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NERI Technical Report no. 76
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Data sheet

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Finally, to those who really did all the work, we are very much indebted to the breeding birds in our study area.

Dansk resumé

Der foreligger få detaljerede undersøgelser over ynglende småfugle i kommercielt drevne skovområder. Denne rapport præsenterer resultater af en undersøgelse af skovstrukturens indflydelse på ynglefuglebestandens artssammensætning og bestandstæthed i forstligt drevne nåle- og løvtræsskove samt i semi-naturlige løvskove i Danmark.

Undersøgelsen blev udført i foråret 1992 i 9 østjydske skove, hvor det totale areal udgjorde 197,9 ha., der var fordelt på 24 forskellige skovtyper. Skovtyperne blev inddelt i 5 serier:

- En successionsserie af nåletræ med 9 skovtyper fra nyplantet gran til gammel, moden skov.
- En successionsserie af Bøg med 4 skovtyper fra ung til gammel skov.
- En serie med 4 skovtyper i naturlig løvskov med hhv. 2 unge og 2 modne skovtyper.
- En serie i fragmenteret skov med 5 skovtyper af ung og gammel nåle- og løvskov.
- En serie med skovtyper af Lærk og Vintereg.

Ynglefuglebestandene blev registreret ved hjælp af Tomialojc's kortlægningsmetode. Skovstrukturen er beskrevet ved hjælp af en modificeret version af Berkels metode, og linietransekttegninger af de enkelte skovtyper er udført.

Undersøgelsen antyder, at det er muligt at gøre forstligt drevne skove mere attraktive for ynglefugle end de er i dag. Skovfuglearterne udviser forskellig fordeling både vertikalt og horisontalt. Derfor er vegetationsstrukturen, især den vertikale variation, samt heterogeniteten i vegetationen af stor betydning for fuglebebestanden. Træartsdiversiteten havde en signifikant effekt på ynglefuglerigdommen i skovene. Tilsvarende havde mængden af dødt træ og træernes diameter en signifikant effekt på antal og tæthed af hulrugende arter.

Nåleskov har højere tæthed af ynglefugle end løvskov af samme højde, men antallet af arter er ikke signifikant forskelligt.

Fragmenteret skov, som er en mosaik af bevoksninger af nåletræer og løvfældende træer, har signifikant flere ynglende arter og højere tæthed af fugle end homogen skov af såvel Bøg som nåletræ.

Naturskov har signifikant flere ynglende arter og højere tæthed af fugle end kulturbetingede skove.

Fortolkningen af undersøgelsens resultater besværliggøres af vekselvirkningen mellem de forskellige strukturelle egenskaber i skoven. Hvor en udvikling henimod naturlige, flersidede drifts-

teknikker ønskes, vil det være tilstrækkeligt at betragte komponenter i skovstrukturen som et kompleks af variabler. For at øge ynglefuglerigdommen i skoven kan det tilstræbes at øge den gennemsnitlige trædiameter, tilstedeværelsen af dødt træ i bevoksningerne samt heterogeniteten og træartsdiversiteten i krone- og busklaget. Desuden vil skiftende bevoksninger af løv- og nåletræ forbedre skoven som biotop for fuglene.

English summary

In the new national policy plan of the Danish government, conservation of valuable biological communities in woodland is indicated as one of the purposes of forest management. The area of woods in which ecological processes will be stimulated is planned to increase considerably. We investigated the relationships between breeding birds and forest structure in order to propose measures which are assumed to lead to higher ecological diversity in woods.

Because bird-species number, bird density and bird-species diversity are generally closely correlated, we use the term breeding-bird richness as a substitute to measure the ecological value of bird communities. The theory on the structure and diversity of ecological communities predicts higher richness in structurally diverse forests.

This research showed that it is possible to design commercial forests which are even more attractive to birds than the present-day forests. Forest bird species show different distributions in vertical and horizontal space. Hence, vegetation structure, particularly number of vegetation layers and patchiness (heterogeneity), was of great significance for the bird fauna. Tree species diversity had a significant effect on bird richness in woods. The same can be said of the proportion of dead wood and the tree diameter, which were especially relevant to hole-breeding species.

The correlation of various structural properties in forests complicates the interpretation of results of this study. However, in forest management aimed at the development of natural processes it will be sufficient to consider the components of forest structure as a complex of co-varying variables. To enhance the breeding bird richness in forests, management should aim at increasing the tree diameter, the presence of dead wood and the heterogeneity and species diversity of the canopy and shrub layers. Moreover, alternating forest blocks with stands of broadleaves and conifers will improve the forest for birds.

1 Introduction

1.1 Forestry in Denmark

In the twentieth century, the progressive removal of natural and semi-natural woodlands in Denmark, as in most European countries, has been accompanied by massive tree planting schemes. Technology has enabled large forests to be created quickly, often in inhospitable areas for tree growing, and natural variations in latitude, altitude, soils and climate have not been reflected in many of these modern forests. Most of these are monocultures, which are homogeneous evenaged stands of the same tree species. Especially pine (*Pinus sp.*), Sitka Spruce (*Picea sitchensis*) and Norway Spruce (*Picea abies*) have been used, and to a lesser extent Larch (*Larix sp.*), Silver Fir (*Abies alba*) and Douglas Fir (*Pseudotsuga menziesii*). In reviewing the history of Danish forestry, it is clear that most of the increase in woodland has been for timber or christmas tree production. For the latter the use of pesticides and herbicides can be considerable. These new forests are very different from the native Danish forests wiped out by man centuries before (Nielsen 1980). However, a new policy has been agreed, and in the coming 80-100 years the area of woodlands in Denmark will be doubled (Hedegaard 1992). When planted and managed with care and foresight they should provide good habitat for an important cross section of our wildlife.

1.2 Ecological value and forestry: conflicts and resolutions

The majority of woodlands are managed within commercial constraints. Afforestation has been a major cause of conflict between conservation organisations and foresters. Attempting to obtain the highest financial return, the desire to increase the strategic reserve of timber and create employment has led to the widespread planting of conifers on low value land (where there is less competition with agriculture), such as the west of Denmark. But nowadays, as interest and care for nature is growing more and more, forest policy has begun to secure wider benefits for the public and for all living organisms, plants as well as animals, composing the ecosystem ('ecological value'). Today, for many woodlands, plans are afoot to introduce natural, multiple management techniques, focused at the ecological value of forests. Forestry can deliver a variety of benefits including wood production to sustain processing. Attention to forest design and management can significantly improve woodlands for woodland birds and other wildlife, with very little sacrifice of financial return. Before the management of forests can be focused at the ecological value, it is necessary that more is known about the relations between forest structure on the one hand, and flora and fauna on the other hand. Because birds constitute an important part of the forest ecosystem and can be observed easily, they are extremely appropriate to serve as indicators for the ecological value of the wood.

1.3 Forest breeding bird community

Few detailed studies have looked at the birds of commercial forests (e.g. Janse & Kessler 1981, Komdeur & Vestjens 1982, 1983, Opdam & Bladeren 1981, Opdam & Schotman 1986, Vestjens 1984). This study discusses the general principles which lie behind bird distribution in woodland habitats. A thorough understanding of why birds occur where they do would be very useful in assessing the impact of forestry on birds. In particular, if we could fully understand the status quo we would be in a much stronger position to recommend how to change forestry practice in ways suitable for birds.

A breeding bird community in forests is made up of species that have different requirements for various forest characteristics. The causes leading to observed forest associations may occur in different spatial and/or temporal scales. Although it is known that forests differ in many ways, finding the components of variation that are crucial for the observed forest associations of species has proven to be a difficult task (e.g. Wiens 1989, Orians & Wittenberger 1991). Obviously, the first step in doing this is to use quantitative characteristics in the environment that are related to distributions of different bird species. The patterns of organization in forest bird communities have been explored in several studies (e.g. James 1971, Anderson & Shugart 1974, Rabenold 1978, Prodon & Lebreton 1981, Spindler & Kessel 1980, James & Wamer 1982, Opdam & Schotman 1986, Bibby *et al.* 1989b).

To assess the conservation value of a commercial plantation, one needs information on exactly what the forest will hold at different ages. Therefore, the succession of birds which occur throughout the forest succession in conifer forests needs to be studied. A factor which needs investigation in the search for an understanding of which birds would be expected to occur in different woods is whether the physical structure of the wood might be important. This could either be because some bird species might be influenced by the structure itself, e.g. flycatchers cannot make fly-catching sallies in impenetrable thickets, or perhaps through an effect that structure might have on the plant community of a wood, which may often be determined by the degree of penetration into wood by sunlight. Because it is generally recognized that birds use habitat structure to select breeding territories (MacArthur & MacArthur 1961, Hildén 1965, James 1971, Anderson & Shugart 1974, Smith 1977, Haila *et al.* 1980, Rotenberry & Wiens 1980, Wiens 1989, Orians & Wittenberger 1991), this study is focused on a quantitative and structural description of the forest types selected and used by the forest avifauna.

1.4 Objectives and outline of the report

The main objectives of this study are to: (1) gather population data on woodland breeding birds; (2) quantify the vegetation structure of the forest; (3) associate the forest structure with breeding birds in order to develop a better understanding of woodland breeding bird communities and to predict the outcome of management activities. These will be used to make recommendations for forest design and management, so as to significantly stimulate rich bird populations, and thereby the ecological value of the woodlands. This report presents the results of some of this work, which examined the breeding bird communities of commercially managed deciduous and needle plantations, and semi-natural deciduous woodlands in Denmark. For a list of English and scientific names of birds mentioned in the text see Appendix I.

1.5 Study areas and forest types

For this project breeding birds in different forest types were censused. In order to analyze the relation between vegetation structure and woodland bird populations effectively, the forest types have to meet with two requirements: they have to be homogeneous and, ideally, they should be of the same size without edge effects. Series of forest types were taken in order to obtain results that link better on to the subject-matter of this research. It was possible to fill in a series for needle woodland; for deciduous woodland it was more difficult.

Initially it was planned to conduct the research in woodlands owned and managed by the Aage V. Jensens Charity Foundations only: Høstemark, Hov, Nedergård and Rørbæk situated in eastern Jutland in Denmark (Fig. 1.1). In order to include forest types not present in the above mentioned woodlands, additional forest sites were selected: Hestehaven, Mols Bjerge, Pindstrup, Skaføgård and Thorsager (Fig. 1.1). The total area surveyed was 197.9 ha. These woodlands are situated far apart. It would have been better to study woodlands within the same geographical region, because identical woods in different places would be likely to hold different assemblages of birds. For example, the Black Woodpecker is restricted to the southern part of Denmark, whereas this species has not ever been known to have lived in northern Denmark, where suitable woodlands (e.g. Høstemark) are present.

Five different series of forest types were distinguished leading to a total of 24 forest types (Table 1.1, Fig. 1.2). Of all forest types line-transect drawings were made (Fig. 1.3; for method see section 2.2.2).

1.6 General analytical methods

The bulk of the information presented in this report is based on data collected from March to July 1991. All data collected in field note books were placed on computer files on the mainframe using PlanPerfect Version 5.1 (WordPerfect Corporation 1990), along with information on the context in which the data were collected. The data were then managed and statistically analyzed using SAS/STAT software (SAS Institute Inc. 1988).

In each chapter the statistical methods used will be described, or referred to those already described. For linear correlation coefficients two-tailed tests with 22 degrees of freedom have been employed (24 forest types), unless otherwise stated. When not specified in the text, values of statistical tests are reported in the legends of figures or tables. Statistical tests, means, standard deviations and confidence limits for percentages were calculated by converting percentages into proportions and transforming the square root of each proportion (or percentages/100), p, to its arcsine ($p'=\text{arcsine}\sqrt{p}$). Transformed values, p', may be transformed back to proportions ($p=(\text{sin}p')^2$).

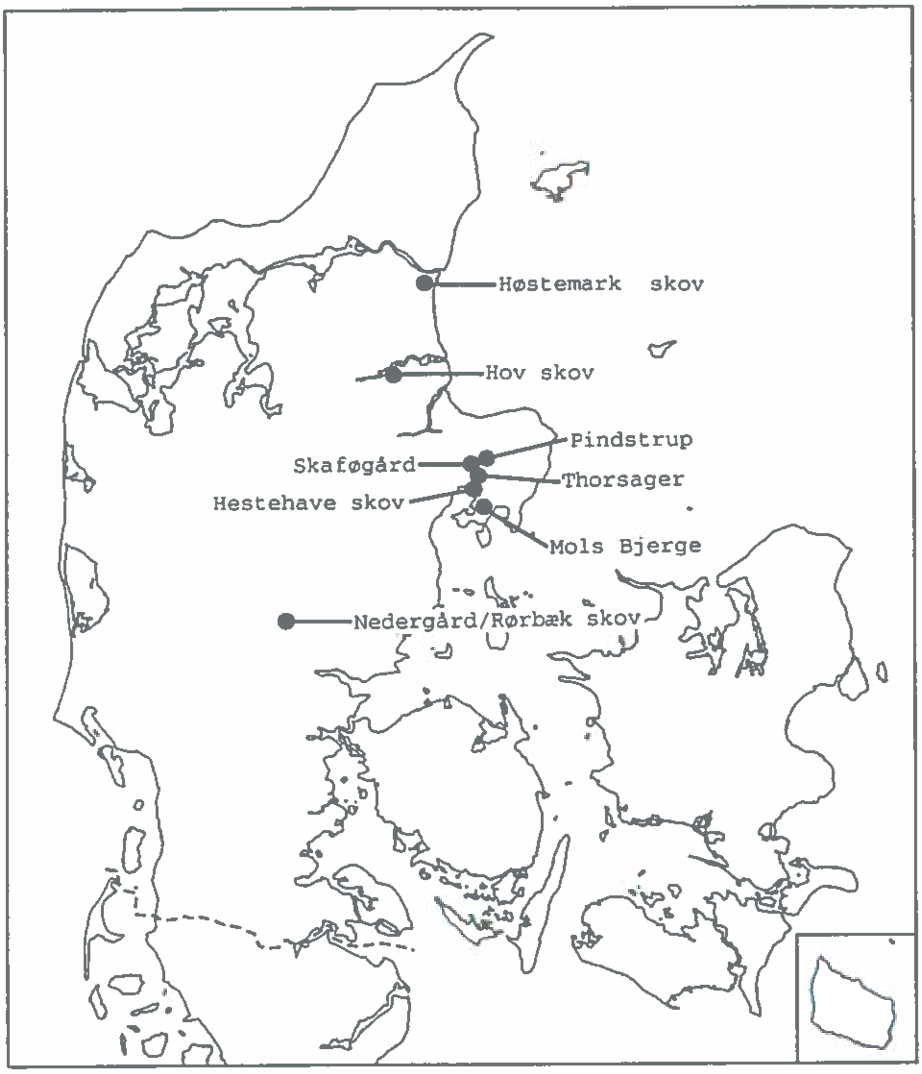


Figure 1.1. Location of woodlands studied in Denmark.

Table 1.1. Series of forest types studied. Under each forest type the study area(s) is (are) mentioned between brackets (see Fig. 1.2).

Series I: A succession series of a combination of Norway Spruce, Sitka Spruce Austrian Pine (*Pinus nigra*), and Scottish Pine (*Pinus sylvestris*). This comprises nine forest types ranging from young (I.1) to mature (I.9) woodlands.

		Area (ha)
I.1	Clear cut with newly planted Norway Spruce (Nedergård 4)	7.6
I.2	Young phase of Norway Spruce (Høstemark 5)	17.4
I.3	Early dense phase of Norway Spruce (Rørbæk 4)	1.2
I.4	Dense phase of Norway Spruce after first thinning (Rørbæk 3)	1.3
I.5	Thicket phase of Norway Spruce (Nedergård 5 and Rørbæk 5)	6.6
I.6	Late thicket phase of Norway Spruce (Rørbæk 2)	1.6
I.7	Mature Norway Spruce (Nedergård 1)	8.5
I.8	Mature Scottish Pine, Austrian Pine, and Sitka Spruce with young shrub (Pindstrup 1, Mols 2, Thorsager 1 and Rørbæk 1)	8.7
I.9	Mature Scottish Pine and Norway Spruce with old shrub (Pindstrup 2, Mols 1, Thorsager 2 and Skaføgård)	10.4

Series II: A succession series of Beech (*Fagus sylvatica*) including four forest types ranging from young (II.2) to mature (II.4) woodlands.

II.1	Young phase of Beech (Hestehave 4)	1.9
II.2	Dense phase of Beech after first thinning (Hestehave 1a and 2)	5.1
II.3	Late thicket phase of Beech (Hestehaven 3)	9.1
II.4	Mature Beech (Hestehave 1b)	13.6

Series III: Young and old semi-natural woodlands including two young (III.1; III.2) and two mature (III.3; III.4) woodlands.

III.1	Young phase of mixed Birch (*Betula sp.*)/Mountain Pine (*Pinus mugo*) woodland with open spaces (Høstemark 3)	9.0
III.2	Dense phase of mixed Birch/Mountain Pine woodland (Høstemark 4)	6.2
III.3	Mature deciduous woodland with Ash (*Fraxinus excelsior*), Beech and Common Alder (*Alnus glutinosa*) without shrubs (Høstemark 1)	10.7
III.4	Mature deciduous woodland with Beech, Common Alder and Birch without shrubs (Høstemark 2)	14.0

Series IV: Fragmented woodlands consisting mainly of plots of mature beech and mature Norway Spruce (Fig. 1.2.b). Besides, small clearcuts, small plots of young beech and newly planted Noble Fir (*Abies procera*) occur. The woodland includes five forest types.

IV.1	Clear cuts, some with newly planted Noble Firs (Hov 1)	5.7
IV.2	Mature Beech without shrubs (Hov 3)	23.8
IV.3	Young Norway Spruce (Hov 4)	4.7
IV.4	Mature Norway Spruce (Hov 5)	16.0
IV.5	Hov total (IV.1 to IV.4, and small patches of self seeded young Beech (Hov 2, 1.2ha))	51.4

Series V: Larch and Sessile Oak (*Quercus petraea*) woodlands including two forest types.

V. 1	Late thicket phase of Larch after second thinning (Nedergård 2 and 3)	5.1
V. 2	Late thicket phase of Oak (Nedergård 6)	8.5

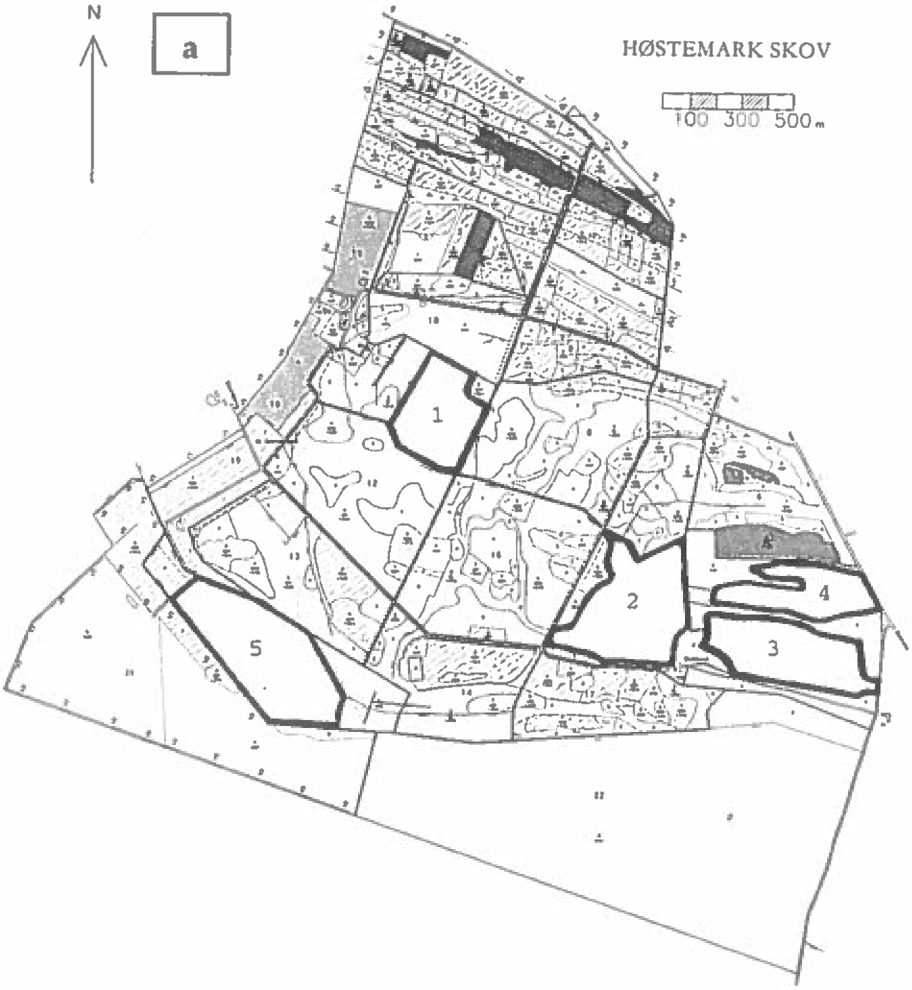
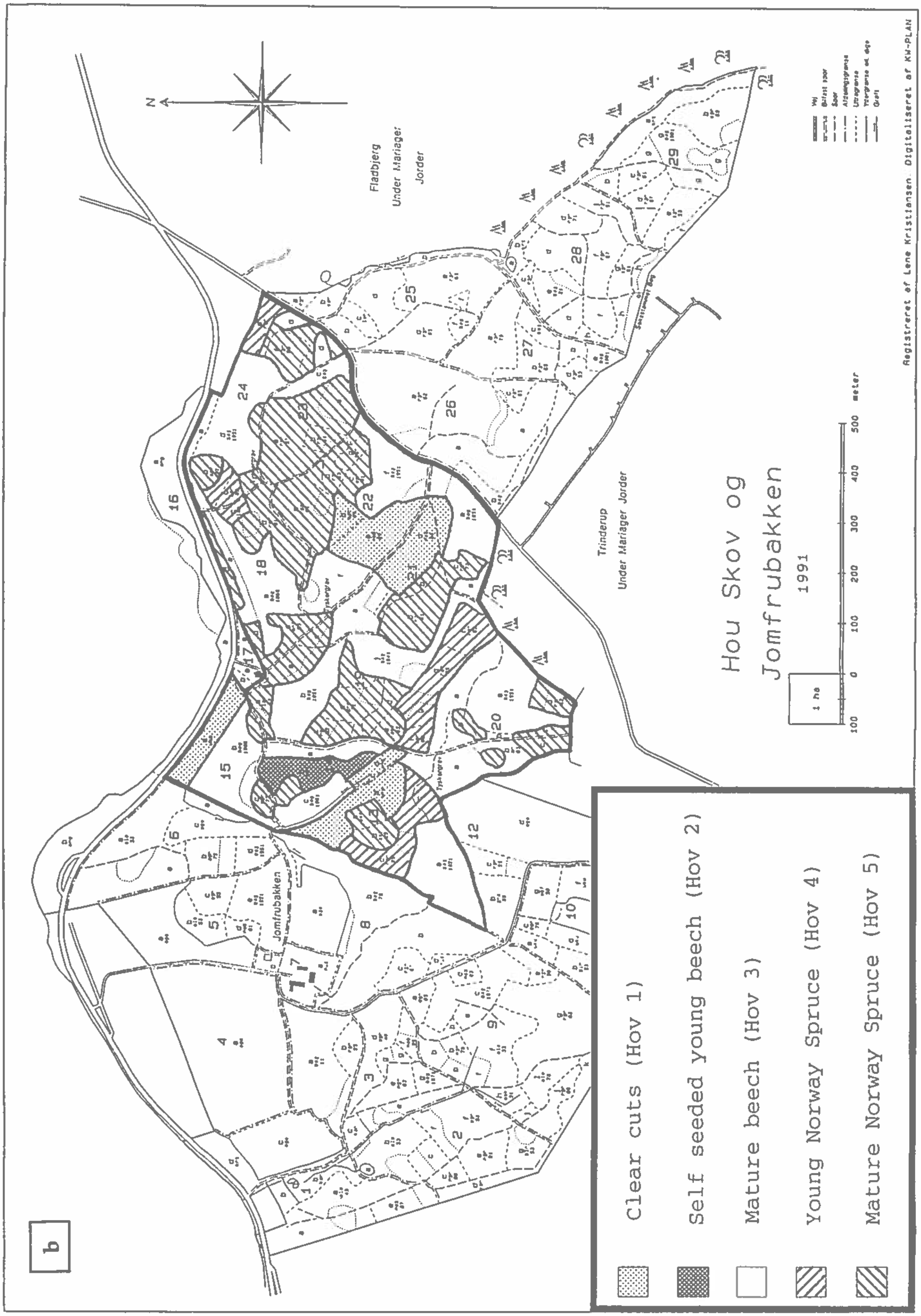


Figure 1.2. Position of the study areas in the woodlands of Høstemark (a), Hov (b), Pindstrup, Skaføgård and Thorsager (c), Hestehaven (d), Mols Bjerge (e), Nedergård (f) and Rørbæk (g). Numbers refer to study areas mentioned in the text.



