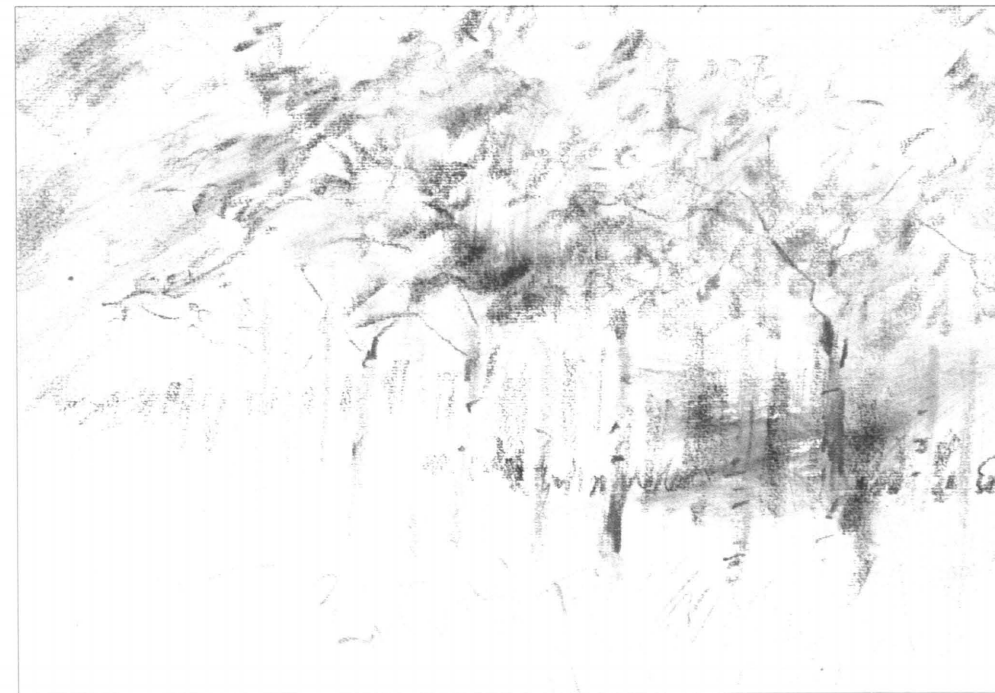


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Rauno Väisänen and Kari Heliövaara

Assessment of Insect Occurrence in Boreal
Forests based on Satellite Imagery and Field
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Assessment of Insect Occurrence in Boreal Forests based on Satellite Imagery and Field Measurements

Contents

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The presence/absence data of twenty-seven forest insect taxa (e.g. *Retinia resinella*, *Formica* spp., *Pissodes* spp., several scolytids) and recorded environmental variation were used to investigate the applicability of modelling insect occurrence based on satellite imagery. The sampling was based on 1800 sample plots (25 m by 25 m) placed along the sides of 30 equilateral triangles (side 1 km) in a fragmented forest area (approximately 100 km²) in Evo, S Finland. The triangles were overlaid on land use maps interpreted from satellite images (Landsat TM 30 m multispectral scanner imagery 1991) and digitized geological maps. Insect occurrence was explained using either environmental variables measured in the field or those interpreted from the land use and geological maps. The fit of logistic regression models varied between species, possibly because some species may be associated with the characteristics of single trees while other species with stand characteristics. The occurrence of certain insect species at least, especially those associated with Scots pine, could be relatively accurately assessed indirectly on the basis of satellite imagery and geological maps. Models based on both remotely sensed and geological data better predicted the distribution of forest insects except in the case of *Xylechinus pilosus*, *Dryocoetes* sp. and *Trypodendron lineatum*, where the differences were relatively small in favour of the models based on field measurements. The number of species was related to habitat compartment size and distance from the habitat edge calculated from the land use maps, but logistic regressions suggested that other environmental variables in general masked the effect of these variables in species occurrence at the present scale.

Keywords: Scolytids, biodiversity, logistic regression models, insect pests.

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1	INTRODUCTION	5
2	MATERIALS AND METHODS	6
	2.1 Study area and sampling	6
	2.2 Satellite imagery	8
	2.3 Classification and ordination	8
	2.4 Logistic models	10
	2.5 Forest fragmentation	11
3	RESULTS	12
	3.1 Classification of species and sample plots	12
	3.2 Species assemblages and environmental variation	16
	3.3 Logistic models	18
	3.4 Forest fragmentation	28
4	DISCUSSION	31
	4.1 Classification and grouping of sample plots	31
	4.2 Environmental variables and insect occurrence	31
	4.3 Field measurements vs. satellite image data	33
	4.4 Forest fragmentation	33
	4.5 Applicability of the method	34
5	CONCLUSIONS	36
	REFERENCES	37

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Preface

In the present article we test the applicability of satellite images and geographic information system (GIS) in boreal forest entomology. Our aim is to predict the occurrence of forest insects in different habitats over wide geographic areas by GIS-assisted methods. This may be important in pest risk assessment in future forest entomology.

We wish to express our sincere thanks to the numerous people who have provided their kind guidance and assistance during the course of the present work. It is our pleasure to thank Jaakko Keronen and Jorma Vahala for assistance in the field, Auli Immonen (Finnish Forest Research Institute, Vantaa) for assistance in the calculations, Anders Gyllander, Pekka Härmä, Sari Metsämäki, Yrjö Sucksdorff (Environment Data Center, Hel-

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Rauno Väisänen

Kari Heliövaara

1 Introduction

The dynamics of insect predator-prey systems and the severity of insect pest outbreaks may be strongly affected by the spatial heterogeneity of natural environments (Taylor 1984, Schowalter et al. 1986, Roland 1993). In spite of apparently similar vegetation cover over wide areas, the boreal zone shows great spatial and temporal heterogeneity with a wide range of subhabitats (Danks & Footitt 1989). Changes in forest structure due to silvicultural practices play a major role in shaping species diversity. Forest management also affects landscape mosaics and creates suitable habitats for different insect species (Nuorteva 1968, Eidmann 1985, Buse & Good 1993). The direct effects of silvicultural practices, such as clear-cutting or burning-over, have a striking influence on local insect species composition and diversity. However, these effects are usually transient if the managed areas are small or the frequency of the practices is low. Though the local effects of forest management on insect fauna are usually incidental, the effects of large-scale forest management on biodiversity may be considerable (Heliövaara & Väisänen 1984, Väisänen et al. 1993).

Computerized mapping systems for the capture, storage, retrieval, and analysis of spatial and descriptive data (GIS, geographic information system) have developed rapidly. GIS technology is central in spatial modelling and it can provide illustrative descriptions of geographic relationships. Applying GIS it is possible to display information in different scales, to combine data coverages from different sources and themes, to display relationships involving time dependence, to create modelling capabilities in an intergated computing environment and to provide quick access to linked spatial and attribute information (Coulson et al. 1988, Lee 1989, Lai 1990, McKendry & Machlis 1993).

Remotely sensed satellite data have been used to classify and map land surface cover types based on spectral reflectance characteristics (Timmons et al. 1984, Ioka & Koda 1986, Shasby & Carneg-

gie 1986). Multispectral scanning data have also been applied in entomological research for the rapid identification of areas being attacked e.g. by forest pests (Dottavio & Williams 1983, Rencz & Nemeth 1985, Gimbarzevsky et al. 1992, Heliövaara et al. in press). High-altitude airborne simulations of thematic mapper (TM) performance have been shown to provide acceptable estimates of, for instance, insect defoliation (Dottavio & Williams 1983, Leckie & Ostaff 1988), pine beetle infestation (Rencz & Nemeth 1985, Gimbarzevsky et al. 1992) and locust habitat mapping (Sinha & Chandra 1988). However, methods for interpreting numerical changes have been rather poorly developed, and satellite-based observations have proved at best only partially effective for routine insect surveys (Riley 1989). Image analysis methods have recently been developed which compute estimates of all forest inventory variables for each pixel (Tomppo 1991).

The aim of the present study is to develop GIS-assisted methods using existing remotely sensed and geological data to predict the occurrence of forest insects in different habitats over wide geographical areas. This may be crucial for the pest risk assessment of large forests. Forest insects may be regarded as keystone species the spatial distribution of which affects the whole forest dynamics. In the present study the relationship between the structure of forest stands and the habitat utilization of forest insects is analysed. It is assumed that the distribution of insect species is at least partly controlled by the silvicultural characteristics of each patch of forest and the landscape formed by these patches. Measurement of several environmental variables in the field could be used to determine the most significant variables associated with forest insect diversity. Models on insect distribution based on field measurements are compared with models based on existing geological and remotely sensed information. This is done to test the applicability of satellite images and GIS in boreal forest entomology.

2 Materials and methods

2.1 Study Area and Sampling

The field work was carried out in Evo, southern Finland (midpoint 61°12'N, 25°07'E) in July–August, 1992. The study area covers approximately 100 km² (12 km by 9 km) and includes different types of forest belonging to the southern boreal zone as well as open fields, lakes, wetlands, and farms, houses and villages. Due to the presence of a forestry training school there is a long tradition of forest management in the area. Silvicultural practices have created a fragmented forest area with relatively small habitat compartments in several stages of succession.

The study was conducted on temporary sample plots in this fragmented forest area. The sampling was based on 30 equilateral triangles with sides of 1 km. The location of the midpoint of each triangle was determined randomly using a random number generator for the latitudinal and longitudinal coordinates. For practical reasons, the triangles were placed on a topographical map with one corner of each triangle pointing towards the nearest road. The sample plots were 25 × 25 m quadrats spaced at 25 m from each other along the sides of the triangles. There were 20 sample plots per side, 60 sample plots per triangle, giving a grand total of 1800 sample plots (Fig. 1). This design made it easy to reach and exactly locate the sample plots. The dislocation of sample plots was minimal due to the study design. Coding errors in the data were eliminated by comparing plotted maps of sample plots with the original triangles and by comparing field habitat classifications with remotely sensed land use classes. The potential effect of spatial autocorrelation was considered insignificant due to the heterogeneous structure of the forest, scattered distribution of the breeding substrate of the insects (Väisänen et al. 1993) and the good dispersal capability of the insects (Nuorteva 1956, 1968, Forsse & Solbreck 1985).

Insect occurrence was recorded on each sample

plot using presence/absence data that did not take species abundance into account. Twenty-six easy-to-detect insect taxa were included in the material (Table 1). Special attention was paid to bark beetles, since their gallery systems are easy to identify at the species level, and other taxa whose detectability are not affected by momentary weather conditions or phenology. The occurrence of the listed insect species of each log, stump and logging waste not older than two years and dying trees was thoroughly investigated. The bark was removed from the breeding material using a knife. The surface area and the removed bark were visually examined in the field and systematically scanned by two forest entomologists. The presence of *Aradus cinnamomeus* was investigated by taking bark from young, living pines. The occurrence of *Retinia resinella* was checked by looking for the presence of fresh resin galls on the branches of pines. The occurrence of Diprionidae was studied by examining the typical feeding scars or larval colonies on pine branches. In addition, the number of ant hills (*Formica rufa* group, mostly *F. aquilonia* Yarrow) was determined for each sample plot. The potential bias caused by sampling effort remained constant throughout the study since the field work was performed by the same persons.

In some cases the recorded insect species were grouped into higher taxa since exact species identification was not always possible on the basis of mother galleries and feeding scars. Consequently the variable '*Pissodes* sp.' included the species *P. castaneum*, *P. pini*, *P. harcyniae* and *P. piniphilus*. *Tomicus piniperda* and the less common *T. minor* formed the variable '*Tomicus* sp.', *Polygraphus subopacus*, *P. poligraphus* and *P. punctifrons* formed the variable '*Polygraphus* sp.'. The variable '*Crypturgus* sp.' was formed by *Crypturgus cinereus*, *C. pusillus* and *C. hispidulus*, and the variable '*Orthotomicus* sp.' included *Orthotomicus proximus*, *O. suturalis* and *O. laricis*. The fol-

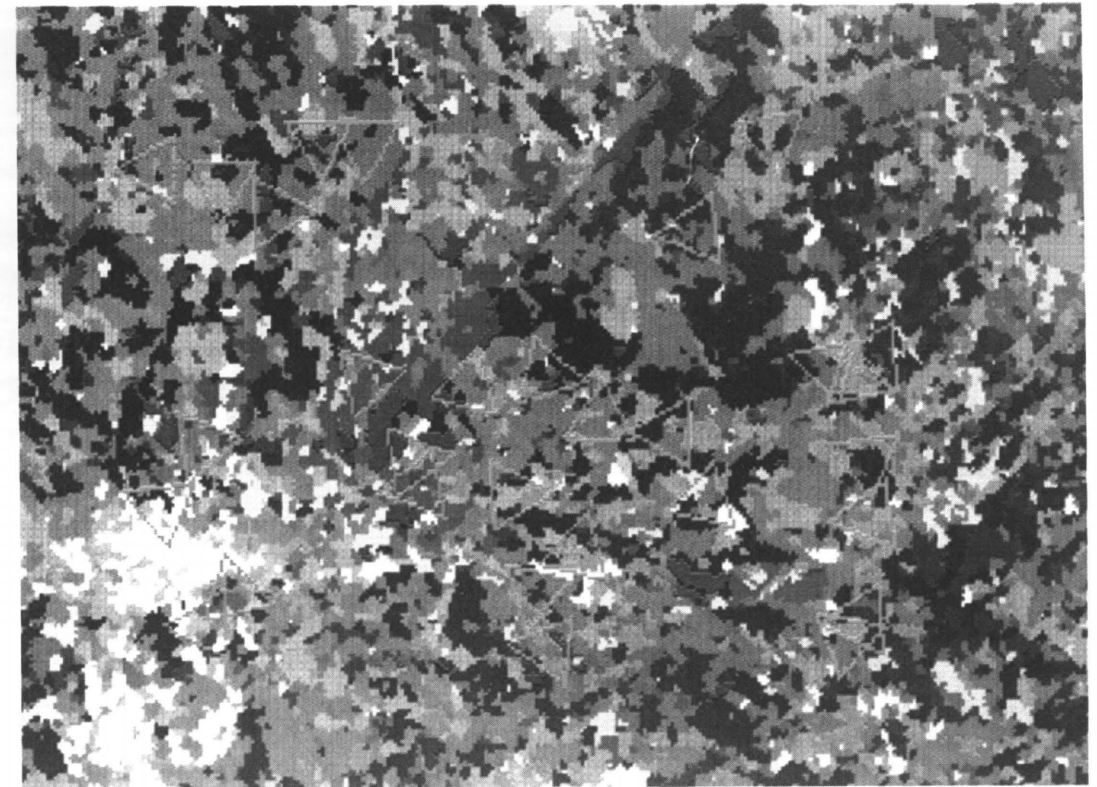


Figure 1. Location of the sample plots on thirty equilateral triangles in Evo, southern Finland. Each triangle has 60 sample plots (25 m by 25 m), 20 sample plots per side.

