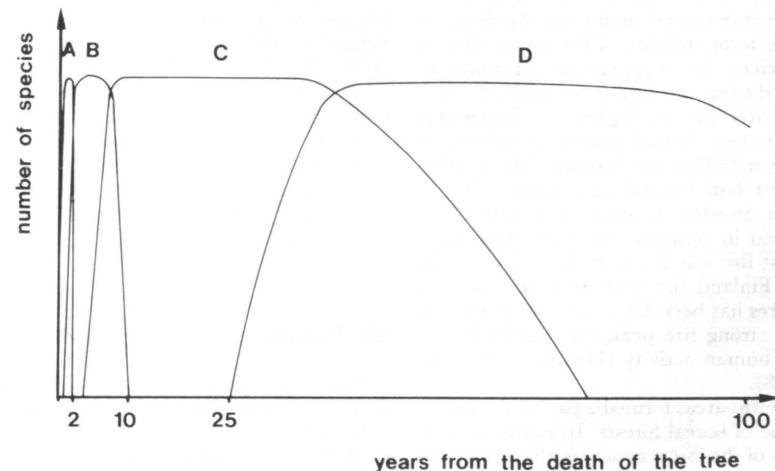

Fig. 5. Successive phases in the invertebrate community exploiting dead wood (for details, see the text). Note that much variation occurs depending on the tree species and geographical areas in question (according to Ehnström 1979).

Kuva 5. Kuolleessa puussa elävän selkärangatonyhteisön sukkessiovaiheet (katso teksti). Kehitys vaihtelee huomattavasti alueittain ja puulajeittain.

Table 4. Invertebrate species associated with natural fires in northern Europe. At least *Aradus* spp. except *A. lugubris*, and *Agonum bogemanni* have drastically declined.

Taulukko 4. Erityisesti kuloalueilta tavattua hyönteislajistoa Pohjois-Euroopassa. Ainakin Aradus-suvun latikat A. lugubrista lukuunottamatta ja Agonum bogemanni ovat suuresti taantuneet.

Heteroptera	**Coleoptera**	Bostrichidae
Anthocoridae	Carabidae	*Stephanopachys substriatus*
Scoloposcelis obscurella	*Pterostichus quadrifoveolatus*	*Stephanopachys linearis*
Scoloposcelidea phryganophila	*Agonum bogemanni*	Cucujidae
Aradidae	*Agonum quadripunctatum*	*Laemophloeus muticus*
Aradus anisotomus	Staphylinidae	Latridiidae
Aradus signaticornis	*Paranopleta inhabilis*	*Corticaria planula*
Aradus angularis	Elateridae	Salpingidae
Aradus aterrimus	*Denticollis borealis*	*Sphaeriestes stockmanni*
Aradus lugubris	Buprestidae	Anthribidae
Aradus laeviusculus	*Melanophila acuminata*	*Platyrhinus resinosus*
	Melanophila cyanea	

change in the age class distribution of forests seems to have caused only few distinct declines, and in general they apparently have a less prominent role in old forests than in cultured young stands.

32. Cessation of natural fires

Fire represents a natural factor in boreal forest ecosystem and maintains the diversity and long term stability of the forest. Due to the efficient fire suppression in northern Europe during the last two hundred years, natural fires are no longer a rejuvenating factor in these boreal forests. According to Zackrisson (1977), for instance, the coniferous forest had burned in a river valley in northern Sweden at mean intervals of 80 years, and in contrast, the mean time since the latest fire was found to be 155 years. In eastern Finland the average time lapse between fires has been 120 years, but in the late 1800s a strong fire peak was caused by increased human activity (Haapanen & Siitonen 1978).

The burnt areas formed a part of the natural mosaic of boreal forests. In northern Sweden 1 % of the forest area was affected by fire every year up to this century (Zackrisson 1977). The fires have thus been an unpredictable but relatively common phenomenon in the boreal ecosystems. This has made it possible that a specialized fauna associated with burnt areas, e.g. burnt tree trunks with fungi,

has developed. Specialized species associated with naturally burnt areas and now declined or vanished in northern Europe are listed in Table 4. The list is entirely based on literature (Palm 1955, Linnavuori 1967, Lindroth 1973, Ehnström 1977a, b, Heliövaara & Väisänen 1983, Lundberg 1984). The faunal succession in burnt areas include also many species of open habitats and that can be found commonly in areas which have been clear-cut, burned over and ploughed (see Hauge & Kvamme 1983, Huhta 1971, Schaefer 1980, Schauermann 1980, Winter 1980, Winter et al. 1980). Especially in North America (see e.g. McLeod 1980 and the references there and Wright & Bailey 1982), concern has recently expressed that the practices suppressing forest fires may ultimately lead to lowered productivity, reduced species diversity, and the distinct possibility of the extinction of some species.

33. Dominance of young stands

The single-species, even-aged forest is undoubtedly easier to manage and more profitable than mixed forest. Therefore foresters tend to favour large-scale, pure-stand silviculture over practices that grow trees in mixture, in rotations that alternate species, or in diversified age-classes and size classes (Knight & Heikkenen 1980). This has led to encouraging pests, especially those of young stands, that under primitive forest conditions

were unknown. The arthropod densities of young stands can be high. According to Martin (1966) the arthropod densities in relation of the crown size of *Pinus resinosa* in Canada increases rapidly until the trees are about 15 years of age, and then declines. In young stands e.g. Orthoptera and Hemiptera are more common than in later successional stages of the forest (e.g. Martin 1965). In Sweden, the number of Arachnida species and individuals is lower on spruce plantations with closed canopy and no field layer then in more open plantations with field layer (Almquist 1982). Moreover, the composition of the forest as a whole is of great significance, for instance, in the composition of invertebrate fauna of pine stumps. In monocultures of pine the fauna of the stumps has been observed to be made up of fewer species, but the density of the invertebrates is greater (Wiackowski 1957).

Hylobius abietis L. was regarded as a serious pest in Central Europe in the early 1800s. In Finland, scattered records on small injuries of planted pines and spruces exist since planting has been used in artificial regeneration of

forests (Saalas 1949). However, from the 1950s natural regeneration has been largely abandoned and seedlings are planted among fresh stumps in clear-cut areas. Nowadays some 1.7×10^8 coniferous seedlings are planted here per year and the damage caused by *H. abietis* destroys every fifth of them on average (Nuorteva 1982). The injuries would be much more serious still if chemical control was not used. Similar records are available from the other northwestern European countries (e.g. Ehnström et al. 1974, Löyttyniemi et al. 1979, Långström 1980, Austarå 1983).

The pine bark bug *Aradus cinnamomeus* is another important pest of young stands which has greatly benefited by the silvicultural practices favouring large-scale pure stands of pine seedlings (Brammanis 1975, Heliövaara 1982, Heliövaara & Väisänen 1983). The first records of this sap-sucking insect from Finland, for instance, are from the end of the 1800s, during this century the records gradually increased, but it was not until the early 1970s that the bug was finally recognized as a pest.

4. SPECIES DIVERSITY IN NATURAL AND CULTIVATED FORESTS

In this section we try to summarize records on the diversity, the numbers and relative abundance of invertebrate species, in natural and cultivated forests. Before this it seems necessary to discuss briefly the concept of the natural equilibrium, so widely used in the forest entomological literature.

41. Equilibrium in virgin forests?

Recently many ecologists have altered their view of ecosystem function, structure, and behaviour from an equilibrium-centred view to an non-equilibrium one dominated by catastrophes (e.g. Connell 1978, McLeod 1980). Consequences of these developments in ecological theory pertaining to the coexistence of insect species in response to forest disturbances have been reviewed from a forest entomological point of view by McLeod (1980) concentrating on the situation in northern boreal forests in Canada.

According to the traditional equilibrium view a system will inevitably return to its equilibrium if it is perturbed from that state. Each species is specialized to its habitat or the resource which it can most efficiently use. In the absence of disturbance, the species assemblage persists at a high level of diversity. An equilibrium condition might be maintained in a community, if the frequency of disturbance were slower than the recovery rate of the community; if not, however, systems would rarely if ever reach the stable state. It has been observed that, if not disturbed, communities would be reduced to a low diversity equilibrium through processes of competitive exclusion (Connell 1978). In fact, a highly diverse community is maintained because of, rather than in spite of, disturbances on a moderate scale.

On the other hand, if these disturbances are short, only those species which quickly mature will form the new community. They must be opportunistic occupiers of empty

space. These pioneer communities will be low in diversity. In graphical form, the curve of diversity as a function of disturbance frequency will be dome-shaped peaking at moderate disturbance frequencies (Connell 1978). Moderate frequencies are referable to the normal replacement rate of the forest. McLeod has reviewed some cases in North American forests supporting Connell's ideas. Auclair and Goff (1971), who studied diversity changes in time in the upland forest of the Great Lakes, related diversity to an environmental gradient and showed that diversity peaked at mesic conditions. According to their results in stressed sites where pioneer species occur, the diversity increased progressively with time.

McLeod (1980) points out that the commonly observed saturating relationship between the diversity of taxa and the area of substrate they occupy seems to contradict Connell's model. He asks, if species/area relationships strongly suggest an equilibrium world, how does this reconcile with non-equilibrium theory? According to him the problem only lies with the choice of the term "equilibrium" to describe the saturation of species assemblages with area. If species assemblages are attuned to disturbance rather than exclusively to competitive coexistence on a finely divided niche space, saturation would still occur at levels determined by the scale of the disturbances, and the rapid return to normalcy following disturbance could be more logically explained.