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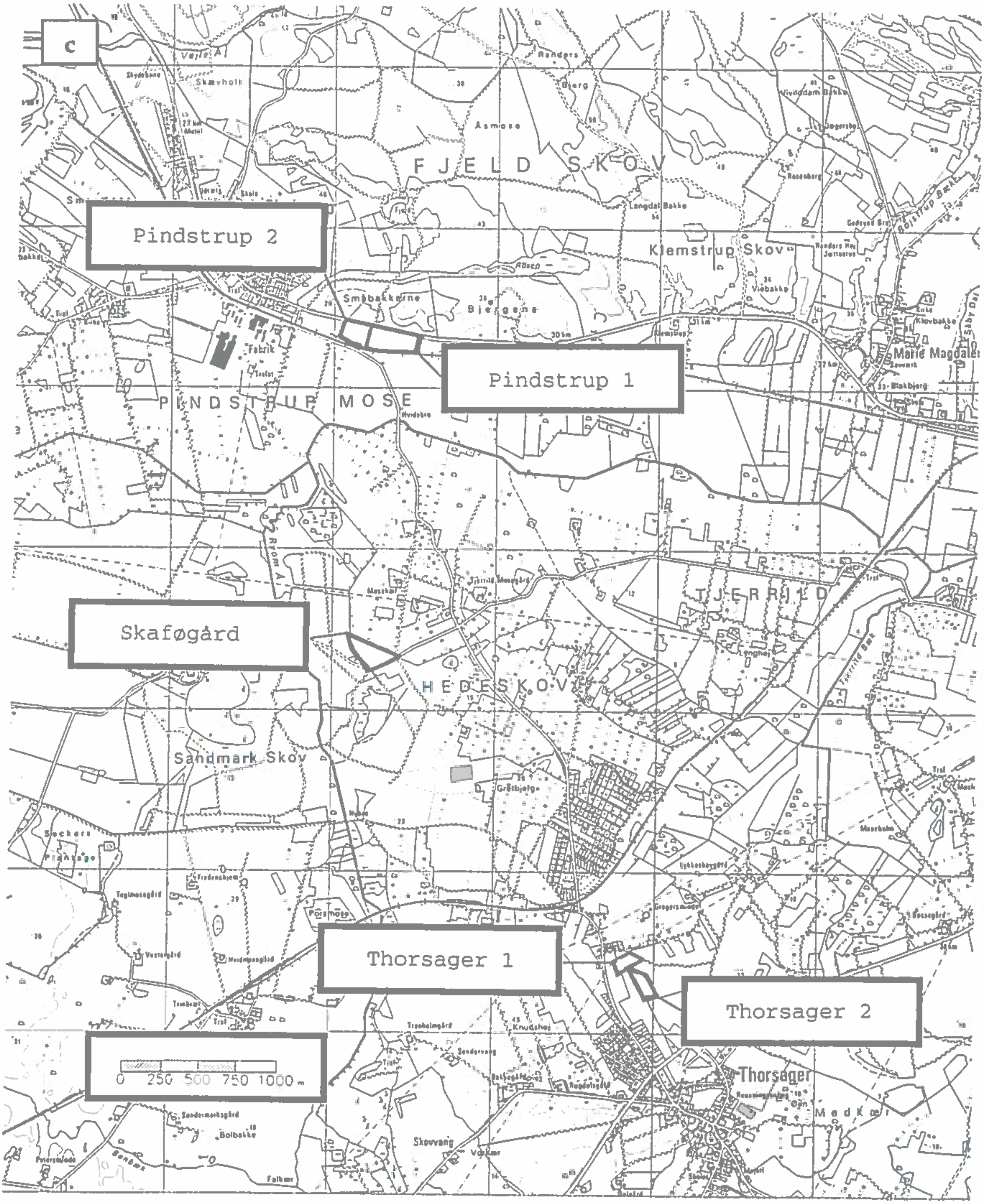

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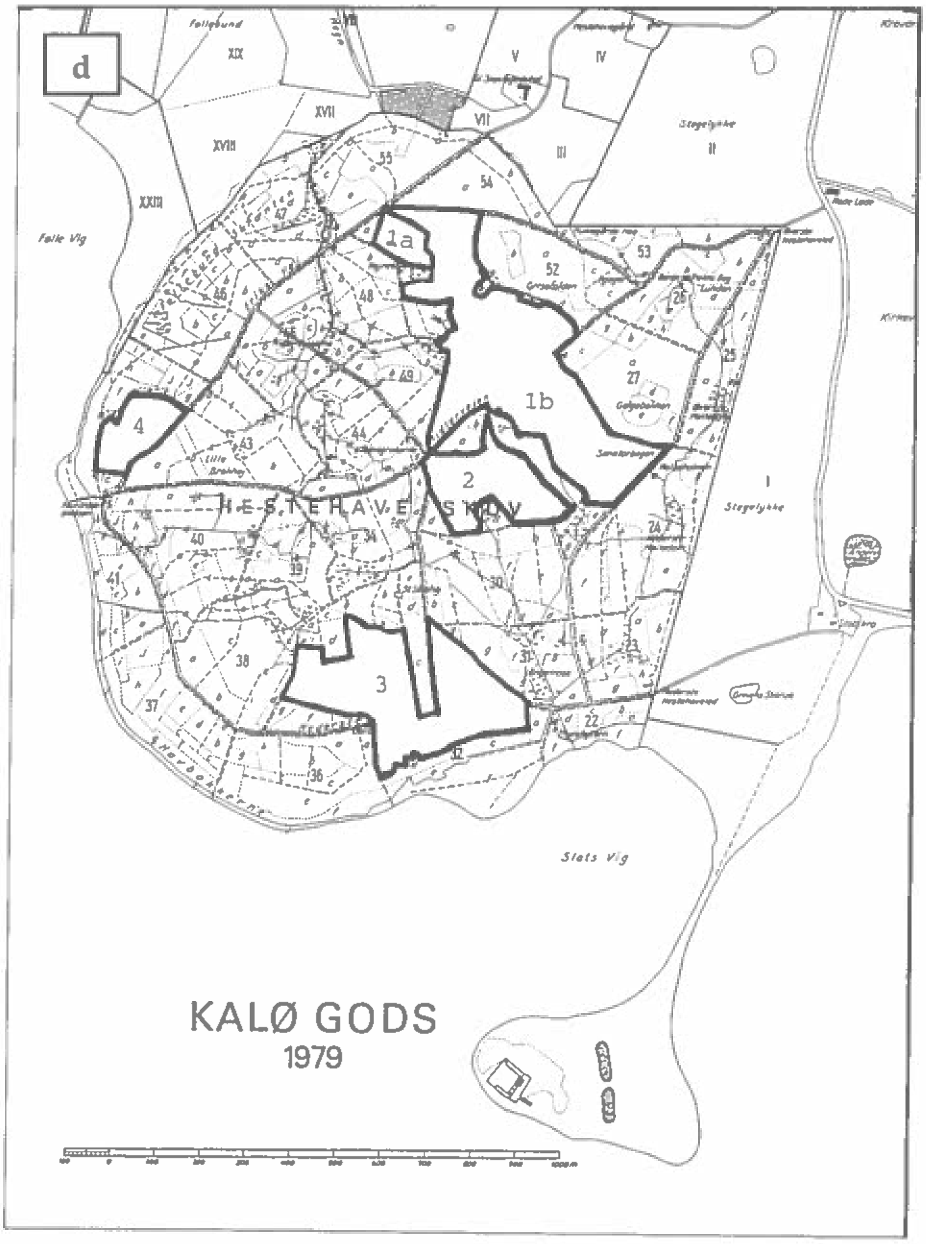

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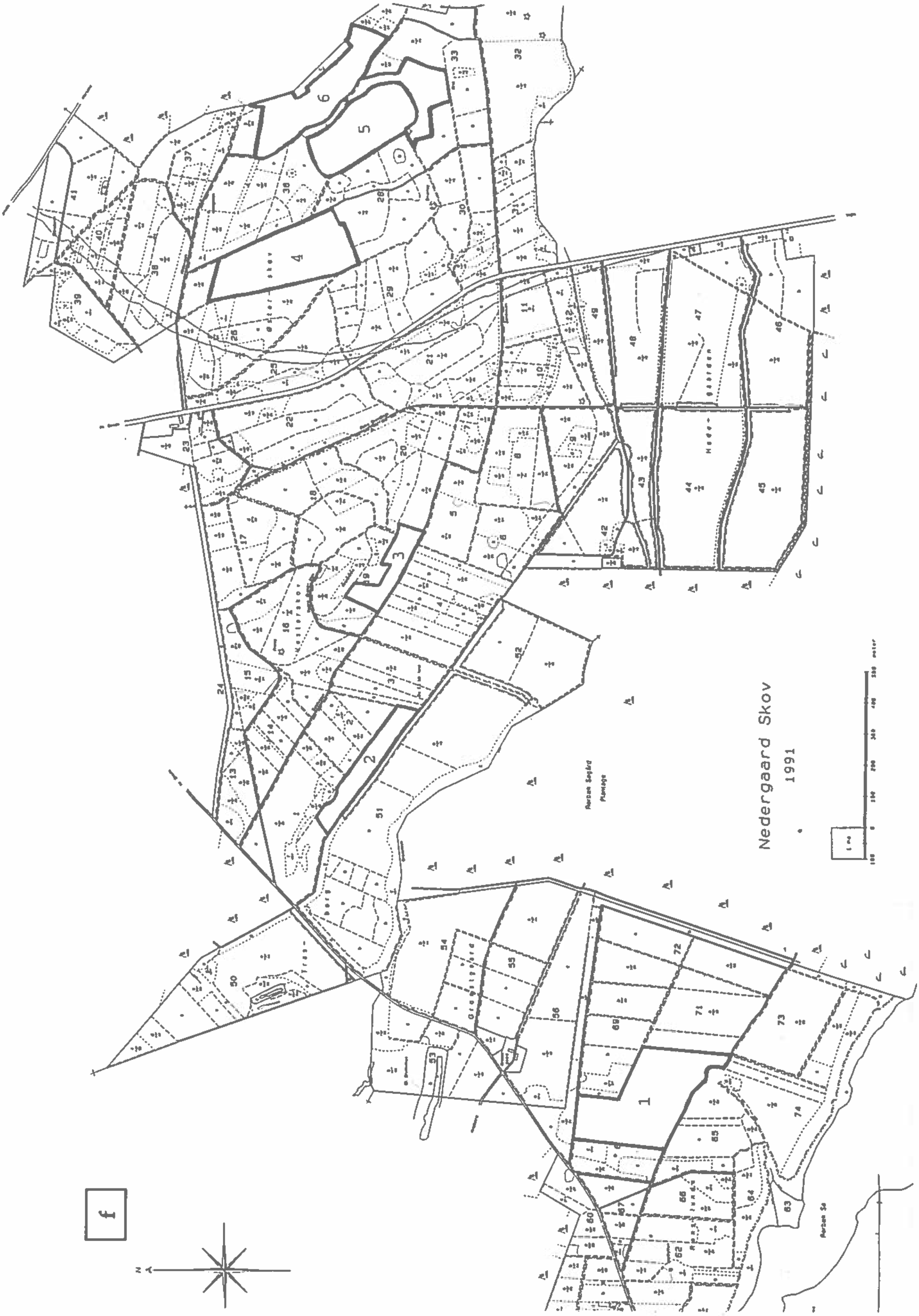

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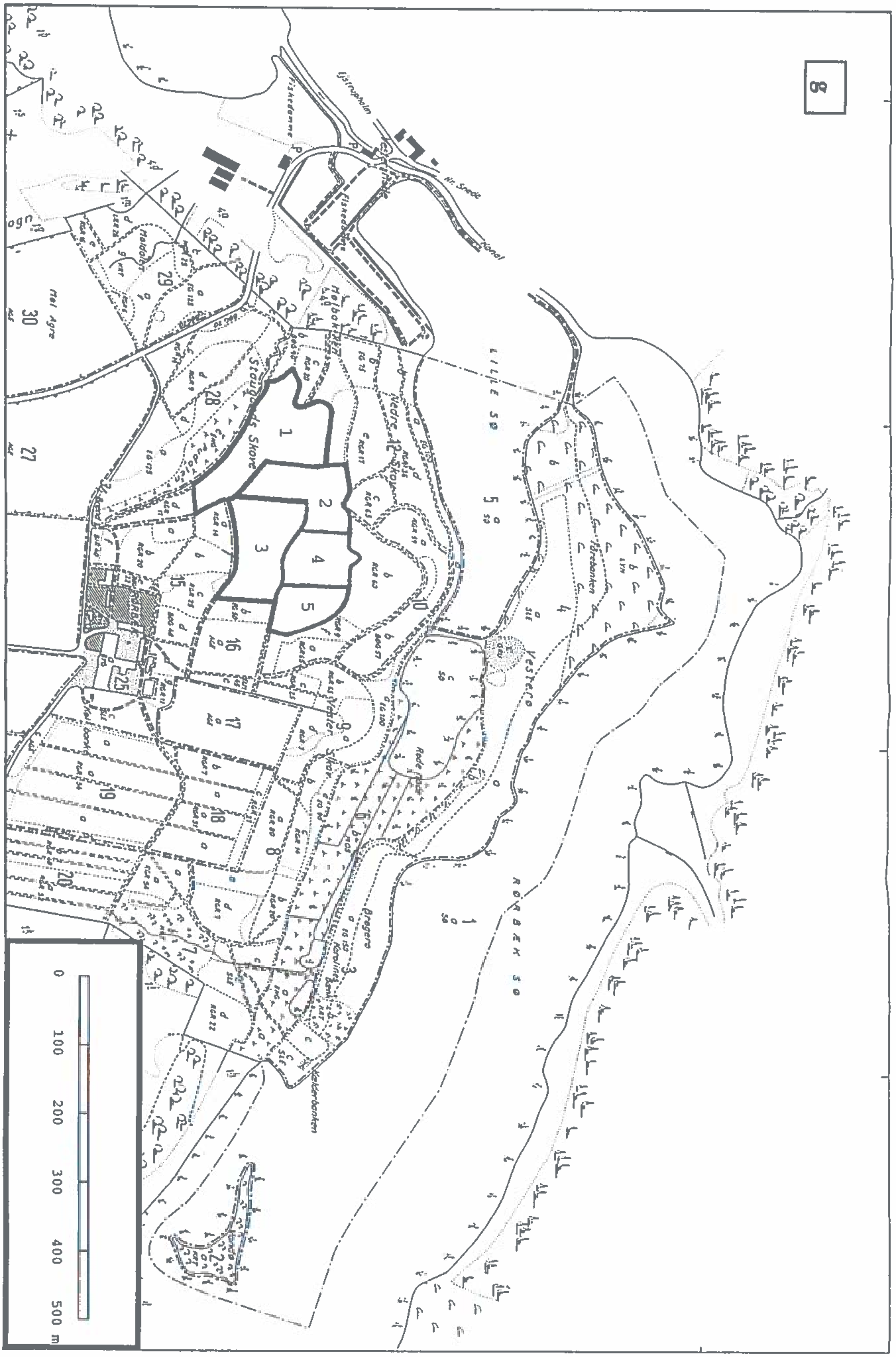

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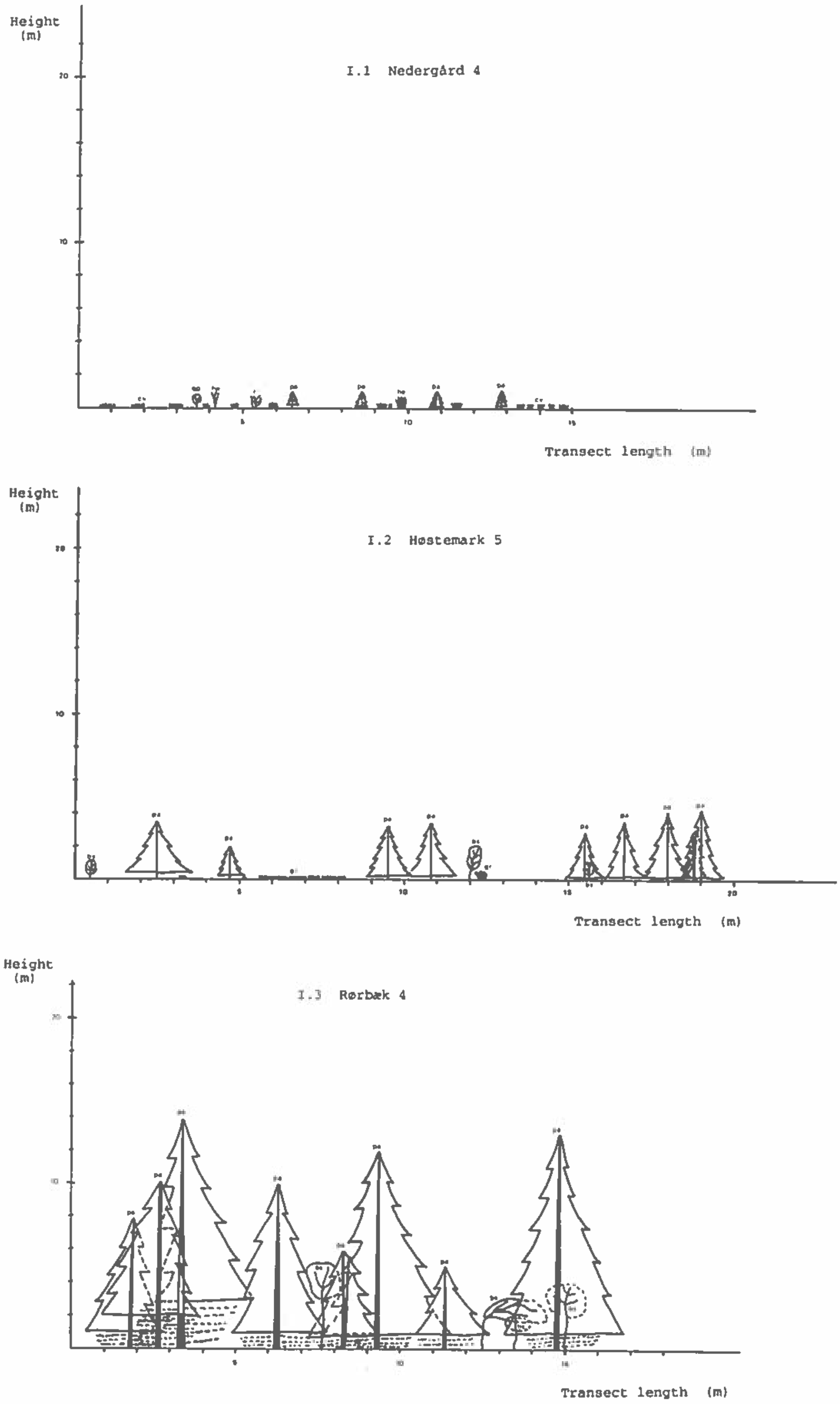
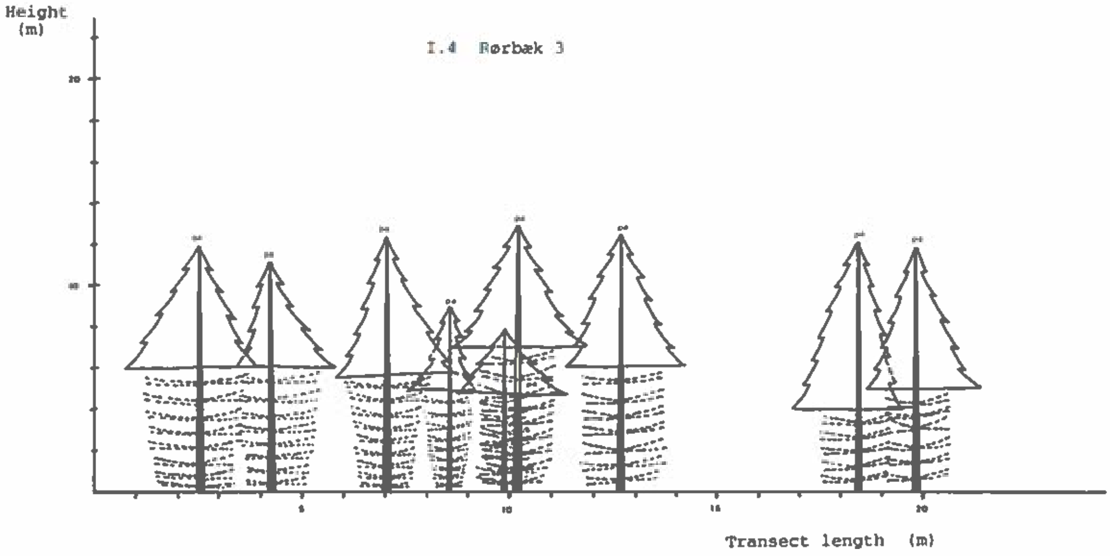
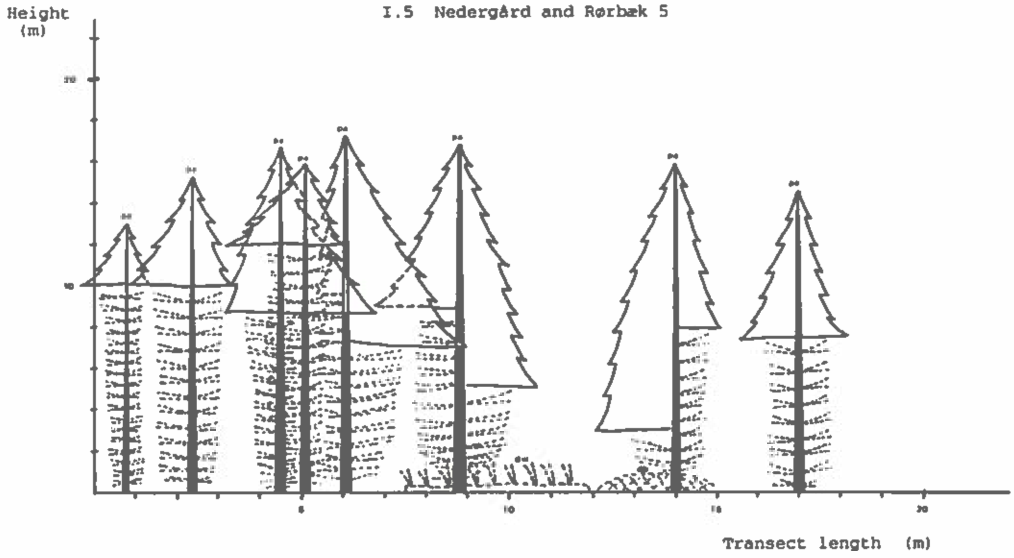
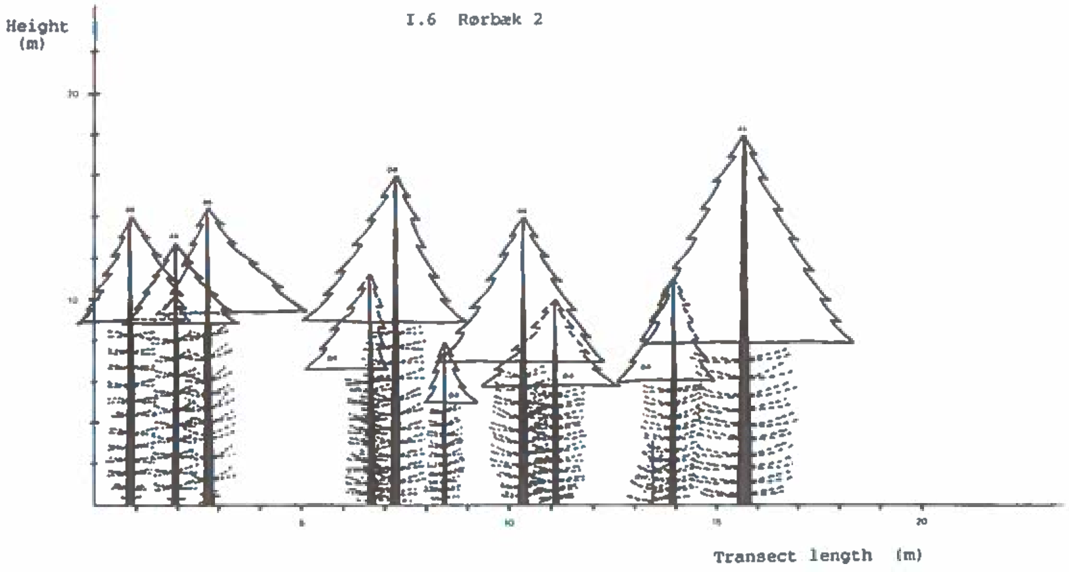


Figure 1.3. Line-transect drawings of all forest types (see section 1.5 for details). Abbreviations refer to plant names mentioned in Appendix II. Note: Forest type II.2 is not illustrated, as it is almost identical with forest type II.1.







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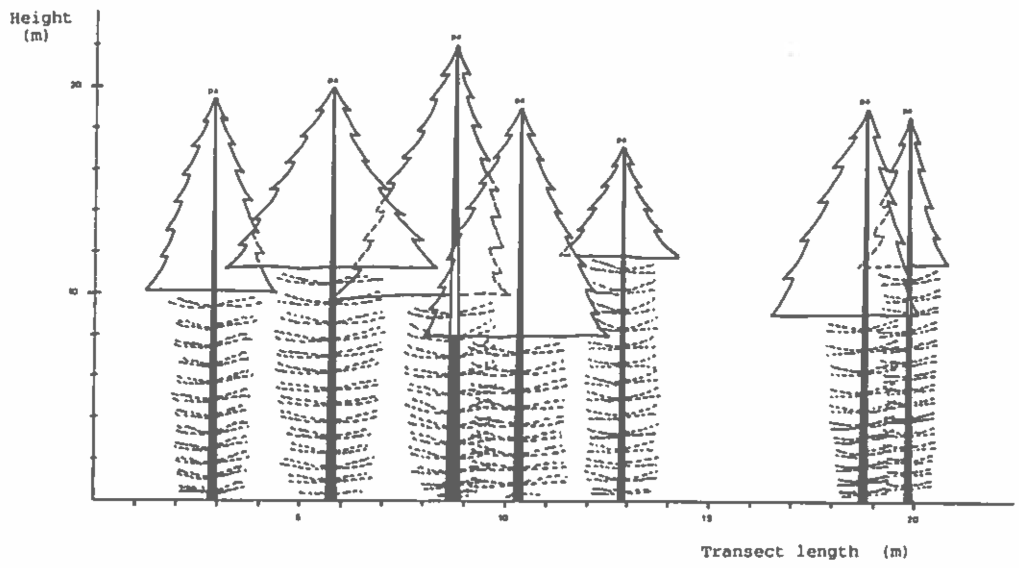
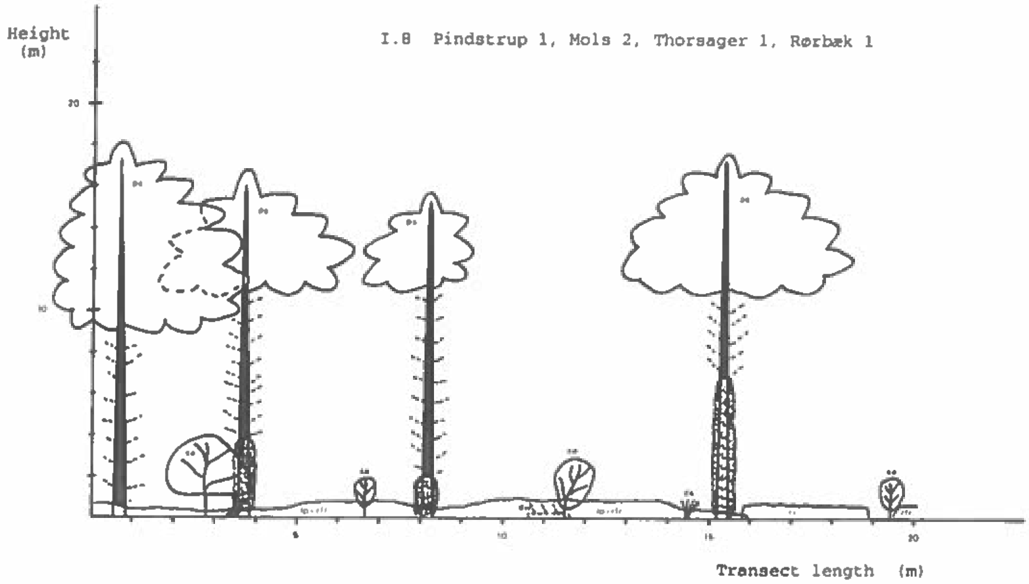
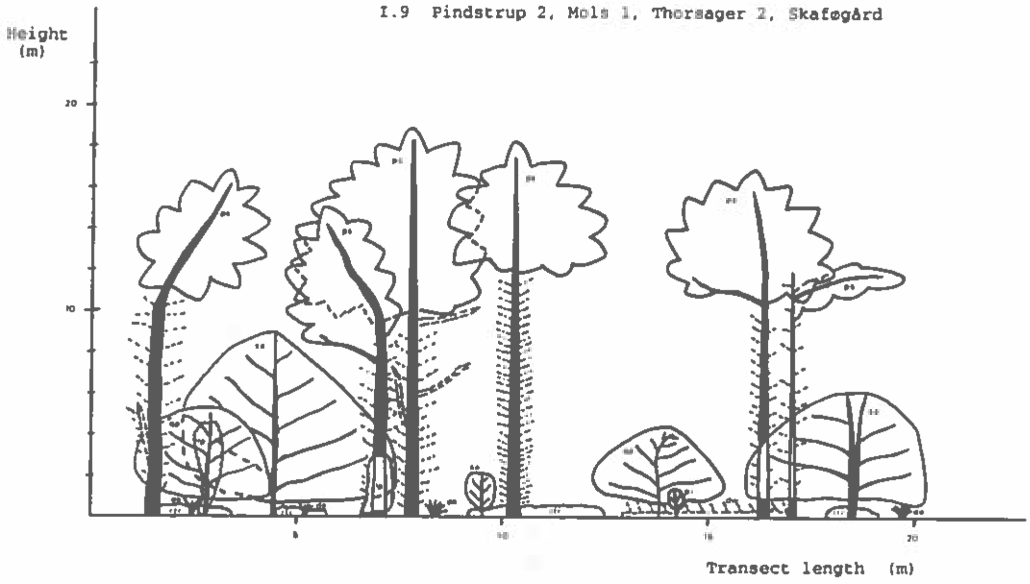
I.7 Nedergård 1