lowing variables were measured in the field for use in the statistical analyses (see chapters 23 and 24):

- number of the sample plot (1–1800);
- coordinates (UTM Grid 27° E) to the nearest 10 m;
- number of the triangle (1–30);
- number of the side of the triangle (1–3);
- land use class: 1 = water, 2 = open field, road, building, etc., 3 = mire, 4 = drained peatland, 5 = forest;
- forest site type according to Cajander (1949): 0 = no forest, 1 = *Cladonia* site type (CIT), 2 = *Calluna* site type (CT), 3 = *Vaccinium* site type (VT), 4 = *Myrtillus* site type (MT), 5 = *Oxalis-myrtillus* site type (OMaT);
- drained peatland: 0 = no peatland, 1 = dwarf shrub

pine swamp, 2 = peatland dominated by *Vaccinium vitis-idaea*, 3 = peatland dominated by *Vaccinium myrtillus*, 4 = herb-rich peatland;

- mire type: 0 = no mire, 1 = open mire, 2 = pine bog, 3 = spruce swamp;
- 'edge effect': 0 = continuous land use class, 1 = border of forest and mire, road, lake or buildings;
- crown canopy coverage using the scale: 1 = <20 %, 2 = 20–40 %, 3 = 40–60 %, 4 = 60–80 %, 5 = >80 %;
- mean height of trees using the scale 1 = <2 m, 2 = 2–8 m, 3 = 8–14 m, 4 = 14–20 m, 5 = >20 m;
- proportion (%) of Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), birches (*Betula verrucosa* and *B. pubescens*), aspen (*Populus tremula*), willows (*Salix* spp.), and alders (*Alnus glutinosa* and *A. incana*) using the scale: 1 = <20 %, 2 = 20–40 %, 3 = 40–60 %, 4 = 60–80 %, 5 = >80 %;

Of the 1800 sample plots, 1276 sample plots were situated in forests, 200 on drained peatlands, 143 sample plots represented cultivated fields or buildings, 115 were on bogs and mires, and 66 on lakes and represented water. The sample plots lying in forests represented the *Cladonia* site type (6 sample plots), *Calluna* site type (42), *Vaccinium* site type (392), *Myrtillus* site type (676), *Oxalis-myrtillus* site type (157) and *Oxalis-Maianthemum* site type (3). The mean crown coverage was 36.7 % (SD 22.8) and the mean tree height 12.0 m (SD 8.3). The mean proportion of spruce was 35.0 % (SD 37.4), that of pine 30.9 % (SD 38.4) and that of birches 18.8 % (SD 25.7). The mean number of tree species recorded was 1.9 (SD 1.1) in each sample plot.

The 200 sample plots lying on drained peatland were classified as dwarf shrub pine swamps (11 sample plots), peatland dominated by *Vaccinium vitis-idaea* (67), peatland dominated by *V. myrtillus* (76) and herb rich peatland (46). The 115 sample plots lying on bogs and mires were classified as open mires (7 sample plots), pine bog (47) and spruce swamp (61). Ninety-nine sample plots were located on the border of forest, mire, road, lake or buildings, while 1701 sample plots were located entirely within a single land use class.

The mean number of insect taxa recorded was 1.4 (SD 1.8) on each sample plot. The number of taxa ranged from 0 to 9.

2.2 Satellite Imagery

Insect occurrence was studied in relation to environmental variables interpreted from remotely sensed data (Landsat Thematic Mapper 30 m multispectral scanner imagery 1991). We used a GIS system (FINGIS) developed by the National Board of Survey in Finland, which contains a central file of drainage basins and is compatible with other environmental filing systems. For this system, the Technical Research Centre of Finland and National Board of Waters and the Environment developed a method of interpreting basin characteristics in satellite images (Kuittinen and Sucksdorff 1987). The interpretation system is hierarchical and starts with the identification of water areas and cultivated areas and ends with peatlands and clear-cut areas. Different algorithms

are used in the different phases. For image enhance purposes principal component analysis was applied. Image segmentation removes noise in the images and the segments are interpreted using the mean values of the pixels in the segments. The edge preserving smoothing was used to eliminate pixel value fluctuations due to the noise without degradation of the improved image information, such as edges. A detailed description of the interpreting procedure is presented by Kuittinen and Sucksdorff (1987). We also utilized standard geological maps available in digitized form in the National Board of Waters and the Environment.

The triangles with the sample plots were overlaid on satellite images (Fig. 1). The following environmental variables were used in the statistical analyses:

- A. Variables from geological maps
 - exposed bedrock (0, 1)
 - ground moraine (0, 1)
 - ablation moraine (0, 1)
 - esker (0, 1)
 - sand (0, 1)
 - silt (0, 1)
 - peat (0, 1)
- B. Remotely sensed variables
 - water (0, 1)
 - open field (0, 1)
 - clear-cut (0, 1)
 - young tree stand (0, 1)
 - growing stock of forest (class means 0, 25, 75, 125, 175, 225 m³/ha)
 - open mire (0, 1)
 - conifer swamp (0, 1)
 - birch swamp (0, 1)
 - pine bog (0, 1)
 - pine forest (0, 1)
 - spruce forest (0, 1)
 - deciduous forest (0, 1)
 - mixed forest (0, 1)

2.3 Classification and Ordination

The insect data were analyzed separately using (i) environmental variables measured in the field (abbreviated: FIELD), and (ii) variables interpreted from the satellite and geological data (SAT).

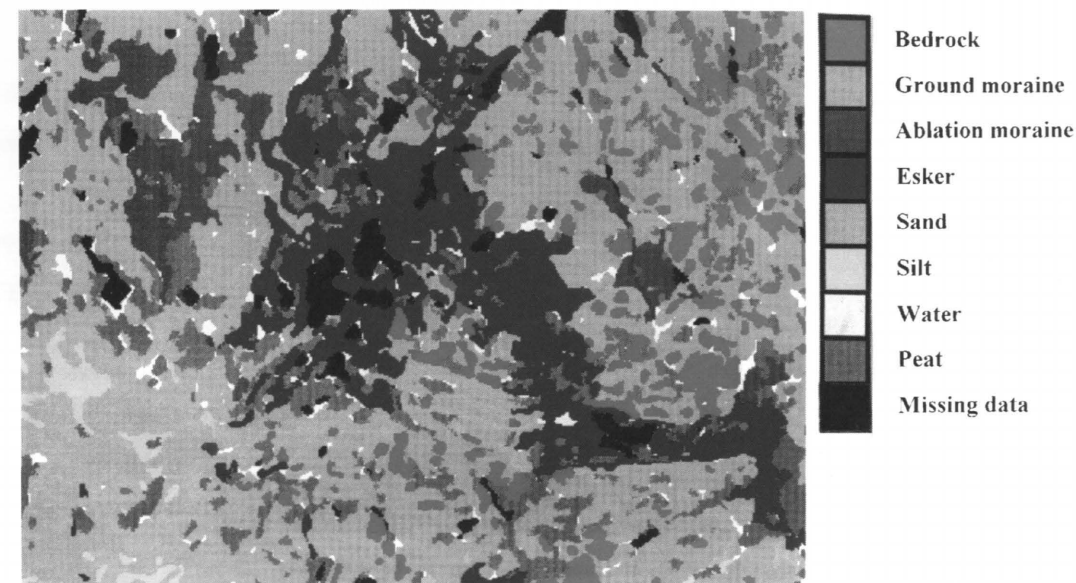


Figure 2. Soil types in the study area.

The statistical programs used in the analyses were TWINSpan (Hill 1979) and CANOCO (Ter Braak 1985). Two-way indicator species analysis is a modification of indicator species analysis which gives both a classification of forest stands and insect species (Hill 1979). These classifications are then used to produce an ordered two-way table of the original data. This analysis was used to classify the sample plots on the basis of their insect species composition and to classify insect species on the basis of their occurrence in the sample plots. The number of indicators was 12. The maximum level of divisions was 6, but the species were regrouped using three division levels in the final tabulation.

Canonical correspondence analysis (CCA) was used to relate the variation in species composition to the environmental variation. The analysis was first carried out using all the variables. The eigenvalue is a measure of the separation of the species' distributions along the ordination axis. The canonical coefficients in the CCA are the coefficients of a weighted multiple regression of the sample scores on the standardized environmental variables. The t-test is not appropriate for tests of significance of canonical coefficients. However,

when the t-value of a variable is less than 2.1 in absolute terms, the variable does not contribute much to the fit of the species data in addition to the contributions of the other variables in the analysis (Ter Braak 1987). In such case the variable was deleted without having any marked effect on the canonical eigenvalues.

Comparing the arrow lengths in the CCA ordination diagrams indicates the importance of the environmental variables in question. The arrow roughly points in the direction of maximum variation of the corresponding variable. Monte Carlo permutation tests of CCA axis 1 for 1800 sample plots were carried out by randomly permutating the sample numbers in the environmental data (99 random permutations). If the observed value is among the 5 % highest values, then the species are significantly related to the environmental variables. The first eigenvalue was used as test statistic.

The inter-set correlations of the environmental variables with the CCA axes are the correlation coefficients between the environmental variables and the species axes consisting of the sample scores. They do not become unstable when the environmental variables are intercorrelated. The fraction of total variance in the standardized envi-

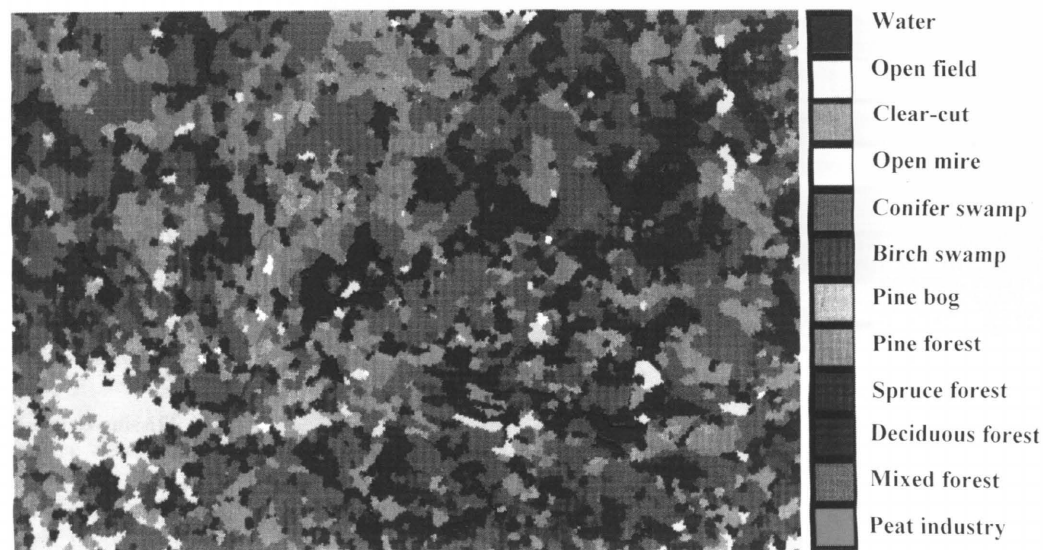


Figure 3. Satellite images of vegetation types and land use patterns in the study area.

ronmental data that is extracted by each species axis is equal to the mean squared inter-set correlation. If the variance inflation factor (VIF) of a variable is large (>20), the variable is highly correlated with the other environmental variables. As a consequence its canonical coefficient is unstable (Ter Braak 1985, 1986).

2.4 Logistic Models

The occurrence of insect species (taxa) was predicted by logistic regression models (stepwise logistic regression computer program, BMDPLR, Engelman 1988; see also Häkkinen & Linnilä 1987, Hosmer & Lemeshow 1989) using separately FIELD and SAT data. This was done in order to determine the significance of the present environmental variables in the geographical distribution of the selected species. The model is as shown below:

$$W = \log \frac{P}{1-P} = b_0 + b_1 x_1 + b_2 x_2 + \dots + b_k x_k$$

where P is the probability of occurrence, b_i are parameters, and x_i are variables $i = 1, \dots, k$.

The log odds W is an increasing function of P and is equal to 0 for $P = 0.5$. Logistic regression assumes that W is a linear function of the covariates and the coefficients of the linear function are estimated by maximum likelihood. The Hosmer-Lemeshow goodness of fit chi-square test (Hosmer and Lemeshow 1989) divides the data into 10 cells and compares the observed and predicted frequencies for these cells. The cells are defined using the predicted frequencies. In the final models, high p values indicate good fit between the observed and predicted frequencies. In the stepwise logistic regression, the criterion for a variable to enter the model was intentionally set loose ($p < 0.1$) in order to obtain the estimated parameters of all variables for further comparisons. We also tested the success of classification by calculating the proportions of correctly classified cases (hit-%). For all the species in the classification, we used cutpoints where the function describing the proportion of decreasing observed failures cuts the function describing the proportion of increasing observed successes. Consequently, the same proportion of new (not used in the construction of the model) cases should become correctly classified when they originate from the same sample pool.