In Fig. 6, McLeod's (1980) hypothetical landscape of insect faunal diversity is shown on a "time since disturbance" vs. area gradient for mesic sites. The time required for species to saturate increases as a function of area. This is because invaders would fill the small patches much more rapidly than the large ones. On small areas, a peak in diversity would occur relatively early following a disturbance, but overall the diversity would be low, simply because of restrictions on the variety of plant species which would occupy
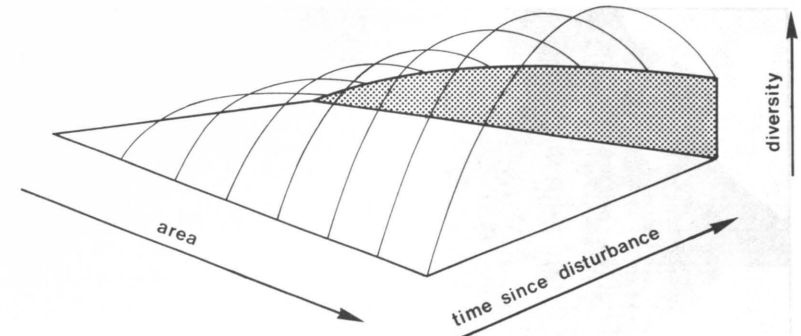
Fig. 6. McLeod's (1980) hypohetical landscape for an insect species assemblage showing diversity in relation to patch size (area) of disturbance, and time since disturbance.
Kuva 6. McLeodin hypoteettinen malli hyönteisten lajistollisesta diversiteetistä suhteessa häiriöalueen laajuuteen ja häiriöstä (esim. kulo, myrskytuho, hakkuu) kuluneeseen aikaan.

the area. As patch size increases, however, the peak of diversity occurs later, and is more pronounced. Thus, diversity/area and diversity/time relationships are difficult to reconcile in the absence of disturbance hypotheses (non-equilibrium).

42. Available data on numbers of species

The extremely low numbers of species in planted tropical monoculture stands when compared to the natural conditions in the same locality is a well-known fact. In forest zoological literature there are also examples of similar cases from other areas, e.g. about the diversity of arthropods in *Pinus radiata* stands in California (Ohmart & Voigt 1981). Thus, the scarcity of available data on the species diversity in natural and cultivated forests in northern Europe becomes still more surprising. In fact, only some pieces of information have been published. Studies, where the invertebrate communities of the same age-class stages in natural and cultived stands would have been compared, seem to be entirely missing.

In the present situation the only possibility is to compile the knowledge from scattered and incomplete sources. Ehnström (1979, 1983) gives an approximation: the numbers of species of a stand could decrease from 8000

to 2000 due to the efficient silviculture in Sweden. Although such an estimate is coarse, of course, it clearly describes the tendency, and something like the maximum diversity (see Fig. 6) and the minimum as well. However, as shown previously the invertebrate diversity can return to a higher level of diversity when the "time since disturbance" becomes longer. One may also ask how many species are really completely missing in the cultivated forests and how many species are only represented in low densities and thus not captured (cf. the holistic and reductionist theories of forest succession).

43. Island biogeographical aspects

When dealing with the species diversity in natural and cultivated forest it is not possible to restrict the discussion to a diversity within a single habitat (e.g. a primeval vs. a clear-cut area) but the natural mosaic including a range of habitats and age-class stages should be compared with that of a cultivated forest. The age-class distribution in a forest today seems to be quite contrary to that of a natural forest (see Fig. 7).

The extremely large boreal zone with long history seems to have been a relatively stable system in spite of the occurrence of fires.
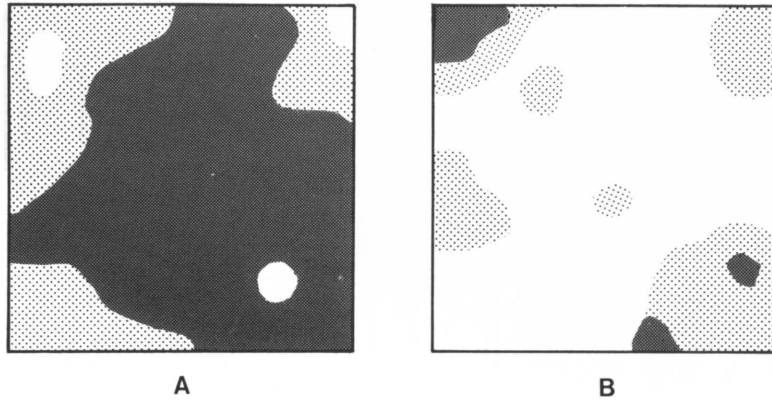
A   **B**

Fig. 7. A schematized illustration on the age-class distribution of forests in natural (A) and cultivated (B) forest areas. White – open field or young forest, shaded – middle-aged forest, black – old forest.

Kuva 7. Kaavio puuston ikäluokkajakaumasta luonnontilaisella (A) ja hoidetulla (B) metsäalueella. Valkea – avoin alue tai nuori metsä, varjostettu – keski-ikäinen metsä, musta – vanha metsä.

Thus, we can expect that specialized species characteristic of old age-classes or even stagnated climax stages can have occurred. Such a situation with a large and relatively continuous net of primeval forests has not necessarily favoured good dispersal abilities, and some of those species cannot have been adapted to the new situation where the habitats are small and far from each other. On the other hand, species of early stages of forest succession seem to have been favoured, as well as those of open biotopes, so that even new pests have appeared. The species associated with fires probably have good dispersion abilities but the practically total loss of fires seems to have been too great a change for some of them to survive.

The conservative influence of the present protected nature reserves on the species associated with primevals is not known. In isolated stands even a single nature catastrophe (or a disease etc.) may destroy any invertebrate population, and since source areas for a recolonization are far away and the dispersal abilities of these species less well developed, a certain gradual reduction can be expected in the numbers of species exlusively associated with primeval forests. In the case of these "taiga species" a suspicuous attitude to the conservative value of very small reserves could be realistic.

When considering the strategy in the design of natural reserves the theory of island biogeography has often been discussed (e.g. Diamond & May 1976, Simberloff & Abele 1976a, b, Gilbert 1980, Gilpin & Diamond 1980, Hanski 1982, Järvinen 1982, Margules et al. 1982, Simberloff 1982). In the case of northern European primeval forests the principal question on the relation of the number of reserves and their area is not of current importance: Only few small forest areas are in primeval state. In those cases when a decision between a single large and several small reserves must still be made, the decision should be based on empirical studies on threatened species.

5. CONCLUSIONS

1. The direct effects of different silvicultural practices of forest invertebrates are usually striking but transient. Invertebrate communities have in most cases a good capability to return to the original composition.

2. Detrimental effects of efficient forestry on forest fauna have become more apparent when larger areas are handled, including the primeval forests which were preserved until our days.

3. The loss of primevals has most seriously affected the decomposition system of timber, especially those invertebrates associated with logs decayed for some years and wood-rotting fungi, as well as some species with strict microclimatic requirements.

4. Cessation of fires has changed the forest dynamics, fire being no longer the main rejuvenating factor in boreal forests. Several forest insects associated with fire have drastically declined and may become extinct in the near future.

5. The abundance of young, even-aged stands and the aim for single-species forests have caused some pest problems, although less serious than in the tropics or in North America, for instance. This is also reflected in the slight usage of chemical control agents in northwestern European forests.

6. The nature reserves are not centres of pest dispersal. Although the injurious species in northern European forests are native, they have only a minor role in primeval ecosystems, much less important than in cultivated forests. The pest problems are mainly caused by the silvicultural practices themselves. As a consequence of strong storms bark beetles can sometimes become abundant in the fallen logs in nature reserves, as well.

7. The "equilibrium" of virgin forests seems to be dynamic, stabilized by disturbances, such as natural fires and storms. As pointed out by McLeod (1980) a highly diverse community is maintained because of, rather than in spite of, disturbances on a moderate scale. However, when very large areas are handled, efficient forestry cannot be a disturbance on a moderate scale, as contrasted to natural fires, etc.

8. Old stagnated primevals belong to the natural boreal forest ecosystem and their loss evidently decreases the faunal diversity on a larger geographical scale, although in a single locality the diversity may be highest in middle-aged stages.

9. Comparative studies on the species numbers in several stages of the succession in cultivated and virgin forests are needed to estimate more accurately the effects of forestry on the natural environment. In addition, studies of the invertebrate fauna of primeval nature reserves is needed to estimate the conservative value of protected areas, and especially in relation to their areal extent.

REFERENCES

Abrahamsen, G. & Thomson, W. N. 1979. A long term study of the enchytraeid (Oligochaeta) fauna of a mixed coniferous forest and the effects of urea fertilization. Oikos 32: 318−327.

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. Ann. Bot. Fenn. 5: 169−211.

Almquist, S. 1982. Spindeldjursfaunan i granplantering i södra Skåne. (Abstract: Spiders, harvestmen, and pseudoscorpions in spruce plantations in south Scania, Sweden (Arachnida)). Ent. Tidskr. 103: 97−105.

Annila, E. 1973. Chemical control of spruce cone insects in seed orchards. Comm. Inst. For Fenn. 78 (8): 1−25.

— 1977. Control of pine cone weevil, Pissodes validirostris Gyll. (Coleoptera: Curculionidae) in pine seed orchards. Commun. Inst. For. Fenn. 90 (6): 1−14.

— 1982a. Lindaanin käyttö männyn paperikennotaimien suojaamiseksi tukkimiehentäin tuhoilta. (Summary: Lindane treatment against Hylobius damage on paper pot seedlings of Scots pine). Folia For. 512: 1−14.

— 1982b. Suojelualueet vaikuttavat ympäristöönsä. Luonnonsuojelutoimiston julk. 4: 71−75.

— ,Heliövaara, K., Puukko, K. & Rousi, M. 1983. Pests on lodgepole pine (Pinus contorta) in Finland. Commun. Inst. For. Fenn. 115: 1−27.