I.8 Pindstrup 1, Mols 2, Thorsager 1, Rørbæk 1



I.9 Pindstrup 2, Mols 1, Thorsager 2, Skaføgård



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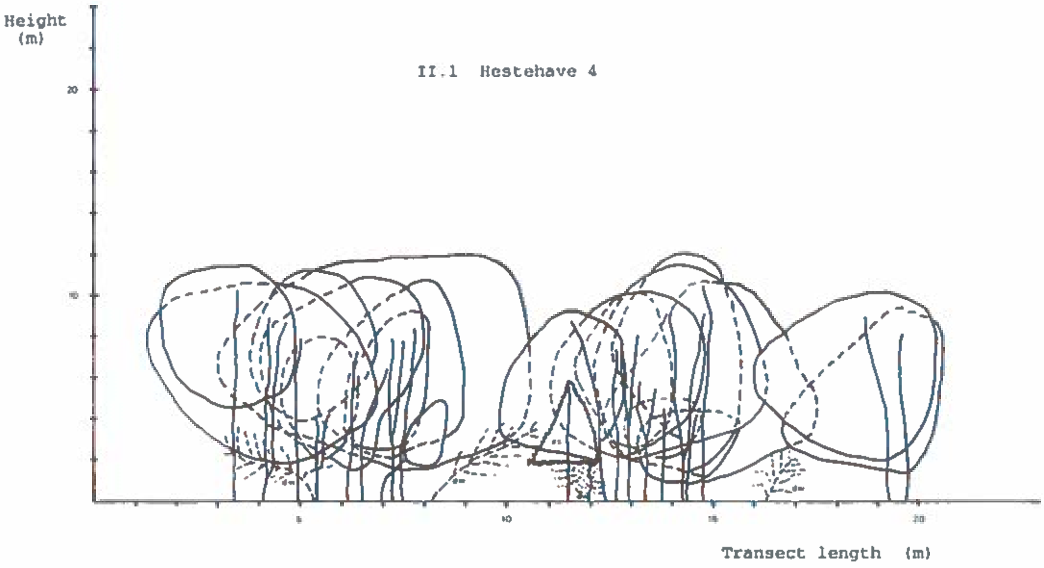
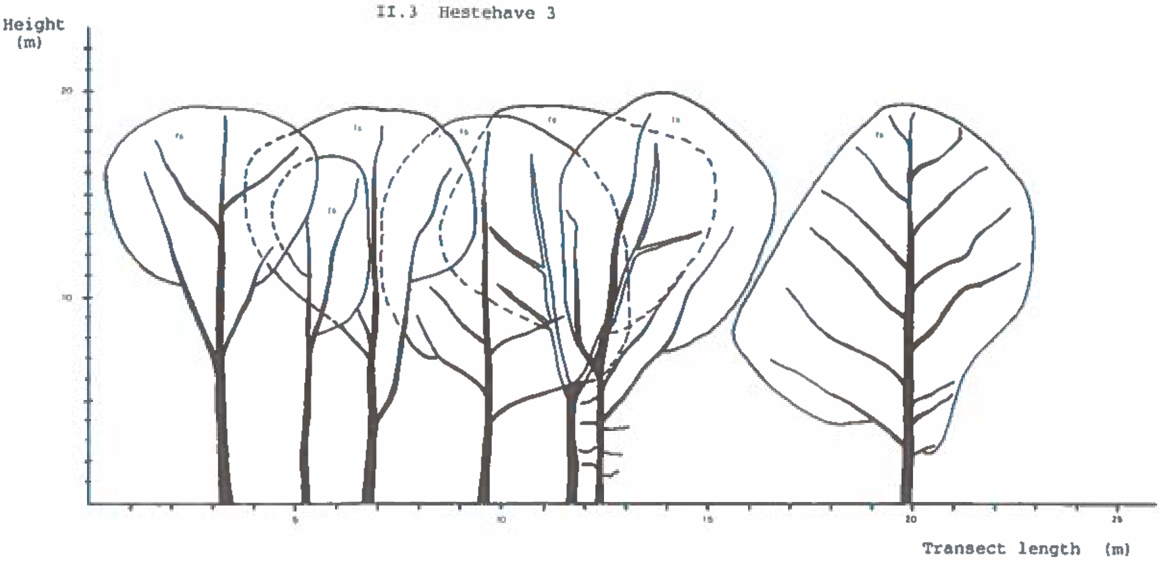
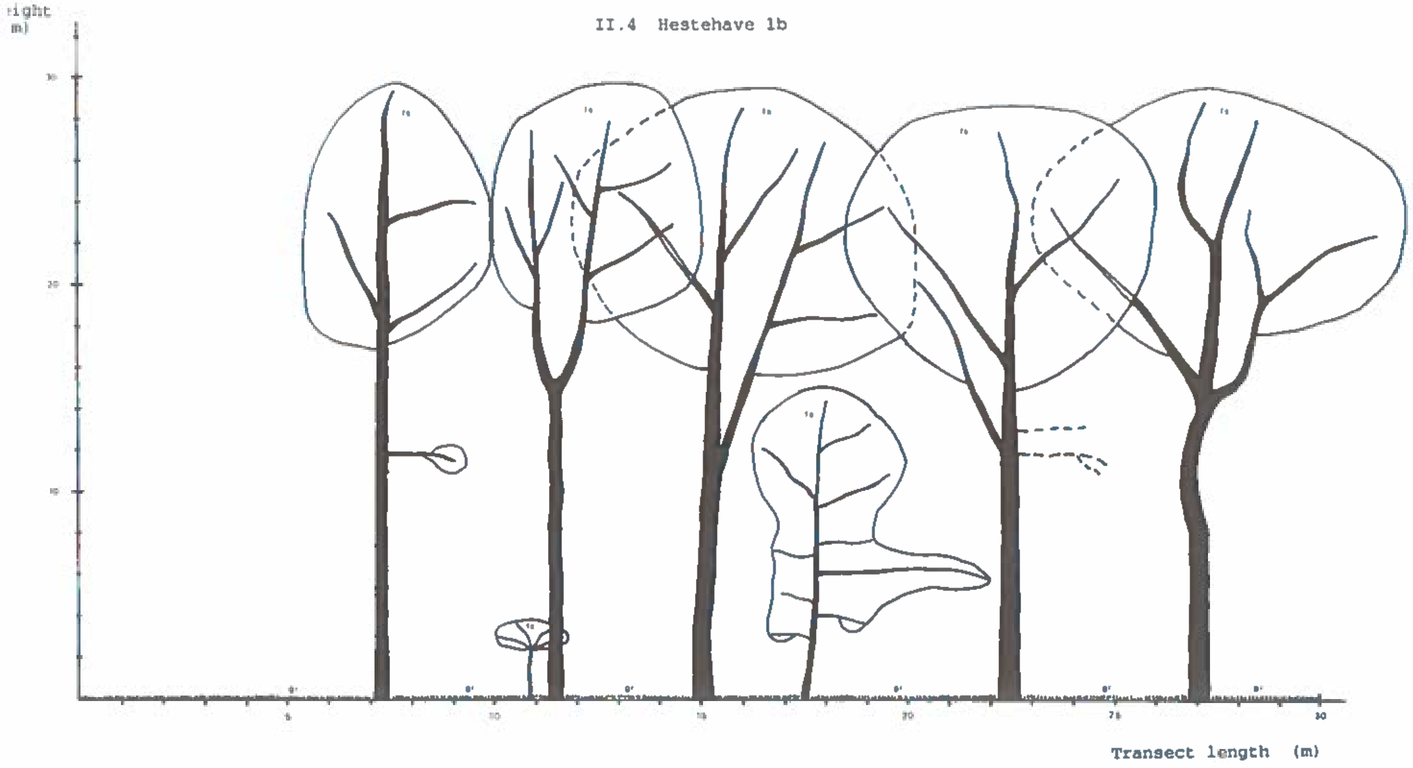

II.1 Hestehave 4


II.3 Hestehave 3


II.4 Hestehave 1b

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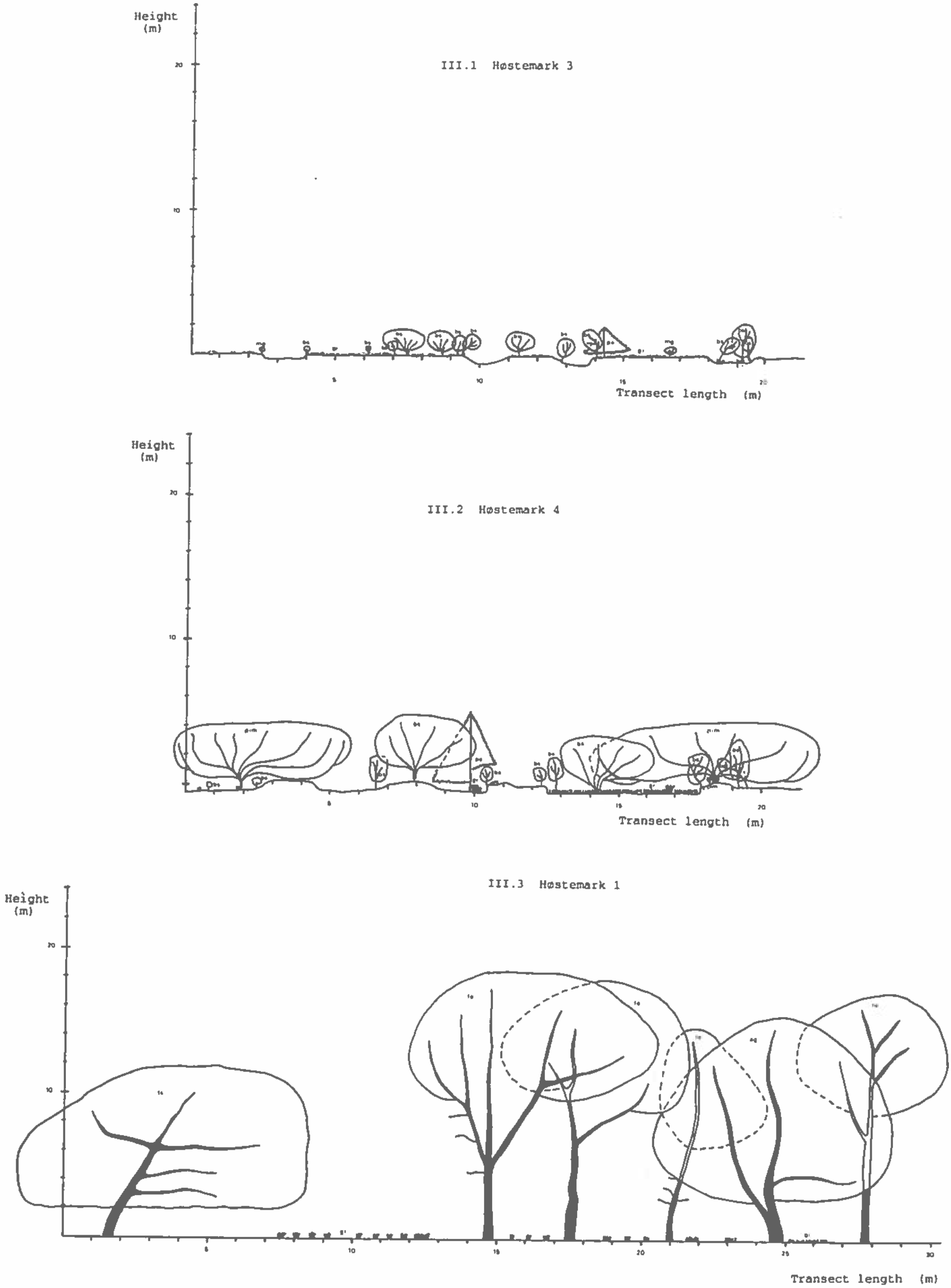

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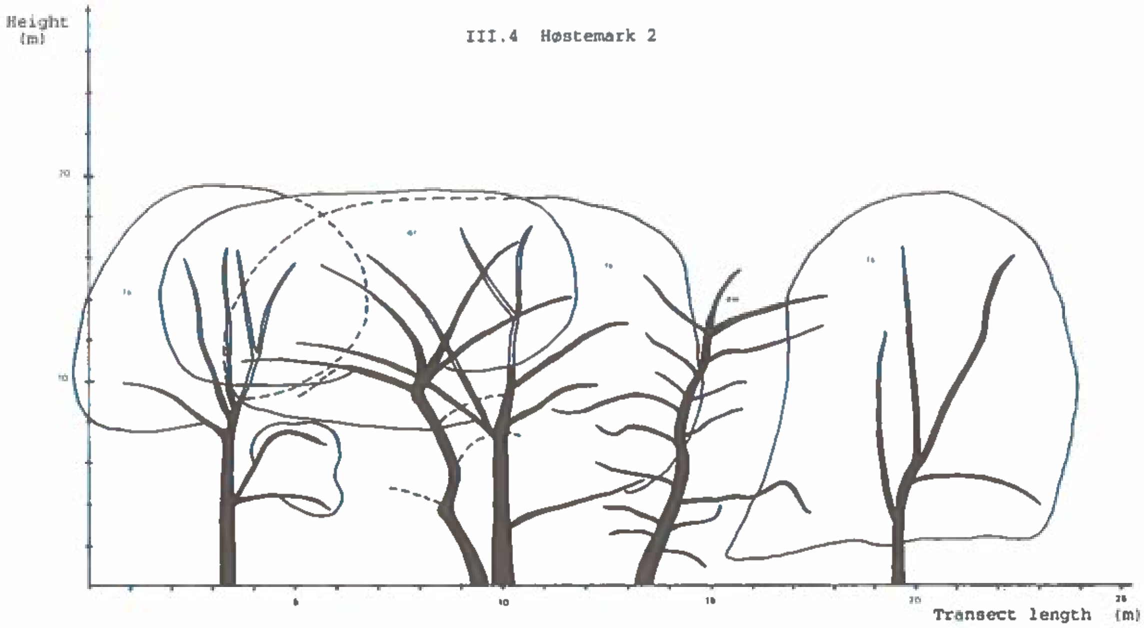
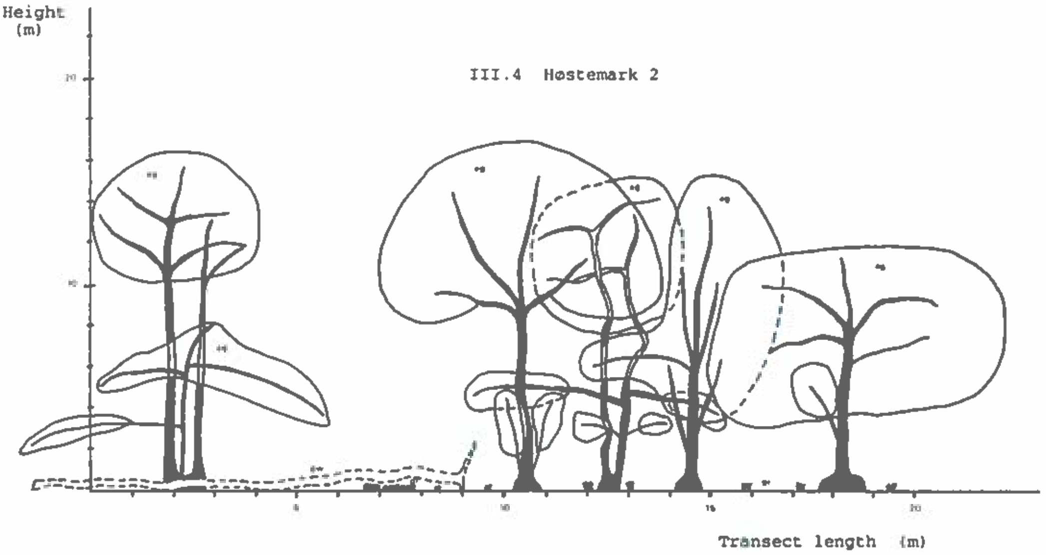
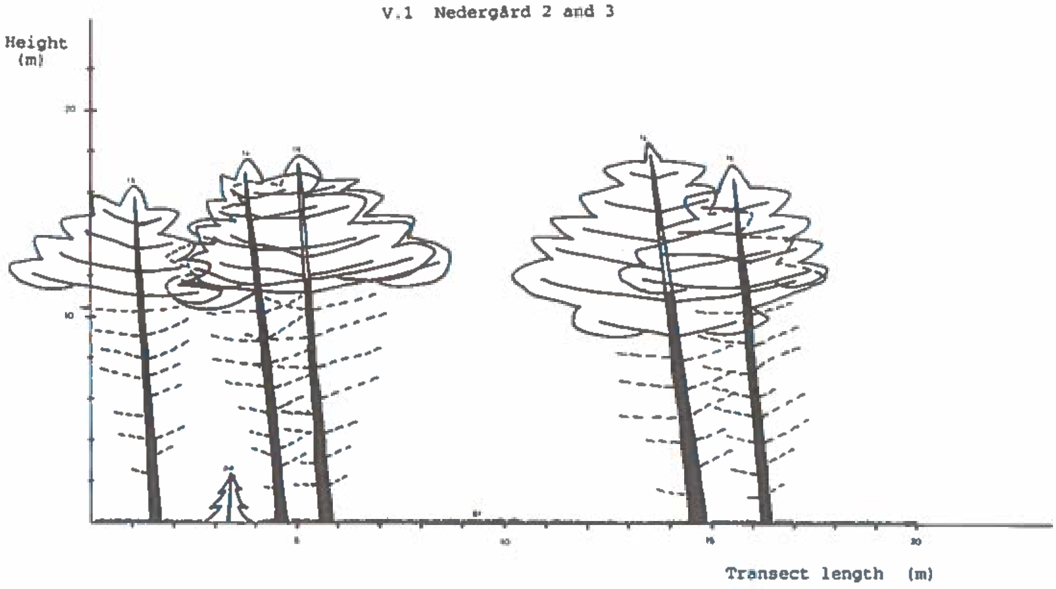

III.4 Høstemark 2


III.4 Høstemark 2

V.1 Nedergård 2 and 3



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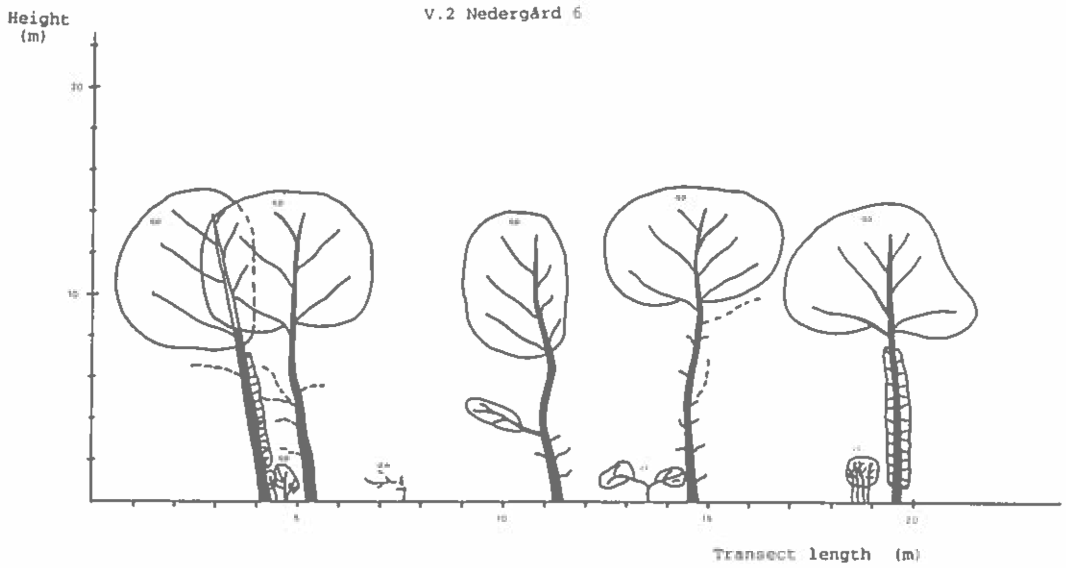


Figure 1.3, continued ...

2 Methods

This chapter describes the bird census method, the vegetation survey method, the analysis of both bird and vegetation parameters, and the clustering procedure.

2.1 The bird census method

The breeding-bird populations were registered using the combined version of the mapping-method (Tomialojc 1979), which yielded the numbers of each species in each plot. Exact positions of the birds, determined either by sight or by sound, and movements of birds were recorded on a species map (1:2,500 or 1:4,000). A different code was used for each recording date. A standard set of symbols indicated the sex and age (juvenile or adult) of the bird, birds singing, foraging, carrying nesting material, feeding young, in flight, or reacting aggressively towards conspecifics. Simultaneous observations between two or more adjacent birds or pairs were connected with a solid line (and the date). When possible, active nests (nests with eggs or young) were recorded (especially woodpecker nests were easy to find in the middle of June, when the nestlings were begging in their nest holes).

Altogether the bird census consisted of 9 to 10 early morning visits from 20 March until 19 June 1992. Each census began ca.

one hour before sunrise, so as to work during the song peak around sunrise (Opdam & Reijnen 1978). During each visit the census started in different woodland plots to avoid bias by species singing earlier or later on the day. To allow for changes in the level of singing and detectability as the breeding season progresses, all woodland plots were visited in the same week.

One of the potential problems of the bird census is that some bird species are more difficult to detect than others, which may lead to a bias towards noisy, easily detected species. For instance, a Songthrush can be heard from a much greater distance than a Goldcrest. A further difficulty, which is particularly relevant in this study when comparing the birds in different habitats, is that the detectability will also depend on the structure of the habitat. In areas with dense foliage, birds will be far more difficult to detect than in open areas. To make allowance for both of these effects the birds in each forest type were counted along routes 50 m apart.

Routes were either on paths, along vegetation borders, or along transects marked with plastic flashes. To help the observer mapping the positions of birds in homogeneous plots without paths (Høstemark), plots were divided into squares of 100 x 100 m. The corners of the squares were double marked with coloured flashes.

2.1.1. Assessing the number of territories

As a measure for bird richness in an area, the number of occupied territories during the breeding season was used; not the number of breeding pairs. Unpaired, non-breeding birds that hold territories also belong to the bird population during the breeding season. Non-territorial birds were thus not incorporated into this research. However they may form a significant part of the bird population as was shown for a local population of Blackbirds; 44% of the total population consisted of non-territorial males (Teixeira 1977).

After the last visit registrations were allocated to territories. Except in the special circumstance of a known nest, the minimal required number of observations of a species before it was considered to have a territory varied from 2 to 4, depending on the number of 'valid visits' in which the bird species could be scored (Table 2.1). For example a sedentary bird like the Wren, present all year round, can be scored during the whole research period, whereas a migratory bird like the Wood Warbler, arriving in May,

Table 2.1. The minimal number of registrations of a species needed to assign a territory, in relation to the number of visits coinciding with the specie's presence in Denmark.

Minimal number of registrations	2	2	2	3	3	4
Number of 'valid visits'	5	6	7	8	9	10

can be scored during a shorter period. Therefore, the number of 'valid visits', coinciding with the species' presence, is higher for the first than for the latter species. Some of the territories included more than one forest type. These territories were treated as comprising equal units, which were allocated to forest type in proportion to their use by the (pair of) birds (Fig. 2.1). For each bird species the number of territories per forest type was counted and the density was calculated for each forest type (number of territories per ten ha; Table 2.2).

2.2 The vegetation survey method

2.2.1 Measurement of vegetation structure

For all forest types (see section 1.5) the vegetation structure was surveyed in June 1992 by use of the transect method developed by Van Berkel (1979) and Komdeur & Vestjens (1982). This method uses transects instead of survey plots, and therefore offers the possibility to calculate a measure for heterogeneity (alteration of absence and presence of vegetation in horizontal direction).

When using the transect method, one walks a transect through the forest facing North, from one forest boundary to the other, taking care to cover every subtype (if any) proportionally. Sub-

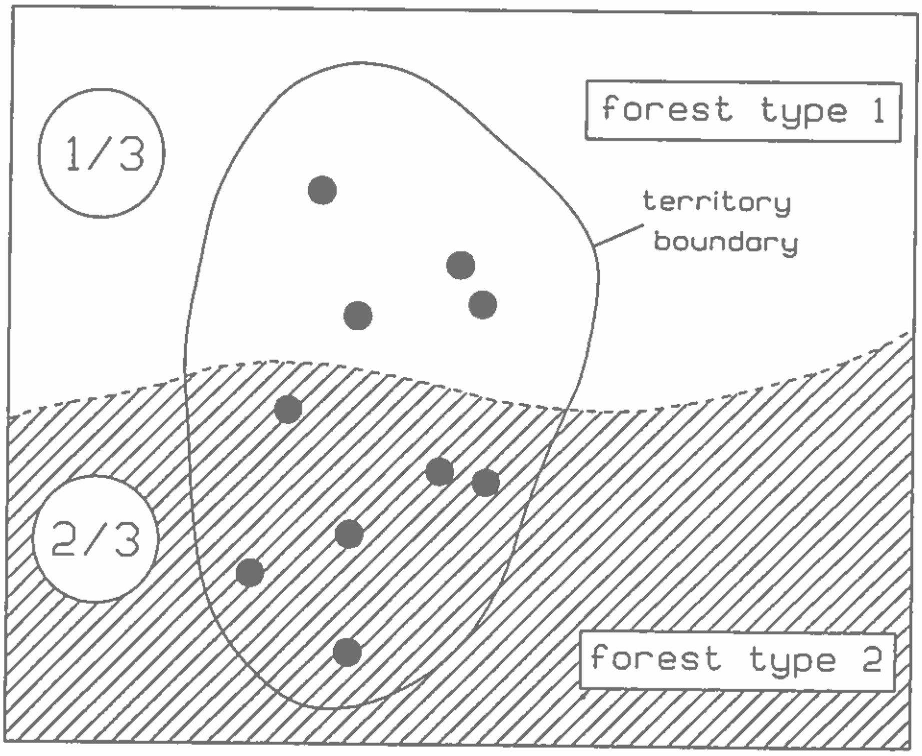


Figure 2.1. Example of dividing a bird territory over two forest types in proportion to its use by the (pair of) birds (black dots are recordings on different days).

Table 2.2. Densities of all breeding bird species in the different forest types given as number of territories/10 ha.

Forest type:	I.1	I.2	I.3	I.4	I.5	I.6	I.7	I.8	I.9	II.1	II.2	II.3	II.4	III.1	III.2	III.3	III.4	IV.1	IV.2	IV.3	IV.4	IV.5	V.1	V.2
Bird species:																								
Wood Pigeon	0	0	8,33	7,69	6,06	18,75	2,35	3,79	0,96	10,53	1,96	4,84	1,84	1,11	3,23	5,61	3,57	0	1,68	2,13	19,38	23,18	0	0
Common Snipe	0	1,72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Woodcock	0	0	0	0	0	0	0	0	0	0	0	0	0	1,11	1,61	0	0	0	0	0	0	0	0	0
Green Woodpecker	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,93	0,71	0	0,84	0	0	0,84	0	0
Great-spotted Woodpecker	0	0	0	0	0	0	0	0	0	0	1,57	0	1,47	0	0	3,74	3,57	0	3,91	0	0,44	4,35	0	0
Red-backed Shrike	0	0,57	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree Pipit	7,89	1,72	0	0	0	0	0	0	0	0	0	0	0	3,33	4,84	1,87	0,71	1,75	0	0,64	0	2,39	0	0
White Wagtail	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1,75	0	0	0	1,75	0	0
Wren	3,95	5,17	0	0	1,52	0	6,24	13,33	12,5	0	0	0	2,94	0	1,61	8,41	9,57	2,98	2,39	3,83	10,69	25,73	0	0
Dunnock	0	8,05	0	0	0	4,38	1,18	3,79	2,88	0	0	0	0	0	0	0	0	0,88	0,21	8,51	1,88	11,47	0	0
Whitethroat	0	6,32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3,51	0	0	0	3,51	0	0
Lesser Whitethroat	0	1,72	0	0	0	0	0	0	0	0	0	0	0	2,22	0	0	0	0	0	0	0	0	0	0
Garden Warbler	0	0	0	0	0	0	0	0,57	0	0	1,96	0	0	1,11	0	0	0	0	0,59	2,13	0	2,72	0	0
Blackcap	0	1,72	0	0	1,06	0	0	6,09	2,88	6,32	3,92	0,77	0,74	0	0	0	2,5	0	4,33	6,17	3,94	16,1	0	0
Icterine Warbler	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Willow Warbler	0	10,34	0	0	0	0	0,35	0,92	1,25	5,26	0	0	0	4,44	20,97	1,87	0	0	1,64	4,89	0	13,2	0	0
Wood Warbler	0	0	0	0	0	0	0	0	0	0	0	0	0,74	0	0	0,93	3,43	0	0,42	0	0	0,42	0	0
Chiffchaff	0	0	0	0	0	0	1,76	6,9	4,42	5,26	0	0	0,74	0	0	0	0	0,53	7,18	3,19	1,69	15,09	0	1,18
Grasshopper Warbler	0	0,57	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Goldcrest	0	0	15	7,69	15,15	22,5	20,59	3,1	9,13	0	0	0	0	1,11	1,61	0,93	0,71	0	0,42	3,62	14,56	18,6	0	0
Pied Flycatcher	0	0	0	0	0	0	0	0	0	0	0	0	0,37	0	0	3,74	3,57	0	0	0	0	0	0	0
Spotted Flycatcher	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1,43	0	0,63	0	0,31	0,94	0	0
Blackbird	0	2,64	0	3,85	1,52	2,5	0	0,92	1,92	5,26	1,96	0	0,37	1,11	1,61	2,8	3,21	0	1,72	5,96	3,06	15,74	0	0
Songthrush	0	2,3	0	7,69	0	0	1,18	0	0	0	0	0	0	0	0	1,87	0	0	1,72	2,13	5,88	17,23	0	0
Mistlethrush	0	0	0	0	0	0	1,18	0,8	0	0	0	0	0	0	0	0	0,71	0	0,42	0	1,25	1,67	0	0
Robin	0	0	0	0	3,03	0	2,35	2,3	2,6	5,26	4,71	0,66	1,1	2,89	1,61	1,87	5,64	0,7	2,94	2,13	5,75	15,69	1,37	0
Redstart	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coal Tit	0	0	0	6,15	10,61	5,63	10,12	2,87	2,88	0	0	0	0	0	0	0,93	0,71	0	0,97	4,04	11,94	16,95	0	0
Marsh Tit	0	0	0	0	0	0	0	0,57	0,96	3,68	0	0	0,74	0	1,61	4,67	3,57	0	2,65	0	0,44	3,08	0	1,18
Great Tit	0	0,57	0	0	0	0	1,18	1,95	0,77	0	1,96	0,44	2,21	1,11	1,61	14,25	10,43	0	8,19	3,19	1,25	12,63	0,98	1,18
Blue Tit	0	0	0	0	0	0	0	0	0	2,11	0	0,77	0	0	0	7,94	5,71	0	2,06	0,64	1,44	8,3	0	1,18
Crested Tit	0	0	0	3,85	1,52	0	2,35	1,15	2,6	0	0	0	0	2,22	3,23	0	0	0	0,88	0	3,69	4,57	1,37	0
Long-tailed Tit	0	0	0	0	0	0	0	0	0	0	0	0	0	1,11	0	0	0	0	0	0	0	0	0	0
Nuthatch	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1,87	2,14	0	1,26	0	0	1,26	0	0
Treecreeper	0	0	0	0	0	0	0,82	0,8	0	0	0	0,66	1,47	0	0	3,74	3,57	0	2,69	0	1	3,69	1,57	0
Chaffinch	0	0,57	12,5	21,54	24,32	3,75	20,82	8,05	13,46	4,21	0	3,08	5,51	0	1,61	12,15	11,07	0	7,52	1,28	9,19	20,49	12,75	4,24
Greenfinch	0	1,72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,5	0	0,21	0	0,31	0,52	0	0
Linnet	0	6,32	0	0	0	0	0	0	0	0	0	0	0	2,22	0	0	0	0	0	0	0	0	0	0
Redpoll	0	0,57	0	0	0	0	0	0	0	0	0	0	0	3,33	0,48	0	0	0	0	0	0	0	0	0
Bullfinch	0	0,57	0	0	0	0	0	0	0	0	1,96	0	0	0	0	0	0	0	0,13	2,77	0,25	3,14	0	0
Siskin	0	0	0	0	0	0	0	1,15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hawfinch	0	0	0	0	0	0	1,18	0	0	0	0	0	2,94	0	0	1,87	0,71	0	4,2	0	0	4,2	0	0
Yellowhammer	0	6,72	0	0	0	0	0	1,15	0	0	0	0	0	7,78	6,45	0	0	0	0	4,26	0,63	4,88	0	0
Reed Bunting	0	0	0	0	0	0	0	0	0	0	0	0	0	2,22	0	0	0	0	0	0	0	0	0	0
Whinchat	0	0	0	0	0	0	0	0	0	0	0	0	0	2,22	0	0	0	0	0	0	0	0	0	0
Starling	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5,23	1,43	0	1,26	0	0	1,26	0	0
Hooded Crow	0	0	0	0	0	0	0	0	0,96	0	0	1,1	0,74	0	0	0,93	0	0	0,67	1,06	0,56	2,3	0	0
Jay	0	0	0	0	3,03	6,25	0	0	0	0	1,96	1,1	1,47	0	0	0	0	0	0,42	1,06	1,56	3,05	0	0

transects were plotted 100 m apart (Fig. 2.2). At each fifth metre the presence or absence of living foliage was noted in the herb, shrub and canopy layer and additionally in the following height bands: 0-0.5 m, 0.5-2 m, 2-4 m, 4-6 m, 6-8 m, 8-10 m, 10-12 m, 12-16 m, 16-20 m, >20 m. Presence or absence of vegetation in different layers was assessed by looking through a tube with a diameter of 4 cm; less than half cover was scored as absence, more than half cover as presence (Fig. 2.3). Only presence was noted as + on the survey form. Together with + for presence of vegetation in a particular layer, the plant species concerned were noted (for the ground vegetation broad classes (e.g. grass) encompassing several species were used). Also leaf litter, dead wood (with a diameter over ca. 5 cm), and piles of dead branches higher than 0.5 m on the forest floor were registered with a + if present. Between registration points one walked with open arms and counted the number of shrub stems touched. Woody vegetation lower than four metres was regarded as shrub and higher than