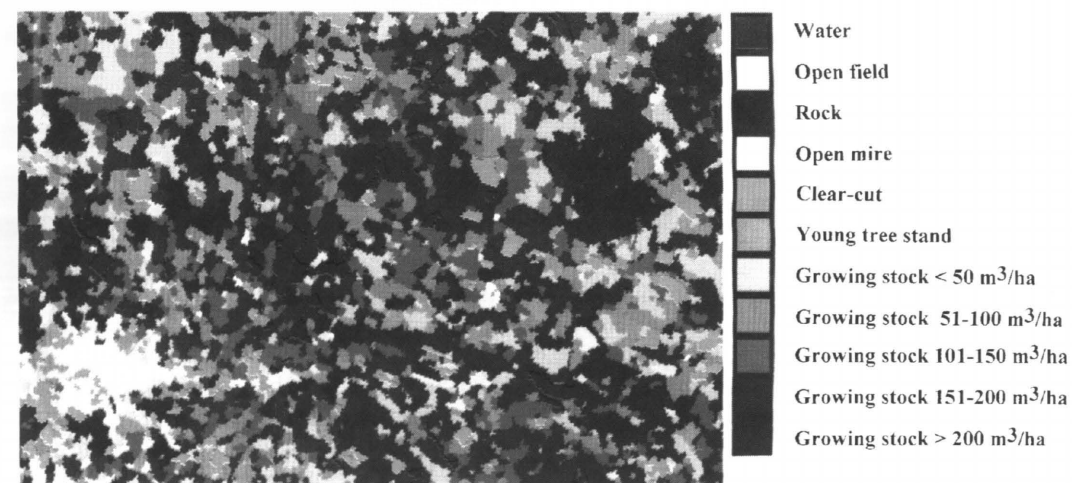


Figure 4. Satellite images of tree volume categories (growing stock) in the study area.

2.5 Forest Fragmentation

The forests of the study area comprise of several compartments which can be interpreted from SAT data according to vegetation type, land use pattern and tree volume category (Figs. 3 and 4; Kuittinen and Sucksdorff 1987). The size of the habitat compartment surrounding each sample plot was measured from the maps (using a trans-

parent paper sheet with 1 mm² grid). Mean values of habitat compartment size were plotted against the number of insect taxa in each vegetation type and tree volume category. The distance of each sample plot from the nearest edge of the surrounding habitat compartment was measured from the maps, and these values were plotted against the number of insect taxa.

3 Results

3.1 Classification of Species and Sample Plots

The insects species were classified into seven groups according to their occurrence as given by TWINSpan (Fig. 5). The primary division among the species was interpreted to be associated with their life histories, since species associated with large (vs. saplings) or weakened trees were classified in the upper branch of the first division, while species associated with young, living trees were classified in the lower main branch. All bark beetles and *Pissodes* weevils with similar life history were grouped in the upper main branch. Species living only on Scots pine were classified in the five lowermost branches, while species associated with Norway spruce, conifers in general, and birch were classified in the two uppermost branches.

Fig. 6 shows the dendrogram of eight sample plot groups as interpreted from the insect data. The number of sample plots varied from 5 to 332 among the groups. There were 15 'borderline or mis-classified' sample plots in the case of groups 1 and 2. The left branch of the primary division was characterized by *Hylurgops palliatus*, *Dryocoetes* sp., *Trypodendron lineatum*, *Pityogenes chalcographus* and *Pissodes* sp., and the right main branch by *Retinia resinella*.

The frequency of occurrence of insect species in the sample plot groups interpreted from the TWINSpan is shown in Table 1. The species richness was much lower in the five latter groups, mainly characterized by pine herbivores, than in the others. The first sample plot group was rather heterogeneous with two common species (*Xylechinus pilosus*, *Cryphalus saltuarius*). The number sample plots as well as the number of species was the highest in sample plot group 2 (21 species) and 3 (17 species), the most characteristic taxa being *Pityogenes chalcographus* and *Tomicus* sp., respectively. *Trypodendron signatum* was the most abundant species in sample plot group 4 with

only four additional species. Sample plot group 5 was characterized by a high frequency of *Tomicus* sp. and *Retinia resinella*, while *R. resinella* was the only abundant species in sample plot group 6. The number of sample plots and the number of species was the lowest in sample plot groups 7 and 8 (three species in both groups), the former being characterized by a high frequency of Diprionidae and *Tomicus* sp. and the latter only by Diprionidae. None of the insect species were recorded in all eight or even seven sample plot groups. *Tomicus* sp. was recorded in six groups, and four taxa (*Retinia resinella*, Diprionidae, *Tomicus* sp., *Trypodendron signatum*) occurred in every sample plot in at least one sample plot group. Five species (*Hylecoetus dermestoides*, *Hylurgops glabratus*, *Scolytus ratzeburgi*, *Pityophthorus micrographus*, *Ips acuminatus*) were recorded in one group only. Of these species,

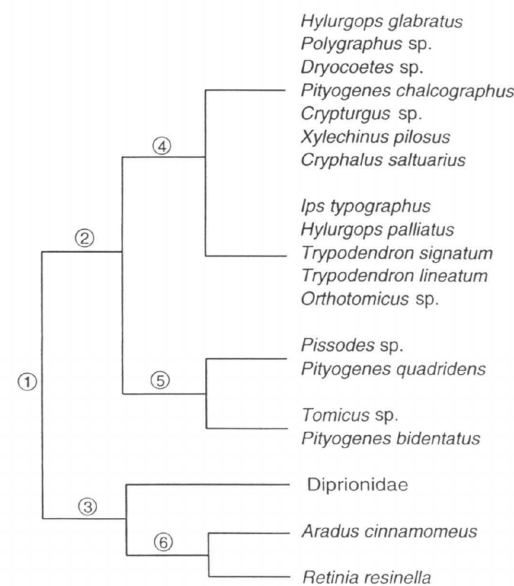


Figure 5. A species dendrogram of a two-way indicator species analysis (TWINSpan). The order of divisions is indicated by encircled numbers.

Table 1. The percentage occurrence frequency of the insect species (taxa) in the eight groups interpreted from the TWINSpan analysis. Species order is as given by TWINSpan. Values greater than 70 are in bold type. The number of sample plots in each group is shown in parentheses. Ants were omitted from the analyses.

Species	Sample plot group							
	1 (46)	2 (332)	3 (322)	4 (7)	5 (106)	6 (194)	7 (6)	8 (5)
<i>Aradus cinnamomeus</i> (Panzer)	–	–	–	–	8	8	–	–
<i>Retinia resinella</i> (Linnaeus, 1758)	–	1	3	–	100	100	–	–
Diprionidae	–	–	1	–	12	–	100	100
<i>Hylecoetus dermestoides</i> (Linnaeus, 1761) ¹	–	–	–	14	–	–	–	–
<i>Hyllobius abietis</i> (Linnaeus, 1758) ¹	–	–	+	–	1	–	–	–
<i>Pissodes</i> sp.	11	45	45	14	32	–	–	–
<i>Xylechinus pilosus</i> (Ratzeburg, 1837)	59	13	1	–	–	1	–	–
<i>Tomicus</i> sp.	4	13	78	43	72	–	100	–
<i>Hylurgops glabratus</i> (Zettstedt, 1828)	–	18	–	–	–	–	–	–
<i>Hylurgops palliatus</i> (Gyllenhal, 1813)	–	45	10	–	2	–	–	–
<i>Hylastes brunneus</i> (Erichson, 1836) ¹	–	–	+	–	1	–	–	20
<i>Polygraphus</i> sp.	2	16	–	–	–	–	–	–
<i>Scolytus ratzeburgi</i> (Janson, 1856) ¹	–	+	–	–	–	–	–	–
<i>Crypturgus</i> sp.	4	26	–	–	–	–	–	–
<i>Dryocoetes</i> sp.	11	53	2	–	–	–	–	–
<i>Cryphalus saltuarius</i> (Weise, 1891)	52	10	1	–	1	1	–	–
<i>Pityophthorus micrographus</i> (Linnaeus, 1758) ¹	–	1	–	–	–	–	–	–
<i>Trypodendron lineatum</i> (Olivier, 1795)	2	41	8	–	–	–	–	–
<i>Trypodendron signatum</i> (Fabricius, 1787)	–	1	–	100	1	–	–	–
<i>Pityogenes chalcographus</i> (Linnaeus, 1761)	9	83	11	–	–	1	–	–
<i>Pityogenes quadridens</i> (Hartig, 1834)	–	4	26	14	7	1	–	–
<i>Pityogenes bidentatus</i> (Herbst, 1783)	–	2	26	–	23	–	33	–
<i>Ips acuminatus</i> (Gyllenhal, 1827) ¹	–	+	–	–	–	–	–	–
<i>Ips typographus</i> (Linnaeus, 1758)	–	4	1	–	–	–	–	–
<i>Ips amitinus</i> (Eichhoff, 1872) ¹	–	2	+	–	–	–	–	–
<i>Orthotomicus</i> sp.	–	5	1	–	–	–	–	20

¹ Species occurs in less than 10 sample plots and has been ignored in further TWINSpan and CCA analyses

H. dermestoides was in sample plot group 4, while the others were in sample plot group 2.

FIELD variables characterizing the sample plot groups are listed in Table 2. Not less than 71.4 % of the sample plots were located in forests in each group, and two groups were characterized by occurring entirely in forests. Note that the groups were not characterized by water, open fields, roads or buildings because the classification was based on recorded insect species. Most of the sample plot groups were characterized by *Vaccinium* or *Myrtillus* forest site types, but there was much variation in forest site types especially in groups

3 and 7. The proportion of sample plots lying on mires varied from 0 to 8.8 % in each group. The sample plots were characterized mainly by spruce swamps in groups 1 and 2, and pine bogs in groups 3, 5 and 6. Mean crown coverage varied from 18.3 to 50.5 %, being slightly higher in the first four groups than in the others. There was almost a fourfold difference in the mean tree height (5.8 vs. 20.3 m) between the groups. A high proportion of Norway spruce characterized the first four groups, while that of Scots pine was especially high in groups 5 and 7. The highest proportion of birches was recorded in groups 6 and 8.

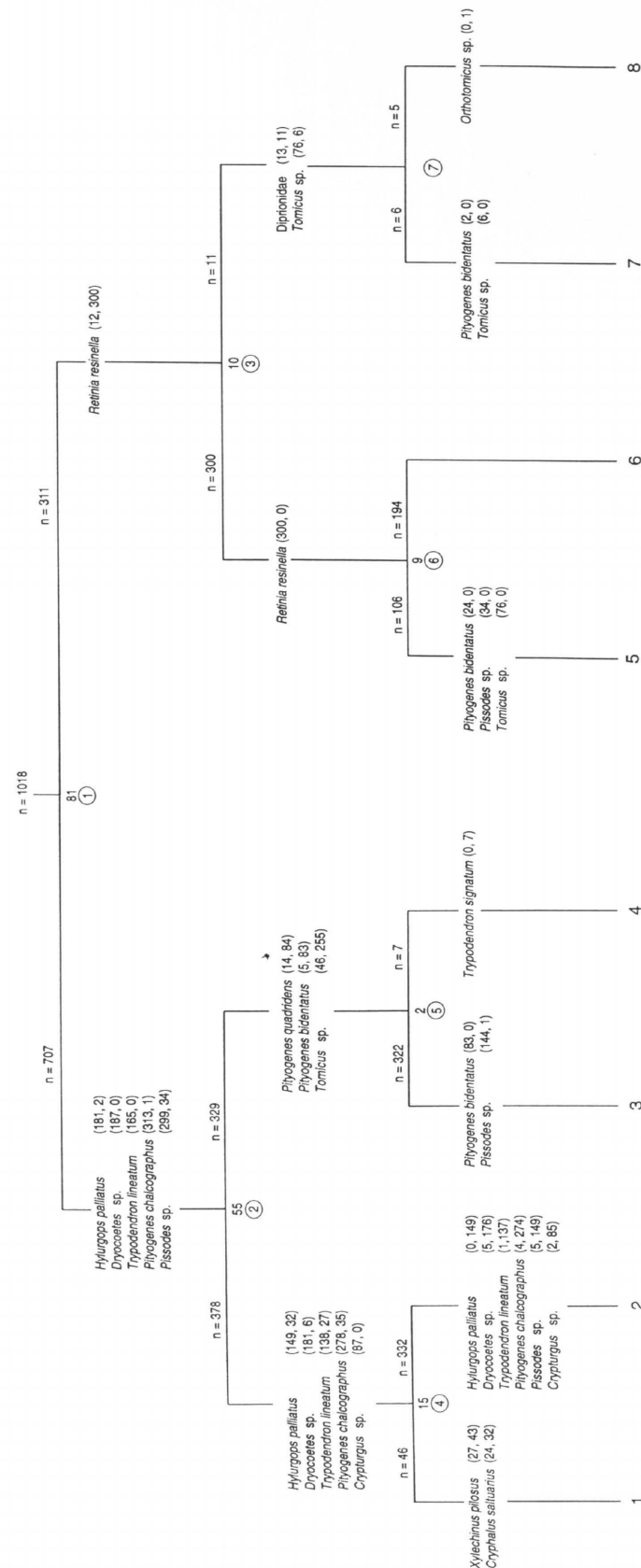


Figure 6. A sample plot dendrogram of a two-way indicator species analysis (TWINSPAN) using the presence/absence data of insects. Numbers in parentheses are the frequencies of each species in the left and right hand cluster, respectively. The number of 'borderline and misclassified plots' is indicated at each division. The order of divisions is indicated by encircled numbers.

Table 2. Mean values and their standard deviations of the FIELD variables for each sample plot group interpreted from TWINSPAN.