Årsmelding for 1981. Landbruksdepartementet, Skogsavdelningen. 56 pp. Oslo.

Auclair, A. N. & Goff, F. G. 1971. Diversity relations of upland forests in the western Great Lakes area. Am. Nat. 105: 499−528.

Austarå, Ø., Annila, E., Bejer, B. & Ehnström, B. 1983. Insect pests in forest of the Nordic countries 1977−1981. Fauna Norw. Ser. B. 31: 8−15.

Äyräpää, T. 1946. Die Makrolepidopterenfauna des Kirschpiels Pielisjärvi und ihre Beziehung zur Kultur. Ann. Zool. Soc. Vanamo 11 (4): 1−65.

Bååth, E., Berg, B., Lohm, U., Lundgren, B., Lundkvist, H., Rosswall, T., Söderström, B. & Wiren, A. 1980. Effects of experimental acidification and liming on soil organisms and decomposition in a Scots pine forest. Pedobiol. 20: 85−100.

Bakke, A., Austarå, Ø. & Christiansen, E. 1984. Forstentomologi. 150 pp. Ås. Norges landsbrukshøgskole.

— & Kvamme, T. 1978. Kairomone response by the predators Thanasimus formicarius and Thanasimus rufipes to the synthetic pheromone of Ips typographus. Norw. J. Ent. 25: 41−43.

— & Kvamme, T. 1981. Kairomone response in Thanasimus predators to pheromone components of Ips typographus. J. Chem. Ecol. 7: 305−312.

— , Saether, T. & Kvamme, T. 1983. Mass trapping of the spruce bark beetle Ips typographus. Pheromone and trap technology. Medd. Norsk Inst. Skogforsk. 38 (3): 1−35.

Baranowski, R. 1977: Ein fund vor Boros schneideri in Finnland (Coleoptera, Boridae). Notulae Ent. 57: 45−46.

Baule, H. 1969. Zusammenhänge zwischen Nährstoffgehalten und Krankheiten bei Forstpflanzen. Landw. Forschg. 23: 92−104.

Behan, V. M., Hill, S. B. & Kevan, D. K. M. 1978. Effects of nitrogen fertilizers, as urea, on Acarina and other arthropods in Quebec black spruce humus. Pedobiol. 18: 249−263.

Bejer, B. 1979. Skovbrugets skadedyr 1978. Skoven 11: 42−43.

— 1980. Skovbrugets skadedyr 1979. Skoven 12: 40−41.

— 1981a. Skovens skadeinsekter 1980. Skoven 13: 38−39.

— 1981b. Insect risks for introduced and native conifers in Northern Europe, especially in the Nordic Countries. EPPO Bull. 11: 183−185.

— 1982. Skovbrugets skadelinge insekter 1981. Skoven 14: 98−99.

Bejer-Petersen, B. 1974. Angrebene af nonnen (Lymantria monacha L.) i Danmark. Dansk Skovforen. Tidsskr. 59: 59−80.

Bílý, S. 1982. The Buprestidae (Coleoptera) of Fennoscandia and Denmark. Fauna Ent. Scand. 10: 1−109.

Birch, M. C. & Haynes, K. F. 1982. Insect pheromones. 58 pp. London.

Biström, O. 1978. Coleoptera and Heteroptera in a natural forest in Mäntyharju (southern Finland). Notulae Ent. 58: 95−100.

Bracher, G. A. & Bider, J. R. 1981. Changes in terrestrial animal activity of a forest community after application of aminocarb (Matacil®). Can. J. Zool. 60: 1981−1997.

Brammanis, L. 1975. Die Kiefernrindenwanze, Aradus cinnamomeus Panz. (Hemiptera-Heteroptera). Ein Beitrag zur Kenntnis der Lebensweise und der forstlichen Bedeutung. Stud. For. Suecica 123: 1−81.

Butovitsch, V. & Eidmann, H. H. 1962. Die Behandlung von berindeten Nutzholz mit Insektiziden. Versuche über die Einwirkung von Applikation, Dosierung und Konzentration auf den Befall durch Rindenbrüter. Forstwiss. Centralblatt 81: 212−222.

— & Spaak, H. 1939. Studier och försök att skydda i skogen kvarliggande timmer mot insekter och svampar. Norrl. Skogsvårdsförb. Tidskr. 3: 1−120.

Cajander, A. K. 1926. Metsätyyppiteoria. Acta For. Fenn. 29: 1−84.

— 1949 (†). Forest types and their significance. Acta For Fenn. 56: 1−71.

Christiansen, E. & Sandvik, M. 1974. Skade av gransnutebille på furuplanter i markberedningsflekker. Norsk Skogsbruk 1974 (5): 8−9.

Clayhills, T. 1982. The distribution of Ipidia sexguttata sexguttata (Coleoptera, Nitidulidae). Notulae Ent. 62: 145−146.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302−1310.

Coyle, F. A. 1981. Effects of clearcutting on the spider community of a southern Appalachian forest. J. Arachnol. 9: 285−298.

Dahl, J. & Beier Petersen, B. 1960. Om virkningen af kemisk skadedyrbekoempelse på insekter og spindler i en granskov. (Summary: On the influence of chemical control on the arthropod fauna of a spruce forest). Forstlige Forsøgsvaesen i Denmark 26: 271−312.

Dehlén, R. & Långström, B. 1977. Randbarkning av massaved − en skogsskyddåtgärd? (Summary: Strip-barking of pulpwood − a measure of forest protection?). Skogshögskolan, Inst. Skogsteknik, Rapp. Uppsatser 118: 1−22.

Diamond, J. M. & May, R. M. 1976. Island biogeography and the design of natural reserves. In: May, R. D. (ed.): Theoretical ecology, pp. 163−186. Oxford.

Dindal, D. L. Metz, L. J. 1977. Community structure of Collembola affected by fire frequency. In: Mattson, W. J. (ed): The role of arthropods in forest ecosystems, pp. 88−95. N. Y.

Edwards, C. A. & Heath, G. W. 1963. The role of soil animals in breakdown of leaf material. In: Doeksen, J. & van der Drift, J. (eds.): Soil organisms, pp. 76−84. Amsterdam.

Edwards, C. A., Reichle, D. E. & Crossley, D. A. Jr. 1970. The role of soil invertebrates in turnover of organic matter and nutrients. In: Reichle, D. E. (ed.): Analysis of temperate forest ecosystems, pp. 147−172. Berlin.

Ehnström, B. 1976. Barkborreangrepp i massavedsvältor. In: Skogs- och virkesskydd, pp. 146−157. Sveriges Skogsvårdsförbund.

— 1977a. Reivo-projektet. Den brända skogens ekologi. Undersökningar över träinsekter 1976. Skogshögskolans sekt. för skogsentomologi. Rapport 4(1977): 1−11.

— 1977b. Reivo-projektet. Den brända skogens ekologi. Undersökningar över träinsekter 1977. Sveriges Lantbruksuniv. Inst. för skogsentomologi. Rapport 5(1977): 1−10.

— 1978. Genom det moderna skogsbruket hotade insektarter. Norw. J. Ent. 25: 77−78.

— 1979. Vård av den lägre faunan i skogsbruket. In: Fauna vård i skogsbruket, pp. 31−39. Jönköping.

— 1983. Skogens hotade insekter. Skogsfakta 3: 1−4.

— , Bejer-Petersen, B., Löyttyniemi, K. & Tvermyr, S. 1974. Insect pests in forests of the nordic countries 1967−1971. Ann. Ent. Fenn. 40: 37−47.

Eidmann, H. H. 1965. Lärchenschädling in Schweden und ihre Verbreitung. Zeitschr. Angew. Ent. 55: 377−388.

— 1972. Insekticiderna och snytbaggen. Skogen 59: 19−20.

— 1974. Skyddsbehandling mot snytbagge. Skogen 61: 52−54.

— , Henningsson, B. & Möller, C. 1979. DDT and lindane residues on treated conifer seedlings and in soil. Ambio 8: 214−217.

Eijsackers, H. & van der Drift, J. 1976. Effects on the soil fauna. In: Audus, L. J. (ed.): Herbicides. Physiology, biochemistry, ecology, pp. 149−174. London.

Elton, E. T. G., Blankwaardt, H. F. H., Burger, H. C., Steemers, W. F. & Tichelman, L. G. 1964. Insect communities in barked and unbarked pine stumps with special reference to the large pine weevil (Hylobius abietis L., Col., Curculionidae). Zeitschr. Angew. Ent. 55: 1−54.

Finegan, B. 1984. Forest succession. Nature 312 (November): 109−114.

Forest statistics of Finland 1950−67. Folia For. 47: 1−93.

Franz, J. 1948. Über die Zonenbildung der Insektenkalamitäten in Urwäldern. Forstwiss. Centralblatt 67: 38−48.

— 1963. Biozönotische und synökologische Untersuchungen über die Bodenfauna und ihre Beziehungen zur Mikro- und Makroflora. In: Doeksen, J. & van der Drift, J. (eds.): Soil organisms, pp. 345−367. Amsterdam.

Gilbert, F. S. 1980. The equilibrium theory of island biogeography: fact or fiction? J. Biogeogr. 7: 209−235.

Gilpin, M. & Diamond, J. M. 1980. Subdivision of nature reserves and the maintenance of species diversity. Nature, Lond. 285: 567−568.

Graham, K. 1963. Concepts of forest entomology. 388 pp. N. Y.

Gustafsson, M. 1960. Bekämpningsmedelsrester i gröde och jord. (Summary: Residues of pesticides in crop and soil). J. R. Swedish Acad. Agric. For. 4: 1−107.

Györfi, J. 1952. Die Schlupwespen und der Unterwuchs des Waldes. Zeitschr. Angew. Ent. 33: 32−47.