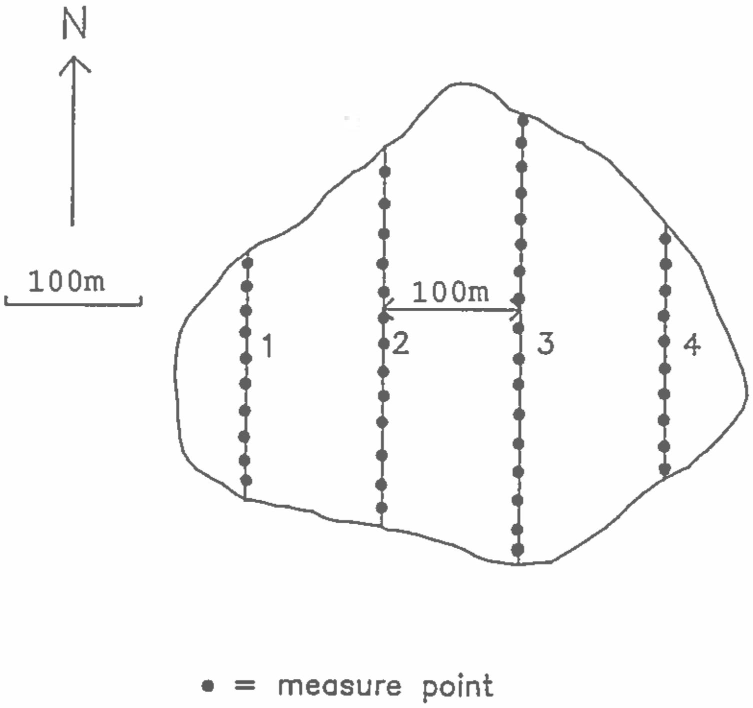


Figure 2.2. Positioning of vegetation transects (1-4) separated by 100 m in an imaginary woodland.

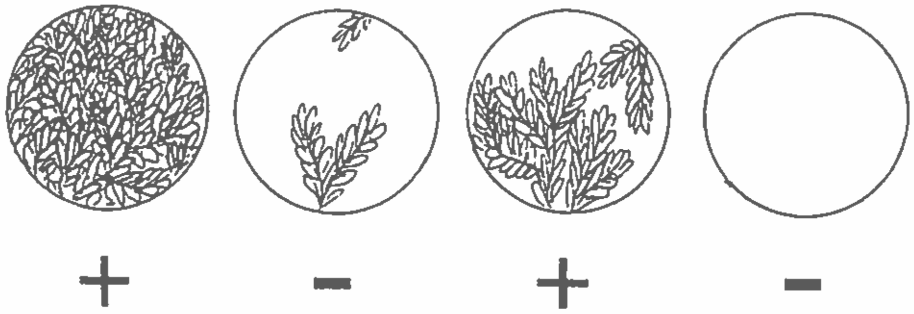


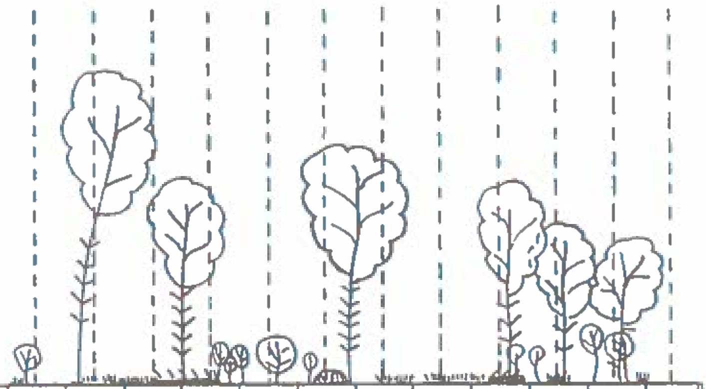
Figure 2.3. Examples of presence (+) or absence (-) of vegetation in a layer when looking through a tube with a diameter of 4 cm.

four metres as trees. At each fifth measure point a wooden cross was thrown on the ground and in every quadrant the following recordings of the nearest tree were taken: the distance to the cross, the species name, the diameter at breast-height, the height of the lowest green branch, the total height, and whether it was dead or alive (using a circle around the code if dead). The diameter and height of the tree were measured with a diameter-meter and a height-meter, respectively. Figure 2.4 shows an example of a transect and the vegetation survey-form.

For an accurate survey the number of measure points (and the length of the transect walked) will depend much upon the degree of uniformity of the forest concerned. For a very homogeneous forest 50 measure points (ca. 250 m), and for a very heterogeneous forest 100 or more measure points were taken.

2.2.2 Method of drawing the forest types

Line-transect drawings of all forest types were made in order to get a picture true to nature (Fig. 1.3). These are used for forestry studies and for clarifying the forest types for people reading this report. In a representative part of the forest type a measure tape of 15 or 30 m was laid, depending on the homogeneity of the forest structure. All trees, shrubs and herbs, whose vertical (crown) projections hit or overlapped with the tape, were drawn from the side. Of each tree or shrub the height, the lowest green branch, the width and shape of the crown, and vertical projection of the crown on the tape were measured.



Leaf litter	+	+			+	+		+			+	+
Dead wood			+	+					+			
Herb		Gr	Gr				He	He		Gr		
Shrub	Bs			Bs	Rf	Ri					Bs	
Canopy		Ps	Ps	Ps		Ps	Ps		Ps	Ps	Qp	
Shrub stems	1	0	0	0	3	2	0	1	0	2	1	1
Etc.												
Etc.												

Figure 2.4. The measurement of vegetation structure in horizontal and vertical direction and an example of a vegetation survey-form (see section 2.2.1, abbreviations refer to plant names mentioned in Appendix II).

The following rules were made when making the drawings:

- Stems of trees either alive or dead were depicted by a solid line, whose thickness is on scale with the diameter of the trees.
- Dead branches were stippled.
- Whenever possible, crown projections were depicted with a solid line.
- With each drawing of a tree or a shrub an abbreviation of the species name was given (see list of abbreviations in Fig. 1.3).

One problem arising with line-transect drawings is that a forest type is partly observed from beneath, whereas the drawings are horizontal projections. This may hinder the recognition of the forest type.

2.3 Forest structure and bird parameters

For each forest type 55 forest parameters (Table 2.3) and 40 bird parameters (Table 2.4) were calculated from the data obtained by the vegetation surveys and bird census. The actual values for the forest and bird parameters are given in Appendices III and IV, respectively.

Table 2.3. The 55 forest structure parameters (1-55, see Appendix III).

1. H(t) - the tree height (m).

2. H(lg) - the height of the lowest green tree branch (m).

3. De(t) - the percentage of dead trees.

4. Di(t) - the mean distance to the nearest tree (m).

5. σ(di) - the standard deviation of the distance to the nearest tree.

6. V(di) - the coefficient of variance of distance, defined as:

$$V(di) = \frac{\sigma(di)*100}{Di(t)}$$

The coefficient of variance expresses sample variability relative to the mean of the sampled distance. The greater the V(di), the more patchy the distribution pattern of trees; the smaller the V(di), the more regular the distribution pattern of trees.

7. diam(t) - the mean diameter of the measured trees (cm). This is a measure for the development (age) of the forest and for the stem surface (in view of stem foragers).

8. σ(diam) - the standard deviation of the diameter.

9. V(diam) - the coefficient of variance of the diameter, defined as

$$V(diam) = \frac{\sigma(diam)*100}{diam(t)}$$

This is a measure of variability in stem diameters.

10. H(s) - the shrub height (m).

11. S/are - the number of shrub-stems per are (100 m^2).

12. Cov(l) - percentage cover of leaf litter.

13. Cov(dw) - percentage cover of dead wood and tree stumps (both with a diameter over ca 5 cm) on the forest floor.

14. Cov(b) - the cover of piles of dead branches (higher than 0.5 m).

15. Cov(h) - the cover of the herb layer.

16. Cov(s) - the cover of the shrub layer.

17. Cov(t) - the cover of the canopy layer.

18. Cov(hst) - the total cover of herb, shrub and canopy layer.

19. FHD(hst) - the Foliage Height Diversity for herb, shrub and canopy layer combined, calculated with the Shannon-Weaver index:

$$FHD(hst) = -\sum_{i=1}^{3} (p_i * \ln p_i)$$

$$\text{where } p_i = \frac{\text{cov.layer } i}{\text{cov(hst)}}$$

20. SD(h) - the species diversity of the herb layer, calculated with the Shannon-Weaver index:

$$SD(h) = -\sum_{i=1}^{n} (p_i * \ln p_i)$$

in which n is the number of species present and p_i is the proportion of species in the herb layer.

21. SD(s) - the species diversity of the shrub layer.

22. SD(t) - the species diversity of the canopy layer.

23. SD(hst) - the total species diversity: parameters 20, 21, 22 summed.

24. Het(h) - the heterogeneity of the herb layer. The heterogeneity is calculated per transect of 50 points as:

$$Het(h) = {}^{10}\log(1 + (p * dp * da))$$

where:
p = the number of groups with presence scores,
dp = the number of different sized groups with presence scores,
da = the number of different sized groups with absence scores.

25. Het(s) - the heterogeneity of the shrub layer.

26. Het(t) - the heterogeneity of the tree layer.

27. Het(hsd) - the total heterogeneity for herb, shrub and tree layer: parameters 24, 25 and 26 summed.

The division of forest types into herb, shrub and canopy layer was made in order to investigate its value for this research. However, this has caused some errors in data analyses, because trees in young forest types were regarded as canopy; in fact they were no more than 'shrubs'. This affected the above parameters expressing cover, foliage height diversity, heterogeneity and species diversity. For a more objective, and thus better method of data gathering, each forest type was divided into four layers: 0-0.5 m, 0.5-6 m, 6-16 m, and >16 m. For each layer the cover (parameters 28-31), the species diversity (parameters 33-36) and the heterogeneity (parameters 38-41) were calculated. In addition, total cover (parameter 32), total species diversity (parameter 37), total heterogeneity (parameter 42) and foliage height diversity (parameter 43) were calculated, using the four layers.

For calculating the vegetation mass present in a forest type, a division into 10 layers was made: 0-0.5 m, 0.5-2 m, 2-4 m, 4-6 m, 6-8 m, 8-10 m, 10-12 m, 12-16 m, 16-20 m, and >20 m. The cover for each layer (parameter 28, and parameters 44-52 starting from cover of the layer between 0.5 and 2 m), total cover (parameter 53) and foliage height diversity (parameter 54) for the 10 layers combined were calculated. Vegetation mass (parameter 55) was calculated as volume vegetation per unit area (m^3/m^2), measured from the wood profiles as the area enclosed by the curve (Fig. 2.5). For all the covers the 'cover' in a layer is the added cover per meter in that layer.

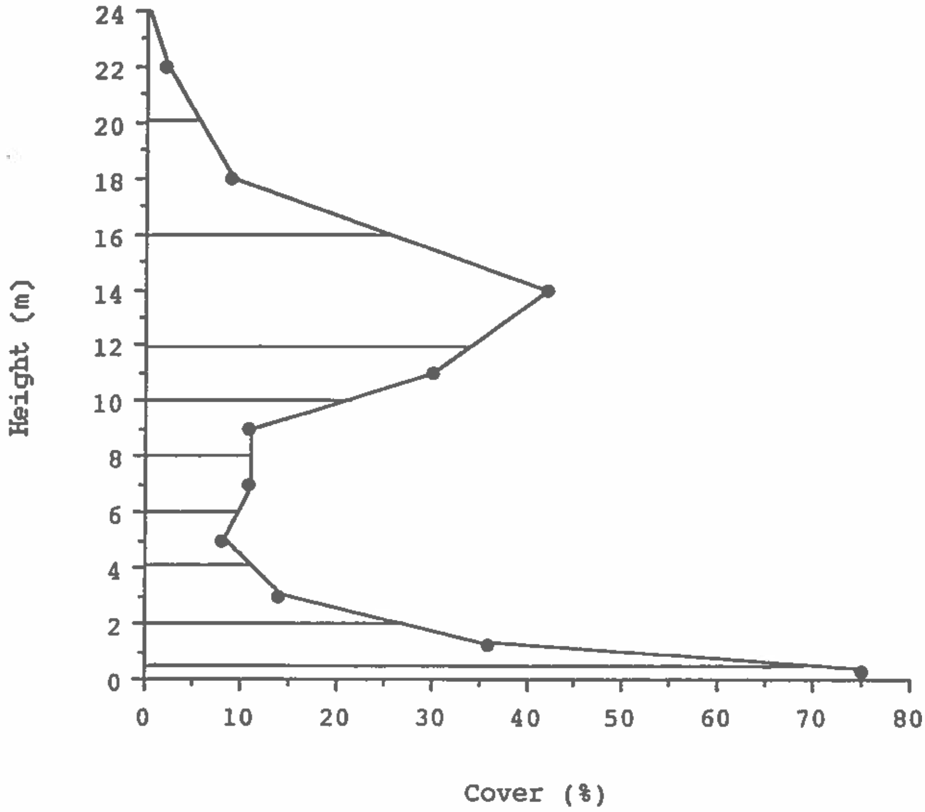


Figure 2.5. Wood profiles (as % cover in each layer) of forest types (see also section 1.5, Fig. 1.3).

Table 2.4. The 40 bird parameters (56-96, see Appendix IV).

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56. S - the number of territorial species of birds.

57. S′ - the area-corrected number of species, or ′species density′:

$$S' = S/A^{0.2}$$

in which A is the area in ha. Thus the theoretical number of species on one hectare is estimated (see also section 3.1)

58. D - total density of all occurring species.

59. BSD - the Bird Species Diversity, calculated with the Shannon-Weaver index:

$$BSD = -\sum_{i=1}^{S} (p_i{*}\ln(p_i))$$

in which S is the number of bird species and p_i is the proportion species i constitutes in the total density D: $p_i = D_i/D$.

60. Y - Yule′s index of diversity (Williams 1964):

$$Y = D^2/\sum_{i=1}^{S}(D_i^2)$$

which is the simplified form of the original formula. In this formula D is the total density of all the birds and D_i is the density of species i. The Yule′s index is a measure of the chance that, if two occurrences are taken at random, they will not be of the same species (Yapp 1979).

61. PIE - the Probability of Interspecific Encounter (Hurlbert 1971) is yet another index which can be used as a diversity index:

$$PIE = 1 - \sum_{i=1}^{S}(p_i^2)$$

This index is a measure of the chance that, if one enters the bird community and encounters two birds at random, these birds belong to different species.

62. E - the evenness of distribution of bird numbers among the occurring species:

$$E = BSD/\ln(S)$$

The evenness is maximal when all species are present in equal numbers.

63. DI - the Dominance Index:

$$DI = (D1 + D2)/D$$

in which D1 and D2 are the densities of the two most numerous species and D is the total density of all species.

The now following parameters are densities of ecological groups; groups of bird species which are related in the way in which they use their habitat for breeding or foraging (information was used from ′Fuglene i

Danmark' by H. Meltofte and J. Fjeldså (1989)). If a species belonged to more than one group within either breeding or foraging groups, then equal proportions of its density were allocated to these groups (proportions between brackets). It is expected that birds belonging to an ecological group will react in the same way on certain structural parameters of the forest.

Birds grouped according to breeding-site selection (parameters 64-72):

64. S(hob) - the number of bird species breeding in holes: Green Woodpecker, Great-spotted Woodpecker, Great Tit, Blue Tit, Coal Tit (½), Crested Tit, Marsh Tit, Nuthatch, Treecreeper, Spotted Flycatcher, Pied Flycatcher, White Wagtail (½) and Starling.

65. S(nhb) - the number of occurring bird species not breeding in treeholes:

S(nhb) = S - S(hob)

66. D(hob) - the density of all bird species breeding in treeholes (for species see S(hob)).

67. D(nhb) - the density of bird species not breeding in treeholes.

68. D(hoc) - the density of holecutters: Green Woodpecker, Great-spotted Woodpecker and Crested Tit.

69. D(hbnc) - the density of holebreeders that are not holecutters:

D(hbnc) = D(hob) - D(hoc)

70. D(grb) - the density of bird species breeding on the ground: Woodcock, Coal Tit (½), Whinchat, Robin, Grasshopper Warbler, Wood Warbler, Tree Pipit, White Wagtail (½), Yellowhammer and Reed Bunting.

71. D(shb) - the density of bird species breeding in shrubs: Long-tailed Tit, Wren, Songthrush, Blackbird, Blackcap, Garden Warbler, Whitethroat, Lesser Whitethroat, Willow Warbler, Chiffchaff, Dunnock, Red-backed Shrike, Greenfinch, Sisken, Linnet, Redpoll and Bullfinch.

72. D(cab) - the density of bird species breeding in the canopy of the forest: Wood Pigeon, Hooded Crow, Jay, Mistle-thrush, Goldcrest, Hawfinch and Chaffinch.

Birds grouped according to foraging behaviour during the breeding season (parameters 73-77):

73. D(grf) - the density of bird species foraging on the ground: Woodcock, Wood Pigeon, Green Woodpecker (½), Hooded Crow, Jay (½), Great Tit (1/3), Wren (½), Mistlethrush, Songthrush, Blackbird, Whinchat, Robin (½), Grasshopper Warbler (½), Spotted Flycatcher (½), Dunnock (½), Tree Pipit, White Wagtail, Red-backed Shrike (½), Starling, Greenfinch (½), Chaffinch (½), Yellowhammer (½) and Reed Bunting (½).

74. D(shf) - the density of bird species foraging in shrubs: Great Tit (1/3), Blue Tit (½), Marsh Tit (½), Long-tailed Tit, Wren (½), Robin (½), Grasshopper Warbler (½), Blackcap (½), Garden Warbler, Whitethroat, Lesser Whitethroat, Willow Warbler, Chiffchaff (½), Dunnock (½), Greenfinch (½), Linnet, Redpoll (½), Bullfinch, Yellowhammer (½) and Reed Bunting (½).

75. D(caf) - the density of bird species foraging in the canopy: Jay (½), Great Tit (1/3), Blue Tit (½), Coal Tit, Crested Tit, Marsh Tit (½), Blackcap (½), Chiffchaff (½), Wood Warbler, Goldcrest, Pied Flycatcher (½), Sisken, Redpoll (½), Chaffinch (½) and Hawfinch.

76. D(aif) - the density of air-foragers: Red-backed Shrike (½), Spotted Flycatcher (½) and Pied Flycatcher (½).

77. D(stf) - the density of bird species foraging on stems: Green Woodpecker (½), Great-spotted Woodpecker, Nuthatch and Treecreeper.

In the following parameters the densities of individual bird species or bird species groups were taken, because they occurred in different densities depending on the forest type and may therefore be good indicator species or indicator groups (parameters 78-95). The abbreviation between brackets is the first character of the genus and the species name, respectively, of the bird species (Appendix II):

78. D(cp) - density of Woodpigeons.

79. D(wp) - the total density of woodpeckers (in this study: Green Woodpecker and Great-spotted Woodpecker).

80. D(pm) - density of Great Tits.

81. D(pa) - density of Coal Tits.

82. D(tt) - density of Wrens.

83. D(tp) - density of Songthrushes.

84. D(tm) - density of Blackbirds.

85. D(er) - density of Robins.

86. D(sa) - density of Blackcaps.

87. D(sapmo) - density of Blackcap and Dunnocks (both species are typical shrub-foragers and shrub-breeders).

88. D(sy) - density of occurring *Sylvia* species: Blackcap, Garden Warbler, Whitethroat and Lesser Whitethroat.

89. D(pt) - density of Willow Warblers.

90. D(ph) - density of occuring *Phylloscopus* species: Willow Warbler, Chiffchaff and Wood Warbler.

91. D(rr) - density of Goldcrests.

92. D(at) - density of Tree Pipits.

93. D(cc) - density of Hawfinches.

94. D(fc) - density of Chaffinches.

95. D(pafc) - density of Coal Tits and Chaffinches (both species are canopy-foragers and canopy-breeders).

2.4 Clustering method of vegetation and bird parameters

The aim of the analysis is to find the structure within and between groups of vegetation and bird parameters. For the set of all vegetation and bird parameters, 95 in total, a correlation matrix was calculated (Table 4.1, chapter 4). It was impossible to recognize the structure in this large correlation matrix. Therefore the vegetation and bird parameters were rearranged separately and reduced using the VARCLUS procedure described in the SAS/ STAT^{r} User's Guide (1988). This showed the groups in the variables and therefore offered the opportunity to reduce the dimension of the problem.

The first step was to reduce the bird parameters to logical, easily understandable groups. The result was a correlation matrix in which bird variables which correlated strongly were grouped together. In this matrix triangles of high correlation coefficients were placed just below the diagonal showing the groups of variables. This procedure was repeated for the vegetation parameters. Thereafter both rearrangements were combined yielding the structured matrix (Table 4.1). Blocks of comparable correlation coefficients indicated the correlations between different groups.

In order to reduce the dimensionality, parameters belonging to a group were replaced by a 'group parameter'. The 95x95 matrix was thus reduced to a 15x15 matrix (see Tables 3.1 and 3.3). In this matrix the values of each parameter were standardized to a mean of 0 and a standard deviation of 1. For each forest type (i) the group-parameter (z_i) was calculated as the mean value of the standardized parameters within one group:

$$z_i = 1/J_g {}^* \sum_{j=1}^{J_g} ((y_{ij}-m_j)/sd_j)$$

where: J_g = number of variables within group g
y_{ij} = value of parameter j for forest type i
m_j = mean value of parameter j
s_{dj} = standard deviation of parameter j

The correlation coefficients between groups indicate how groups of bird parameters will react on groups of forest parameters.

The question may arise why not all variables have been treated together with the VARCLUS-method, in order to get mixed groups of forest and bird variables. In fact this was done in the beginning of the analysis, but yielded rather poor results, caused by the fact that the correlation levels of the bird parameters were, in general, higher than those of the vegetation parameters. Thus only few forest parameters were put in groups together with bird parameters and hardly any mixed groups (as hoped for) were obtained. Another reason for treating bird and vegetation parameters separately and putting them together later on was that only 'pure' forest groups and 'pure' bird groups can be reduced to logical, easily understandable group parameters.

It must be stressed that significantly non-linear relations will not be detected when using the VARCLUS method starting from a matrix of linear correlation coefficients. However, this method revealed a large part of the coherence between the vegetation and bird parameters.

A problem in this analysis, in which variables are lumped, is that one cannot point out one single variable in a group as the (real) determining one. This is however to a large extent only a theoretical problem because in the management of forests one can never treat 'single variables'. The forest structure can be seen as a complex of the groups of parameters which had been detected. These groups can be used as a measure in dealing with the forest and can be treated separately to a certain extent.

3 Results

3.1 The meaning of bird parameters concerning richness and diversity

3.1.1 The area corrected number of bird species

In recent years great interest was shown in the relationship between the size of an area and the birdlife which it holds. This interest was stimulated by the theory of island biogeography (MacArthur & Wilson 1967), which provided a theoretical background to the observations that larger, less isolated islands tended to have more species of breeding landbirds than did small, more isolated islands. Since the start of studies on bird communities parameters have been used to express the richness of the bird community as a whole. At a very early stage the number of species (S) and the total density of all bird species together (D) were used (Peet 1974). Many authors have treated woodlands as 'habitat islands', and have shown that larger woods tend to have more breeding bird species than smaller woods (Williams 1964, Opdam & Van Bladeren 1981, Komdeur & Vestjens 1982). Although such a result indicates that given the choice it would usually be better to protect a single large woodland than a single small wood, even that is not unquestionably true. For example, a wood whose bird community consisted solely of Goshawks which preyed upon Black Grouses (an admittedly unlikely scenario) would be rated by most people as of high conservation interest, whereas a community with many more species, all of which were very common, widespread species, would almost certainly be rated more moderately. The point is that species-area relationships predict the number of species which will occur in a wood, but do not of themselves predict which species they will be, and conservation value is critically related to the identity of the species present. The precision with which even species number can be predicted is in fact so low that it would be rash to use the general relationship between area and species richness, for example, to formulate a strategy for woodland reserve acquisition.

Despite this, the species-area relationship itself is of ecological interest. Also in this study a significant positive relation exists between woodland area (A) and the number of species in a certain forest type ($r=76$, $p<0.001$; $S = 0.643*A + 7.598$). Larger woods were found to contain a larger number of species than smaller woods, and as a rough guide it is suggested that to double the number of species to be found in a wood it is necessary to increase the size of a wood 5.2-fold. A 10-fold increase was found in a study in British woods by Moore and Hooper (1975). However, an uncritical acceptance of Moore's and Hooper's 10-fold rule would be unwise. The work of Woolhouse (1983) showed that biases in surveying effort can greatly affect the observed species-area relationship, and Fuller (1982) suggested that the form of the species-area relationship differs from region to region in the British Isles.

In order to eliminate the influence of the area, an area corrected number of species (S') was introduced (Gleason 1992, Williams 1964). The relation between the number of species and the area (A) for a particular habitat is exponential, expressed by the following formula:

$$S = S'*A^z$$

where S' is the number of species to be expected in an area of one hectare (S' is also called the species density), and z is a constant dependent on the type of animals studied. S' depends mainly on the structure of the forest type, and has also been used in other studies (e.g. Opdam & Van Bladeren 1981, Komdeur & Vestjens 1982). For each woodland type S' has a certain value independent of the area. When z is known, the above formula can be used to calculate S'. This is essential for our research because forest types vary considerably in size, ranging from 1.2 ha to 51.4 ha (see section 1.5). When plotting log S versus log A, z can be calculated as the slope of the regression line (Fig. 3.1), defined as:

$$\log S = \log S' + z*\log A$$

The increase in number of species was linear and did not level off to a maximum for larger areas (there was no significant relation between S and A^z, after A was accounted for). However, other studies found that the increase in number of species was not linear, but levelled off to a maximum for larger areas (Preston 1960). Therefore z becomes smaller for bigger areas. In Fig. 3.1 all forest types have been plotted, but in fact the above theory is only valid for different sized plots of a certain forest type. As in this research no species numbers for parts of the forest types are known, it is impossible to calculate the z-value. For the calculation of S' a z-value of 0.2 has been used, obtained from a Dutch research (Opdam & Van Bladeren 1981).