	1 (46)	2 (332)	3 (322)	Sample plot group 4 (7)	5 (106)	6 (194)	7 (6)	8 (5)
LAND USE CLASS								
Water	-	-	-	-	-	-	-	-
Open field, road, building etc.	-	-	-	-	-	-	-	-
Bog, mire	4.4	3.9	7.1	-	8.5	8.8	-	-
Drained peatland	17.4	14.8	12.7	28.6	3.8	7.2	-	-
Forest	78.3	81.3	80.1	71.4	87.7	84.0	100	100
FOREST SITE TYPE								
No forest	21.7	18.7	19.9	28.6	12.3	16.0	-	-
CIT	-	-	0.3	-	-	2.1	-	-
CT	-	-	5.3	-	11.3	3.6	-	20.0
VT	4.4	3.9	41.9	-	63.2	53.1	100	20.0
MT	47.8	59.0	28.6	42.9	13.2	24.7	-	60.0
OMT	26.1	18.4	3.1	28.6	-	0.5	-	-
OMaT	-	-	0.9	-	-	-	-	-
DRAINED PEATLAND								
No peatland	82.6	85.2	87.3	71.4	96.2	92.8	100	100
Dwarf shrub pine swamp	-	-	0.6	-	1.9	1.6	-	-
Peatland dominated by <i>Vaccinium vitis-idaea</i>	2.2	4.8	9.0	-	-	3.1	-	-
<i>Vaccinium myrtillus</i>	4.4	6.0	2.5	28.6	0.9	1.6	-	-
Herbrich peatland	10.9	3.9	0.6	-	0.9	1.0	-	-
MIRE TYPE								
No mire	95.7	96.1	92.9	100	91.5	91.2	100	100
Open mire	-	-	-	-	-	2.6	-	-
Pine bog	2.1	-	6.2	-	8.5	3.6	-	-
Spruce swamp	2.2	3.9	0.9	-	-	2.6	-	-
'EDGE EFFECT'								
Continuous land use class	93.5	97.6	96.3	100	90.6	94.9	100	80.0
Border of forest, mire, road, lake or human residences	6.5	2.4	3.7	-	9.4	5.1	-	20.0
Crown coverage (%)	mean 50.5	46.3	39.8	39.3	28.3	18.3	37.5	28.0
SD	17.5	19.8	18.4	15.1	19.0	20.6	21.9	20.2
Mean height of trees (m)	mean 20.1	18.3	14.2	20.3	8.8	5.8	18.5	15.1
SD	3.2	6.0	6.3	3.9	5.9	4.4	6.2	7.9
Proportion of (%)								
<i>Picea abies</i>	mean 74.4	71.4	18.4	57.9	8.8	14.9	0.8	11.0
SD	19.5	31.8	26.7	40.9	18.0	22.6	2.0	21.9
<i>Pinus sylvestris</i>	mean 9.2	12.2	69.0	31.7	77.9	59.2	90.8	58.0
SD	15.3	24.9	32.4	35.3	28.6	34.8	18.0	37.7
<i>Betula verrucosa</i> and <i>B. pubescens</i>	mean 14.2	10.4	11.3	9.3	12.2	23.3	8.3	31.0
SD	15.1	15.7	17.6	10.6	19.7	25.3	16.0	22.5
<i>Populus tremula</i> and <i>Salix</i> spp.	mean 0.8	1.3	1.0	-	0.7	1.7	-	-
SD	3.2	6.2	5.0	-	4.6	7.7	-	-
<i>Alnus glutinosa</i> and <i>A. incana</i>	mean 0.8	1.0	0.2	2.1	0.3	0.8	-	-
SD	3.3	5.0	1.4	3.9	1.6	4.5	-	-
Number of ant hills	mean 0.2	0.2	0.2	0.1	0.1	0.1	-	-
SD	0.4	0.4	0.4	0.4	0.3	0.3	-	-

Table 3. Mean values of the SAT variables for each sample plot group interpreted from TWINSpan.

	Sample plot group							
	1 (46)	2 (332)	3 (322)	4 (7)	5 (106)	6 (194)	7 (6)	8 (5)
Exposed bedrock	17.4	16.0	16.5	42.9	7.6	27.8	—	—
Ground moraine	52.2	50.9	21.7	28.6	27.4	32.0	—	40.0
Ablation moraine	13.0	6.3	5.9	—	12.3	10.8	—	—
Esker	2.2	13.3	34.8	14.3	38.7	17.5	100	60.0
Sand	4.4	3.3	8.1	—	0.9	0.5	—	—
Silt	—	0.3	—	—	—	—	—	—
Peat	6.5	7.8	9.6	14.3	8.5	8.8	—	—
Water	4.4	0.3	3.4	—	0.9	1.6	—	—
Open field	—	—	0.9	—	2.8	—	—	—
Clear-cut	—	2.7	1.9	—	5.7	21.1	—	—
Young stand	4.4	1.2	2.2	—	13.2	13.4	—	—
Growing stock								
0 m ³ /ha	6.5	4.2	7.8	—	22.6	35.1	—	—
< 50 m ³ /ha	13.0	11.8	14.0	—	18.9	18.6	—	40.0
51–100 m ³ /ha	13.0	7.8	15.5	28.6	8.5	12.9	—	—
101–150 m ³ /ha	2.2	3.3	7.8	—	13.2	9.3	—	—
151–200 m ³ /ha	37.0	40.7	38.8	28.6	24.5	17.5	83.3	20.0
> 200 m ³ /ha	28.3	32.2	16.2	42.9	12.3	6.7	16.7	40.0
Conifer swamp	6.5	8.1	7.1	28.6	1.9	4.1	—	—
Birch swamp	—	1.8	2.5	14.3	3.8	5.2	—	—
Pine bog	6.5	2.7	8.4	—	1.9	1.6	—	—
Pine forest	2.2	1.5	16.2	—	14.2	7.7	83.3	40.0
Spruce forest	37.0	45.8	14.0	57.1	8.5	5.2	—	—
Deciduous forest	4.4	3.6	4.0	—	0.9	7.7	16.7	—
Mixed forest	37.0	32.2	40.1	—	46.2	33.5	—	60.0

while the relatively low proportion of other deciduous trees was fairly evenly distributed between the groups, apart from groups 7 and 8 where they were lacking.

According to the SAT data the proportion of sample plots characterized by exposed bedrock varied from 7.6 to 42.9 % in the sample plot groups, not including two groups characterized by esker only (group 7) or esker and ground moraine (group 8) (Table 3). The proportion of ground moraine sample plots exceeded 50 % in the first two groups. The highest proportions of clear-cut areas and young stands were recorded in groups 5 and 6. These groups were also characterized by the highest proportion of treeless area. The proportion of the highest growing stock category (more than 200 m³/ha) exceeded 40 % in groups 4 and 8. The

proportion of both conifer swamp and birch swamp was the highest in group 4. No sample plots were characterized by swamp or mire in groups 7 and 8 according to the satellite images. The proportion of pine forests was the highest in groups 7 and 8, while it varied from 0 to 16.2 % in the others. The highest proportion of spruce forests was recorded in group 4.

3.2 Species Assemblages and Environmental Variation

The faunistic data were related to variation in the environment using CCA. The CCA ordination diagram illustrates the insect fauna in relation to FIELD variables (Fig. 7). The Monte Carlo per-

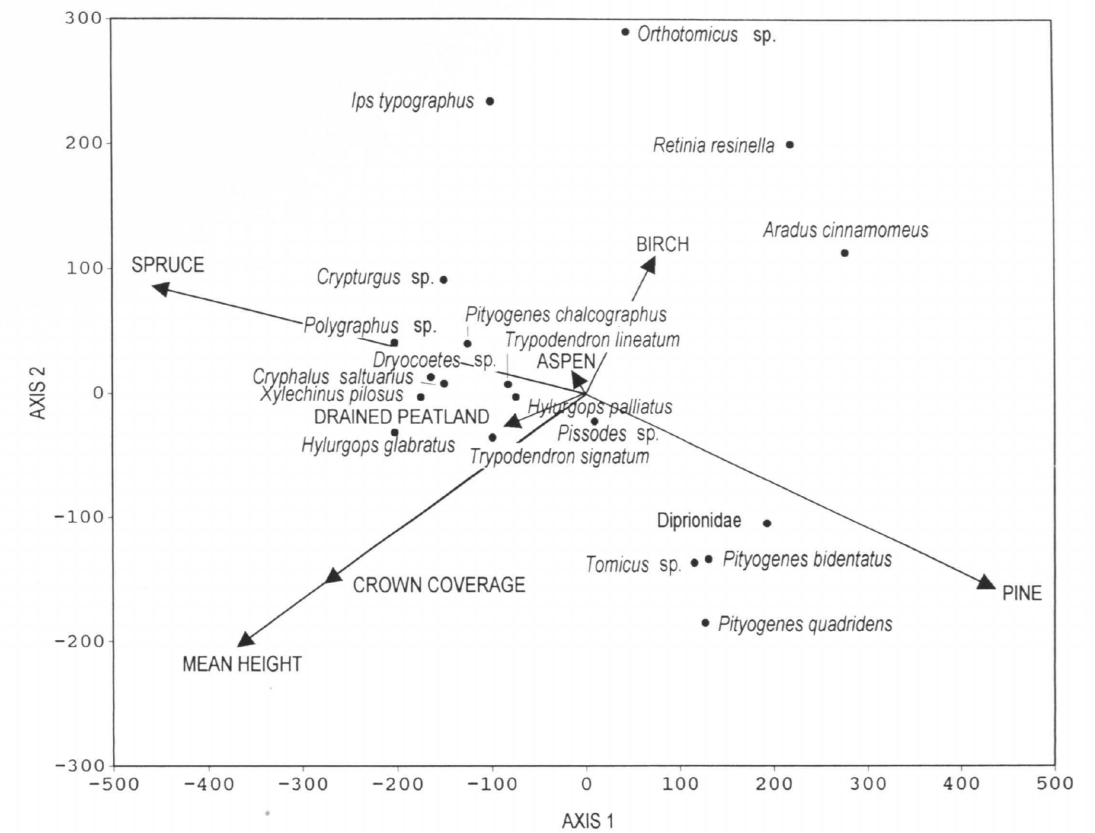


Figure 7. Ordination diagram based on canonical correspondence analysis (CCA) of the distribution of insects in sample plots in the study area with respect to seven environmental variables (arrows) of FIELD data. In each variable, the *t*-value of canonical coefficients in absolute values is higher than 2.2. Eigenvalue for the axis 1 is 0.49 and 0.16 for the axis 2.

mutation test showed that the occurrence of the insect taxa were indeed related to these variables (99 random permutations, $p < 0.01$ for the first canonical axis).

The canonical coefficients for the proportion of pine, birch and spruce received the highest absolute value on the first axis, but other variables (mean height, crown coverage, proportion of peatland, aspen) contributed to the fit of the species data (Table 4). The proportion of spruce and pine and mean height seemed to determine the trends in the assemblages of insect taxa along axis 1. This axis correlated with these variables, positively (pine) or negatively (spruce, mean height). On the second axis, the mean height of the forest and the proportion of spruce had the highest canonical coefficients of opposite sign. The species-

environment scatter plot shows that the second axis was mainly related to mean stand height and the proportion of pine and spruce, all with negative coefficients. The variance inflation factors (Ter Braak 1986) were relatively low indicating that the environmental variables used were not correlated with other variables. The fraction of the total variance in the standardized environmental data extracted by species axis 1 was 22.6 %, that extracted by axis 2 was 3.3 %, and that by axis 3 was 4 %.

Species associated with Scots pine lay on the right-hand side of the diagram and those associated with Norway spruce on the upper left-hand side (Fig. 7). Species living on both spruce and pine tended to concentrate near the centre of the diagram.

Table 4. Canonical coefficients, variance inflation factors (VIFs) and the inter-set correlations of FIELD variables with the first four axes of canonical correspondence analysis (CCA). Canonical coefficients with a t -value > 2.0 in absolute values are indicated by x .

Variable	Axis Eigenvalue	Canonical coefficients				Correlation coefficients				VIFs
		1	2	3	4	1	2	3	4	
Drained peatland	0.49	-0.06 ^x	-0.03	0.03 ^x	0.00	-0.13	-0.04	0.03	-0.04	1.0
Crown coverage	0.16	-0.18 ^x	-0.17 ^x	-0.19 ^x	0.19 ^x	-0.44	-0.22	-0.29	0.15	1.4
Spruce	0.11	0.28 ^x	0.35 ^x	-0.95 ^x	-0.42 ^x	-0.73	0.12	-0.12	-0.07	12.6
Pine	0.05	0.99 ^x	-0.09 ^x	-0.88	-0.40 ^x	0.69	-0.23	-0.01	0.03	11.2
Birch		0.36 ^x	0.08 ^x	-0.33	-0.23 ^x	0.12	0.16	0.01	-0.09	2.6
Aspen		0.08 ^x	0.00 ^x	-0.12	-0.07 ^x	-0.02	0.02	-0.01	-0.03	1.2
Mean height		-0.30 ^x	-0.40 ^x	0.23	-0.13 ^x	-0.59	-0.30	0.01	-0.15	1.8

Table 5. Canonical coefficients, variance inflation factors (VIFs) and the inter-set correlations of SAT variables with the first four axes of canonical correspondence analysis (CCA). Canonical coefficients with a t -value > 2.0 in absolute values are indicated by x .

Variable	Axis Eigenvalue	Canonical coefficients				Correlation coefficients				VIFs
		1	2	3	4	1	2	3	4	
Sand	0.15	-0.06 ^x	0.12 ^x	0.03	0.04 ^x	-0.06	0.18	0.05	0.08	1.0
Clear-cut	0.03	0.18 ^x	-0.10 ^x	-0.02	0.06 ^x	0.26	-0.07	-0.07	0.08	1.2
Young stand	0.01	0.18 ^x	-0.05 ^x	0.10 ^x	0.02	0.27	-0.02	0.14	-0.02	1.2
Growing stock	0.01	-0.24 ^x	-0.12 ^x	0.05 ^x	0.03	-0.37	-0.11	0.04	0.02	1.3

The faunistic data were also related (CCA) to variation in the SAT data (Fig. 8). The Monte Carlo permutation test showed that the occurrence of the insect taxa were related to these environmental variables (99 random permutations, $p < 0.01$ for the first canonical axis). On the first axis the canonical coefficients of the growing stock volume and the proportion of young stands obtained the highest absolute values (of opposite sign) (Table 5). The canonical coefficients of the growing stock and sand received the highest absolute value on the second axis. The first axis was correlated with the growing stock and young stand, and the second axis with the growing stock and sand, but the correlation coefficients were relatively low. The fraction of the total variance in the environmental data extracted by species axis 1 was 7.0 %, while axis 2 extracted 1.2 %, and axis 3 extracted 0.6 %.