Haapanen, A. & Siitonen, P. 1978. Kulojen esiintyminen Ulvinsalon luonnonpuistossa. (Summary: Forest fires in Ulvinsalo strict nature reserve). Silva Fenn. 12: 187−200.

Haeggström, C.-A. 1983. Vegetation and soil of the wooded meadows in Nåtö, Åland. Acta Bot. Fenn. 120: 1−66.

Hågvar, S. & Abrahamsen, G. 1980. Colonisation by Enchytraeidae, Collembola and Acari in sterile soil samples with adjusted pH levels. Oikos 34: 245−258.

— & Amundsen, T. 1981. Effects of liming and artificial acid rain on the mite (Acari) fauna in coniferous soil. Oikos 37: 7−20.

Hanski, I. 1982. Suojelualueet ekologisena saaristona. Luonnonvarainhoitotoimiston julk. 4: 64−70.

Hauge, E. & Kvamme, T. 1983. Spiders from forest-fire areas in southern Norway. Fauna Norw. Ser. B. 30: 39−45.

Heath, J. 1981. Threatened Rhopalocera (butterflies) in Europe. Council of Europe, Nature and Environment Ser. 23: 1−157.

Heikinheimo, O. 1915. Kaskiviljelyn vaikutus Suomen metsiin. Acta For. Fenn. 4 (2): 1−264.

Heikkilä, R. 1978. Mäntykuitupuupinojen suojaaminen pystynävertäjän iskeytymistä vastaan Pohjois-Suomessa. (Summary: Protection of pine pulpwood stacks against the common pine-shoot beetle in northern Finland). Folia For. 351: 1−11.

— 1981. Männyn istutustaimikkojen tuhot Pohjois-Suomessa. (Summary: Damage in Scots pine plantations in northern Finland). Folia For. 497: 1−22.

Heimpel, A. M. 1966. Exposure of white mice and guinea pigs to the nuclear-polyhedrosis virus of the cab-

bage-looper, Trichoplusia ni. J. Inverteb. Path. 8: 98−102.
— 1967. Human feeding tests using a nuclear-polyhedrosis virus of Heliothis zea. J. Inverteb. Path. 9: 55−57.
Heliövaara, K. 1982. The pine bark bug, Aradus cinnamomeus (Heteroptera, Aradidae) and the height growth rate of young Scots pines. Silva Fenn. 16: 357−361.
— , Terho, E. & Annila, E. 1983. Effect of nitrogen fertilization and insecticides on the population density of the pine bark bug, Aradus cinnamomeus (Heteroptera, Aradidae). Silva Fenn. 17: 351−357.
— & Väisänen, R. 1983. Environmental changes and the flat bugs (Heteroptera, Aradidae and Aneuridae). Distribution and abundance in Eastern Fennoscandia. Ann. Ent. Fenn. 49: 103−109.
Hellqvist, C. 1984. Produktion av större märgborre i tallstubbar. (Summary: Production of Tomicus piniperda in pine stumps). Sveriges Skogsvårdsförb. Tidskr. 82: 37−47.
Helve, E. 1981. Eucinetus caucasicus (Reitt.) Kuhmosta (Eucinetidae). Notulae Ent. 61: 224.
Hoffmann, F. 1966. Düngung und Schadlingsbefall in der Forstwirtschaft. Wiss. Zeitschr. Techn. Univ. Dresden 15: 643−648.
Hokkanen, H. & Raatikainen, M. 1977. Faunal communities of the field stratum and their succession in reserved fields. J. Sci. Agric. Soc. Finland 49: 390−405.
Huhta, V. 1965. Ecology of spiders in the soil and litter of Finnish forests. Ann. Zool. Fenn. 2: 260−308.
— 1971. Succession in the spider communities of the forest floor after clear-cutting and prescribed burning. Ann. Zool. Fenn. 8: 483−542.
— , Karppinen, E., Nurminen, M. & Valpas, A. 1967. Effect of silvicultural practices upon arthropod, annelid and nematode populations in coniferous forest soil. Ann. Zool. Fenn. 4: 87−143.
— , Nurminen, M. & Valpas, A. 1969. Further notes on the effect of silvicultural practices upon the fauna of coniferous forest soil. Ann. Zool. Fenn. 6: 327−334.
— , Hyvönen, R., Koskenniemi, A., Vilkamaa, P., Kaasalainen, P. & Sulander, M. 1984. Metsälannoituksen ja pH:n vaikutus maaperäeläimistöön. Jyväskylän yliopiston biologian laitoksen tiedonantoja 36: 1−35.
Ignoffo, C. M. & Heimpel, A. M. 1965. The nuclear-polyhedrosis virus of Heliothis zea (Boddie) and Heliothis virescens (Fabricius). J. Inverteb. Path. 7: 329−340.
Imby, L. & Palmqvist, G. 1978. De svenska Anomogynaarternas utseende, biologi och utbredning (Lep., Noctuidae). Abstract: The biology and occurrence of the Swedish Anomogyna species (Lep., Noctuidae)). Ent. Tidskr. 99: 97−107.
Jalas, J. & Suominen, J. (eds.) 1973. Gymnospermae (Pinaceae to Ephedraceae). Atlas Florae Europaeae 2: 1−40.
Järvinen, O. 1982. Conservation of endangered plant populations: single large or several small reserves? Oikos 38: 301−307.
Juutinen, P. 1962. Tutkimuksia metsätuhojen esiintymisestä männyn ja kuusen viljelytaimistoissa Etelä-Suomessa. (Referat: Untersuchungen über das Auftreten von Waldschäden in den Kiefern- und Fichtenkulturen Südfinnlands). Commun. Inst. For. Fenn. 54 (5): 1−80.
— 1978. Kuitupuupinot pystynävertäjän (Tomicus piniperda L.) lisääntymispaikkoina Pohjois-Suomessa. (Summary: Pulpwood stacks as breeding sites for pine shoot beetle (Tomicus piniperda L.) in northern Finland). Folia For. 335: 1−28.
Kaisila, J. 1960. The influence of culture on the Finnish lepidopterous fauna. Fennia 85: 106−111.
Kalliola, R. 1973. Suomen kasvimaantiede. 308 pp. Porvoo, Helsinki.
Kangas, E. 1947. Kovakuoriaisfaunamme erikoisuuksia luonnonsuojelun kannalta. Suomen Luonto 1947: 45−55.
— 1961. Hyönteisten, erityisesti tuholaisina esiintyvien lajien reagoinnista voimistuvaan inhimilliseen kulttuuriin. (Summary: The impact of human culture on insects, and especially on insect pests). Fennia 85: 100−105.
— 1971. Det 15. nordiska entomologmötet i Helsingfors 27−29 juli 1970. Acta Ent. Fenn. 28: 10−13.
— 1979. Eicolyctus brunneus (Gyll.) (Cucujidae) tavattu Ilomantsissa. Notulae Ent. 59: 169.
— 1983. Cucujus cinnaberinus (Scopoli) (Cucujidae) Lammin Evolta (EH). Notulae Ent. 63: 214.
— & Kangas, J. 1944. Über die Lebensweise und die Larve von Xylophilus cruentatus Gyll. (Col., Eucnemidae). Ann. Ent. Fenn. 10: 7−16.
Karppinen, E. 1957. Die Oribatiden-Fauna einiger Schlag- und Brandflächen. Ann. Ent. Fenn. 23: 181−203.
Kellomäki, S. 1972. Maanpinnan reliefin ja kasvillisuuden kehityksestä aurauksen jälkeisinä vuosina Perä-Pohjolan metsänuudistusaloilla. Helsingin yliopiston metsänhoitotieteen laitoksen julk. 8: 1−56.
Knight, F. B. & Heikkenen, H. J. 1980. Principles of forest entomology. 461 pp. N. Y.
Kolbe, H. 1980. Gefährdung von Wirtschaftsbeständen durch Insektenvermehrungen in Naturwaldreservaten. Natur und Landsch. 55: 159−161.
Köppä, P. 1964. The sales of plant protection chemicals in Finland in 1963. Tekn. Kem. Aikakauslehti 13: 502−505.
Krauss, A. 1969. Einfluss der Ernährung der Pflanzen mit Mineralstoffen auf den Befall mit parasitären Krankheiten und Schädlingen. Z. Pflanzenern., Düng., Bodenk. 124: 129−147.
Krogerus, R. 1943. Suomalaisen aarniometsän hyönteisiä. Havaintoja Pyhähäkin luonnonpuistosta. Suomen Luonto 3: 42−45.
— 1960. Ökologische Studien über nordische Moorarthropoden. Artenbestand, ökologische Faktoren, Korrelation der Arten. Soc. Sci. Fenn. Comm. Biol. 21 (3): 1−238.
Król, A. 1983. Omfattende masseherjinger av insekter på skogen i Polen. Norsk Skogbruk 29 (10): 28−29.
Långström, B. 1979. Märgborrarnas förökning i röjningsavfall av tall och kronskadegörelse på kvarstående träd. (Summary: Breeding of pine shoot beetles in clearing waste of Scots pine and subsequent shoot-damage on remaining trees). Sveriges Lantbruksuniv., Skogsent. Rapp. 1: 1−52.
— 1980. Kan snytbaggeskadorna förutspås? Skogsbruket 50: 176−177.
— 1981. Ecology of the larch shoot moth, Blastotere laevigatella (Lepidoptera, Yponomeutidae) in Finland. Notulae Ent. 61: 1−7.
— 1982. Abundance and seasonal activity of adult Hylobius-weevils in reforestation areas during first years following final felling. Commun. Inst. For. Fenn. 106: 1−23.
— , Hellqvist, C. & Ehnström, B. 1984. Fördelning och produktion av större märgborren i tallvältor. (Summary: Distribution and production of Tomicus piniperda in pine wood stacks). Sveriges Skogsvårdsförb. Tidskr. 82: 23−35.
Larsson, S. & Tenow, O. 1984. Areal distribution of a Neodiprion sertifer (Hym., Diprionidae) outbreak on Scots pine as related to stand condition. Holarctic Ecol. 7: 81−90.
— & Bejer-Petersen, B., Kangas, E. & Bakke, A., 1977. The distribution of bark beetles in the Nordic Countries. Acta Ent. Fenn. 32: 1−37.
Lekander, B. 1954. Skogsinsekternas uppträdande i Sverige under tiden 1946−1950. (Zusammenfassung: Das Auftreten von Waldinsekten in Schweden in der Zeit 1946−1950). Medd. Stat. Skogsforsk. 44: 1−46.
Lenski, R. E. 1982. The impact of forest cutting on the diversity of ground beetles (Coleoptera: Carabidae) in the southern Appalachians. Ecol. Ent. 7: 385−390.
Levula, T. & Heikkilä, R. 1981. Maanmuokkauksen vaikutus männyntaimien alkukehitykseen Pohjois-Karjalassa. Metsäntutkimuslaitoksen tiedonantoja 11: 1−8.
Lindberg, H. & Saris, N. E. 1952. Insektfaunan i Pisavaara naturpark. Acta Soc. Fauna Flora Fenn. 69 (2): 1−82.
Lindroth, C. H. 1973. Sentida förändringar i den nordiska insektfaunan. Exempel från carabiderna. Entomologen 2: 1−8.
Linnavuori, R. 1967. Nivelkärsäiset II. Luteet 2. Geocorisae. Suomen Eläimet Animalia Fenn. 11: 1−232. Porvoo−Helsinki.
Lohm, U., Lundqvist, H., Persson, T. & Wirén, A. 1977. Effects of nitrogen fertilization on the abundance of enchytraeids and microarthropods in Scots pine forests. Stud. For. Suecica 140: 1−23.
Löyttyniemi, K. 1978. Metsälannoituksen vaikutuksesta ytimennävertäjiin (Tomicus spp., Col., Scolytidae). (Summary: Effect of forest fertilization on pine shoot beetles (Tomicus spp., Col., Scolytidae)). Folia For. 348: 1−19.
— , Austarå, Ø., Bejer, B. & Ehnström, B. 1979. Insect pests in forests of the Nordic Countries 1972−1976. Folia For. 395: 1−13.
Lundberg, S. 1977a. Skalbaggsarter, som inte återfunnits i Sverige på lång tid − några tips (Coleoptera). (Abstract: Beetles which have not been recovered in a long time in Sweden − some tips (Coleoptera). Ent. Tidskr. 99: 121−126.
— 1977b. Fynd av två för Norden nya skalbaggsarter (Coleoptera). Ent. Tidskr. 98: 5−6.
— 1978. Agathidium pulchrum och Tachinus basalis nya för Europa, samt andra sällsynta skalbaggsarter från Pallosenvaara-området (östra Finland) (Coleoptera). Notulae Ent. 58: 71−72.
— 1984. Den brända skogens skalbaggsfauna i Sverige. (Abstract: The beetle fauna of burnt forest in Sweden). Ent. Tidskr. 105: 129−141.
Lundblad, O. 1950. Studier över insektfaunan i Fiby urskog. Kungl. Svenska Vetenskabsacad. Avhandl. i Naturskyddsärenden 6: 1−235.
Lyon, L. J., Grawford, H. S., Cuzuhai, E., Fredriksen, R. L., Harlow, F. R., Metz, L. J. & Pearson, H. A. 1978. Effects of fire on fauna: a state-of-knowledge review. U. S. Dept. Agric. For. Serv. Gen. Techn. Rep. WO-6.
Margules, C., Higgs, A. J. & Rafe, R. W. 1982. Modern biogeographic theory: Are there any lessons for nature reserve design? Biol. Conserv. 24: 115−128.
Markkula, M. 1974. Sales of pesticides in Finland 1973. Kemia-Kemi 9: 625−628.
Marshall, V. G. 1977. Effects of manures and fertilization on soil fauna: a review. Commonwealth Bureau of soils, Special Publ. 3: 1−79.
Martin, J. L. 1965. The insect ecology of red pine plantations in Central Ontario. III. Soil-surface fauna as indicators of stand change. Proc. Ent. Soc. Ontario 95: 87−102.
— 1966. The insect eicology of red pine plantations in Central Ontario. IV. The crown fauna. Can. Ent. 98: 10−27.
McLeod, J. M. 1980. Forests, disturbances, and insects. Can. Ent. 112: 1185−1192.
Meinecke, C. F., McLane, W. C. & Rehnborg, C. S. 1970. Inhalation and dermal allergenicity studies of a nuclear-polyhedrosis virus of Heliothis zea in guinea pigs. J. Inverteb. Path. 15: 207−210.
Mikkola, K. 1974. Hyönteistemme perintöaineksen suojelu. Suomen Luonto 33: 78−81.
— 1979. Vanishing and declining species of Finnish Lepidoptera. Notulae Ent. 59: 1−9.
Mitchell, R. G., Waring, R. H. & Pitman, G. B. 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. Forest Sci. 29: 204−211.
Mitscherlich, G. 1975. Wald Wachstum und Umwelt. 352 pp. Frankfurt am Main.
Muona, J. 1978. Harvinaisia kovakuoriaisia Kb: Pallosenvaarasta. Notulae Ent. 58: 174.
— 1984a. Trixagus caucasicus Reitter found in Finland. Notulae Ent. 64: 89−90.
— 1984b. Contribution to the knowledge of Finnish false click-beetles (Coleoptera, Eucnemidae). Notulae Ent. 64: 91.
Nuorteva, M. 1956. Hakkuiden vaikutuksesta kaarnakuoriaisten esiintymiseen eräällä metsäalueella Etelä-Hämeessä. (Zusammenfassung: Über den Einfluss der Hiebe auf das Auftreten der Borkenkäfer in Südfinnland (Süd-Häme). Acta For. Fenn. 63: 1−38.
— 1957. Kaarnakuoriaiset metsänhoidollisten toimenpiteiden arvostelijoina. (Summary: Bark beetles as judges of silviculture). Metsätal. Aikakauslehti 11: 1−2.
— 1964a. Über den Einfluss der Menge des Brutmaterials auf die Vermehrlichkeit und die natürlichen Feinde des Grossen Waldgärtners, Blastophagus piniperda L. (Col., Scolytidae). Ann. Ent. Fenn. 30: 1−17.
— 1964b. Eine Möglichkeit, die Kernpolyhedrose bei latent verseuchten Imagines von Neodiprion sertifer Geoffr. (Hym., Diprionidae) nachzuweisen. Ann. Ent. Fenn. 30: 172−177.