A finding which is related to the existence of species-area relationships is that some particular species are found in a greater proportion of large woods than of small woods. This suggests that certain species require woods of above a certain critical size before they will occupy them. If so, this could be of great conservation importance; it would suggest that steps should be taken to protect the integrity of current sites and perhaps to manage unused sites in such a way that their size increased. The species most likely to show minimum area effects will be those who hold large territories and hunt only inside single woods. Most of the species with large territories in Denmark which might fall into this category are raptors, such as Goshawks, which spend much of their time hunting for prey inside the single wood in which they nest.

In the present research the number of species (S), and especially the species density (S'), are strongly correlated with the total density (D; Fig. 3.2). The same correlations are found in other researches (e.g. Janse & Kessler 1981, Komdeur & Vestjens 1982, Opdam & Van Bladeren 1981).

3.1.2 Breeding bird richness

With a given density and number of species it is, however, (at least theoretically) possible that the proportions of the individual species are largely different. For example for D=50 and S=5 one could have 20, 10, 10, 5 and 5 territories or 40, 5, 3, 1 and 1 territories. To express this difference in diversity (with the second

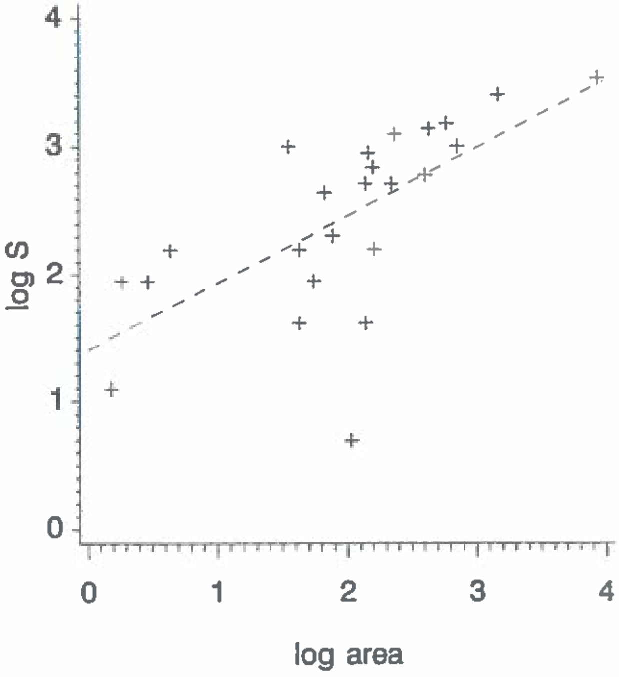


Figure 3.1. Relationship between numbers of bird species (S) and forest area (log area) (r=76, p<0.001, y = 0.528x + 1.403).

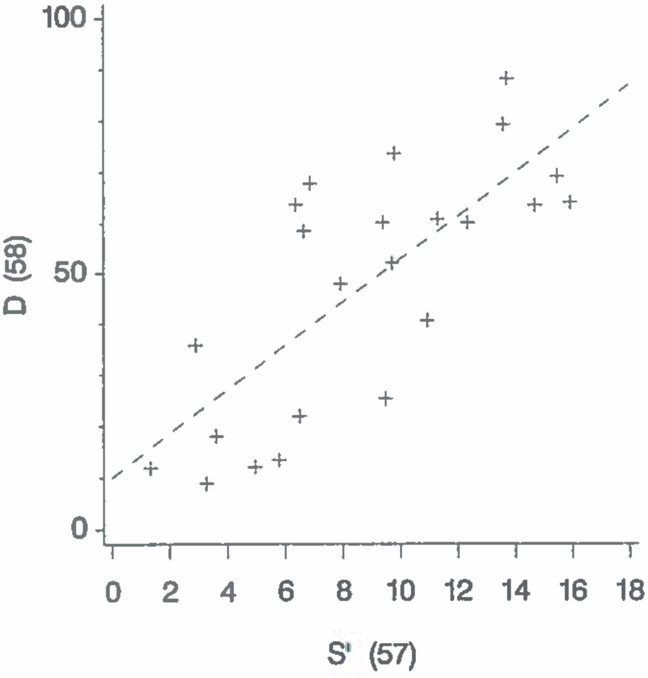


Figure 3.2. Relationship between bird species density (S') and total density (D) (r=78, p<0.001, y = 4.648x + 8.079).

example being less diverse than the first because one species is very dominant) some diversity-indices have been devised, of which the Shannon-Weaver index is the most widely used (Shannon & Weaver 1949; for formula see section 2.3.2). For a given number of species the Shannon-Weaver index reaches a maximum value, when the birds are evenly distributed over species (for the above mentioned example 10 territories for each species). Then BSD is equal to lnS:

$$BSD_{max} = -(\Sigma p_i{*}\ln p_i)_{max} = -S{*}1/S{*}\ln(1/S) = \ln S$$

Generally, BSD is strongly correlated with S (in this research: r=77, p<0.001). To eliminate this relation the evenness index (E = BSD/lnS) is often used (e.g. Erdelen 1978, Komdeur & Vestjens 1982, Opdam & Van Bladeren 1981); it is a measure for the evenness of distribution of numbers over species. Its maximum value is 1, which is reached when the BSD is at its maximum (lnS); all species are present in equal numbers. However, E has proved to be very similar for poor and rich (in terms of S and D) bird communities (Fig. 3.3). When the factor S is eliminated nothing much remains of the BSD index. Therefore the BSD index is of little value, at least in this field of ornithological study. It is better to use the much simpler indices S and D (in most cases even one of these is sufficient). Only if two bird communities with (approximately) the same S and D have to be compared, BSD (or E) may be useful.

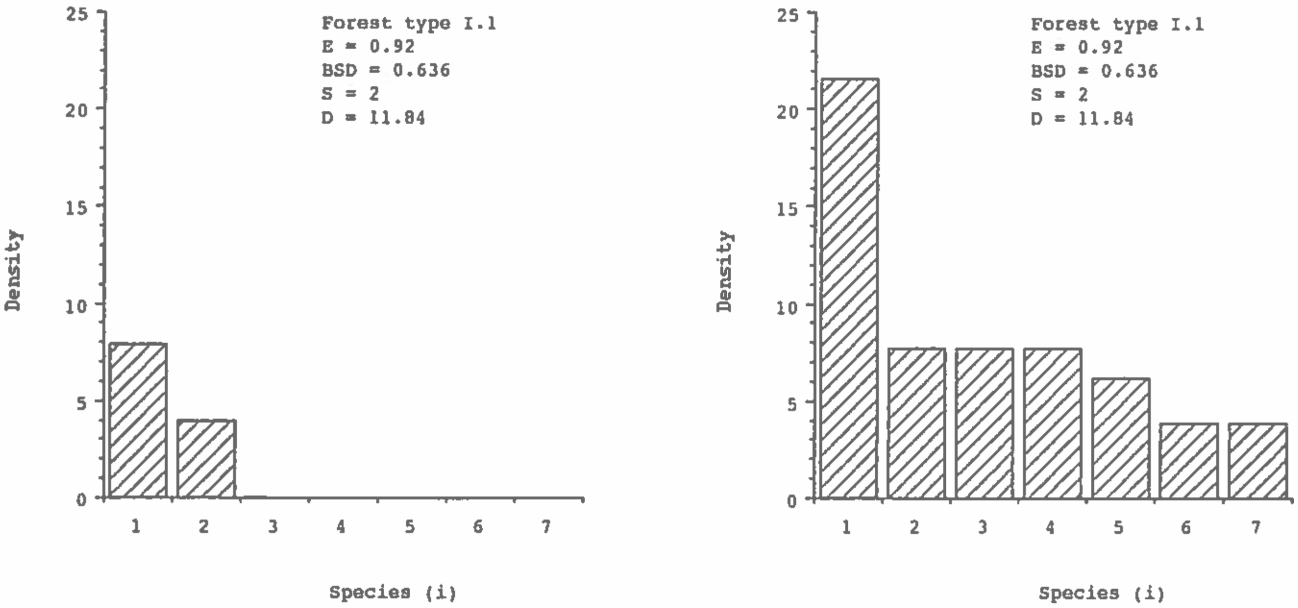


Figure 3.3. An example of a rich (forest type I.1) and a poor forest (forest type I.4) in terms of birds with very similar E, showing that the difference in BSD is largely due to difference in S (same species numbers do not necessarily refer to same bird species).

Two other diversity indices, Yule's index Y and an index named PIE, were used to assess their value for this type of research (see section 2.3.2). Figure 3.4 shows the maximum value (for E=1) of BSD, Y and PIE for a given number of species. Over a certain interval with low values of S, the PIE index increases more than the BSD index, but over the same interval with high values of S the increase is smaller. Y, however, increases linearly with S. It is clear that PIE and BSD chiefly express differences for low species numbers and become less discriminative at higher values of S, whereas Y shows no such pattern. This is caused by the fact that the maximum BSD, PIE and Y are lnS, 1-1/S, and S, respectively (Fig. 3.4). Therefore Y is probably a better parameter for research on communities with many species.

For the three diversity indices the evenness index varies most, and has thus highest discriminative ability when values of Y are used (Fig. 3.5).

For a bird community it is important to know how evenly the bird numbers are distributed among the species. The evenness index appeared not to be a good measure. The dominance index (DI, see section 2.3.2.) can provide useful information. A significant negative correlation exists between the bird species density (S') and the dominance index (Fig. 3.6). In other words, the higher the number of species the smaller the dominance index, and thus the less dominating the most numerous species.

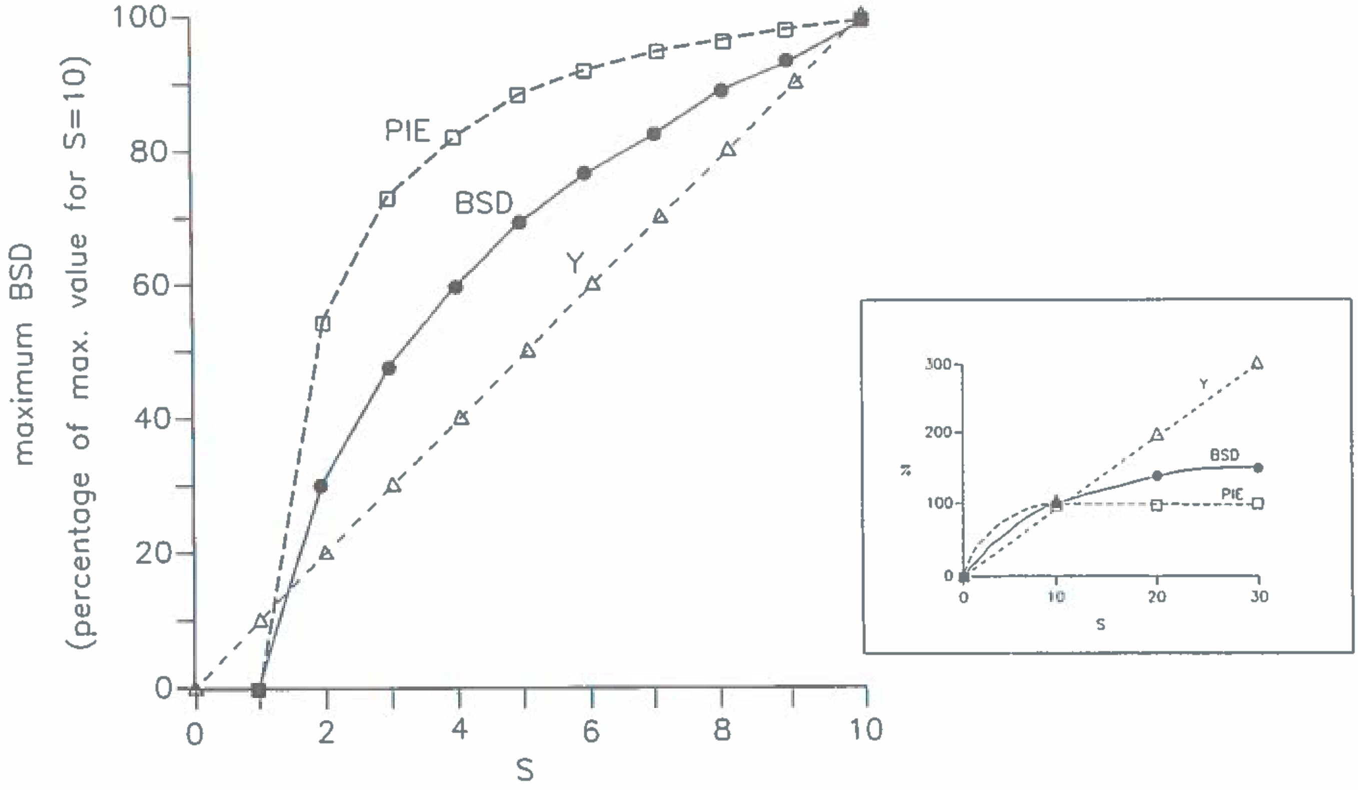
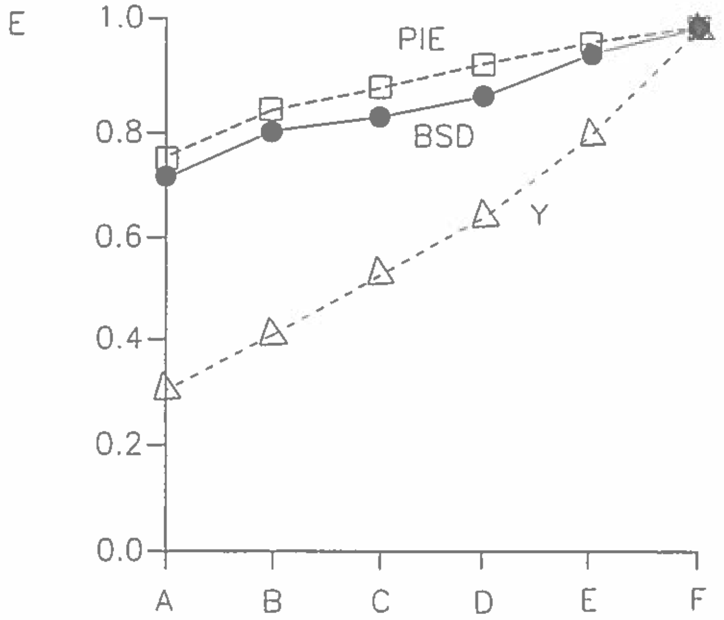


Figure 3.4. Maximal values for the three diversity indices BSD, Y and PIE in relation to the number of bird species S (maximum value is reached when E=1; BSD_{max} = ln S, Y_{max} = S, PIE_{max} = 1 - 1/S).



A: 11, 1, 1, 1, 1, 1, 1, 1, 1, 1
B: 9, 2, 2, 1, 1, 1, 1, 1, 1, 1
C: 6, 6, 1, 1, 1, 1, 1, 1, 1, 1
D: 5, 4, 2, 2, 2, 1, 1, 1, 1, 1
E: 3, 3, 3, 3, 3, 1, 1, 1, 1, 1
F: 2, 2, 2, 2, 2, 2, 2, 2, 2, 2

Figure 3.5. The evenness (E) calculated as the actual value divided by the maximum value of the bird diversity indices of BSD, Y and PIE for six hypothetical cases with S=10 and D=20 (Inset shows the evenness for S values between 0 and 30).

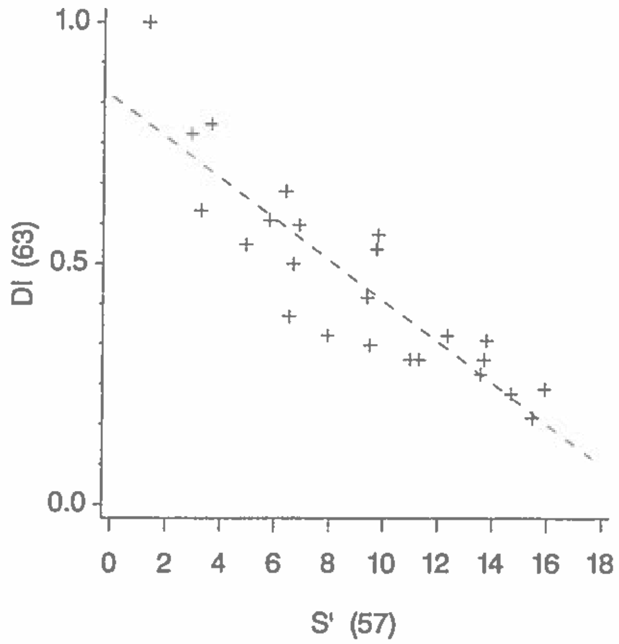
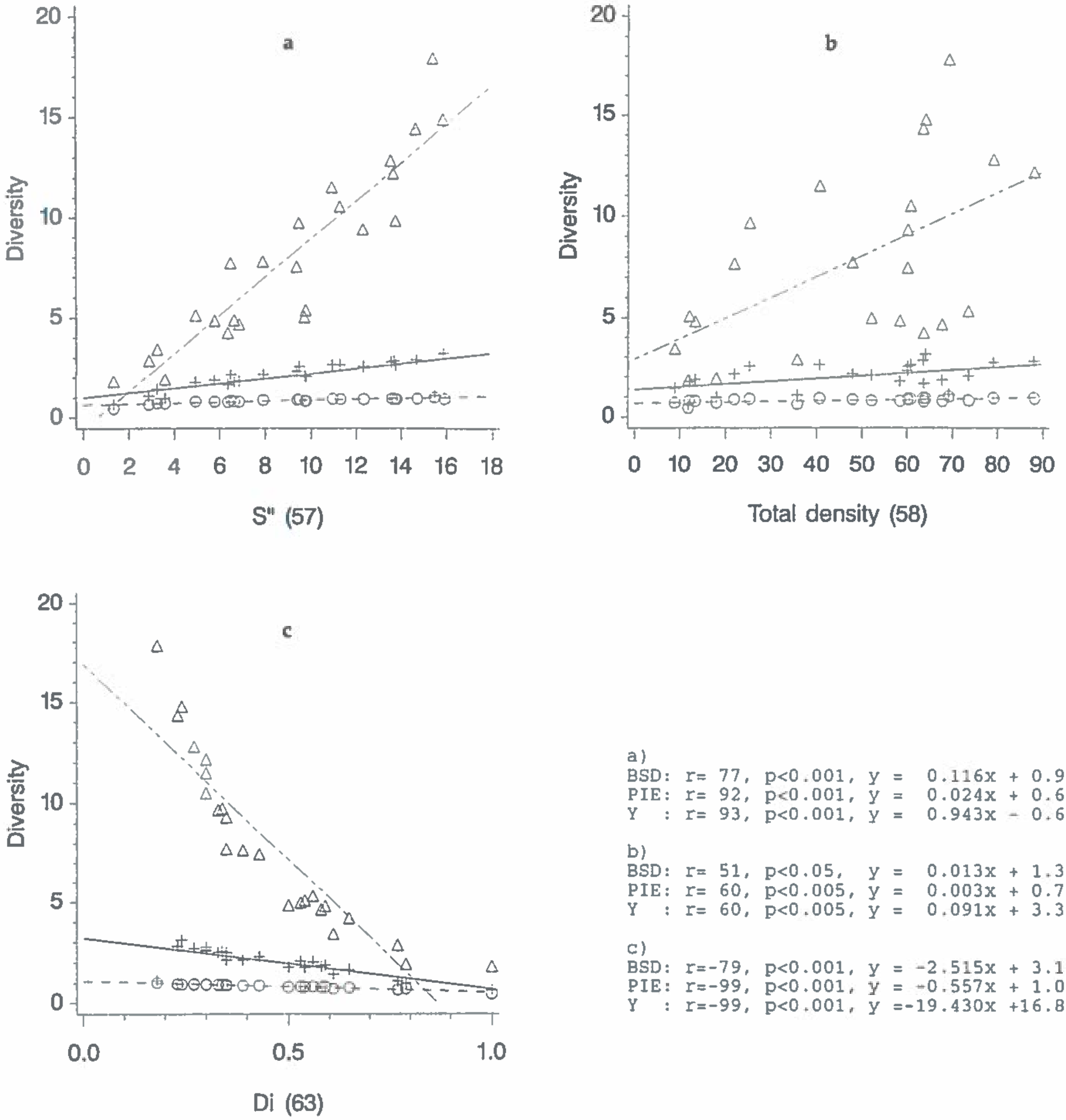


Figure 3.6. Relation between bird species density (S') and the dominance index (DI) (r=-90, p<0.001, y = -0.043x + 0.047).

The diversity indice BSD is correlated with bird species density (S') and total density (D) (Fig. 3.7). Instead of the three diversity indices easier calculable indices can be used. Therefore the term breeding bird richness can be used as a substitute to measure the ecological value of bird communities.



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a)
BSD: r= 77, p<0.001, y =  0.116x + 0.991
PIE: r= 92, p<0.001, y =  0.024x + 0.613
Y  : r= 93, p<0.001, y =  0.943x - 0.619

b)
BSD: r= 51, p<0.05,  y =  0.013x + 1.375
PIE: r= 60, p<0.005, y =  0.003x + 0.701
Y  : r= 60, p<0.005, y =  0.091x + 3.317