Species associated with pine also lay on the

right-hand side in this diagram (Fig. 8). Species of young pine stands (*Retinia resinella*, *Aradus cinnamomeus*) were clearly separated from the other species on the right side of the diagram. Species associated with spruce were widely distributed on the left-hand side.

3.3 Logistic Models

The SAT models better predicted (Hosmer-Lemeshow test) the distribution of forest insects, except in the cases of *Xylechinus pilosus*, *Dryocoetes* sp. and *Trypodendron lineatum*, where the differences were relatively small in favour of the FIELD models (Table 6 and 7). The FIELD models best predicted the distributions of *Tomicus* sp., *Pityogenes quadridens*, *Pissodes* sp. and to a lesser degree *Pityogenes bidentatus* and ant

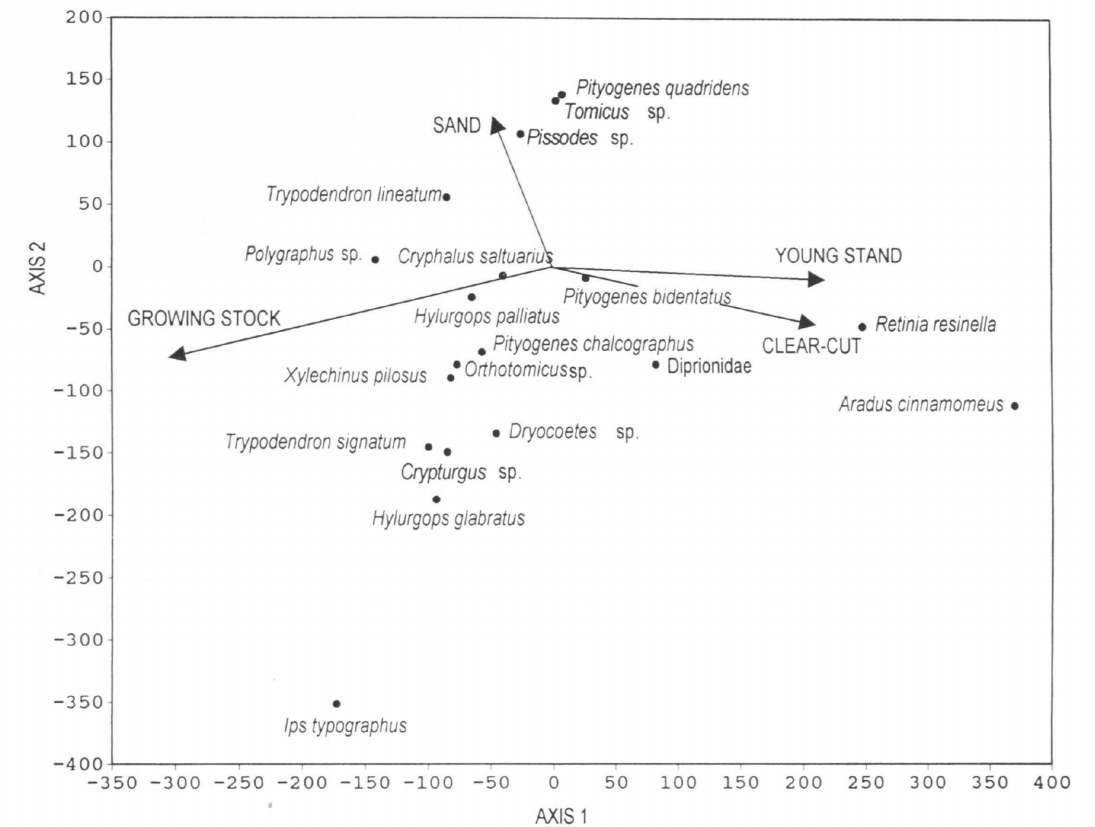


Figure 8. Ordination diagram based on canonical correspondence analysis (CCA) of the distribution of insects in sample plots in the study area with respect to four environmental variables (arrows) of SAT data. In each variable, the t -value of canonical coefficients in absolute values is higher than 2.2. Eigenvalue for the axis 1 is 0.14 and 0.03 for the axis 2.

hills. The models were poor for *Retinia resinella* and especially for *Trypodendron lineatum* and *Pityogenes chalcographus*.

According to the FIELD models, the proportion of pine, land use class and forest site type, together with mean height and crown coverage with negative coefficients, best predicted the distribution of *Retinia resinella* (Table 6). The occurrence of ant nests was best predicted by the mean tree height, land use class and the distribution of birch (with a negative sign). The distribution of *Dryocoetes* sp. was related to the variables spruce, mean height and crown coverage of the forest. The models for *Trypodendron lineatum* and *Pityogenes chalcographus* were poor. The first two terms of the models for *Pityogenes quadridens* and *P. bidentatus* were the distribution of pine and mean height of the forest. Drained peat-

mire type. The occurrence of *Tomicus* sp. was closely associated with the distribution of pine, crown coverage, mean height and site type of forest, drained peatland and mire type, as well as edge, spruce, birch and alder (the latter four with negative signs). The distribution of *Hylurgops palliatus* was best predicted by land use class, mean height, site type and crown coverage of forest as well as the distribution of birch and forest edges with negative coefficients. The occurrence of *Dryocoetes* sp. was related to the variables spruce, mean height and crown coverage of the forest. The models for *Trypodendron lineatum* and *Pityogenes chalcographus* were poor. The first two terms of the models for *Pityogenes quadridens* and *P. bidentatus* were the distribution of pine and mean height of the forest. Drained peat-

Table 6. Constants and terms with their coefficients used in the logistic regression FIELD models of distribution of the insect species. X^2 refers to the Hosmer-Lemeshow test.

Term	<i>Retinia resinella</i>	Ant hills	<i>Pissodes</i> sp.	<i>Xylechinus pilosus</i>	<i>Tomicus</i> sp.	<i>Hylurgops palliatus</i>
Constant	-7.723	-6.533	-3.264	-10.34	8.787	-12.80
Constant/SE	-54.3	-21.3	0.00	-25.0	0.00	-53.60
Term 1	Pine	Mean height	Crown coverage	Spruce	Pine	Mean height
Coefficient	0.411	0.307	0.584	0.546	0.461	0.192
Coefficient/SE	0.00	0.00	0.00	0.00	0.00	0.00
Term 2	Mean height	Land use class	Birch	Crown coverage	Crown coverage	Birch
Coefficient	-0.711	Several	-0.443	0.625	0.732	-0.564
Coefficient/SE	0.00	0.00	0.00	0.00	0.00	0.00
Term 3	Land use class	Birch	Land use class	Mean height	Mean height	Land use class
Coefficient	Several	-0.228	Several	0.459	0.385	Several
Coefficient/SE	-2.52	0.00	0.00	0.00	0.00	0.00
Term 4	Crown coverage		Pine	Mire type	Forest site type	Forest site type
Coefficient	-0.438		0.396	Several	Several	Several
Coefficient/SE	0.00		0.00			
Term 5	Forest site type		Spruce	Edge	Crown coverage	
Coefficient	Several		0.227	-0.455	0.271	
Coefficient/SE	0.00		0.00	0.00	0.00	
Term 6			Edge	Drained peatland	Edge	
Coefficient			-0.507	Several	-0.614	
Coefficient/SE			0.00		0.00	
Term 7			Alder	Mire type		
Coefficient			-5.001	Several		
Coefficient/SE			0.27			
Term 8			Aspen	Spruce		
Coefficient			-0.737	-0.440		
Coefficient/SE			0.00	0.00		
Term 9				Birch		
Coefficient				-0.416		
Coefficient/SE				0.00		
Term 10				Alder		
Coefficient				-5.565		
Coefficient/SE				-1.92		
X^2 value	11.47	7.23	6.20	9.80	5.80	9.69
p	0.18	0.51	0.63	0.28	0.67	0.29

Term	<i>Dryocoetes</i> sp.	<i>Trypodendron lineatum</i>	<i>Pityogenes chalcographus</i>	<i>Pityogenes quadridens</i>	<i>Pityogenes bidentatus</i>
Constant	-6.975	-6.930	-4.918	-5.130	-6.889
Constant/SE	-15.10	14.90	-23.00	-7.66	0.00
Term 1	Spruce	Mean height	Mean height	Pine	Pine
Coefficient	0.557	0.259	0.353	0.557	0.659
Coefficient/SE	8.08	0.00	0.00	5.51	0.00
Term 2	Mean height	Land use class	Land use class	Mean height	Mean height
Coefficient	0.518	Several	Several	0.675	0.694
Coefficient/SE	5.03	0.00	0.00	7.13	7.55
Term 3	Crown coverage	Birch	Forest type	Drained peatland	Birch
Coefficient	0.415	-0.494	Several	Several	0.443
Coefficient/SE	4.39	-3.74	0.00	0.00	0.00
Term 4		Spruce	Birch	Spruce	Forest site type
Coefficient		0.146	-0.612	-0.353	Several
Coefficient/SE		0.00	0.00	-2.40	
Term 5		Crown coverage	Pine	Crown coverage	Edge
Coefficient		0.194	-0.343	-0.261	0.472
Coefficient/SE		0.00	0.00	-2.06	0.00
Term 6			Alder		Crown coverage
Coefficient			-0.539		-0.250
Coefficient/SE			0.00		0.00
Term 7			Crown coverage		Drained peatland
Coefficient			0.149		Several
Coefficient/SE			0.00		
Term 8					
Coefficient					
Coefficient/SE					
Term 9					
Coefficient					
Coefficient/SE					
Term 10					
Coefficient					
Coefficient/SE					
X^2 value	10.83	14.71	16.25	5.92	7.26
p	0.21	0.07	0.04	0.66	0.51

Table 7. Constants and terms with their coefficients used in the logistic regression SAT models of distribution of the insect species. X^2 refers to Hosmer-Lemeshow test.

Term	<i>Retinia resinella</i>	Ant hills	<i>Pissodes</i> sp.	<i>Xylechinus pilosus</i>	<i>Tomicus</i> sp.	<i>Hylurgops palliatus</i>
Constant	-9.906	-2.568	-13.94	-6.190	-2.613	-9.152
Constant/SE	0.00	-6.25	0.00	-8.47	-5.71	0.00
Term 1	Spruce forest	Growing stock	Deciduous forest	Growing stock	Esker	Growing stock
Coefficient	-0.470	0.219	-1.251	0.475	0.581	0.408
Coefficient/SE	-3.35	4.33	-4.25	5.65	7.55	7.62
Term 2	Sand	Bedrock	Water	Esker	Pine bog	Pine forest
Coefficient	-1.645	0.271	-4.538	-1.018	1.485	-0.720
Coefficient/SE	-4.54	2.94	0.00	-2.79	9.02	-3.03
Term 3	Clear-cut	Ablation moraine	Silt	Conifer swamp	Mixed forest	Deciduous forest
Coefficient	0.271	0.417	-3.897	0.594	0.720	-0.604
Coefficient/SE	2.22	3.10	-6.48	3.53	7.55	-2.32
Term 4	Silt	Clear cut	Open field	Pine forest	Pine forest	Silt
Coefficient	-4.954	0.325	-1.282	-0.729	0.759	-5.411
Coefficient/SE	-7.29	1.88	-3.57	-1.42	5.98	-9.80
Term 5	Ground moraine	Open field	Clear cut		Conifer swamp	Pine bog
Coefficient	-0.367	-0.526	-0.871		0.774	0.559
Coefficient/SE	-4.84	-1.42	-4.09		5.38	3.22
Term 6	Water		Young stand		Silt	Conifer swamp
Coefficient	-1.164		-0.779		-5.535	0.481
Coefficient/SE	-4.34		-4.19		0.00	3.20
Term 7	Conifer swamp		Birch swamp		Birch swamp	Ablation moraine
Coefficient	-0.859		-0.435		0.697	0.383
Coefficient/SE	-4.22		-1.97		3.65	2.32
Term 8	Growing stock		Ablation moraine		Ablation moraine	Moraine
Coefficient	-0.295		0.233		0.307	0.203
Coefficient/SE	-5.60		2.04		2.53	2.15
Term 9	Open field				Spruce forest	
Coefficient	-0.939				0.259	
Coefficient/SE	-3.00				2.28	
Term 10	Pine forest					
Coefficient	0.300					
Coefficient/SE	2.40					
Term 11	Peat					
Coefficient	0.435					
Coefficient/SE	2.79					
Term 12	Pine bog					
Coefficient	-0.534					
Coefficient/SE	-2.26					
X^2 value	8.37	7.05	0.083	11.72	4.02	5.95
p	0.40	0.53	0.99	0.16	0.86	0.65

Term	<i>Dryocoetes</i> sp.	<i>Trypodendron lineatum</i>	<i>Pityogenes chalcographus</i>	<i>Pityogenes quadridens</i>	<i>Pityogenes bidentatus</i>
Constant	-12.67	-19.53	-4.259	-5.902	-0.234
Constant/SE	-17.60	0.00	-5.21	-19.90	-0.632
Term 1	Spruce forest	Growing stock	Spruce forest	Pine bog	Esker
Coefficient	0.695	0.271	0.641	1.298	0.783
Coefficient/SE	4.53	3.82	5.26	7.39	6.44
Term 2	Sand	Esker	Growing stock	Esker	Pine bog
Coefficient	-5.515	-0.313	0.253	0.499	0.904
Coefficient/SE	0.00	-2.41	4.74	4.23	4.30
Term 3	Pine forest	Water	Pine forest	Open field	Conifer swamp
Coefficient	-1.131	-5.0096	-0.584	-4.5832	0.652
Coefficient/SE	-2.17	0.00	-2.49	0.00	3.49
Term 4	Growing stock	Clear cut	Sand	Exposed bedrock	Ablation moraine
Coefficient	0.187	-4.108	-0.435	-0.381	0.616
Coefficient/SE	2.82	0.00	-2.24	-2.01	3.30
Term 5	Silt	Open field	Silt	Sand	Pine forest
Coefficient	-4.375	-4.207	-0.992	0.378	0.324
Coefficient/SE	0.00	0.00	-1.90	1.97	2.27
Term 6	Spruce swamp	Silt	Water		
Coefficient	-0.605	-4.070	-0.615		
Coefficient/SE	2.82	0.00	-1.64		
Term 7	Mixed forest	Conifer swamp	Mixed forest		
Coefficient	0.312	0.672	0.285		
Coefficient/SE	2.30	3.68	2.70		
Term 8	Ablation moraine	Spruce forest	Conifer swamp		
Coefficient	0.268	0.496	0.492		
Coefficient/SE	1.81	3.29	3.25		
Term 9		Mixed forest	Moraine		
Coefficient		0.396	0.126		
Coefficient/SE		2.81	1.73		
Term 10		Pine bog			
Coefficient		0.542			
Coefficient/SE		2.41			
Term 11					
Coefficient					
Coefficient/SE					
Term 12					
Coefficient					
Coefficient/SE					
X^2 value	12.25	15.74	7.58	2.02	2.72
p	0.14	0.05	0.48	0.85	0.74

Table 8. Mean values for predicted probabilities of insect taxa in the sample plots according to the logistic regression FIELD models. Predicted probabilities for presence (P_{pred}) are given for the sample plots where species were observed to be present ($P_{\text{obs}} = 1$) or absent ($P_{\text{obs}} = 0$).