— 1965. Seuraustuhojen uhkan varteenottaminen hakkuissa. Kasvinsuojeluseuran julk. 31: 1—4.

— 1972. Tumamonisärmiöviruksen käytöstä ruskean mäntypistiäisen (Neodiprion sertifer Geoffr.) torjunnassa. (Summary: Use of the nuclear polyhedrosis virus in the control of the European pine sawfly (Neodiprion sertifer Geoffr.)). Silva Fenn. 6: 172—186.

— 1982. Muuttuvat metsätuholaisongelmat. Luonnon Tutkija 86: 154—156.

Nuorteva, P., Tulisalo, E., Larsson, B., Lehtinen, A., Nummelin, M., Ojala, A. & Yrjönen, K. 1983. Suomen toukohärkäkantojen romahtaminen. (Abstract: The decline of Finnish meloid populations; Coleoptera, Meloidae). Luonnon Tutkija 87: 84—95.

Ohmart, C. P. & Voigth, W. G. 1981. Arthropod communities in the crowns of the natural and planted stands of Pinus radiata (Monterey pine) in California. Can. Ent. 113: 673—684.

Oldiges, H. 1960. Der Einfluss der Waldbodendüngung auf das Auftreten von Schadeinsekten. Zeitschr. Angew. Ent. 59: 49—59.

Palm, T. 1955. Coleoptera i brandskadad skog vid nedre Dalälven. Ent. Tidskr. 76: 40—45.

— 1982. Förändringar i den svenska skalbaggsfaunan. (Abstract: Changes in the Swedish beetle fauna (Coleoptera)). Ent. Tidskr. 103: 25—32.

Palmgren, P. & Biström, O. 1979. Populations of Araneae (Arachnoidea) and Staphylinidae (Coleoptera) on the floor of a primeval forest in Mäntyharju, southern Finland. Ann. Zool. Fenn. 16: 177—182.

Pulkkinen, M. 1983. Tukkimiehentäit Hylobius abietis, Col. Curculionidae, kalalokkiyhdyskunnan Larus canus ravintona. (Summary: Remains of Hylobius abietis, Col. Curculionidae, in pellets of the Common Gull). Ornis Fenn. 60: 93—95.

Rautapää, J., Myllymäki, A., Siltanen, H. & Mattinen, V. 1976. Endrin, DDT and PCB's in Finnish soils. J. Sci. Agric. Soc. Finland 48: 181—186.

Richardson, R. J. & Holliday, N. J. 1982. Occurrence of carabid beetles (Coleoptera: Carabidae) in a boreal forest damaged by fire. Can. Ent. 114: 509—514.

Richter, G. 1953. Die Auswirkung von Insektiziden auf die terricole Makrofauna (Quantitative Untersuchungen begifteter und unbegifteter Waldboden). Nachr. Dtsch. Pflanzenschutzdienst 4: 61—72.