c)
BSD: r=-79, p<0.001, y = -2.515x + 3.198
PIE: r=-99, p<0.001, y = -0.557x + 1.086
Y  : r=-99, p<0.001, y =-19.430x +16.881
```

Figure 3.7. Relationship between diversity indices (BSD, Y, PIE) and bird species density (S'in a), total bird density (D in b) and the dominance index for birds (DI in c) (correlation coefficients (r), critical values (p) and regression lines are given).

3.2 Forest characteristics and breeding birds

The patterns of habitat distribution that we observe are a consequence of decisions made by individual birds in selecting a place in which to establish a breeding territory. A great many factors influence these decisions, and differences in the effects of these factors produce variation in habitat occupancy patterns both within and between species. A thorough understanding of why birds occur where they do would be very useful in assessing the impact of forestry on birds. This chapter describes the association of forest characteristics with variations in the distribution or abundance of bird species. In this chapter some of the basic determinants of habitat selection by woodland birds will be mentioned. In the next chapter the general principles which lie behind bird distribution in woodland habitat will be discussed. The relation between forest structure and breeding birds was analyzed by means of a correlation matrix of the set of all vegetation and bird parameters (Table 3.1).

3.2.1 Forest succession

All bird species are restricted, to various degrees, in the range of habitats they occupy. By definition, the members of a local community share at least portions of their habitat ranges, but as one moves between different forest types, some species disappear and others appear (see Table 3.2). Such patterns are seen most clearly by following the changes in bird populations that occur during the succession that follows clear-cutting of forests. Here the bird fauna of the conifer stands were studied comprising the succession series (forest types I.1 - I.9): open conifer stand, young, early dense and closed conifer stands, conifer thickets, mature conifer stands without and with shrub understorey.

Commercial forests are always changing so it is meaningless to talk about 'typical' birds of plantations without stating the stage of the succession. The birds present in each successive stage of commercial coniferous plantations differ in accordance with species-specific habitat requirements related to nest sites, cover, food, foraging sites, and so on (Fig. 3.8). The newly planted stands held rather few bird species; Wrens and Tree Pipits. Wrens were present because of the presence of piles of dead branches, and Tree Pipits because their preying habit (feeding at least partly in the air) requires plenty of space. For this reason the latter was absent from closed stands. As trees grew, the Tree Pipits fell in numbers, and were replaced by birds whose characteristic habitat is shrub. At this stage the dominant species was the Willow Warbler, and to a certain extent Dunnock, Yellowhammer and Whitethroat. As the trees grew taller and the canopy closed, Willow Warblers and other shrub species were replaced by species characteristic of true woodland: Chaffinches, Goldcrest and Coal Tits. At a later stage with a more open canopy and more shrub as a direct result of more penetration into the wood by sunlight the shrub-loving birds increased.

It is often overlooked in the arguments about the value of commercial plantations that birds inhabiting the early stages of the forest cycle are every bit as much 'forest birds' as those which live in mature trees. And when the crop is harvested, the

Table 3.1. Correlation matrix of the 55 vegetation and 40 bird parameters, rearranged separately using the VARCLUS procedure (see sections 2.4 and 3.3 concerning method and results).

	18	49	50	53	32	43	42	11	16	19	44	25	27	20	21	23	33	34	37	6	17	47	48	54	30	40	3	10	22	35	36	14	45	46	29	39	24	38	9	12	15	28	2
				V1									V2										V3						V4					V5				V6			V7		
18. Cov(hat)	100																																										
49. Cov(10-12)	49																																										
50. Cov(12-16)	61	91																																									
53. Cov(0->20)	70	82	82																																								
32. Cov(0->16)	85	66	74	91																																							
43. FHD(4)	71	67	71	91	89																																						
42. Het(0->16)	69	64	60	84	83	95																																					
11. S/area	45	33	39	34	31	39	44																																				
16. Cov(m)	43	20	35	15	20	30	37	70																																			
19. FHD(hat)	57	19	37	22	30	38	41	70	92																																		
44. Cov(0.5-2)	29	-21	-8	3	12	12	15	50	41	47																																	
25. Het(m)	42	22	34	22	23	34	44	67	95	85	43																																
27. Het(hat)	29	2	14	3	4	19	25	63	81	88	52	76																															
20. SD(h)	7	3	8	-2	-2	13	26	50	51	43	28	46	51																														
21. SD(m)	40	22	32	17	16	28	37	83	90	87	45	84	84	64																													
23. SD(hat)	47	27	40	24	36	39	49	66	78	74	37	71	58	72	80																												
33. SD(0-0.5)	19	-4	13	-0	2	12	20	67	74	72	49	67	77	76	86	69																											
34. SD(0.5-6)	55	8	23	20	40	45	51	44	67	68	47	63	44	44	56	78	41																										
37. SD(0->16)	59	22	40	28	46	49	54	53	80	80	39	71	57	52	70	89	59	91																									
6. V(di)	-5	-25	-21	-36	-22	-24	-22	-6	24	32	18	21	52	33	21	18	22	38	20																								
17. Cov(t)	22	53	43	64	53	44	41	-3	-36	-45	-22	-24	-59	-16	-34	-17	-35	-21	-24	-67																							
47. Cov(6-8)	6	50	27	54	39	44	44	-5	-32	-44	-32	-21	-54	-19	-29	-12	-43	-15	-22	-60	78																						
48. Cov(8-10)	6	70	53	54	41	49	52	5	-10	-22	-46	-5	-35	7	-7	18	-22	-2	8	-37	59	80																					
54. FHD(10)	59	80	78	94	83	92	88	40	22	24	6	27	9	8	24	31	6	29	37	-25	57	54	60																				
30. Cov(6-16)	22	80	72	60	50	45	50	20	3	-11	-33	5	-26	11	6	29	-10	4	12	-36	65	68	86	63																			
40. Het(6-16)	49	41	27	53	52	62	69	38	4	7	9	16	3	12	13	12	-10	30	15	-26	43	49	34	59	29																		
3. De(t)	40	5	12	12	37	28	23	-19	3	5	18	-5	-13	-15	-26	22	-28	31	43	15	3	3	6	13	12	10																	
10. H(m)	51	46	46	38	43	48	49	37	72	65	9	70	48	12	53	50	25	55	69	33	-11	2	27	45	25	13	30																
22. SD(t)	52	20	32	31	50	46	50	37	36	38	31	30	12	25	31	67	13	81	74	6	7	7	22	39	27	33	62	46															
35. SD(6-16)	44	51	51	47	59	61	66	26	27	21	-8	25	2	27	19	51	4	59	63	8	28	32	57	62	56	53	45	54	71														
36. SD(>16)	50	62	62	65	68	75	66	17	27	34	-11	30	7	-4	17	39	-4	46	54	2	20	32	53	66	38	33	26	59	49	67													
14. Cov(b)	-39	-3	-14	-28	-44	-32	-25	6	7	-2	-10	16	16	-16	11	-27	3	-23	-23	31	-25	-17	-4	-16	-11	-9	-45	9	-25	-10	-8												
45. Cov(2-4)	27	17	10	50	45	43	33	11	-15	-13	37	-7	-20	-17	-12	4	-10	12	5	-24	52	54	18	49	18	29	26	9	33	11	18	-38											
46. Cov(4-6)	19	25	12	56	49	54	46	-7	-32	-33	-2	-22	-44	-19	-30	-10	-34	3	-8	-52	71	83	67	53	33	49	15	-4	21	24	32	-43	82										
29. Cov(0.5-6)	27	-4	-7	29	32	33	27	18	-0	1	61	5	-6	-13	-5	9	-10	30	16	-17	28	33	-5	31	-5	29	36	11	40	7	7	-38	89	66									
39. Het(0.5-6)	19	7	14	26	29	41	38	17	25	29	46	21	20	7	19	39	7	43	39	-2	-8	17	14	32	5	3	33	33	46	16	31	-40	52	36	64								
24. Het(h)	12	1	18	10	3	9	8	49	45	55	24	48	68	28	59	24	78	-12	13	23	-27	-28	-24	4	-21	-20	-55	18	-12	-32	-4	15	-13	-27	-18	-2							
38. Het(<0.5)	45	33	36	51	41	58	59	66	52	61	33	54	67	54	65	50	67	29	42	1	7	3	9	52	10	32	-28	34	13	13	23	-9	22	15	14	10	66						
9. V(diam)	7	-24	-8	8	20	15	7	-13	-14	-3	38	-16	1	-7	-11	0	15	32	21	32	-3	-20	-20	15	-23	-21	33	-8	34	11	12	-13	35	16	33	21	10	6					
12. Cov(l)	-9	37	28	45	20	27	30	5	-24	-38	-17	-13	-34	16	-11	-10	1	-29	-29	-62	76	66	52	45	58	22	-31	-24	-15	2	-9	-8	37	54	11	-13	-1	32	-4				
15. Cov(h)	48	-10	-0	4	24	5	-4	-15	9	33	7	5	22	-25	8	2	-1	9	18	44	-37	-45	-42	-11	-45	-18	20	26	-0	-16	21	-20	-5	-20	-3	7	26	5	23	-60			
28. Cov(<0.5)	43	-19	0	-10	14	-7	-13	5	28	49	30	19	41	-19	24	12	16	21	28	43	-55	-63	-59	-24	-48	-24	22	20	4	-19	7	-15	-21	-42	-7	12	30	-9	15	-76	82		
26. Het(t)	14	-13	-8	-16	-3	-1	0	5	0	24	36	-14	39	11	10	9	6	20	15	46	-51	-45	-33	-9	-28	8	32	-5	21	2	-11	-9	-12	-33	6	27	-2	1	13	-51	26	42	
4. Di(t)	64	69	75	79	75	78	80	28	25	32	-6	33	20	7	22	25	8	26	31	-5	32	23	40	78	45	67	33	66	24	49	60	-8	10	18	-5	20	9	37	-3	17	22	8	3
5. σ(di)	59	52	62	58	61	63	63	20	39	52	4	43	46	11	34	34	16	35	47	39	-4	-12	15	60	20	29	15	59	26	67	61	5	-4	-10	-13	10	25	40	12	-17	43	32	24
7. Diam(t)	58	74	79	81	79	83	82	22	11	20	-18	14	6	15	11	28	-4	25	33	-14	46	33	55	82	58	55	28	35	38	68	65	-21	12	27	-6	14	-4	38	2	26	3	-11	8
8. σ(diam)	66	59	71	79	84	85	84	24	16	26	3	18	11	18	16	38	9	42	49	-3	39	23	43	82	47	49	36	38	57	71	64	-25	26	32	13	22	-3	43	36	23	11	-5	12
51. Cov(16-20)	67	63	76	80	80	86	82	25	23	36	-7	27	16	1	19	24	10	32	41	-15	32	18	36	79	36	45	17	37	33	54	71	-12	6	21	-5	8	11	45	21	16	20	7	-1
52. Cov(>20)	50	58	68	72	65	73	65	32	22	33	-7	26	23	17	23	22	21	20	32	-12	32	9	30	69	31	34	-1	24	20	48	60	-6	-0	13	-16	-8	26	55	21	26	6	-4	-8
55. VM	64	80	81	97	88	84	79	27	7	12	-5	16	-7	-2	11	20	-4	13	19	-41	73	57	57	89	65	51	6	31	28	45	59	-24	46	56	20	16	6	46	3	54	-1	-16	-25
31. Cov(>16)	63	59	74	76	81	82	79	19	18	29	-16	21	8	6	13	26	7	33	42	-15	35	21	43	75	44	42	23	34	37	61	70	-17	2	21	-12	3	5	39	22	20	12	1	-4
41. Het(>16)	59	60	69	68	73	80	82	30	26	35	-9	30	15	13	22	34	11	42	48	-9	26	39	45	74	44	53	28	38	41	69	72	-8	-5	13	-11	5	1	37	14	8	5	-3	4
13. Cov(dw)	-10	36	31	17	1	30	33	-0	18	8	-23	12	7	-1	6	1	-8	10	12	-11	8	21	46	38	32	9	31	26	8	32	23	28	-28	-5	-13	15	-15	5	-10	15	-19	-19	7
1. H(t)	53	75	77	75	70	73	75	25	5	16	-22	9	5	13	11	18	-0	8	17	-21	44	30	54	74	58	52	4	21	20	50	51	-8	-3	14	-21	-6	7	44	-9	33	0	-15	10
2. H(lg)	34	52	47	42	40	47	56	14	-3	1	-33	-5	-3	25	5	15	-7	15	12	-21	31	25	49	47	51	59	19	7	27	54	25	-3	-22	4	-32	-23	-24	22	-23	27	-22	-29	24
56. S	25	25	48	37	38	49	47	29	32	41	42	30	36	19	28	41	21	48	50	19	-8	-16	8	47	10	7	19	38	34	41	50	4	16	-5	19	55	7	22	24	-12	1	12	26
59. BSD	18	9	33	27	31	30	26	11	15	23	47	13	13	-8	3	16	2	20	24	-11	0	-15	-10	26	1	-12	29	8	33	6	22	-10	21	-2	31	54	-4	-1	23	-9	-2	18	29
60. T	20	8	29	33	33	44	40	25	29	36	52	30	30	12	24	32	19	46	41	6	-8	-13	-4	48	-5	3	13	25	46	23	39	-3	27	6	34	66	6	17	35	-10	2	15	24
61. PIE	21	7	28	31	33	43	39	24	29	37	51	29	28	9	23	33	17	48	43	6	-10	-14	-4	38	-5	1	18	26	51	23	40	-5	28	6	35	69	4	15	36	-13	4	17	26
63. DI	-17	-5	-24	-30	-29	-41	-36	-21	-25	-32	-53	-26	-28	-11	-22	-28	-17	-42	-36	-2	7	12	6	-35	8	0	-10	-21	-43	-16	-34	8	-30	-10	-37	-71	-8	-15	-34	8	-2	-15	-24
65. S(nhb)	11	2	24	14	18	27	27	26	31	41	54	29	42	23	30	37	38	46	45	32	-27	-36	-14	25	-10	-6	13	21	40	25	30	12	7	-20	17	51	11	15	39	-24	2	20	44
57. S'	17	14	33	27	29	42	41	30	28	39	43	26	35	22	27	41	19	49	46	16	-15	-17	3	37	3	9	17	23	56	35	42	0	15	-4	21	60	3	18	27	-17	-4	10	42
82. D(tt)	27	18	33	10	16	26	28	37	62	64	21	54	60	13	44	40	27	48	56	44	-35	-42	-12	22	-4	5	22	65	43	42	29	28	-21	-42	-7	21	17	20	5	-42	9	25	34
85. D(er)	19	36	37	39	27	40	41	22	17	11	23	25	-0	4	12	21	-10	42	29	-14	25	16	19	52	26	34	30	24	52	39	39	17	32	18	31	27	-37	5	8	15	-20	-27	-1
62. E	-21	-38	-35	-14	-17	-19	-24	-7	-9	-20	37	-4	-13	-18	-17	-30	-8	-24	-27	-40	10	8	-32	-20	-38	-17	-18	-27	-25	-47	-17	-22	32	25	37	26	6	-17	8	15	-8	1	-18
72. D(cab)	1	39	27	24	20	31	37	15	-9	-18	-26	-11	-18	37	-6	23	-14	15	12	-20	41	45	64	35	57	50	11	8	41	66	23	-6	3	24	-6	-5	-39	10	-25	33	-56	-60	6
75. D(caf)	-3	36	29	21	15	28	33	17	-3	-10	-20	-7	-9	38	-2	26	-13	20	15	-14	28	31	54	33	51	41	14	8	45	61	22	-6	-0	14	-7	7	-40	5	-26	23	-54	-52	17
95. D(pafc)	14	51	40	28	23	34	35	15	-2	-4	-31	-8	-8	22	-3	16	-22	13	11	-18	29	32	53	33	48	52	10	15	34	59	30	-7	-11	11	-15	-4	-36	5	-43	10	-34	-33	22
92. D(at)	-18	-46	-32	-40	-28	-32	-43	-26	13	18	13	8	16	-28	-6	2	-3	12	18	56	-58	-49	-46	-41	-53	-63	20	22	8	-22	6	4	2	-25	12	31	8	-29	39	-64	51	50	7
91. D(rr)	-22	3	-3	-16	-15	-4	1	18	-1	-9	-4	-12	-1	51	4	30	6	20	19	9	0	5	28	1	25	16	15	-3	42	46	-6	-6	-4	-5	-1	1	-33	3	-8	8	-50	-46	29
81. D(pa)	-18	28	26	1	-7	15	24	27	22	11	-16	14	15	53	25	42	14	27	28	-3	-4	10	47	19	62	19	2	17	39	51	18	13	-26	-15	-26	12	-21	8	-31	10	-57	-44	21
94. D(fc)	22	55	42	36	29	38	38	13	-8	-8	-28	-11	-11	12	-10	5	-30	4	1	-23	39	37	49	37	47	59	8	10	24	52	25	-13	-3	20	-7	-5	-35	6	-45	14	-27	-30	19
79. D(wp)	38	45	55	66	68	71	63	1	14	16	-8	19	3	-8	4	17	-2	27	35	-8	32	28	34	73	29	33	17	33	29	50	66	-16	35	40	18	41	-3	22	21	28	8	-8	-15
68. D(hoc)	21	43	46	47	40	59	53	-3	6	13	-2	7	12	7	-3	20	-19	31	32	11	10	18	32	58	27	30	42	29	42	50	55	-22	28	28	21	47	-27	12	17	0	-4	-11	31
66. D(hob)	21	50	54	51	40	58	57	12	10	17	-10	12	8	11	5	28	-17	30	27	-10	20	26	43	57	40	34	19	29	47	47	54	-13	19	24	10	47	-20	18	-11	9	-13	-21	20
76. D(aif)	24	33	46	50	52	56	46	-2	12	21	5	16	13	-10	-0	12	-4	19	29	16	15	5	21	51	13	6	8	39	24	42	66	-3	16	16	6	39	15	12	33	-9	19	17	3
77. D(etf)	50	55	64	72	71	80	75	8	12	22	-16	15	1	-11	4	14	-10	30	36	-10	28	25	40	77	32	43	22	38	35	60	76	-9	14	29	2	24	-7	24	22	8	19	2	-1
64. S(hob)	63	64	77	75	74	81	79	40	35	49	11	34	32	15	33	48	11	47	53	-4	19	11	33	77	41	41	29	47	57	56	66	-22	21	16	13	44	8	44	8	2	13	9	26
80. D(pm)	48	35	54	56	59	63	56	25	26	43	21	19	24	1	23	35	12	43	49	2	2	-5	7	61	15	13	31	33	48	36	52	-30	29	14	25	59	9	28	33	-10	28	25	28
93. D(cc)	27	36	53	56	52	58	49	8	4	13	-13	9	9	2	-2	8	-3	8	17	1	23	9	23	56	23	20	-7	18	17	38	47	-11	11	18	-6	19	11	26	21	15	13	-1	-4
69. D(hbnc)	29	52	60	55	47	56	57	10	21	26	-3	24	9	15	18	39	-6	36	33	-17	26	25	42	58	48	32	13	33	53	48	53	-8	20	19	8	42	-11	23	-18	13	-15	-18	6
70. D(gfb)	-32	-24	-17	-32	-33	-36	-27	-8	2	6	22	-3	11	-16	-4	2	-11	22	8	39	-40	-40	-27	-20	-29	-36	24	8	29	-5	6	35	1	-21	11	28	-16	-31	30	-44	8	11	37
71. D(ehb)	0	-20	-6	-8	-3	10	16	31	36	42	64	33	49	17	33	34	26	49	37	28	-37	-32	-26	4	-22	-0	21	19	45	8	4	14	13	-17	34	50	9	9	21	-31	-14	16	52
74. D(ehf)	7	-23	-2	-7	5	1	2	10	18	28	61	17	26	-10	11	21	7	40	30	32	-31	-30	-37	-1	-24	-20	33	12	45	0	6	5	23	-16	40	57	-3	-12	40	-39	14	33	43
90. D(ph)	18	-18	1	6	14	12	13	31	22	38	68	28	42	3	23	25	16	37	25	29	-22	-32	-39	6	-24	4	12	7	38	-5	3	3	28	-8	41	49	18	14	25	-29	12	31	42
89. D(pt)	10	-30	-11	-11	1	-6	-7	21	10	23	65	11	31	-7	12	16	7	33	17	30	-29	-32	-45	-11	-25	-2	23	-8	39	-9	-13	-1	27	-7	42	40	-2	-8	26	-33	7	36	51
58. D	-5	26	33	18	17	31	32	14	9	8	2	5	4	19	-2	22	-9	35	33	13	6	10	33	27	33	18	22	25	58	63	48	28	3	1	3	26	-22	-8	5	-7	-15	-26	22
65. D(nhb)	-30	-3	-2	-20	-20	-8	-1	14	-3	-4	7	-9	7	27	3	18	1	19	11	13	-11	-9	16	-4	15	7	11	-4	41	35	-3	27	-10	-23	-10	9	-25	-12	-2	-7	-53	-33	42
73. D(grf)	-21	7	6	1	1	16	20	5	4	-3	-3	1	-3	16	-2	27	-12	26	21	1	3	21	42	13	24	10	17	23	51	47	32	9	6	12	8	41	-27	-12	-4	-6	-41	-31	16
78. D(cp)	-12	16	0	19	12	26	31	11	-15	-24	-8	-10	-27	23	-8	18	-12	13	5	27	42	58	59	29	37	37	-1	7	42	43	23	4	38	51	27	15	-28	19	-5	43	-51	-70	-16
83. D(tp)	-21	6	5	3	-7	20	16	16	14	22	7	8	34	18	21	14	13	14	13	15	-33	-2	54	12	-7	8	-25	9	9	15	32	18	-12	-5	-11	38	17	14	-10	-19	-15	2	38
88. D(ey)	-2	-11	1	8	-3	7	25	34	37	32	47	42	33	17	38	21	39	36	25	-3	-14	-23	-25	10	-19	2	-11	6	19	-5	-1	32	9	-15	26	33	14	9	17	-2	-21	7	9
87. D(aapmo)	-0	-2	10	2	2	12	25	50	40	33	48	43	33	32	44	34	42	43	32	-6	-4	-13	-2	16	8	17	-8	11	35	23	1	37	-9	-20	7	17	11	16	3	7	-40	-15	9
86. D(aa)	19	19	29	31	23	35	45	55	40	35	53	46	27	22	46	33	36	40	31	-30	19	6	-4	40	14	32	-9	13	37	18	16	23	20	9	29	30	13	28	4	23	-40	-15	-4
84. D(tm)	-19	-7	-4	6	8	18	18	1	1	-4	21	1	-9	-0	-3	16	-12	29	13	-26	11	27	21	13	10	4	19	6	41	17	20	-9	32	33	37	63	-23	-15	4	6	-43	-22	4

Spearman-correlationmatrix:
R > 40; P < 0.05
R > 52; P < 0.01
R > 55; P < 0.005

4	5	7	8	51 V8	52	55	31	41	13	1 V9	2	56	59	60	61	63 B1	65	57	82	85	62	72	75	95	92 B2	91	81	94	79	68	66	76	77 B3	64	80	93	69	70	71	74 B4	90	89	58	65	73 B5	78	83	88	87	86 B6	84
38																																																			
39	75																																																		
41	72	91																																																	
43	73	86	89																																																
58	62	76	75	87																																															
30	55	82	77	77	69																																														
10	70	88	90	97	87	75																																													
76	68	84	85	92	81	63	94																																												
6	16	30	25	33	24	11	31	30																																											
32	66	92	81	84	75	77	84	83	32																																										
63	36	72	62	58	51	45	63	67	44	81																																									
19	59	51	58	43	44	33	46	46	25	36	14																																								
25	27	27	30	29	19	22	27	25	15	20	-3	77																																							
12	47	36	44	38	32	29	34	31	15	17	-8	93	80																																						
10	45	34	44	37	30	27	32	30	16	16	-8	93	80	99																																					
17	-40	-31	-38	-32	-27	-27	-27	-22	-13	-11	12	-90	-79	-99	-99																																				
10	47	29	40	30	28	10	26	28	15	16	-1	96	75	92	92	-89																																			
10	50	45	49	39	34	23	36	39	19	29	12	97	77	92	93	-90	95																																		
13	57	34	35	34	27	3	31	36	43	22	17	63	41	49	50	-44	61	59																																	
10	32	39	43	36	34	38	31	39	26	27	24	62	47	59	60	-55	54	60	33																																
3	-45	-43	-43	-35	-39	-15	-38	-46	-30	-47	-57	-23	21	7	4	-11	-17	-18	-33	-13																															
8	5	52	40	19	22	29	20	33	34	47	69	10	-5	-1	-2	4	4	20	16	24	-39																														
22	12	54	39	17	23	24	26	31	36	44	65	35	12	18	17	-15	23	40	29	37	-38	95																													
19	10	59	37	27	27	30	31	36	39	53	72	19	-2	-2	-2	3	4	21	29	21	-46	89	89																												
0	2	-43	-27	-27	-30	-46	-30	-34	-21	-59	-72	17	15	24	27	-26	28	18	25	-9	11	-55	-63	-48																											
1	-17	15	12	-16	-6	-16	-7	2	23	8	40	18	-2	1	1	1	18	25	22	15	-31	82	85	68	-22																										
3	11	37	23	9	15	3	16	26	51	32	55	41	15	24	23	-21	35	47	42	33	-41	80	89	75	-30	80																									
5	19	60	37	30	28	37	31	35	33	55	69	9	-7	-10	-10	10	-7	11	21	16	-41	81	79	96	-52	55	59																								