Insect taxon	$P_{\text{pred}}(P_{\text{obs}} = 0)$		$P_{\text{pred}}(P_{\text{obs}} = 1)$	
	Mean	SD	Mean	SD
<i>Retinia resinella</i>	0.050	0.096	0.442	0.231
Number of ant hills	0.026	0.033	0.159	0.057
<i>Pissodes</i> sp.	0.059	0.091	0.305	0.125
<i>Xylechinus pilosus</i>	0.014	0.032	0.136	0.088
<i>Tomicus</i> sp.	0.089	0.128	0.512	0.262
<i>Hylurgops palliatus</i>	0.044	0.051	0.181	0.085
<i>Dryocoetes</i> sp.	0.032	0.046	0.275	0.141
<i>Trypodendron lineatum</i>	0.052	0.056	0.162	0.109
<i>Pityogenes chalcographus</i>	0.079	0.091	0.342	0.153
<i>Pityogenes quadridens</i>	0.033	0.056	0.226	0.178
<i>Pityogenes bidentatus</i>	0.038	0.067	0.207	0.165

Table 9. Mean values for predicted probabilities of insect taxa in the sample plots according to the logistic regression SAT models. Predicted probabilities for presence (P_{pred}) are given for the sample plots where species were observed to be present ($P_{\text{obs}} = 1$) or absent ($P_{\text{obs}} = 0$).

Insect taxon	$P_{\text{pred}}(P_{\text{obs}} = 0)$		$P_{\text{pred}}(P_{\text{obs}} = 1)$	
	Mean	SD	Mean	SD
<i>Retinia resinella</i>	0.038	0.085	0.289	0.145
Number of ant hills	0.041	0.050	0.139	0.051
<i>Pissodes</i> sp.	0.043	0.077	0.241	0.184
<i>Xylechinus pilosus</i>	0.006	0.005	0.087	0.060
<i>Tomicus</i> sp.	0.013	0.003	0.165	0.087
<i>Dryocoetes</i> sp.	0.009	0.016	0.180	0.092
<i>Trypodendron lineatum</i>	0.007	0.018	0.148	0.082
<i>Pityogenes chalcographus</i>	0.033	0.050	0.275	0.133
<i>Pityogenes quadridens</i>	0.000	0.000	0.112	0.106
<i>Pityogenes bidentatus</i>	0.000	0.000	0.109	0.060

land and crown coverage contributed to both models, spruce to that for *P. quadridens*, and birch, forest site type and edge to that for *P. bidentatus*.

The mean values for the predicted FIELD probabilities of the occurrence of different species varied from 0.14 (*Xylechinus pilosus*) to 0.44 (*Retinia resinella*) and 0.51 (*Tomicus* sp.) in the sample plots occupied by insect taxa (Table 8).

The SAT models were good for *Tomicus* sp., *Pityogenes quadridens* and *P. bidentatus* and especially for *Pissodes* sp. The worst model predic-

tions were for the distribution of *Xylechinus pilosus*, *Dryocoetes* sp. and *Trypodendron lineatum* (Table 7).

The predicted distributions of the insect taxa in the study area are given in Fig. 9 on maps based on the logistic regression models of the SAT data (see Tables 8 and 9). The 12-term-model including clear-cut, pine forest and peat with positive coefficients moderately predicted the distribution of *Retinia resinella* (Table 7). The models gave the highest probabilities for *Retinia resinella* to

Table 10. The percentage of correctly classified sample plots (hit %) of the logistic FIELD and SAT models. N = the observed number of occupied sample plots.

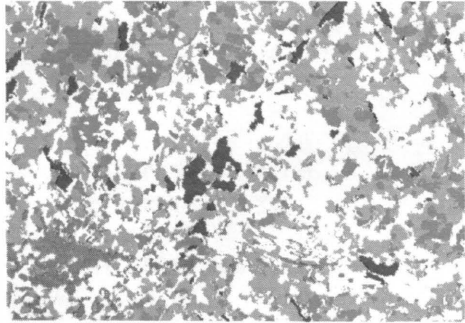
Insect taxon	FIELD		SAT		N
	Cutpoint	Hit %	Cutpoint	Hit %	
<i>Retinia resinella</i>	0.225	80.56	0.208	70.78	312
Number of ant hills	0.125	62.06	0.125	68.39	209
<i>Pissodes</i> sp.	0.225	71.11	0.242	47.89	333
<i>Xylechinus pilosus</i>	0.058	78.17	0.058	65.89	73
<i>Tomicus</i> sp.	0.225	81.33	0.225	60.33	383
<i>Hylurgops palliatus</i>	0.142	70.17	0.125	70.89	183
<i>Dryocoetes</i> sp.	0.125	77.61	0.108	65.83	187
<i>Trypodendron lineatum</i>	0.092	64.28	0.108	65.83	165
<i>Pityogenes chalcographus</i>	0.225	75.67	0.175	69.50	314
<i>Pityogenes quadridens</i>	0.058	76.61	0.092	69.30	107
<i>Pityogenes bidentatus</i>	0.075	80.17	0.092	69.33	114
Mean		74.34		65.81	

occur in relatively large areas in the northwest and eastern parts, and the lowest probabilities in the central parts of the study area. Models for ant nests, with a relatively low probability, included growing stock, exposed bedrock, ablation moraine and clear-cut, suggesting a very patchy distribution (Fig. 9). The occurrence of *Pissodes* sp. was positively associated only with ablation moraine and negatively with deciduous forest, water, silt, open field, clear-cut, young stand and birch swamp. The model for *Xylechinus pilosus* was relatively poor. The largest areas with the highest probability were concentrated in the northeast parts of the study area. The distribution of *Tomicus* sp. was best predicted by a model consisting of ten terms including esker, pine bog, mixed forest, pine forest, conifer swamp, silt (negative sign), birch swamp, ablation moraine and spruce forest. According to the models, these beetles were clearly concentrated in the central parts of the study area. The distribution of *Hylurgops palliatus* was associated with growing stock, pine bog, conifer swamp, ablation moraine and moraine with positive coefficients, and pine and deciduous forest and silt with negative coefficients. The occurrence of *Dryocoetes* sp. was positively associated with spruce and mixed forest, growing stock and ablation moraine. The distribution of *Trypodendron lineatum* was predicted to some degree by growing stock, conifer swamp, spruce and mixed for-

est and pine bog. The predicted distribution of this species was very patchy without any clear pattern in the study area. The best predictors for *Pityogenes chalcographus* were spruce forest and growing stock, but seven other variables contributed to the model. The predicted distributions for *H. palliatus*, *Dryocoetes* sp. and *P. chalcographus* were rather similar, suggesting the highest probabilities of occurrence for the western, northeastern and southern parts of the study area. The best predictors for *P. quadridens* and *P. bidentatus* included pine bog and esker. Sand (positive sign) and open field and exposed bedrock (negative sign) contributed to the model for *P. quadridens*. Conifer swamp, ablation moraine, and pine forest (positive sign) contributed to the model for *P. bidentatus*, which indicated a more or less continuous distribution in the central parts of the study area.

The mean values of predicted SAT probabilities for the occurrence of different insect species varied from 0.09 (*Xylechinus pilosus*) to 0.29 (*Retinia resinella*, *Pityogenes chalcographus*) and 0.32 (*Tomicus* sp.) in the sample plots occupied by the insect taxa (Table 9).

According to the FIELD models, the percentage of correctly classified sample plots varied from 62.1 % (number of ant hills) to 81.3 % (*Tomicus* sp.) (Table 10). According to the SAT models, the percentage varied from 47.9 % (*Pissodes* sp.)

Retinia resinella

Ant hills

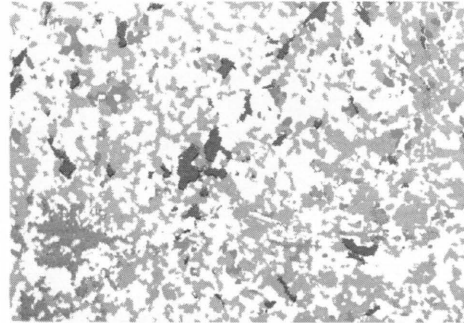
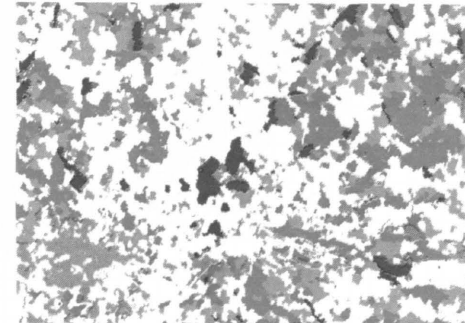
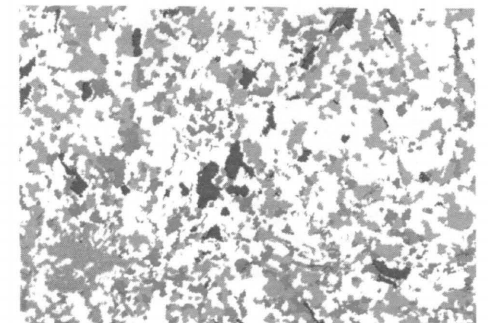
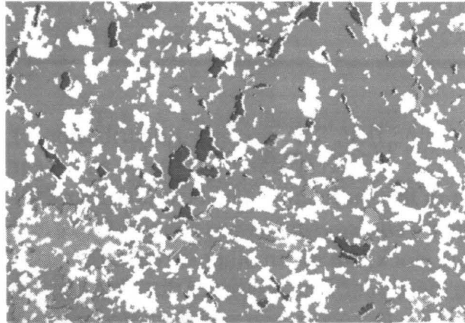
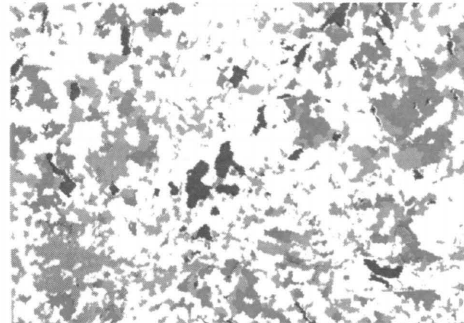
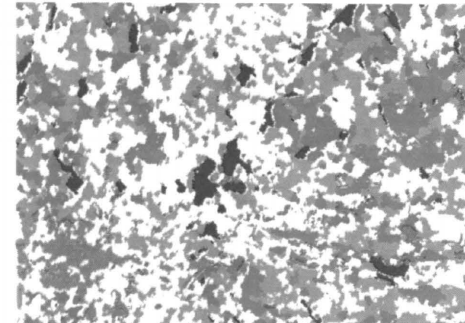
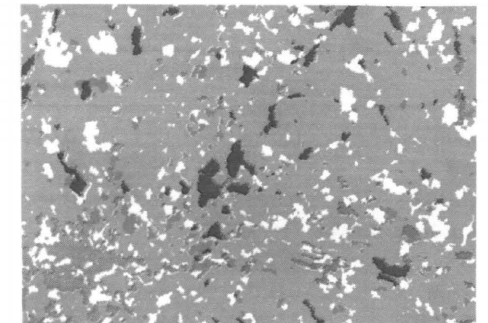
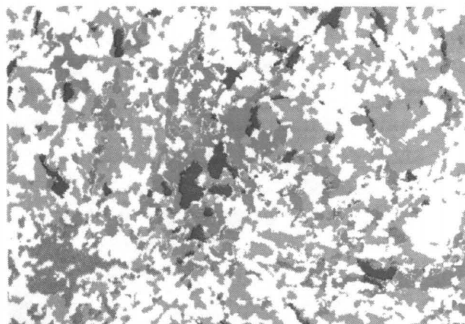
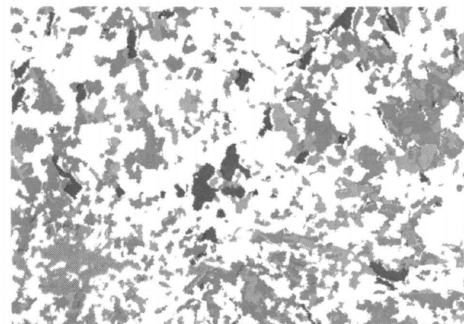
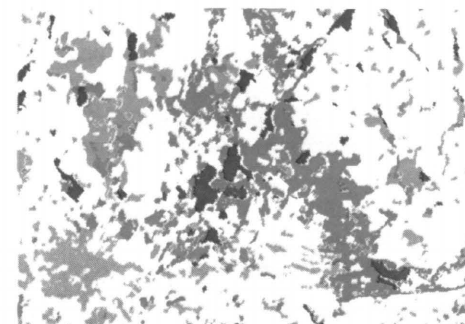
*Drycoetes* sp.*Trypodendron lineatum**Pissodes* sp.*Xylechinus pilosus**Pityogenes chalcographus**Pityogenes quadridens**Tomicus* sp.*Hylurgops palliatus**Pityogenes bidentatus*

Figure 9. The predicted distribution of the insect taxa in the study area based on the SAT models. The maps show the sample plots with the predicted probability of occurrence higher than the mean observed probability for occupied sample plots (red), and that minus 1 SD (orange). Lakes are indicated by blue and open fields by grey.