Rummukainen, U. 1964. Hyönteisten aiheuttamasta tuoreen kuorellisen havupuutavaran pilaantumisesta ja sen kemiallisesta estämisestä. (Summary: On deterioration of green softwood caused by insects and its chemical control). Commun. Inst. For. Fenn. 58 (5): 1—67.

Rutanen, I. 1980. Lajien Ceruchus chrysomelinus (Hochenw.) ja Tragosoma depsarium (L.) (Cerambycidae) esiintymisestä Pallosenvaaran—Suomunjärven aarnialueilla. Notulae Ent. 60: 230.

Saalas, U. 1932. Muistiinpanoja hyönteiskeräysretkiltä Yläneen Kolvassa ym. toistasataa vuotta sitten. Luonnon Ystävä 36: 190—193.

— 1939. Über einige kulturbeeinträchtigte Käferarten sowie einige Neuankömmlinge in der Käferfauna Finnlands. VII. Int. Kongr. Ent. Berlin,

pp. 361—376.

— 1949. Suomen metsähyönteiset. 719 pp. Porvoo, Helsinki.

Salonen, H., Marttila, V. & Ormio, H. 1980. Luonnonsuojelualueiden edustavuus. Luonnonvarainhoitotoimiston julk. 2: 1—72.

Schaefer, M. 1980. Sukzession von Arthropoden in verbrannten Kiefernforsten. II. Spinnen (Araneida) und Weberknechte (Opilionida). Forstwiss. Centralblatt 99: 341—356.

Schauermann, J. 1980. Sukzession von Arthropoden in verbrannten Kiefernforsten. IV. Moderkäfer (Lathridiidae). Forstwiss. Centralblatt 99: 366—371.

Schimitschek, E. 1952. Über Krankheitsbegriff, Disposition und Vorbeugung im Forstschutz. Zeitschr. Angew. Ent. 33: 18—31.

— 1953a. Forstentomologische Studien in Urwald Rotwald. Teil I. Zeitschr. Angew. Ent. 34: 178—215.

— 1953b. Forstentomologische Studien im Urwald Rotwald. Teil II. Zeitschr. Angew. Ent. 34: 513—542.

— 1954. Forstentomologische Studien im Urwald Rotwald. Teil III. Zeitschr. Angew. Ent. 35: 1—54.

Schwenke, W. 1960. Über die Wirkung der Walddüngung auf die Massenvermehrung der Kiefernbuschhornblattwespe (Diprion pini L.) 1959 in Mittelfranken und die heraus ableitbaren gradologischen Folgerungen. Zeitschr. Angew. Ent. 46: 371—378.

— 1961. Walddüngung und Schadeinsekten. Anz. Schädlingskunde 34: 129—134.

Selander, J. & Nuorteva, M. 1980. Feromonivalmisteen käyttö kirjanpainajien torjumiseksi kuolevassa kuusikossa. (Summary: Use of synthetic pheromones for the control of spruce bark beetles in a heavily infested spruce stand). Silva Fenn. 14: 113—121.

Sheals, J. G. 1955. The effects of DDT and BHC on soil Collembola and Acarina. In: Kevan, D. K. M. (ed.): Soil Zoology, pp. 241—252. London.

Simberloff, D. S. 1982. Island biogeographic theory and the design of wildlife refuges. Ekologiya 1982 (4): 3—13 (In Russian).

— & Abele, L. G. 1976a. Island biogeography theory and conservation practice. Science 191: 285—286.

— & Abele, L. G. 1976b. Island biogeography and conservation: strategy and limitations. Science 193: 1032.

Simolinna, J., Juutinen, P. & Nuortimo, T. 1959. Kertomus mäntymittarin (Bupalus piniarius L.) torjumiseksi Taipalsaarella, Ruokolahdella ja Puumalassa kesällä 1959 suoritetusta lentopölytyksestä. Manuscript, 29 pp. [Available at Univ. Helsinki, Unionink. 40 A, SF-00170 Helsinki, Finland].

Skogsdata 83. Sveriges Lantbruksuniv., Inst. Skogstaxering. 55 pp.

Skogsskyddsutredningen 1977. Virkeslagringen. Skogsstyrelsen 1979. 71 pp. Jönköping.

Skogsstatistisk årsbok 1981—1983. Skogsstyrelsen 1983. 245 pp. Jönköping.

Söderström, V. 1976. Analys av markberedningseffekterna vid plantering på några färska hyggen.

Sveriges Skogsvårdsförb. Tidskr. 2—3: 1—133.

Stark, R. 1965. Recent trends in forest entomology. Ann. Rev. Ent. 10: 303—324.

Svensson, I. 1982. Skogsbrukets inverkan på fjärilfaunan. XIX Nordiska entomologmötet, Helsingfors 1982, p. 23 (pages not numbered).

Szujecki, A. 1979. Some problems of zoocoenosis restoration in degraded forest habitats. Memorabilia Zool. 32: 57—67.

—, Szyszko, J., Mazur, S., & Perliński, S. 1983. The process of forest soil macrofauna formation after afforestation of farmland. 196 pp. Warsaw.

Szyszko, J. 1984. Effect of fire on the plasticity of Carabidae (Coleoptera) communities. IInd symposium on the protection of forest ecosystems. Organisation of biocenosis as a basis of the prevention methods in protection of forest ecosystems. Rogów 7—8 December 1981. pp. 205—209. Warsaw.

Trägårdh, I. & Butovitsch, V. 1934. Redogörelse för barkborrekampanjen efter storm härjningarna 1931—32. (Zusammenfassung: Bericht über die Bekämpfungsaktion gegen Borkenkäfer nach den Sturmverheerungen 1931—1932). Medd. Stat. Skogsförsöksanst. 28: 1—268.

Väisänen, R. 1982. Vanishing and vulnerable Diptera of Finland. Notulae Ent. 62: 111—121.

Wallace, H. R. 1953. The ecology of insect fauna of pine stumps. J. Anim. Ecol. 22: 154—168.

West, D. C., Shugart, H. H. & Botkin, D. B. (eds.) 1981. Forest succession. Concepts and application. 517 pp. Berlin.

Wiackowski, S. 1957. Entomofauna pniakow sosnowych w zaleznoski od wieku i rozmiary pniaka. (Summary: The entomofauna of pine stumps in relation to the age and size of stump). Ekol. Polska Ser. A. 3: 1—128.

Winter, K. 1980. Sukzession von Arthropoden in verbrannten Kiefernforsten. I. Methoden und allgemeiner Überblick. Forstwiss. Centralblatt 99: 324—340.

Wright, H. A. & Bailey, A. W. 1982. Fire ecology. United States and Southern Canada. 501 pp. N. Y.

Yearbook of forest statistics 1983. Folia For. 559: 1—224.

Zackrisson, O. 1977. Influence of forest fires on the North Swedish boreal forest. Oikos 29: 22—32.

Zethner, O. 1976. Control experiments on the nun moth (Lymantria monacha L.) by nuclear-polyhedrosis virus in Danish coniferous forests. Zeitschr. Angew. Ent. 81: 192—207.

Zoebelein, G. 1957. Zur Beeinflussung der Insektenfauna des Waldes durch chemische Grossschädlingsbekampfungen. I. Mitteilungen. Zeitschr. Angew. Ent. 41: 320—332.

— 1958. Zur Beeinflussung der Insektenfauna des Waldes durch chemische Grossschädlingsbekampfungen. 2. Mitteilungen. Zeitschr. Angew. Ent. 43: 432—438.

— 1960. Zur Beeinflussung der Insektenfauna des Waldes durch chemische Grossschädlingsbekampfungen. 3. Mitteilungen. Zeitschr. Angew. Ent. 45: 320—330.

Total of 209 references

SELOSTE

*NYKYAIKAISEN METSÄNKÄSITTELYN VAIKUTUKSET LUOTEISEUROOPPALAISEN METSÄN
SELKÄRANGATTOMIIN: SYNTEESI*

1. Johdanto

Voimaperäistä metsätaloutta on usein moitittu luonnon tasapainon järkyttämisestä. Puuston ikärakenteessa ja lajikoostumuksessa tapahtuneiden muutosten sekä aarnimetsien vähenemisen on ajateltu yksipuolistaneen metsien selkärangatonlajistoa. Toisaalta vanhoja metsiä on joskus pidetty kuolleina, jähmettyneinä ekosysteemeinä tai tuholaisten leviämiskeskuksina, joista on vaaraa ympäristön hoidetuille metsille.

Nykyaikaisen metsänkäsittelyn vaikutukset metsän selkärangattomiin tunnetaan yleensä varsin puutteellisesti. Käsillä olevan yhteenvedon tarkoituksena on esitellä ja analysoida metsän rakenteessa tapahtuneiden muutosten ja metsänkäsittelyn sekä suoria että epäsuoria vaikutuksia selkärangatonlajistoon sekä osoittaa tärkeimmät tietämyksen aukot. Tutkimuksessa keskitytään Luoteis-Euroopan – Norjan, Ruotsin ja erityisesti Suomen – boreaalisiin metsiin. Artikkeliin on sisällytetty myös muilta alueilta saatavilla olevia valaisevia lisätietoja.

2. Metsänkäsittelyn suorat vaikutukset selkärangattomiin

Metsänkäsittelyn suorat selkärangattomiin kohdistuvat vaikutukset on työssä käsitelty kuutena kokonaisuutena, joiden lisäksi etenkin soiden ojitus ja maatalousmaan metsittäminen ovat ympäristöä muuttamalla vaikuttaneet selkärangattomiin. Soiden kuivattaminen merkitsee monille hyönteislajeille elinympäristön totaalista katoamista, mutta yksityiskohtaista tietoa aiheutuneista muutoksista on vähän saatavilla. Eräiden perhoslajien tiedetään hävinneen kokonaan ojitetulta suolta, ja monien lajien tiedetään olevan herkkiä pienillekin suoympäristön muutoksille. Maatalousmaan metsittäminen on puolestaan luonut uutta metsää ja lisännyt metsissä elävien selkärangattomien määrää. Toisaalta vanhojen laidun- ja hakamaiden metsittyminen on vähentänyt tiettyjä lajeja. Kuusettaminen on vähentänyt eräitä lehtoniittyjen lajeja kuten pikkuapolloa ja maitikkaverkkoperhosta Etelä-Skandinaviassa.