9	64	68	68	67	52	64	65	56	22	46	14	63	46	64	62	-61	47	56	31	51	4	13	21	12	4	-11	14	9																							
4	55	65	62	50	44	41	49	49	36	44	37	63	43	52	52	-51	49	63	40	57	-27	39	54	47	5	30	45	45	69																						
2	55	72	60	51	42	50	49	49	36	57	45	68	46	57	58	-56	52	72	44	60	-34	51	66	59	-8	32	60	55	64	84																					
9	68	60	56	57	50	49	56	47	15	39	2	74	53	69	67	-68	62	65	48	29	-10	10	17	15	22	-12	12	12	82	56	56																				
3	75	83	82	89	66	68	86	83	34	72	46	56	36	50	49	-44	37	49	35	46	-24	18	22	26	-11	-14	13	26	85	63	64	69																			
1	78	86	83	79	68	70	76	76	27	75	50	74	53	62	63	-58	57	72	55	55	-39	31	43	43	-14	10	37	41	68	73	83	62	78																		
2	65	61	66	62	43	48	57	54	13	45	14	75	62	73	75	-71	64	73	46	47	-11	-4	12	6	16	-8	12	3	76	61	66	64	76	83																	
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Table 3.2. Number of bird species, total bird densities and the densities of bird groups based on nesting and feeding ecology in managed and natural young dense conifer stands (a), and in managed and natural climax stands of deciduous woodlands (b).

a	Managed	Natural
Forest type:	I.3	III.2
Number of species (S')	2.9	9.7
Total density (D)	35.8	52.1
Breeding groups:		
S hole breeders	0	3
D hole breeders	0	6.5
D hole cutters	0	3.2
D ground breeders	0	14.5
D shrub breeders	0	24.7
D canopy breeders	35.8	6.5
Foraging groups:		
D ground foragers	14.6	17.5
D shrub foragers	0	27.4
D canopy foragers	21.3	7.2
D airforagers	0	0
D stem foragers	0	0

b	Managed	Natural	
Forest type:	II.4	III.3	III.4
Number of species (S')	16	22	23
Total density (D)	25.4	88.2	79.2
Breeding groups:			
S hole breeders	5	10	11
D hole breeders	6.3	46.6	36.5
D hole cutters	1.5	4.7	4.3
D ground breeders	1.8	5.1	10.1
D shrub breeders	4.8	15.0	15.8
D canopy breeders	12.5	21.5	16.8
Foraging groups:			
D ground foragers	9.2	34.8	27.6
D shrub foragers	3.9	18.1	17.2
D canopy foragers	9.2	23.7	22.3
D airforagers	0.2	1.9	2.5
D stem foragers	2.9	9.8	9.6

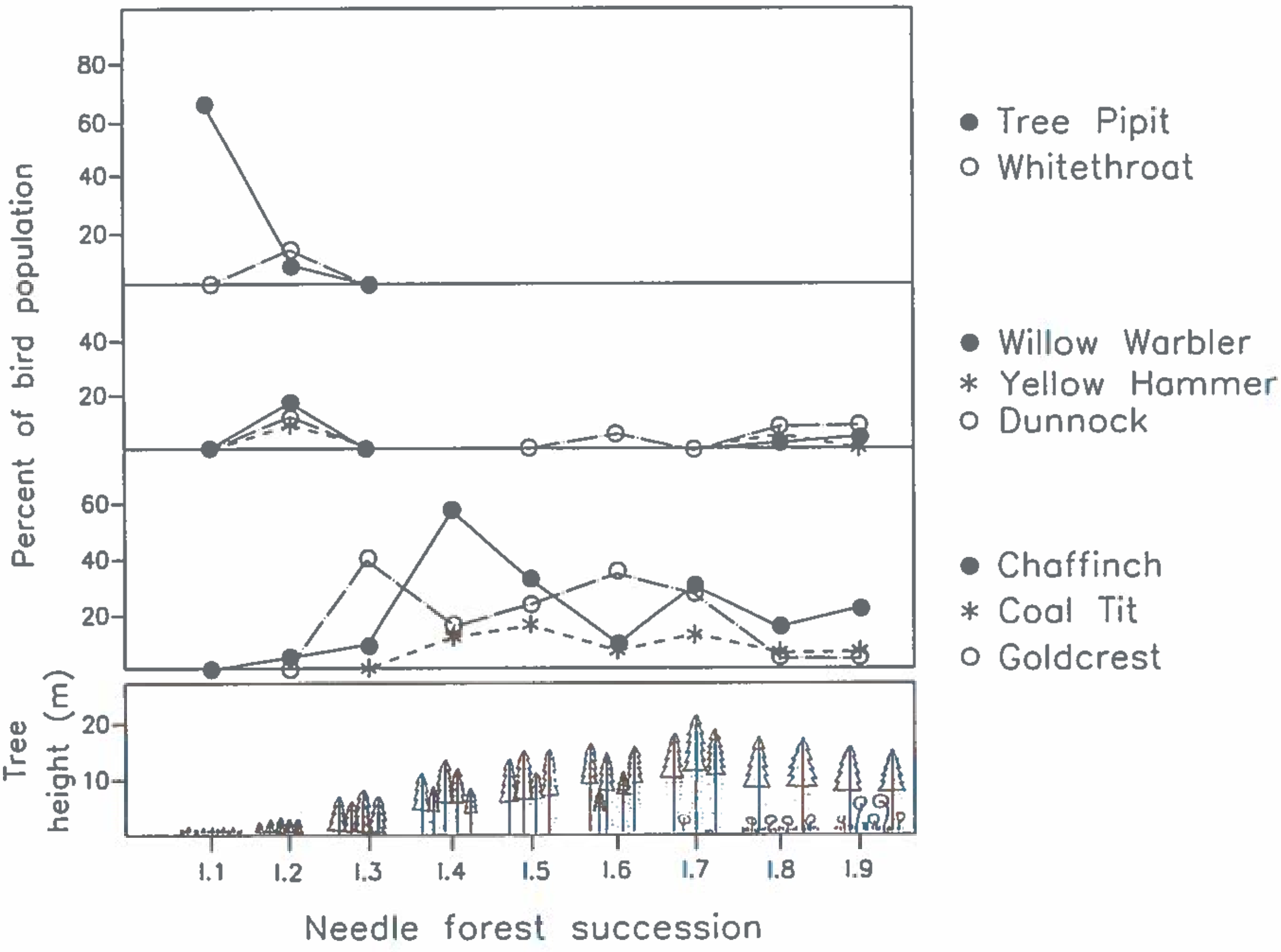


Figure 3.8. Changes in the relative dominance of eight bird species in Danish habitats arrayed on a successional sequence from open young conifer stands (I.1) to mature conifer stands with an understorey of shrub (I.9).

colonizers of the restock site again have to be regarded as 'forest birds'. Thus, to assess the conservation value of a commercial plantation, one needs information on exactly what the forest will hold at different stages.

The total densities of feeding-ecology and breeding-ecology species groups changed considerably during the successional sequence of forest succession (Fig. 3.9 and Fig. 3.10, respectively).

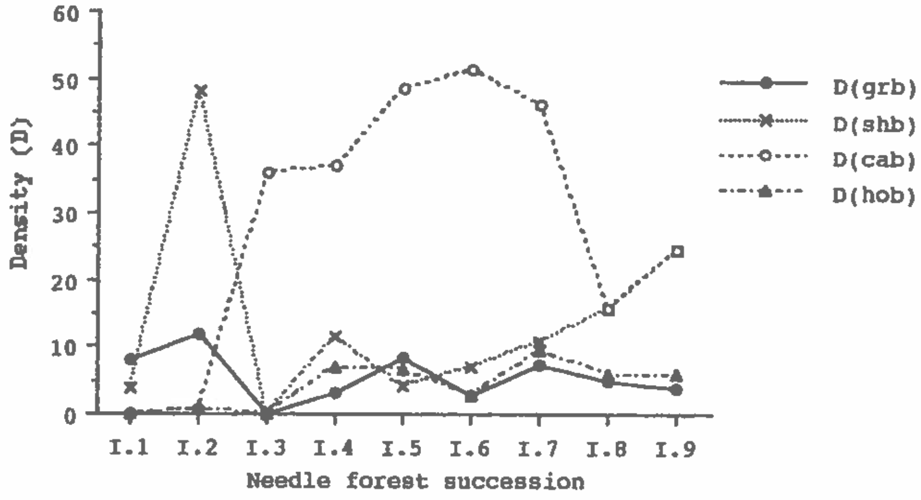


Figure 3.9. The densities of breeding-ecology species groups in various stages of coniferous forest succession (forest types I.1 - I.9). D(grb) = density of species nesting on the ground, D(shb) = density of species nesting in shrub, D(cab) = density of species nesting in the canopy, and D(hob) = density of species nesting in holes.

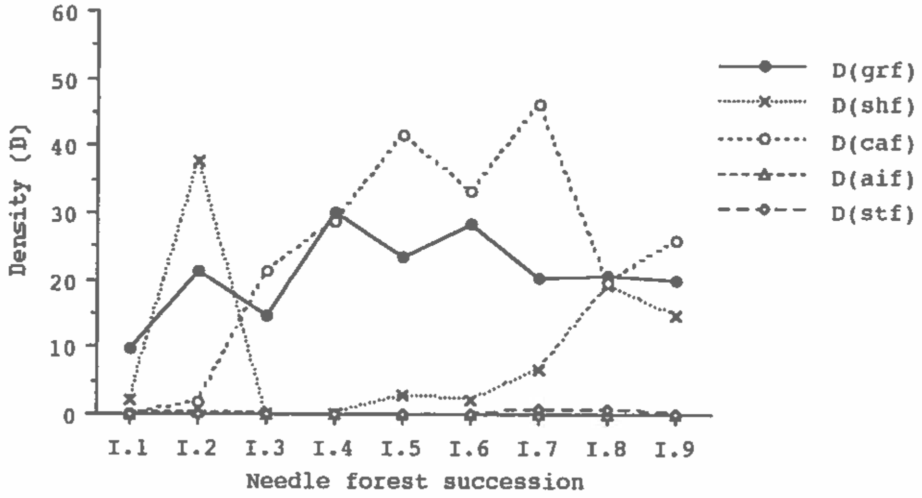


Figure 3.10. The densities of feeding-ecology species groups in various stages of coniferous forest succession (forest types I.1 - I.9). D(grf) = density of species feeding on the ground, D(shf) = density of species feeding in shrub, D(caf) = density of species feeding in the canopy, D(aif) = density of species feeding in the air, and D(stf) = density of species feeding on stems.

The number of birds feeding and breeding in trees at first increased very rapidly, because the forest canopy increased. However, in stands with shrub the canopy was more open and as a result the number of canopy-feeders showed a decline. The density of birds feeding and breeding in bushes at first increased to the young dense. In conifer thickets very few individuals of these species occurred. During the development of the stand from the thicket stage to a mature pine forest with shrubs, the abundance of this species group again increased considerably.

The densities of birds and number of species on coniferous forest sites varied with successional stages. They were much higher in the young stand than the newly planted stand, but were quite small in a conifer thicket (Fig. 3.11). The poor development of the ground vegetation, the lack of a bush stratum, the crotch structure, the slenderness of the trees and the density of the stand cause the absence or sparsity of the following species groups in conifer thickets:

- nesting in trees or holes
- nesting or feeding in shrub
- feeding in the air

The bird density and species number increased again with successional stage and in climax conifer stands they reached their maximum value. However, the bird density and number of species in climax conifer stands was only slightly greater than that of the young stand (forest type I.2). It has already been shown that forest succession did not very greatly affect the total density of birds feeding on the ground. Consequently the changes of bird density during forest succession were mainly due to the improvement of the conditions for the birds feeding in trees and bushes.

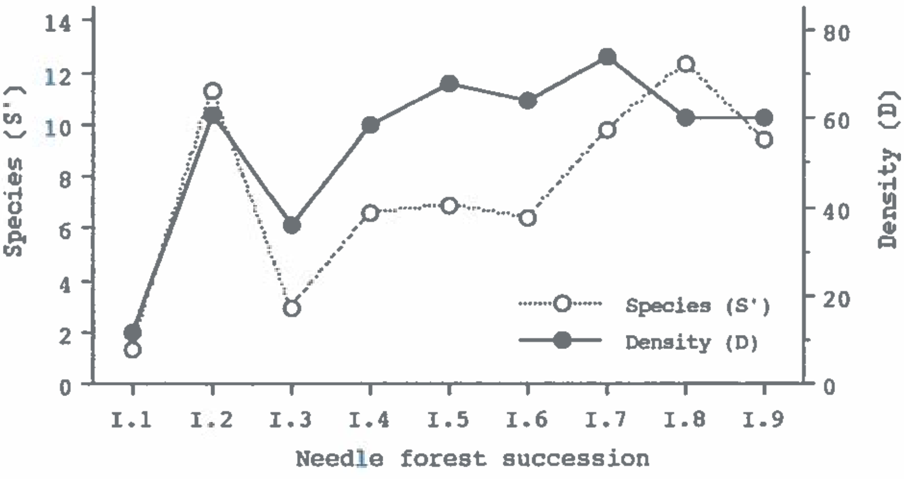


Figure 3.11. The total number of birds species (S') and total bird density (D) varied with needle forest succession (forest types I.1 - I.9).

As can be seen from the discussion above, many changes take place in the forest in connection with its development and apparently have a considerable effect on the feeding and nesting environment of birds. But as more specific studies on the relationships between prey animals and forest succession are lacking, conclusions concerning the dependence of birds on factors relating to feeding ecology are very difficult.

3.2.2 Coniferous and deciduous woodlands

It is quite likely that different tree species will support different bird species; both because they provide nesting opportunities, and, probably much more importantly, because they contain different feeding opportunities. However, there appear to be very few species whose habitat requirements are so specific that they are met only by one tree species. Excellent evidence of this comes from the large number of common species which can use Sitka Spruce for nesting and feeding (e.g. in Rørbæk area no. 1; Fig. 1.2g), even though this is a recent addition to the potential tree species on offer to the Danish avifauna.

The most obvious division between different tree species is between broadleaves and conifers. Most species will nest in both types of wood. However a number of species prefer broadleaves (e.g. Marsh Tit, Nuthatch, Wood Warbler, Hawfinch; Table 3.2) and another group of species prefer conifers (e.g. Goldcrest, Coal Tit, Crested Tit; Table 3.2). In this section the numbers and densities of bird species were compared between conifer and Beech stands of different heights (Fig. 3.12). Over the height interval 7-23 m the number of species was the same for both woodlands ($t=0.66$, $df=9$, $p>0.50$). Despite the fact that Beech woodlands are beautiful places, their bird numbers are rather unimpressive; coniferous woods are much better in terms of densities ($t=32.24$, $df=9$, $p<0.001$).

3.2.3 Fragmented and homogeneous woodlands

Between the two extremes as mentioned in section 4.2, there are forests with a mosaic of broadleaved trees and coniferous trees. The latter had a more diverse avifauna than did pure broadleaf and conifer stands. For example the mature stands of Beech and Norway Spruce (types IV.2 and IV.4, respectively) in the fragmented woodland of Hov (type IV.5, Fig. 1.2b) had considerably more species, higher densities and Bird Species Diversity than even-aged, homogeneous woodlands of either Beech or Norway Spruce (types II.4 and I.7, respectively) (Fig. 3.13). For example the total number of bird species and the total density of birds in conifer stands were two-thirds of that in conifer mosaics. A group of bird species was absent altogether from pure coniferous forests, not surrounded by broadleaves (e.g. Blackcap, Blackbird, Blue Tit), and a different group from deciduous forests with no conifers (e.g. Willow Warbler and Chiffchaff). This might be explained by the fact that a conifer stand surrounded by blocks of deciduous, and vice versa, has edge habitats, habitats which qualitatively and quantitatively differ from the forest interior in the sense that they are comprised of a vegetation including features of both bordering plant communities. The edge condition is attractive to birds for several reasons: (1) Edge vegetation supports a greater proportion of utilized food resources (McDiarmid *et al.* 1977). (2) Some species use conifer trees for nesting and deciduous trees for foraging and are thus often observed at habitat edges. In this study no Chaffinch territories were recorded in a leafless Oak woodland (study area 6 in Nedergård); they were situated in coniferous woodlands just along the border of the Oak/coniferous woodland (Fig. 3.14). Possibly leafless Oaks had fewer prey items than conifers, so birds mainly use the food resources of conifers. However, after the Oaks came into leaf, the Chaffinches expanded their territories into the Oak woodland and family groups were seen foraging mainly in Oaks (Fig. 3.14). Probably the birds exploited a more profitable food source in deciduous trees at that time. (3) Some species tend to use an edge location for singing.

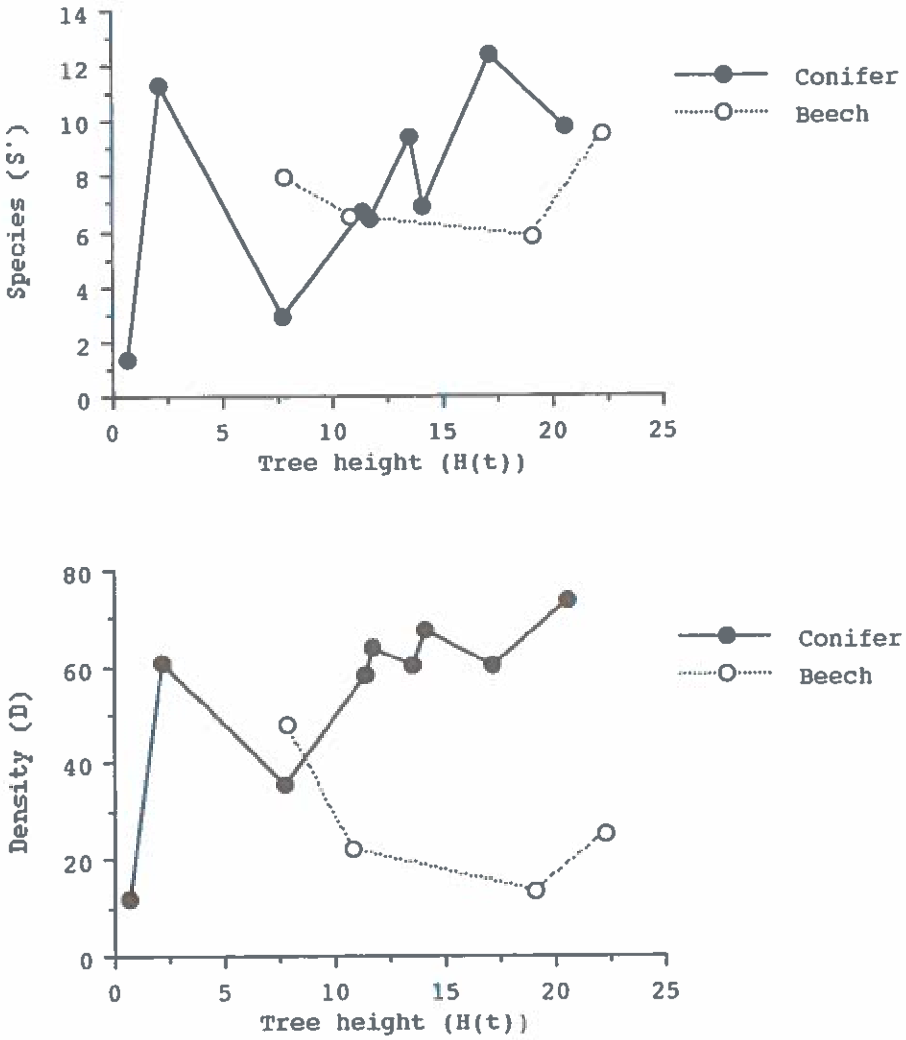


Figure 3.12. The total number of bird species (S') and total bird density (D) for coniferous and deciduous (Beech) woodlands of different heights.

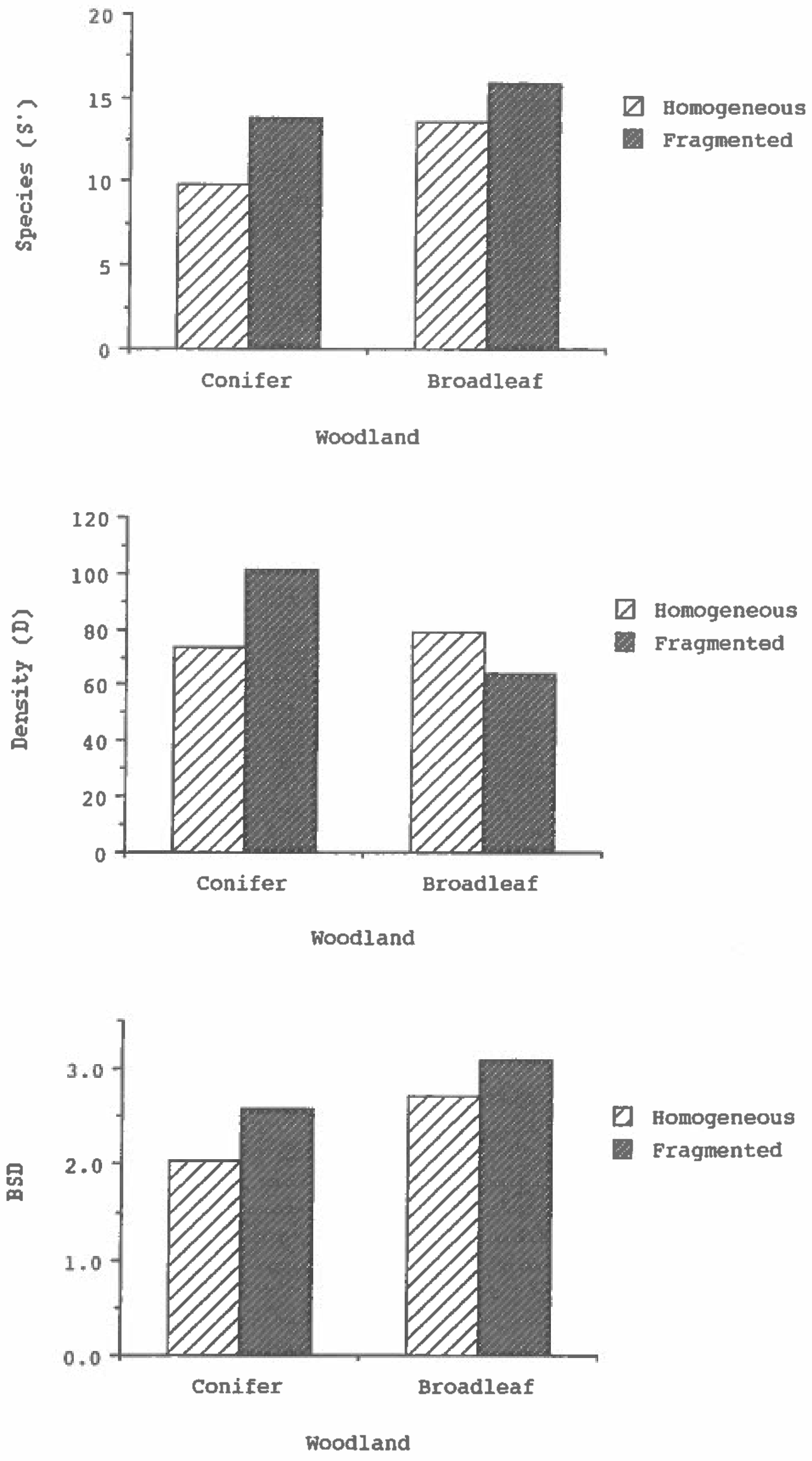


Figure 3.13. The total number of bird species (S'), total bird density (D) and Bird Species Diversity (BSD) for evenaged, homogeneous coniferous and broadleaved woodlands (Norway Spruce and Beech, respectively) and fragmented woodland (a mosaic of Beech and Norway Spruce) .

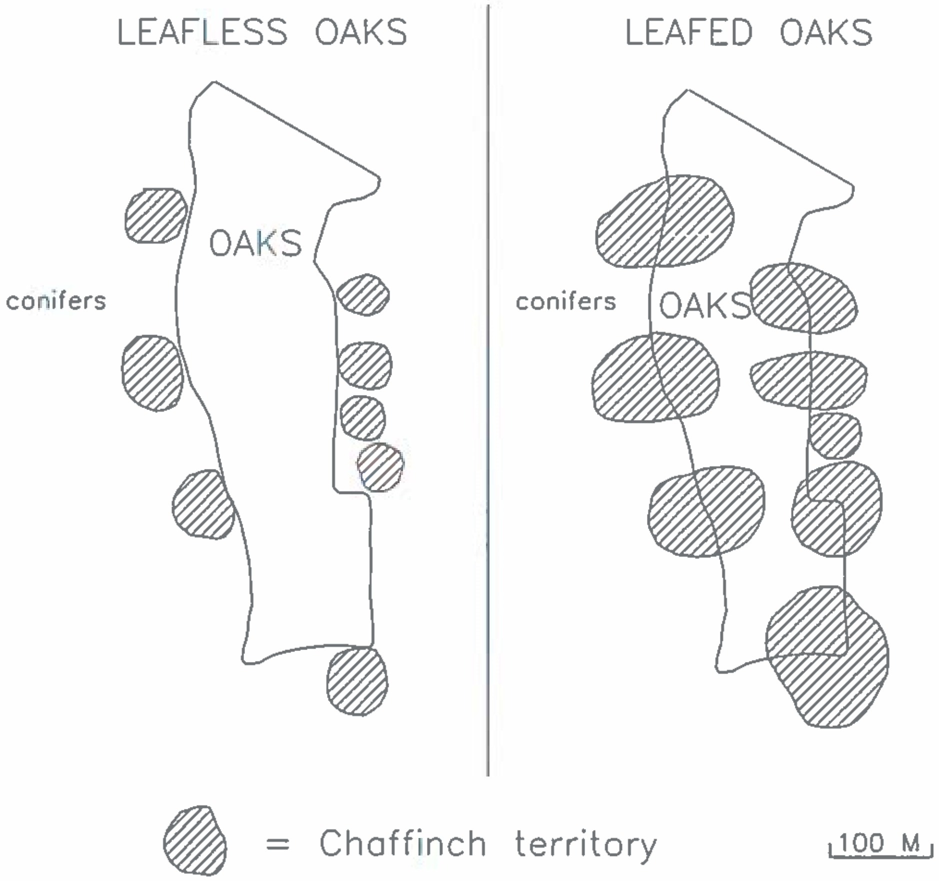


Figure 3.14. Positions of Chaffinch territories in a fragmented conifer/oak woodland before (left) and after leafing of the Oak trees.

Thus there is more potential for birds using both types of trees. In Welsh conifer forests, it was shown that certain species, notably Wood Warblers, Chiffchaffs and Pied Flycatchers, nested in the conifer plantations but only in areas where there were at least a few broadleaved trees (Bibby *et al.* 1989a). Small patches of broadleaves were enough to attract these species. Thus the most obvious way of trying to improve the forest for birds is to plant both blocks of broadleaves and conifers. However, there is clear evidence that mixtures of conifers and broadleaves are better for birds than either on their own (Moss 1978), and this is a subject on which more information is urgently needed for practical management. In this study the number of bird species and the total density of birds correlated positively with the species diversity of the canopy layer (>16 m; Fig. 3.15).

3.2.4 Managed and natural woodlands

Silviculture considerably changes the natural course of forest succession, and these changes in turn affect the bird fauna. After regeneration cutting, and especially after clear-cutting which promotes regeneration of conifers, hardwood brush (e.g. Birch) invades the area, but as soon as the slower-growing conifer

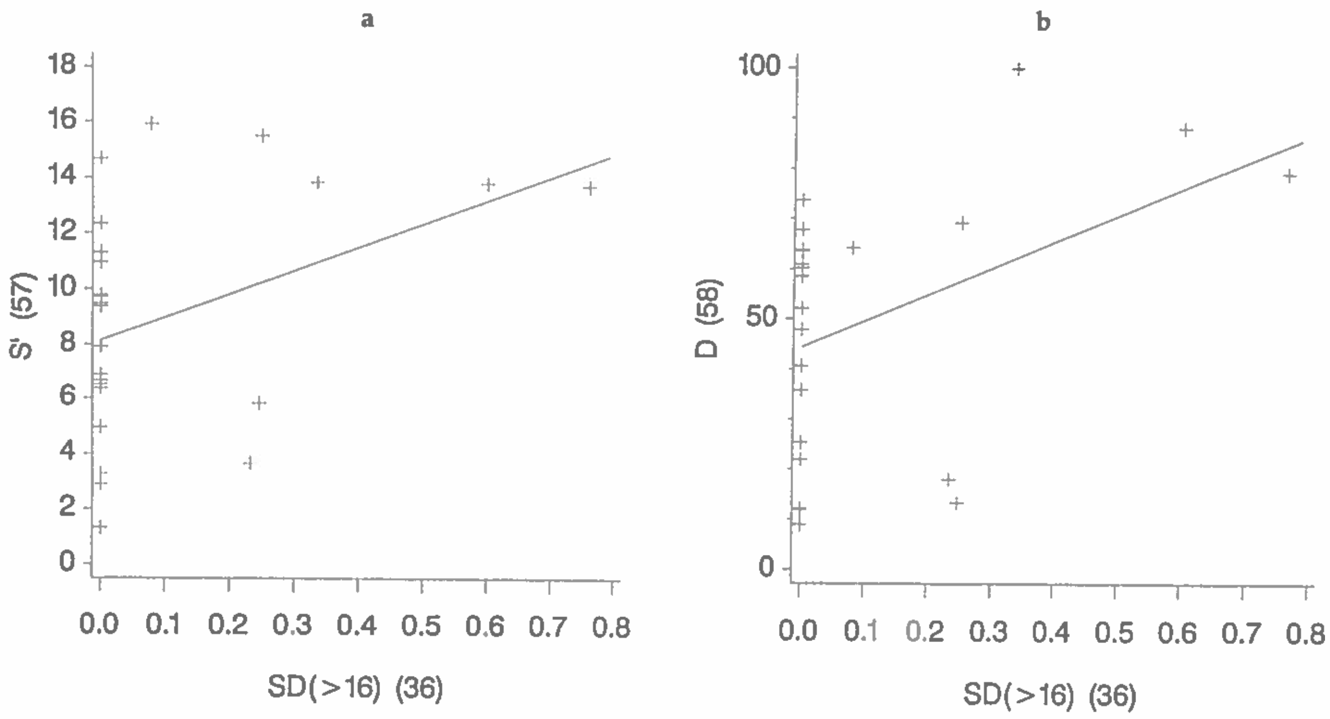


Figure 3.15. Number of bird species (S') and total bird density (D) in relation to species diversity of the canopy layer higher than 16 m (SD(>16)) (S': r=42, $p<0.05$, y = 8.165 + 8.151; D: r=44, $p<0.05$, y = 52.777x + 44.364).

seedlings have grown large enough, the development of the stand is interrupted. At this time the tree species composition, for instance, is determined. Practically all hardwood bushes are removed from the regeneration area. Conifers remain the main species, and the stand gradually develops to the timber stage. Hardwood cannot gain a footing before the stand starts regenerating again. Under natural conditions mixed stands will be formed.

In this study comparisons were made between the bird diversity of managed and natural woodlands of roughly the same ages; managed versus natural young dense conifer stands (forest types I.3 vs. III.2) and managed versus natural climax stands of deciduous woodlands (forest type II.4 vs. forest types III.3 and III.4). (For a list of forest types see Table 1.1). Natural woodlands held more species and higher densities of birds than managed woodlands (Table 3.2).

In managed young conifer stands the density of canopy-breeders and canopy-foragers was higher than in natural stands, whereas the densities of the other ecological groups were lower (Table 3.2a). Air-foragers, hole, ground and shrub-breeders were completely absent in managed stands, whereas they occurred in natural stands. Generally for birds that nest in holes it may be important that there are trees large enough and at the right rotting stage. However, some hole-breeders can occur in the early stages of succession; they can nest in holes in the ground (e.g. the Coal Tit nests successfully in raised stumps).

It is evident that the high number of species and bird density in mature natural deciduous stands as compared with mature managed deciduous stands was due to the considerably larger densities of all ecological groups found in the former. The densities of birds boring their holes themselves in natural forests were so high because there were so many dead trees present (8.8%) in comparison with managed woodlands (0%). The number of species and density of hole-nesting birds is significantly higher in natural than in managed woodlands (Table 3.2b), because the density of the birds nesting in holes of others is directly correlated with the density of hole-cutters (section 3.2.5).

According to these observations, no bird species derives any advantage from managed woodlands.

3.2.5 The importance of dead wood for birds

Dead wood is one of the scarcest features of the forests of today. The value of dead wood to other wildlife groups is considerable; Steele (1972) estimates that as much as 20% of a wood's animal species are associated with dead wood, and it is especially important to some beetles. Dead wood is important in supplying food for birds. Together with dependent organisms it constitutes an important part of a complete forest ecosystem. Dead wood forms a part of the base of the feeding pyramid in the forest: plants and animals living on it, in their turn are food for higher organisms, including birds. Hole-nesters profit by the presence of dead wood, not only as source of food but also as nesting site. Hole-nesters can be divided into those boring their holes themselves, and those nesting in the holes of others. The latter is largely dependent on the former (Fig. 3.16). The diameter of the tree is an important factor to the species excavating their own holes in trees and various species differ considerably from each other in this respect (Pynnönen 1939). For hole-cutting birds it is easier to cut a nesting hole in dead wood than in live wood. In the Netherlands evidence exists that woodpeckers prefer to nest in dead or decaying wood (Komdeur & Vestjens 1983). The increased food and nest-site supply through the presence of dead wood promotes a higher density of hole-cutters (Fig. 3.17). With a higher density of hole-cutting birds the density of hole-breeders that are not hole-cutters increased too (Fig. 3.18), because the latter depends on the availability of second hand nest holes. The observed linking between dead wood, hole-cutters and hole-breeders that are not hole-cutters was also found in Dutch needle forests (Komdeur & Vestjens 1983). The presence of dead wood is clearly the icing on the forest conservation cake.

3.2.6 Vertical and horizontal variation in forest structure

During the development of a forest the trees grow taller and the number of foliage layers increases. One effect of the additional vegetation strata may be to provide an enlarged habitat space in

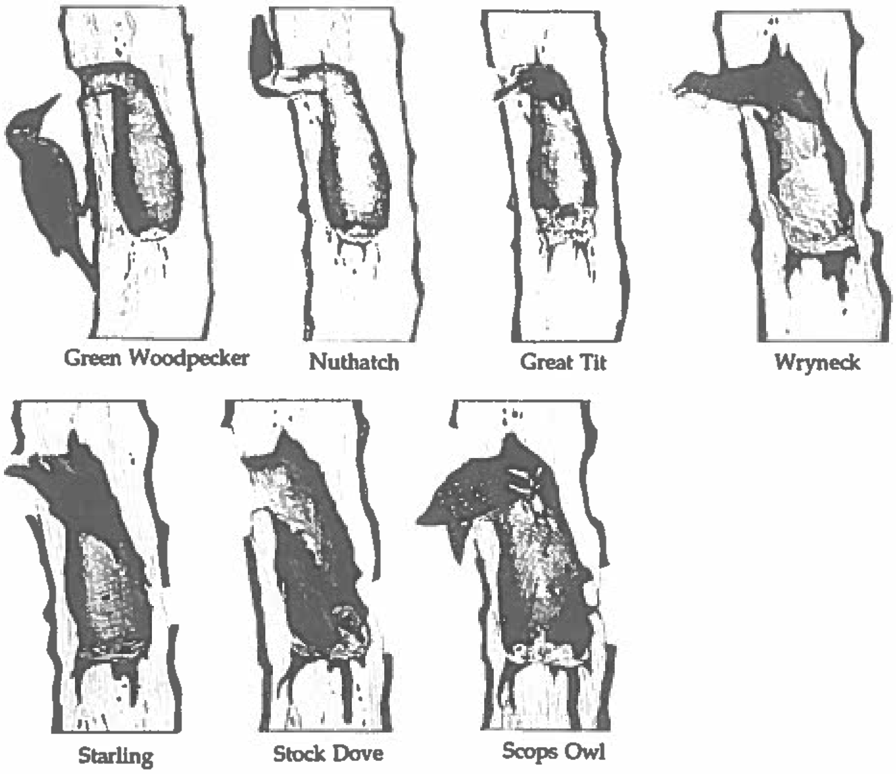
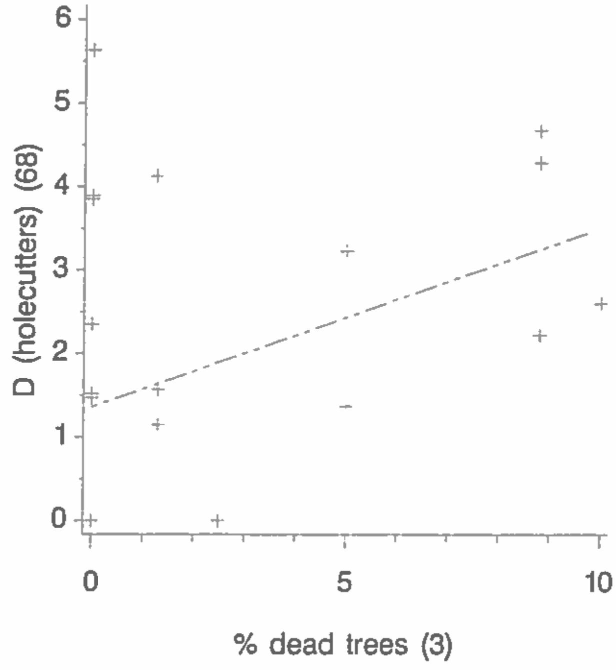


Figure 3.16. Several bird species may use one nest-hole, but not all cut the holes themselves. Woodpeckers are eminent holecutters; when they have bored a hole, it can be used by other bird species season after season. These species may enlarge or reduce the nest-hole according their own needs.



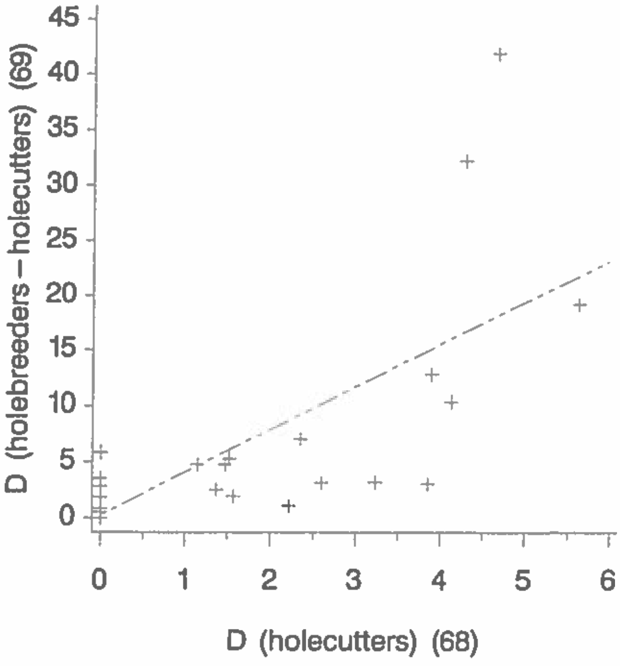


Figure 3.17. The density of holecutters in relation to the percentage of dead trees in the forest with a diameter of more than 10 cm at breast height (r=42, p<0.05, y = 0.192x + 1.296).

Figure 3.18. The density of holebreeders that are not holecutters in relation to the density of hole-cutting birds (r=68, p<0.001, y = 3.824x + 0.287).

which additional species can be accommodated through vertical segregation. A second effect may be the provision of new substrates which support more food sources for birds, e.g. more foliage arthropods. In this study habitat diversity was expressed by a measure of the evenness of the distribution of foliage among vertical height strata, foliage height diversity (FHD). Because bird species occupy different layers in the woodland, and because the Foliage Height Diversity measure is correlated with the number of vegetation layers, it is not surprising that the number of bird species showed a significant relationship with FHD (Fig. 3.19). In managed woodlands the shrub layer is normally absent, because the trees are felled before a shrub layer can develop. The presence of a shrub layer, however, is very important for birds foraging and breeding in shrubs; the higher the cover of shrubs, the higher the density of shrub-birds (Fig. 3.20). As a consequence, the more shrub is present in a woodland the higher the species number and species diversity (r=43 and r=47, respectively (P<0.05)).