Table 11. Size and number of habitat compartments according to vegetation type and land use class.

Type	Compartment size, km ²			Number of compartments	Number of sample plots
	Min.	Max.	Mean		
Clear-cut etc.	0.005	1.093	0.389	41	220
Open mire	0.005	0.010	0.008	2	2
Conifer swamp	0.005	0.278	0.083	35	102
Birch swamp	0.008	0.105	0.037	20	47
Pine bog	0.010	0.113	0.043	13	36
Pine forest	0.002	1.458	0.657	18	121
Spruce forest	0.010	5.003	0.994	51	347
Deciduous forest	0.008	0.250	0.093	31	109
Mixed forest	0.008	5.345	1.554	56	570

Table 12. Size and number of habitat compartments according to the growing stock volume.

Type	Compartment size, km ²			Number of compartments	Number of sample plots
	Min.	Max.	Mean		
Open mire	0.010	0.023	0.019	2	4
Clear-cut	0.008	0.335	0.145	22	108
Young stand	0.010	0.785	0.182	26	114
Growing stock, m ³ /ha					
<50	0.008	0.386	0.178	46	225
51–100	0.010	0.386	0.128	31	152
101–150	0.005	0.483	0.113	49	161
151–200	0.003	1.890	0.662	65	522
>200	0.008	3.168	0.394	52	260

to 70.9% (*Hylurgops palliatus*). The overall mean percentage of correctly classified sample plots was higher for the FIELD (74.3%) than for the SAT data (65.8%) (Table 10). Both methods gave similar hit percentages for *Hylurgops palliatus* and *Trypodendron lineatum*. Only in the case of the number of ant hills was the hit percentage higher for the SAT than for the FIELD data.

3.4 Forest Fragmentation

The size of habitat compartments was calculated from the satellite images for the whole Evo forest area covering about 100 km². The number of habitat compartments varied from two open mire areas to 56 areas of mixed forest, where most of the sample plots (579) were located according to

the classification based on vegetation types and land use classes. The largest habitat compartment covered 5.3 km² of mixed forest (Table 11). In the classification based on growing stock, both the number of compartments (65) and the number of sample plots (522) were the highest in the tree volume category of 151–200 m³/ha (Table 12; the inconsistencies in the number and size of habitat compartments between Tables 11 and 12 are due to differences in original interpretation of remotely sensed data). The area of the largest compartments varied from 0.023 km² (open mire) to 3.2 km² (growing stock >200 m³/ha). In general, the number of insect species recorded was the highest in spruce forests and the lowest in pine forests (Fig 10 A). There was much variation and only slight tendencies in the number of insect species recorded in relation to

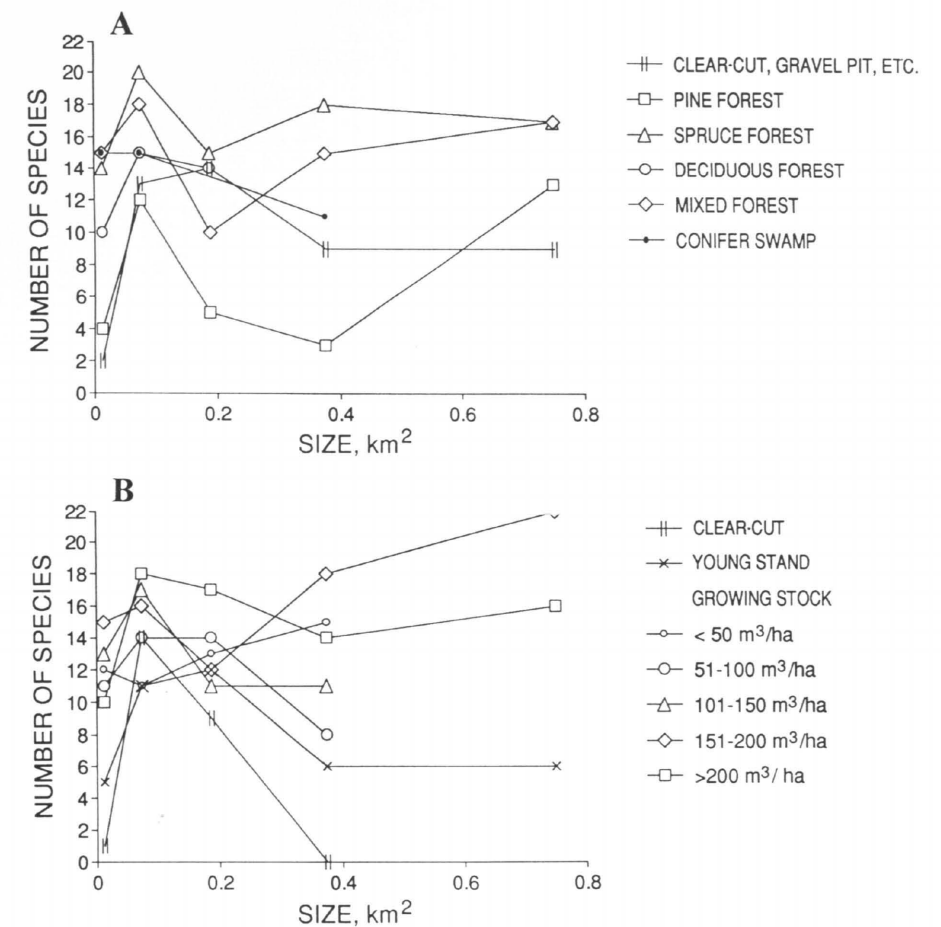


Figure 10. Number of insect species per sample plot in relation to the size of habitat compartment according to vegetation type and land use class (A) and tree volume category (B) interpreted from the SAT data.

the compartment size. However, the lowest number of insect species was usually recorded in the smallest compartments, and the highest number of species in the second smallest ones (mean 0.1 km²). This slight tendency can also be observed in different tree volume categories excluding the categories of less than 50 and 151–200 m³/ha (Fig. 10 B).

The number of insect species seemed to be the higher, the closer to the edge of the compartment the sample plot was located in each vegetation type and tree volume class (Fig 11 A and B). At the edge of the compartment, the number of species was 1.2 to 13 times higher than at 250 meters from the edge. This tendency was most evident

for clear-cut areas, young stands and mixed forests. Both the compartment size and the distance from the forest edge were added as predictor variables in the logistic regression models. However, these variables improved the fit of the species data only in the cases of *Retinia resinella* and *Xylechinus pilosus* (patch size), *Pityogenes chalcographus* (distance from the forest edge) and *Dryocoetes* sp. (both variables). Even in these cases the variables represented the last or second last steps in the models, indicating that in general other environmental variables masked the effect of compartment size and distance from the edge in species occurrence.

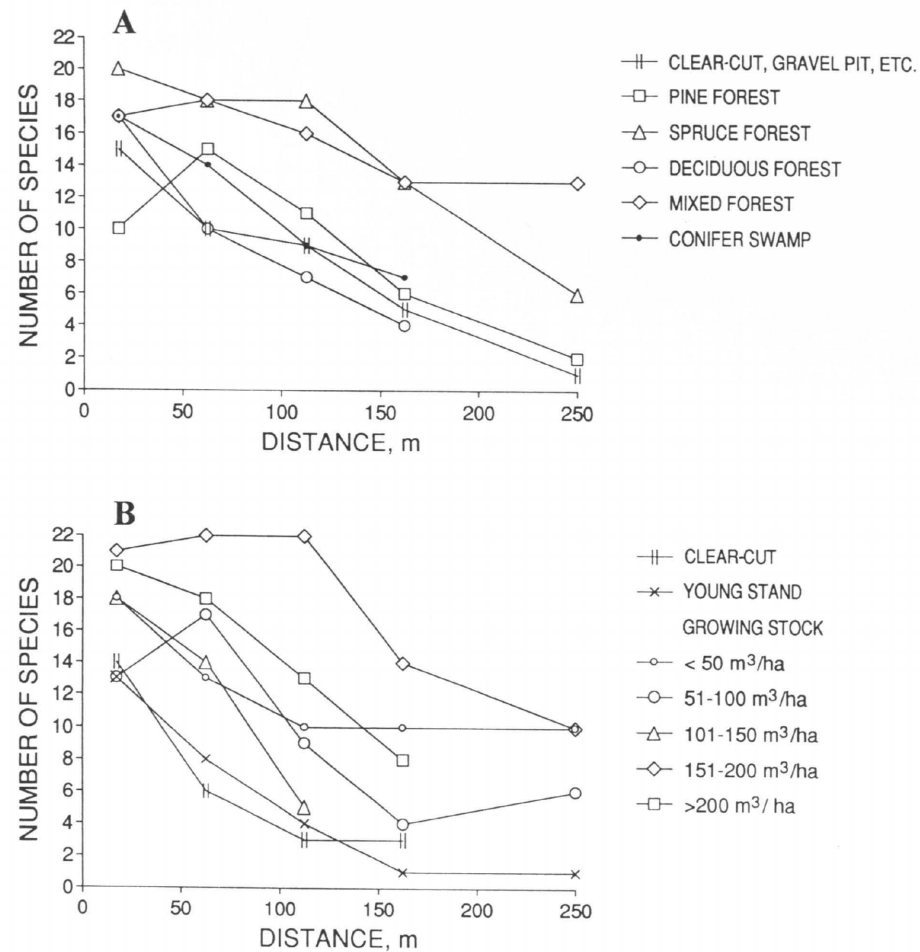


Figure 11. Number of insect species per sample plot in relation to the distance from the nearest edge of the habitat compartment according to vegetation type and land use classes (A) and tree volume category (B) interpreted from the SAT data.

4 Discussion

4.1 Classification and Grouping of Sample Plots

In quantitative biogeography, multivariate analysis techniques such as canonical correspondence analysis (CCA), have been developed to relate community composition directly to the known variation in the environment (Ter Braak 1986). Two-way indicator species analysis (TWINSPAN) can be used to classify insect communities (e.g. Eyre & Foster 1989). These methods can reveal patterns in species assemblages that are impossible to recognize when the sequential single species approach is used (e.g. Väisänen et al. 1992).

In this study a two-way indicator species analysis based on insect presence/absence data produced eight sample plot groups. Though the FIELD and SAT data were largely independent, the sample plot groups showed similar tendencies as regards habitat characteristics irrespective of the method. When FIELD variables were used, the first two groups were characterized by a relatively high proportion of spruce-dominated and spruce-birch mixed forests of the *Myrtillus* and *Oxalis-myrtillus* site type. This classification was also clearly visible when using SAT data. The third group was mainly characterized by pine-dominated forests of the *Vaccinium* site type in the FIELD measurements. This was also true for the SAT analyses, but the high proportion of mixed forests may represent misclassification of different forest types. The fourth sample plot group was otherwise similar to the first two groups, but the proportion of peatlands dominated by *Vaccinium myrtillus* is higher. This was reflected in the high proportion of conifer swamps in the SAT data. The next two groups (5 and 6) were characterized by relatively short and sparse pine and mixed forests of the *Vaccinium* and *Myrtillus* site type. A similar forest type classification, high proportion of clear-cut areas and young stands as well as a

relatively low growing stock volume were also readily seen in the SAT classification. The small groups 7 and 8 were characterized by continuous pine forests with some birch mixture, and were classified similarly as pine and mixed forests growing on eskers on the basis of the SAT data.

4.2 Environmental Variables and Insect Occurrence

Insect species distributions are limited by both abiotic factors such as temperature and precipitation, and biotic factors such as predation and competition (for reviews, see Taylor 1984, Gaston 1990). The distribution of bark beetles is determined largely by the distribution and abundance of their host tree species and breeding material and climate (Rudinsky 1962, Lekander et al. 1977, Coulson 1979). In addition, most bark beetles are very sensitive to the size, age and resistance of the host tree, and the site conditions and previous forest management.

Forest insects reproducing in dead or dying trees must be able to detect and locate suitable breeding substrate, which generally occurs sporadically and is usually scarce (Lindelöw et al. 1992). Most bark beetle species live only in recently cut or injured tissues of woody plants that are in the process of dying (Wood 1982). Scolytids are the first pioneer group of insects exploiting dead wood. Human activities, especially forest management, shape the distribution of forest insect species. It has been shown that thinning and clear-cutting increase bark beetle numbers. Heavy forest fellings, which removed a half of the original trees, almost doubled the population densities of bark beetles and *Pissodes* spp. in a forested area (Nuorteva 1968). Silvicultural practices create a fragmented forest area with relatively small compartments in several successional stages. It is likely that forest management has changed the between-

species competition and species assemblages of bark beetles (Heliövaara et al. 1991). Increased amounts of stumps and logging waste have benefited certain species, while the removal of dead wood has decreased some other species. In small areas, a peak in scolytid diversity would occur relatively early following any form of a silvicultural practice.