Avohakkuussa puihin tavalla tai toisella sitoutuneet eläimet luonnollisesti katoavat puuston mukana. Valon määrä maanpinnassa kasvaa, kenttäkerroksen kasvillisuus lisääntyy lämpö- ja kosteusolot muuttuvat. Maaperäeläimistössä tapahtuva muutos avohakkuun jälkeen ei kuitenkaan ole kovin huomattava, samat lajit näyttävät dominoivan, vaikka yksilömäärät pienenevätkin. Maassa elävien selkärangattomien reaktiot avohakkuun jälkeen on ryhmitelty neljään ryhmään: 1. kaksisiipisten toukat ja aikuiset kovakuoriaiset lisääntyvät voimakkaasti; 2. sukkulamadot, änkyrimadot ja hyppyhäntäiset lisääntyvät hitaasti; 3. punkit ja kovakuoriaistoukat lisääntyvät aluksi, mutta vähenevät pian; 4. lierot ja hämähäkkieläimet vähenevät. Avohakkuun jälkeen ravinteet maassa vapautuvat ja vadelma, maitohorsma, kastikat ja metsälauha valtaavat alaa. Samalla esimerkiksi eräät perhoset ja kukkakärpäset lisääntyvät.

Harvennuksen vaikutuksen maaperän eläimistöön oletetaan olevan avohakkuun kaltainen, mutta heikompi. Sukkulamatojen, änkyrimatojen ja hyppyhäntäisten väheneminen ovat huomattavimmat erot avohakkuun seurauksiin nähden. Alaharvennuksen on todettu lisäävän jäävän puuston resistenssia kaarnakuoriaisia vastaan.

Avohakkuut ja kuorelliset puutavarapinot ovat luoneet tuholaisongelmia. Käsillä olevassa työssä tähän laajaan metsäentomologian osa-alueeseen puututaan vain lyhyesti: Erityisesti pystynävertäjä ja kirjanpainajat ovat lisääntyneet puutavarapinoissa. Avohakkuualoille jääneet kannot ovat hyödyttäneet erityisesti tukkimiehentäitä.

Kulotuksessa syntyvä kuumuus on tuhoisa miltei kaikille maaperäeläimille. Kulotuksen jälkeen alkuperäinen eläimistö, erityisesti änkyrimadot ja hyppyhäntäiset, kuitenkin palautuu melko nopeasti. Lierot näyttävät olevan kulotukselle herkkä ryhmä. Hämähäkkieläimet palautuvat jonkin verran kulotuksen jälkeisinä vuosina, mutta lajistossa tapahtuu kvalitatiivisia muutoksia. Monien pohjoiseurooppalaisten hyönteislajien tiedetään suosivan tai elävän vain palaneissa metsissä. On ilmeistä, ettei kulotus entomologisessa mielessä korvaa luonnonkuloja.

Aurauksen on havaittu lisäävän kenttäkerroksen määrää. Tämä saattaa suosia eräitä hyönteislajeja. Toisaalta esimerkiksi aurauksella voidaan jossain määrin estää tukkimiehentäin aiheuttamia tuhoja.

Useita puulajeja kasvavat metsät ovat tuholaisia vastaan kestävämpiä kuin yhtä puulajia kasvavat tasaikäiset metsät. Tuhohyönteisten petojen ja loisten laji- ja yksilömäärät ovat sekametsissä huomattavasti suurempia kuin yhtä puulajia kasvavissa metsissä. Vesakonmuodostajana ja männynversoruosteen väli-isäntänä tunnettu haapa on vähentynyt metsistämme (etenkin järeät puut), ja useat sillä elävät selkärangatonlajit ovat niin ikään taantuneet. Vieraista puulajeista pääasiassa siemenenä tuotettu kontortamänty ei ole tuonut mukanaan uusia tuholaislajeja. Eräät ainoastaan lehtikuusella elävät lajit ovat kulkeutuneet Pohjois-Eurooppaan ravintokasvinsa mukana.

Lannoitus lisää maaperän ravinteita ja siten kasvillisuuden ja mikro-organismien määrää. Mikrobiaktiivisuus lisääntyy lannoituksen jälkeen lähinnä happamuuden vähenemisen seurauksena. Änkyrimatojen, hyppyhäntäisten ja kaksisiipistoukkien määrän on havaittu lisääntyneen, mutta lierojen vähentyneen lannoituksen jälkeen. Maaperän suurempiin niveljalkaisiin lannoituksella ei ole todettu olevan vaikutusta. Typpilannoituksen tiedetään vaikuttavan eräisiin puulla eläviin tuhohyönteisiin. Se lisää esimerkiksi männystä nesteitä imevän punalatikan runsautta, mutta vähentää neulasia syöviä mäntypistiäisiä. Nilassa elävien kaarnakuoriaisten määrissä ei ole havaittu lannoituksen aiheuttamia muutoksia.

Hyönteismyrkyt vaikuttavat populaatiotiheyksiä alentavasti kaikkiin eläinryhmiin ilmeisesti kuoripunkkeja lukuunottamatta. Eniten hyönteismyrkyt näyttävät vaikuttavan maanpinnalla eläviin lajeihin, erityisesti hämähäkkeihin ja petokovakuoriaisiin. Käytännön metsänhoidossa myrkkien käyttö on Luoteis-Euroopassa varsin vähäistä. DDT:tä on Suomessa käytetty laajalti vuodesta 1945 syyskuuhun 1971, jolloin sen käyttö rajoitettiin taimitarhoihin. Norjassa DDT:tä käytetään yhä tukkimiehentäin torjuntaan. Suomessa tukkimiehentäin tuhoja pyritään vähentämään käsittelemällä istutettavia taimia lindaanilla, mutta Ruotsissa sekä DDT:n että lindaanin käyttö on nykyisin täysin kielletty. Laaja-alaisemmin kemiallista torjuntaa on käytetty Suomessa mäntymittaria vastaan kahdesti ja mäntypistiäistä vastaan kerran. Muiden hyönteisten kemiallinen torjunta metsissä on ollut lähinnä kokeellista. Feromonipyydysten avulla on pyritty Ruotsissa ja Norjassa kaarnakuoriaisten, lähinnä kirjanpainajan ja tikaskuoriaisen vähentämiseen. Biologista torjuntaeliöistä Luoteis-Euroopassa käytetään tuumanonisärmiöviruksta ruskean mäntypistiäisen torjuntaan. Kokonaisuutena hyönteismyrkkyjen, feromonien ja biologisten torjuntaeliöiden käyttö käytännön metsänhoidossa on ollut melko pienimuotoista, eikä niiden vaikutuksia metsien selkärangattomien runsauteen voida juuri havaita. Toisaalta on huomattava, että erityisesti maataloudessa käytetyt pestisidit ovat aiheuttaneet eräiden selkärankaisten kannanromahduksia.

3. Yleiset muutokset metsien dynamiikassa

Luonnontilaiset boreaaliset metsät käsittävät useita peräkkäisiä ikäluokkavaiheita tietyllä paikalla ja eri vaiheissa olevien metsiköiden mosaiikkimaisia komplekseja. Aarnimetsissä suhteellisen vanhat ikäluokat ovat vallitsevia. Tilastot metsien ikäluokkajakaumista osoittavat kuitenkin, että jopa keski-ikäiset metsät ovat harvinaisia ja alueellisesti rajoittuneita koko Pohjois-Euroopassa.

Ikimetsien väheneminen on vaikuttanut eniten lahoavia puita ja lahottajasieniä hyväksikäyttäviin spesialistilajeihin sekä lajeihin, joilla on ahtaat mikroklimaattiset vaatimukset (tasainen kosteus ja varjoisuus). Monet tällaiset lajit ovat vähentyneet ja eräät jopa näyttävät kokonaan hävinneen Pohjois-Euroopasta (esimerkkilajeja taulukossa 1). Useat taksonomisesti ja faunistisesti heikosti tunnetut ryhmät, esimerkiksi loispistiäiset ja sienisääsket ovat ilmeisesti myös kärsineet laajamittaisesta metsien käsittelystä.

Palaneet metsät muodostivat osan luonnontilaisten metsien mosaiikista, ja niissä eli spesialisoitunutta selkärangatonlajistoa, joka on voimakkaasti taantunut Pohjois-Euroopassa (ks. taulukko 2).

Nuorten, pääasiassa yhtä puulajia kasvavien, istutettujen metsien osuus on voimakkaasti lisääntynyt. On ilmeistä, että eräät tuholaislajit ovat suuresti hyötyneet tästä kehityksestä.

4. Lajiston diversiteetti luonnontilaisissa ja viljellyissä metsissä

Artikkelin tässä osassa tarkastellaan luonnon tasapainon käsitettä metsäeläintieteelliseltä kannalta. Nykyisin katsotaan usein, että yhteisön suuri diversiteetti säilyy lähinnä pienten häiriöiden takia eikä siis niistä huolimatta. Tällaisista vähäistä metsien uudistumisen ja dynaamisen tasapainon kannalta keskeisistä häiriötekijöistä voidaan mainita luonnonkulot ja myrskytuhot.

On yleisesti tunnettua, että trooppisilla yhden puulajin metsänviljelmillä lajistollinen monimuotoisuus on huomattavasti pienempi kuin luonnontilaisissa trooppisissa metsissä. Sen sijaan Pohjois-Euroopassa näyttää suhteessa olevan huomattavaa aukko vertailevaa tutkimuksessa: luonnontilaisten ja viljeltyjen metsiköiden selkärangattomien laji- ja yksilömääriä käsittelevät tutkimukset näyttävät tyystin puuttuvan. Erään arvion mukaan metsikön selkärangatonlajimäärä voisi pudota 8000:sta 2000:een voimaperäisen metsätalouden seurauksena Ruotsissa.

Tarkasteltaessa lajistollista diversiteettiä luonnontilaisissa ja viljellyissä metsissä ei voida rajoittua vertaile-

maan yksittäisiä habitaatteja vaan koko luonnontilaisten metsien ikäluokkakirjoa tulisi verrata vastaavaan viljelymetsissä. Arvioitaessa luonnonsuojelualueiden merkitystä vanhojen metsien selkärangatonlajiston suojelussa ja uusia suojelualueita perustettaessa korostetaan empiiristen tutkimusten kiireellistä tarvetta.

5. Päätelmiä

1. Useiden metsänkäsittelymenetelmien vaikutus selkärangatonlajistoon on yleensä voimakas mutta ohimenevä. Useimmilla selkärangatonyhteisöillä näyttää olevan hyvä palautumiskyky.

2. Voimaperäisen metsätalouden tuhoisat vaikutukset lajistoon ovat käyneet ilmeisiksi, kun laajoja alueita, myös tähän päivään saakka säilyneitä ikimetsiä, on hakattu.

3. Ikimetsien väheneminen on vaikuttanut voimakkaimmin puunhajottajalajistoon sekä lajeihin, joilla on tiukat pienilmastolliset vaatimukset.

4. Kulojen harvinaistumisen seurauksena metsien dynamiikka on muuttunut, ja eräät palaneiden metsien spesialistilajit ovat voimakkaasti harvinaistuneet ja saattavat kokonaan hävitä lähitulevaisuudessa.

5. Nuoret, tasaikäiset metsät, joissa pyritään yhden pääpuulajin kasvatukseen, ovat runsastuneet Luoteis-Euroopassa. Näin on aiheutunut eräitä tuholaisongelmia, jotka ovat kuitenkin pienempiä kuin esimerkiksi trooppisissa maissa tai Pohjois-Amerikassa. Tämä näkyy myös vähäisessä hyönteismyrkkyjen käytössä luoteiseurooppalaisissa metsissä.

6. Luonnonsuojelualueet eivät ole tuholaisten leviämiskeskuksia. Vaikka pohjoiseurooppalaiset tuholaislajit ovat alkuperäisiä, niillä on vain vähäinen merkitys aarnimetsissä verrattuna viljelymetsiin. Tuholaisongelmat aiheutuvat pääasiassa itse metsänkäsittelymenetelmistä. Myrskyjen jälkeen eräät kaarnakuoriaiset saattavat kuitenkin runsastua kaatuneissa puissa myös luonnonsuojelualueilla.

7. Luonnon tasapaino näyttää olevan luonnontilaisissa metsissä dynaaminen, erilaisten häiriöiden kuten myrskyjen ja kulojen tasapainottama. Kuitenkin laajoja metsäalueita käsiteltäessä intensiivistä metsätaloutta ei voida enää pitää tasapainottavana vähäisenä häiriönä ekosysteemin tai selkärangatonlajiston kannalta.

8. Puustoltaan vanhat aarnimetsät kuuluvat olennaisena osana havumetsävyöhykkeen ekosysteemiin. Niiden häviäminen vähentää väistämättä lajistollista diversiteettiä tarkasteltaessa laajoja maantieteellisiä alueita, vaikka tietyllä paikalla diversiteetti voikin olla suurin keski-ikäisissä metsiköissä.

9. Vertailevia tutkimuksia selkärangatonlajistosta metsänhoidollisesti käsitellyissä ja luonnontilaisissa metsissä tarvitaan, jotta metsänhoidon vaikutuksia luontoon voidaan tarkemmin arvioida. Ikimetsiä käsittävien suojelualueiden selkärangatonlajiston tutkimuksia tarvitaan myös alueiden suojeluarvon arvioimiseksi.

168 Wuolijoki, E. 1981. Effects of simulated tractor vibration on the psychophysiological and mechanical functions of the driver: Comparison of some exitatory frequencies. Seloste: Traktorin simuloidun tärinän vaikutukset kuljettajan psykofysiologisiin ja mekaanisiin toimintoihin: Eräiden herätetaajuuksien vertailu.

169 Chung, M.-S. 1981. Flowering characteristics of *Pinus sylvestris* L. with special emphasis on the reproductive adaptation to local temperature factor. Seloste: Männyn (*Pinus sylvestris* L.) kukkimisominaisuuksista, erityisesti kukkimisen sopeutumisesta paikalliseen lämpöilmastoon.

170 Savolainen, R. & Kellomäki, S. 1981. Metsän maisemallinen arvostus. Summary: Scenic value of forest landscape.

171 Thammincha, S. 1981. Climatic variation in radial growth of Scots pine and Norway spruce and its importance to growth estimation. Seloste: Männyn ja kuusen sädekasvun ilmastollinen vaihtelu ja sen merkitys kasvun arvioinnissa.

172 Westman, C. J. 1981. Fertility of surface peat in relation to the site type class and potential stand growth. Seloste: Pintaturpeen viljavuuden tunnukset suhteessa kasvupaikkatyyppiin ja puuston kasvupotentiaaliin.

173 Chung, M.-S. 1981. Biochemical methods for determining population structure in *Pinus sylvestris* L. Seloste: Männyn (*Pinus sylvestris* L.) populaatiorakenteesta biokemiallisten tutkimusten valossa.

174 Kilkki, P. & Varmola, M. 1981. Taper curve models for Scots pine and their applications. Seloste: Männyn runkokäyrämalleja ja niiden sovellutuksia.

175 Leikola, M. 1981. Suomen metsätieteellisen julkaisutoiminnan rakenne ja määrällinen kehitys vv. 1909–1978. Summary: Structure and development of publishing activity in Finnish forest sciences in 1909–1978.

176 Saarilahti, M. 1982. Tutkimuksia radioaaltomenetelmien soveltuvuudesta turvemaiden kulkukelpoisuuden arvioimiseen. Summary: Studies on the possibilities of using radar techniques in detecting the trafficability of peatlands.

177 Hari, P., Kellomäki, S., Mäkelä, A., Ilonen, P., Kanninen, M., Korpilahti, E. & Nygrén, M. 1982. Metsikön varhaiskehityksen dynamiikkaa. Summary: Dynamics of early development of tree stand.

178 Turakka, A., Luukkanen, O. & Bhumibhamon, S. 1982. Notes on *Pinus kesiya* and *P. merkusii* and their natural regeneration in watershed areas of northern Thailand. Seloste: Havaintoja männyistä (*Pinus kesiya* ja *P. merkusii*) ja mäntyjen luontaisesta uudistumisesta Pohjois-Thaimaan vedenjakaja-alueilla.

179 Nyyssönen, A. & Ojansuu, R. 1982. Metsikön puutavaralajirakenteen, arvon ja arvokasvun arviointi. Summary: Assessment of timber assortments, value and value increment of tree stands.

180 Simula, M. 1983. Productivity differentials in the Finnish forest industry. Seloste: Tuottavuuden vaihtelu Suomen metsäteollisuudessa.

181 Pohtila, E. & Pohjola, T. 1983. Lehvästöruiskutuksen ajoitus kasvukauden aikana. Summary: The timing of foliage spraying during the growing season.

182 Kilkki, P. 1983. Sample trees in timber volume estimation. Seloste: Koepuut puuston tilavuuden estimoinnissa.

183 Mikkonen, E. 1983. Eräiden matemaattisen ohjelmoinnin menetelmien käyttö puunkorjuun ja kuljetuksen sekä tehdaskäsittelyn menetelmävalinnan apuvälineenä. Abstract: The usefulness of some techniques of the mathematical programming as a tool for the choice of timber harvesting system.

184 Westman, C. J. 1983. Taimitarhamaiden fysikaalisia ja kemiallisia ominaisuuksia sekä niiden suhde orgaanisen aineen määrään. Summary: Physical and physico-chemical properties of forest tree nursery soils and their relation to the amount of organic matter.

185 Kauppi, P. 1984. Stress, strain, and injury: Scots pine transplants from lifting to acclimation on the planting site. Tiivistelmä: Metsänviljelytaimien vaurioituminen noston ja istutuksen välillä.

186 Henttonen, H. 1984. The dependence of annual ring indices on some climatic factors. Seloste: Vuosilustoindeksien riippuvuus ilmastotekijöistä.

187 Smolander, H. 1984. Measurement of fluctuating irradiance in field studies of photosynthesis. Seloste: Säteilyn vaihtelun mittaaminen fotosynteesin maastotutkimuksissa.

188 Pulkki, R. 1984. A spatial database – heuristic programming system for aiding decision-making in long-distance transport of wood. Seloste: Sijaintitietokanta – heuristinen ohjelmointijärjestelmä puutavaran kaukokuljetuksen päätöksenteossa.

189 Heliövaara, K. & Väisänen, R. 1984. Effects of modern forestry on northwestern European forest invertebrates: a synthesis. Seloste: Nykyaikaisen metsänkäsittelyn vaikutukset luoteiseurooppalaisen metsän selkärangattomiin: synteesi.

190 Suomen Metsätieteellinen Seura 75 vuotta. The Society of Forestry in Finland – 75 years. 1984.

KANNATTAJAJÄSENET – SUPPORTING MEMBERS