In a previous study on the biogeographical patterns of the Scolytidae in northern Europe, temperature variables associated with the locality of the study sample plot (latitude, longitude) were the most important determinants of the biogeographical variation, but annual precipitation and the distribution of *Picea abies* also contributed to the fit of the model (Heliövaara et al. 1991). In the present study on a much smaller geographical scale, tree species was the first term entering the FIELD models for those insect species associated with one tree species only (pine for *Retinia resinella*, *Tomicus* sp., *Pityogenes quadridens* and *P. bidentatus*, spruce for *Xylechinus pilosus*, and *Dryocoetes* sp.). The only exception was spruce-associated *Pityogenes chalcographus*, in which the mean height of the forest was the first variable.

Closer examination of the maps of predicted distributions based on SAT data revealed very different patterns for different species. These emerging predicted distributions showed specific features even for monophagous species associated with Scots pine. *Retinia resinella* seemed to be associated with pine stands of low tree volume growing on ground moraine. The models gave low probabilities of occurrence in high-density stands, mostly dominated by spruce, and unexpectedly also in stands growing on eskers. *R. resinella* is known to occur abundantly in sunny, dry upland forests (Väisänen and Heliövaara 1991), but the species is associated with a rather short period of early forest succession. The SAT data suggested a relatively high growing stock volume on the eskers. It is likely that these stands have already passed the most favourable phase of succession for attack of this moth. This was also supported by the fact that the highest predicted probabilities of the occurrence of *Tomicus* sp. were concentrated on pine-dominated eskers. These beetles colonize fresh timber or wind-thrown or otherwise severely weakened pines with a preference for large diameter trunks with a rough bark structure (Långström

1983, Schroeder 1987, Schlyter and Löfqvist 1990), but adults also attack the shoots of pole-stage trees (Långström and Hellqvist 1990) characterizing the present esker area. The predicted occurrence of *Pityogenes bidentatus* was similar to that of *Tomicus* sp., but this species was even more clearly restricted to the esker area. Both *Pityogenes* species associated with pine characteristically infest trees of small diameter. *P. bidentatus* lives under the thin bark of pines, especially in the branches and crowns of felled pines, but is usually less abundant than *P. quadridens* (Saalas 1949). The closely related *P. quadridens* has a similar life style. It is the most abundant scolytid species in the crowns and branches of felled pines in Finland (Saalas 1949). The models suggested that the highest probabilities of the occurrence of *P. quadridens* were restricted to pine bogs.

The logistic regression models less accurately predicted the distributions of insect species associated with spruce than those associated with pine, as indicated by the generally lower p values in Table 7. *Xylechinus pilosus* is a late-swarving scolytid which breeds in dominated, slowly growing or recently died young spruces (Postner 1974). After forest cuttings, the proportional number of *X. pilosus* has been observed to increase (Nuorteva 1968). Though the fit of the model, ignoring the distribution of spruce as a variable, was relatively poor for *Xylechinus pilosus*, the predicted distribution of this species was clearly restricted to spruce dominated areas around the esker zone lying in the middle of the study area. This tendency was even more evident for *Dryocoetes* sp., another taxon associated with spruce. These species prefer stumps and the lower parts of spruce trunks growing in moist conditions (Saalas 1949) which are characterized by high growing stock volume in the satellite images. The predicted distribution of *Pityogenes chalcographus* is otherwise similar but more patchy. This species lives mainly under the thin bark of both standing and fallen spruces most severely attacking those trees with a deficient water supply (Merker and Müller 1951), but it can occasionally also breed on other conifers (Saalas 1949). For example, it was found in the pine stands on the esker area. *P. chalcographus* is the most frequent species as measured by the surface covered by the galleries in an untouched forest area in Finland (Nuorteva 1956).

Of the present insect taxa examined, *Pissodes* sp., *Hylurgops palliatus* and *Trypodendron lineatum* live on both pine and spruce. According to the logistic regression models, the predicted occurrence of *Pissodes* weevils covered almost the whole study area excluding clear cut areas and deciduous forests. This is explained by the fact that the taxon *Pissodes* sp. contains several species whose larvae live under the bark of fallen trees and whose adults feed on small conifer saplings. *Hylurgops palliatus* and *T. lineatum* are generally found in somewhat aged substrate (Sjödin et al. 1989). The distribution of *H. palliatus* was clearly restricted to areas with high growing stock volumes. *Trypodendron lineatum* is polyphagous, feeding on many species of conifers. In virgin forests, the species lives at the base of standing trees that have just died, or in fallen trees (Annala et al. 1972). The model, which is poor as indicated by a low p value, predicted a very patchy distribution for *T. lineatum*.

The present models produced a very patchy distribution for ant hills. The highest probabilities were associated with high growing stock in spruce or mixed forests, and clear cut areas. The long-lasting ant societies are bound to their nest sites and foraging areas and are susceptible to environmental disturbances such as forest fires and silvicultural practices. The societies of most ants are dependent on the vegetation structure as well as the physical conditions (temperature, moisture, etc.) of the soil. The most abundant ant species of mature taiga forest benefit from the changes in microclimate caused by clear cutting, but wood-ants (*Formica* spp.) especially prevail in later successional stages of forest (Punttila et al. 1991). According to Wuorenrinne (1974), *Formica* ants prefer 40 to 80-year-old mixed forests of spruce, pine and birch, but avoid pure one-tree species forests.

4.3 Field Measurements vs. Satellite Image Data

There was more variation in the first variables, and the number of variables in the SAT models was higher. Although the fit of the SAT models was generally better, there were striking differences among the species. In the case of *Pityo-*

genes chalcographus, *Retinia resinella* and *Hylurgops palliatus* the fit of the SAT models was much better than the fit of the FIELD models, but in the case of *Xylechinus pilosus*, and *Dryocoetes* sp. the opposite was true. Both procedures produced relatively good models for *Pissodes* sp., *Tomicus* sp., *Pityogenes quadridens* and even for *P. bidentatus*, but both failed especially in the case of *Trypodendron lineatum*.

The maximum percentage of correctly classified sample plots exceeded 80 % in three insect taxa associated with pine (*Retinia resinella*, *Tomicus* sp., *Pityogenes bidentatus*) in the FIELD models. The maximum percentage of correctly classified sample plots was 5–23 % lower (overall mean 65.81 vs. 74.34 %) for any insect taxa when the SAT variables were used, but for the number of ant hills, *Hylurgops palliatus* and *Trypodendron lineatum*, it was similar or slightly higher. The discrepancy between the fit of the FIELD and SAT models and hit percentages may appear unexpected but they are measures of different dimensions. While p values are measures of the concordance and dependent on the selection of cutpoints, hit percentages are associated with the success of classification.

4.4 Forest Fragmentation

Stand dynamics and the population dynamics of forest insects are highly interrelated. The present results show that the size and shape of habitat compartments in the forest landscape also affected insect occurrence. The smaller the size of the fragments, the higher is the proportion of forest edges out of the total forest area. The number of insect species had a peaked distribution in relation to compartment size. More interestingly, the number of insect species was the higher the closer to the compartment edge the sample plot was located. This is understandable, since most scolytids are associated with fallen and wind-damaged trees. Wind-induced forest damage is most frequent at stand-edge conditions around clear cut areas (Peltola et al. 1993). The microclimate of edges also differs from that of forest interiors. In a forest edge of deciduous trees in Eastern United States, significant edge effects were detected in light, temperature, litter

moisture, vapour pressure deficit, humidity and shrub cover, in some cases reaching up to 50 meters from the edge (Matlack 1993).

There is relatively little information about the effect of forest edge on invertebrates. Forest edges may reflect predator-parasite abundance or disruption of pheromone communication. Trees growing close to the edges experience differing exposure and edaphic factors, affecting tree physiology and phenology and altering insect survival (Schowalter et al. 1986). Comparisons among subplots within natural stands of *Pinus radiata* in California indicated that insect communities on the edges of the stands contained more species at higher population densities than in the middle of the stands (Ohmart and Voigt 1981). Especially herbivorous insects and predators were attracted to the edges of stands where floral and structural diversity was greatest. Shade has been shown to be an important factor influencing the numbers of butterflies (Warren 1985, Greatorex-Davies et al. 1993), as well as Heteroptera, Chrysomelidae and Curculionidae (Greatorex-Davies et al. 1994) frequenting woodland rides. Schlyter and Lundgren (1993) suggested that higher scolytid numbers outside old growth forest reserves were associated with a higher sustained level of available breeding material in managed forests as a result wind-falls at newly exposed forest edges, logging slash and log piles. Higher temperatures in thinned stands and along felled area edges may have also accelerated the reproduction by the bark beetles. Helle and Muona (1985) observed that Coleoptera in general preferred edges on both sides of the forest edge between clear-fellings and mature forests in northern Finland.

In the present study, the habitat compartments appear larger in the satellite images than they are in the field, and do not represent actual stand compartments in terms of silviculture. This is due to the fact that some variables have been lumped together resulting in one habitat compartment in the satellite images. For instance, clear-cut areas cover both old and new clear-cut areas, and spruce forests cover three different successional stages of spruce forests. In addition, habitat edges have been combined with the habitats in some cases (smoothing). Consequently, the effect of the habitat edge and forest fragmentation on forest insects deserves more detailed investigations.

4.5 Applicability of the Method

Modern statistical methods and remote sensing techniques provide tools for assessing the distribution of insect diversity in forests (Liebhold et al. 1993, Riley 1993). The special benefits of images from natural resources satellites are that they regularly contain full coverage data from a wide area, they contain information invisible to the human eye, they are in digital format, and their price per unit is low. Spectral characteristics of environmental variables (land use patterns, tree species, growing stock, soil types) and even rapid changes in these characteristics can be studied, for instance, through the analysis of satellite scanner images. The value of the interpretation is that field work is only checking instead of total inventory and that the whole area does not need to be checked (Häme 1991).

Logistic regression models are useful for evaluating the impacts of different variables on insect occurrence, and even for developing a pest hazard rating forecasting system for larger areas. Unless most of the probabilities of a set of data are very small or very large, or the fit of the model is extremely poor in an identifiable systematic manner, it is unlikely that any alternative model will provide a better fit (Hosmer & Lemeshow 1989). Applications of the model of insect occurrence are sufficiently flexible for frequent updating in response to changes in environmental conditions. The fit of models would benefit from the addition of new environmental variables (e.g. topography, exposition) already available in GIS databases. Combination of variables associated with silvicultural practices (timing of felling, amount of logging waste, forest road network etc.) and insect behaviour (e.g. dispersal capability) would be likely to improve the models. Although current GIS technology may have a few limitations in operational situations, computer based GIS has been proven to be an invaluable tool for resource managers by providing flexible spatial data handling capabilities (Lee 1989). The capabilities of conventional GIS can also be enhanced by incorporating artificial intelligence techniques (Coulson et al. 1988).

The present analyses presuppose that the composition of the observed forest insect fauna of a sample plot is not affected by the neighbouring

plots. Any similarities are considered to result from habitat characteristics and independent insect attacks. The forest insects selected for the present study mostly represent species that have a good dispersal ability (Forsse and Solbreck 1985, Forsse 1989), and they are very common in the study area. In principle, the whole study area is saturated by the insects examined, partly due to intensive forest management. The distribution of the insects is mainly directly associated with the distribution and availability of breeding material in suitable habitats (Coulson and Witter 1984). Forest insects reproducing in dead or dying trees must be able to detect and localize suitable breeding substrate, which generally occurs sporadically and is usually scarce (Lindelöw et al. 1992). In an untouched forest breeding material mostly consists of snowbreaks and wind-thrown trees. This material appears in patches with a size varying from single trees, scattered throughout the forest, to less common larger patches when groups of trees or whole stands have been affected. Intensive forest management probably shifts the distribution of patch sizes towards larger patches (Forsse 1989).

In contrast to large-scale homogeneity of boreal forests small-scale heterogeneity predominates

the landscape characteristics in the scale of the present study, although both the poor resolution and the edge preserving smoothing of the remotely sensed land use data partly mask this variation. The mosaic-like landscape structure, sporadic distribution and availability of breeding material, and good dispersal ability of forest insects studied both decrease the potential effects of autocorrelation at the present scale (see Sokal and Oden 1978, Chou et al. 1993). Within a single tree, some of the forest insects are more uniformly spaced than random (Byers 1984), at least in higher densities (Saarenmaa 1983).

Though satellite-based observations have proved at best only partially effective for routine insect damage surveys, the present results show that they can be useful in analysing and predicting the distribution of insects on the basis of certain environmental variables. The present presence/absence data of several forest insect species were gathered on temporary sample plots in a fragmented forest area in southern Finland. These data did not take into account the abundances of different species. Estimating population densities presupposes more detailed and laborious faunal analyses and will make the field work much more expensive and time-consuming.

5 Conclusions

1. The results suggest that the occurrence of at least some forest insect species, especially those associated with Scots pine, can be relatively accurately assessed indirectly on the basis of habitat characteristics visible at the present spatial scale. A very high spatial resolution requires advanced contextual interpretation (Häme 1991), but the 30 x 30 m pixel size of the Landsat Thematic Mapper used in the present study seemed to be adequate in the present forest entomological study.
2. The success of the models varied between species. This may be explained by the fact that all habitat characteristics are not bound to the present measurements or site classes. Some species may be associated with the characteristics of single trees, whereas others may be associated with stand characteristics.
3. It is likely that the addition of new environmental variables to the models, as well as even a rough classification of species into different abundance categories, would improve the results of the analyses. The analyses can be repeated easily with up-to-date information.
4. Overlaying the maps of the probable occurrence of a large number of species belonging to taxonomically and ecologically diverse and representative groups of organisms, would highlight the hot-spot areas with a high degree of biodiversity at the landscape scale. Restricted to forest pests the method could show those forests with a high risk of damage.
5. The results indicate that silvicultural practices are a major force controlling the species composition of the insect groups examined at the landscape level.

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- 243 **Rauno Väisänen** and **Kari Heliövaara**: Assessment of insect occurrence in boreal forests based on satellite imagery and field measurements.
- 244 **Eero Kubin** and **Lauri Kemppainen**: Effect of soil preparation of boreal spruce forest on air and soil temperature conditions in forest regeneration areas.
Instructions to authors.
- 245 **Mykkänen, Reijo**: Aspiration-based utility functions in a planning model for timber flow management.

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