However, not only vertical stratification in habitats, but also horizontal patchiness might be important. In this research the horizontal heterogeneity of a woodland showed a close relationship with the number of species (Fig. 3.21). A strong relation was found between the heterogeneity of the canopy layer (>16 m) and the density of air-foragers (Fig. 3.22). It is assumed that this is caused by the fact that air-foragers require plenty of gaps in the canopy for feeding. In dense woodlands these birds are unable to practice their specific feeding habits.

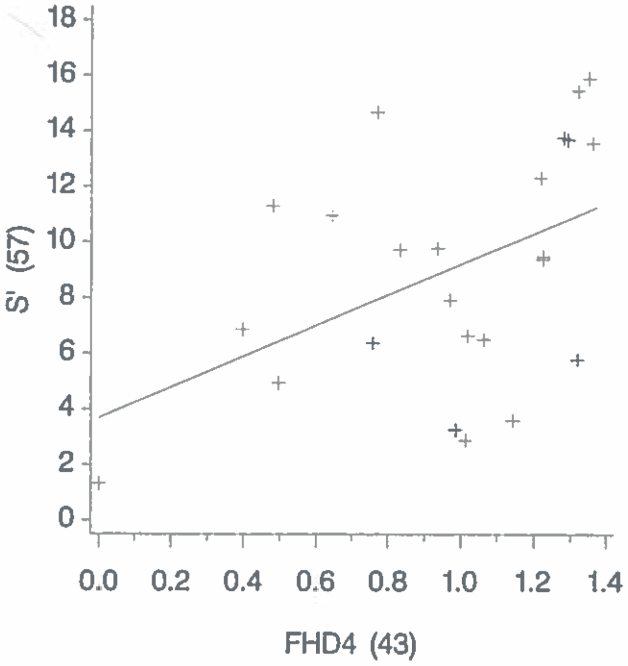


Figure 3.19. The number of bird species (S') in relation to Foliage Height Diversity (FHD4) (r=42, p<0.05, y = 5.508x + 3.751).

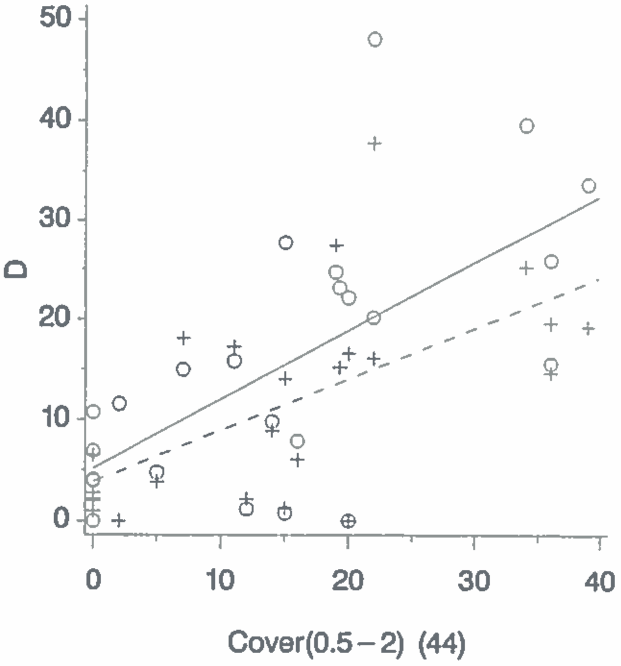


Figure 3.20. The density (D) of shrub-breeding (0; r=64, p<0.001, y = 0.668x + 5.011) and shrub-foraging birds (+; r=61, p<0.005, y= 0.501x + 4.332) in relation to vegetation cover between 0.5 and 2 m.

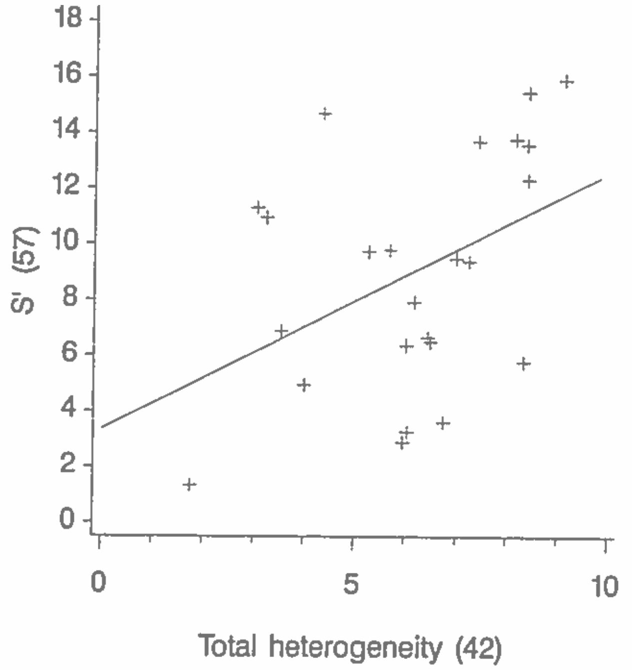


Figure 3.21. The total number of bird species (S') in relation to horizontal heterogeneity of a woodland (r=41, p<0.05, y = 0.924x + 3.351).

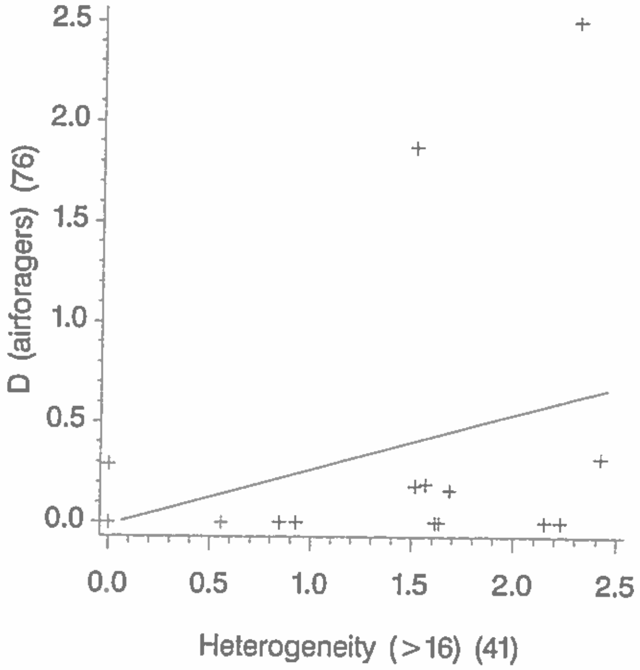


*Figure 3.22.*The density of air-foragers and heterogeneity of the canopy layer higher than 16 m (Het(>16)). (r=47, p<0.05, y = 0.267x - 0.009).

As the foliage height diversity was significantly correlated with the heterogeneity of the woodland (see section 3.3.1), it was not clear whether the increase in bird variables was due to the one or the other parameter. However, it can be concluded that an older and further developed forest with varied layers, both vertically and horizontally, supports a richer and more varied bird population.

3.2.7 Density of bird species as a measure for habitat preference

Generally the density of a bird species in a particular habitat type is related with the species' preference for that habitat type; the higher the density the better the habitat. However, this does not mean that two habitat types with the same bird densities are of the same quality. For example the densities of Willow Warblers in the dense phase of mixed Birch/Mountain Pine woodland (forest type III.2) and in the young phase of Norway Spruce (forest type I.2) were the same (11.8 vs. 10.3 territories/10ha), but the occupation rates by which the species occupied their territories in both forest types were different (Fig. 3.23). The birds established territories in forest type III.2 first, and in forest type I.2 after the former was saturated with territories, ca. two weeks later. This phenomenon was not due to geographical constraints as the

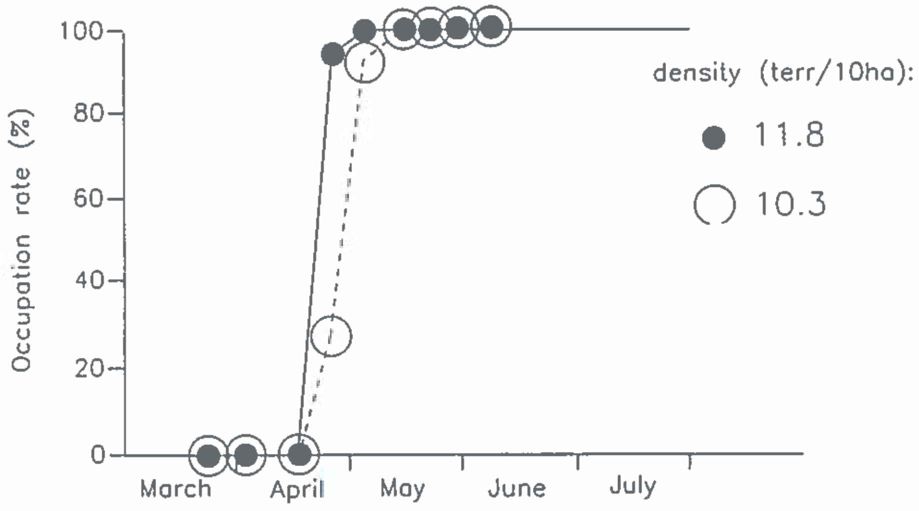


Figure 3.23. Willow Warbler occupation rate (% of total density) of the dense phase of mixed Birch/Mountain Pine woodland (forest type III.2; closed dots) and of the young phase of Norway Spruce (forest type I.2; open dots), March - July 1992.

woodlands are separated by only two km and Willow Warblers arrived at the same time. Clearly birds occupied the best habitats first.

3.3 Groups of vegetation and bird parameters

As it was impossible to recognize the structure in the large correlation matrix of the 95 forest and bird parameters (Table 3.1), the vegetation and bird parameters were rearranged separately using the VARCLUS procedure (section 2.4), thereby reducing it to a 15 x 15 matrix (Table 3.3). This reduced matrix offered an excellent opportunity to study the major correlations between groups of parameters. In this chapter these groups of forest and bird parameters will be described as well as relevant correlations between these groups.

In the VARCLUS matrix nine groups of vegetation parameters ('V groups') and six groups of bird parameters ('B groups') can be distinguished (Tables 3.4 and 3.5, respectively).

The reduced VARCLUS matrix offers an excellent opportunity to study major correlations between groups of parameters which are described below.

3.3.1 Correlations between groups of vegetation parameters

- Heterogeneity (V1) and foliage height diversity (V3) correlated positively with species diversity of trees and dead trees (V4).

Table 3.3 The reduced 15 x 15 VARCLUS matrix with correlations between groups of vegetation parameters ("V groups") and bird parameters ("B groups") (see also Table 3.1).

Spearman-correlationmatrix:

R > 40: P > 0.05
R > 52: P < 0.01
R > 55: P < 0.005

	V1	V2	V3	V4	V5	V6	V7	V8	V9	B1	B2	B3	B4	B5	B6
V1	100														
V2	30.6														
V3	74.1	-1.1													
V4	50.7	44.6	43.5												
V5	35.6	5.0	53.4	34.8											
V6	37.5	65.4	9.3	-13.4	7.0										
V7	18.0	33.3	-23.9	24.1	-4.1	18.4									
V8	89.7	15.0	71.0	44.7	12.5	27.6	20.1								
V9	56.6	-9.7	42.8	17.9	-6.4	9.2	-13.3	68.1							
B1	38.6	45.0	27.6	52.3	24.5	14.3	30.0	38.3	20.0						
B2	10.5	-7.7	20.0	24.0	-2.2	-18.5	-38.1	11.1	43.7	12.9					
B3	65.4	12.2	48.7	49.2	22.3	7.3	31.4	70.9	51.7	69.8	24.5				
B4	-16.7	27.4	-21.7	26.3	22.1	-11.7	29.9	-24.0	-24.1	70.2	0.0	29.5			
B5	63.5	-3.7	34.9	32.2	21.8	-21.8	-23.5	10.4	31.4	52.6	67.8	39.1	33.7		
B6	17.9	22.9	14.0	23.1	33.6	-3.0	-11.5	-2.5	6.1	70.8	4.4	25.7	67.1	56.0	100

Table 3.4 Groups of vegetation parameters ("V groups") (see also Table 3.3).

V1. Total cover and heterogeneity.
Parameters: 18.Cov(hst), 49.Cov(10-12), 50.Cov(12-16), 53.Cov(0->20), 32.Cov(0->16), 43.FHD(4), 42.Het(0->16).
Mean internal correlation: 76.3

V2. Cover of shrubs and species diversity of herbs and shrubs.
Parameters: 11.S/are, 16.Cov(s), 19.FHD(hst), 44.Cov(0.5-2), 25.Het(s), 27.Het(hst), 20.SD(h), 21.SD(s), 23.SD.(hst), 33.SD(0-0.5), 34.SD(0.5-6), 37.SD(0->16).
Mean internal correlation: 65.0

V3. Tree cover and Foliage Height Diversity.
Parameters: 6.V(di), 17.Cov(t), 47.Cov(6-8), 48.Cov(8-10), 54.FHD(10), 30.Cov(6-16), 40.Het(6-16).
Mean internal correlation: 54.1

V4. Species Diversity of trees and Dead trees.
Parameters: 3.De(t), 10.H(s), 22.SD(t), 35.SD(6-16), 36.SD(>16).
Mean internal correlation: 50.9

V5. Cover and heterogeneity of vegetation between 0.5 and 6 m.
Parameters: 14.Cov(b), 45.Cov(2-4), 46.Cov(4-6), 29.Cov(0.5-6), 39.Het(0.5-6).
Mean internal correlation: 54.8

V6. Heterogeneity herbs.
Parameters: 24.Het(h), 38.Het(<0.5).
Mean internal correlation: 66.0

V7. Heterogeneity trees and cover of litter and herbs.
Parameters: 9.V(diam), 12.Cov(l), 15.Cov(h), 28.Cov(<0.5), 26.Het(t).
Mean internal correlation: 39.2

V8. Development.
Parameters: 4.D(t), 5.σ(di), 7.Diam(t), 8.σ(diam), 51.Cov(16-20), 52.Cov(>20), 55.VM, 31.Cov(>16), 41.Het(>16).
Mean internal correlation: 79.7

V9. Tree height.
Parameters: 13.Cov(dw), 1.H(t), 2.H(lg).
Mean internal correlation: 52.3

Table 3.5 Groups of bird parameters ("B groups") (see also Table 3.3).

B1. Species richness and diversity.
Parameters: 56.S, 59.BSD, 60.Y, 61.PIE, 63.DI, 65.S(nbh), 57.S', 82.D(tt), 85.D(er).
Mean internal correlation: 72.0

B2. Canopy-birds.
Parameters: 62.E, 72.D(cab), 75.D(caf), 95.D(pafc), 92.D(at), 91.D(rr), 81.D(pa), 94.D(fc).
Mean internal correlation: 60.7

B3. Hole-breeders and air-foragers.
Parameters: 79.D(wp), 68.D(hoc), 66.D(hob), 76.D(aif), 77.D(stf), 64.S(hob), 80.D(pm), 93.D(cc), 69.D(hbnc).
Mean internal correlation: 70.1

B4. Shrub- and ground-birds.
Parameters: 70.D(grb), 71.D(shb), 74.D(shf), 90.D(ph), 89.D(pt).
Mean internal correlation: 73.9

B5. Total bird density.
Parameters: 56.D, 65.D(nhb), 73.D(grf), 78.D(cp), 83.D(tp).
Mean internal correlation: 60.8

B6. Rest group.
Parameters: 88.D(sy), 87.D(sapmo), 86.D(sa), 84.D(tm).
Mean internal correlation: 66.5

- More vegetation between 0.5 and 6 m (more shrubs; V5) results in a higher foliage height diversity (V3).

- The development of a forest (V8) is highly correlated with both total cover and heterogeneity of a forest (V1), tree cover and foliage height diversity (V3) and species diversity of trees and dead trees present (V4).

- The development of a forest (V8) is highly correlated with tree height (V9).

- Higher trees (V9) result in more cover and heterogeneity (V1) and foliage height diversity of a woodland (V3).

3.3.2 Correlations between groups of bird parameters

- Species richness and diversity (B1) was very highly correlated with all the bird groups, save canopy birds (B2). The more hole-breeding birds and air-foragers (B3), shrub-birds and ground-breeders (B4), and the higher the total bird density (B5), the higher the species richness and diversity of the woodland bird community (B1). The fact that the number of bird species (S) was selected as the first variable in the VARCLUS matrix for bird parameters meant that the number of species is a parameter of paramount importance; it had the highest mean correlation with all the other bird parameters.

- Canopy birds (B2) correlated strongly with total bird density (B5).

3.3.3 Correlations between groups of ovegetation and bird parameters

The total cover and heterogeneity of a forest (V1) and the tree cover and foliage height diversity (V3) were strongly correlated with hole-breeders and air-foragers (B3). This means that a more heterogeneous forest (both in horizontal and vertical direction) with high vegetation cover supported more hole-breeding and air-foraging bird species.

The more shrub present and the higher the species diversity of the shrub layer (V2), the higher the species richness of woodland birds and diversity of woodland birds (B1) (Figs 3.24 and 3.25).

The higher the species diversity of the tree layer and the more dead trees in the woodland (V4), the higher the bird species richness and diversity (B1) and number of hole-breeders and air-foragers (B3). Hole-cutting birds profit by dead trees, not only as a source of food, but also as nesting site. The increased food and nest-site supply through the presence of dead wood enables a higher density of hole-cutters and indirectly by that a higher density of other hole-breeding birds (section 3.2.5).

A further developed woodland (V8) with higher trees (V9) supported more hole-breeding and air-foraging bird species (B3).

The higher the trees in a woodland (V9) the more canopy birds present (B2) (Fig. 3.26).

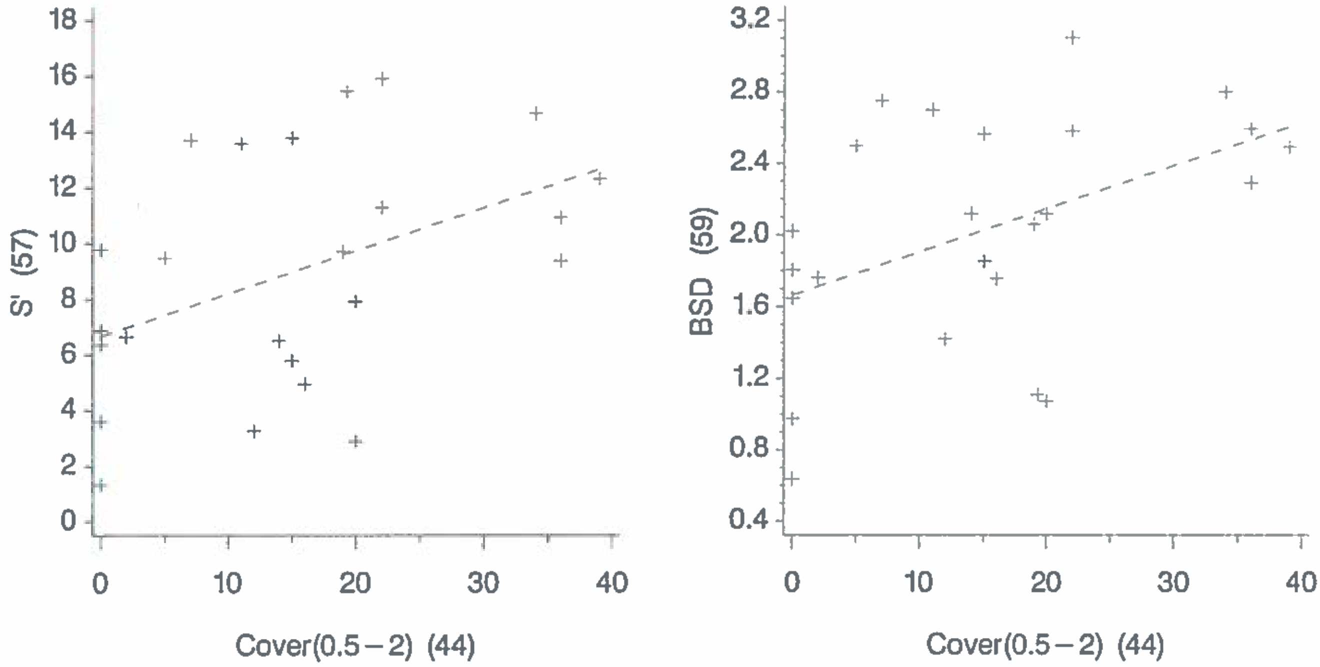


Figure 3.24. The total number of bird species (S') and Bird Species Diversity (BSD) in relation to cover of shrub (Cov(0.5-2); S': r=43, $p<0.05$, $y = 0.152x + 6.381$; BSD: r=47, $p<0.05$, $y = 0.023x + 1.681$).

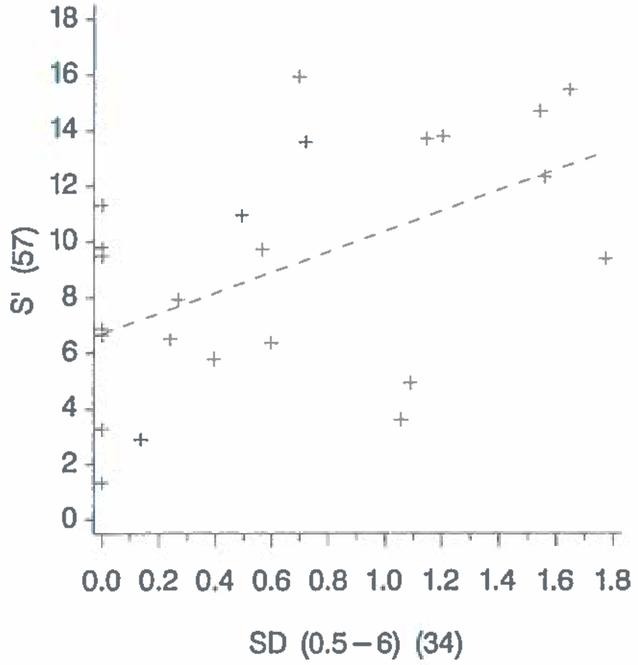


Figure 3.25. The total number of bird species (S') in relation to species diversity of the shrub layer (SD(0.5-6)): r=49, $p<0.05$, $y = 3.704x + 6.614$).

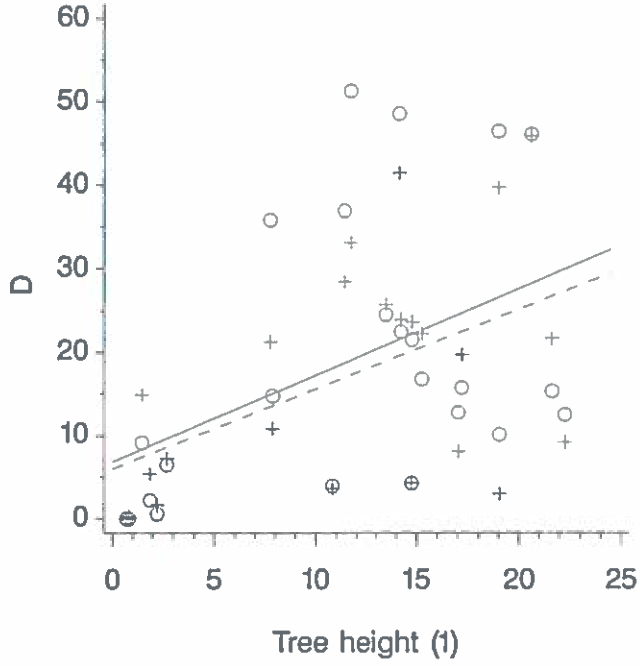


Figure 3.26. The density of canopy breeders (open dots) and canopy foragers (closed dots) in relation to tree height (m) (canopy breeders: r=47, $p<0.05$, $y= 1.043x + 6.811$; canopy foragers: r=44, $p<0.05$; $y = 0.960x + 6.001$).

4 Discussion

4.1 Conservation management

Denmark's commercial plantations contain many interesting bird species but they are also the workplaces of foresters whose main aims are to grow trees rather than to promote bird conservation. This chapter deals with how the conservation value of these plantations can be increased in the future. Some progress is already being made towards incorporating conservation into the management of the trees in forests, but much remains to be done.

It might be easier to have timber production, recreation and conservation neatly divided up on their own bits of land, but it would loose many opportunities for birds and for the establishment of the sort of approach to woodland management that really integrates and balances conflicting objectives to achieve both environmental and economic aims.

To date, rather little attention has been paid to the conservation gains which can be made within the current area of plantations and so conservationists have been unable to make firm suggestions as to how the forests should be managed. Where suggestions have been made they have often paid no attention to the real world in which the forester has to make his living. Too often conservationists have told foresters what they should be doing in their forests on the flimsiest of evidence. Changes in forestry practice which will cost money can only be introduced on the basis of sound research. Too little such research has so far been done for conservationists to be confident that they have very much to teach foresters about wildlife conservation. This study has developed a critical consideration of the effects of the forest structure (and indirectly that of forest management) on birds. The outcome of this study can be used to give some recommendations for forest management in order to increase the breeding bird richness, which are discussed below.

4.1.1 Restructuring the forest

In the late 1970s the concept of 'restructuring' developed (Hibberd 1985). Restructuring starts by looking at, and questioning, operational methods. It stresses the need to reconsider forest design from first principles at felling, and advocates some redesign for all the forests.

Up to now, conservation in the forest has been seen largely in terms of special sites. There has been a tendency to suggest that a certain percentage of the forest should be 'set aside for wildlife', and forest managers have been rightly alarmed that after one area has been lost for wildlife, some more for recreation, there will be hardly anything left for the production of trees. However, critical consideration of the effects of forest management on birds is developing. Ideas on forest structure, and especially the significance for both birds and mammals of restocking, were developing (Janse & Kessler 1981, Leslie 1981, Opdam & Bladeren 1981, Komdeur & Vestjens 1982, 1983, Opdam & Schotman 1986).

This study shows that some factors are crucial for birds. The breeding bird richness, expressed in terms of species density (S'), total density (D) and Bird Species Diversity (BSD) (section 3.1.2) increases with an increase in species diversity of both the shrub (0.5-6 m) and tree layer, heterogeneity of the shrub and tree layer, diameter of trees, and cover of shrub (Table 4.1). Moreover dead trees play an important role for hole-cutting birds, and thereby indirectly for hole-breeding birds (Table 4.1). Restructuring provides a vehicle for integrating management of these features for forest birds as forest managers started to realize the impractibility of single-purpose plans (e.g. for felling, recreation, conservation) as management became more complex.

This 'restructuring' approach is based on the idea that the entire forest has some value to wildlife. However, rare bird species deserve special attention because general forest management, designed to increase bird species diversity, will not necessarily help them. Their particular needs should be taken into account. This means that if a rare bird, for example a Goshawk, is found nesting in any part of the forest, operations such as felling should not be carried out in the near vicinity during the breeding season.

To enhance breeding-bird richness in forests, management should aim at taking the following measures:

- Longer rotations, when a clearcut system is applied, as diversity, heterogeneity, tree diameter and the presence of dead wood increase with age of the woodland.
- Leave dead wood at harvesting. The existence of dead or dying trees, both standing and lying, in woodlands is of great importance to birds.
- Promote a good vertical division of the vegetation with shrubs or a second tree layer. This can be achieved without any costs, by not eliminating natural regeneration of broadleaves.

Table 4.1. Important correlations between vegetation and bird parameters.

Bird parameters	BSD	S'	D	D (holecutters)
Vegetation parameters:				
Species Diversity (0.5-6 m)	28	49	35	31
Species Diversity trees	33	56	58	42
Species Diversity (0->16 m)	24	46	33	32
Heterogeneity (0.5-6 m)	54	60	35	47
Heterogeneity trees	29	42	27	31
Mean diam trees	27	45	49	65
Cover (0.5-2 m)	47	43	2	- 2
Percentage of dead trees	29	17	22	42

- Promote a small-scale regeneration system (e.g. group or single tree felling) with a tree or groupwise mixture of ages and species. The size of the area felled ('felling coupe') determines the scale of the age class patchwork. Small areas will be of greater benefit to birds because there will be greater numbers of edge species (species who prefer to live at the forest edge).
- Increase the heterogeneity and species diversity of the canopy and shrub layers by irregular felling of coupes differing in size. Younger trees can grow up in these gaps by either natural regeneration or planting.

The above findings enabled reproduction of a hypothetical forest which is rich in birds (high BSD, S and D; Fig. 4.1). Its main features are high age, rich understorey of shrubs of different broadleaved species, high presence of dead wood and various gaps in the canopy layer. If forests are especially managed for their natural value, like in nature reserves, natural processes can be started by these measures and then the forest may be left without treatment after some time. As the greatest diversity of birds will be found in this hypothetical woodland, it seems ideal from conservation's point of view, but not from forest management's point of view. In determining the best way to integrate conservation objectives into forest management one can change Danish forestry plantations to increase the value for birds by making them more heterogeneous in age and space.

Figure 4.1. Transect of a hypothetical forest intended to create a high bird richness. Its main features are high age of trees, rich understorey of shrub, large amounts of dead wood, high species diversity and gaps in the canopy layer. Abbreviations refer to plant names in Appendix II.

4.1.2 Age class distribution and tree species

The totally unnatural nature of Danish forests is one of the major blocks to sensible thinking in terms of conservation value. This study shows that unnatural habitats do have conservation value. A good example of this is the study of fragmented and homogeneous woodlands (section 3.2.3) with the first having a more varied and richer bird community than the latter. Creating a more diverse age class distribution seems to be the best way of improving the diversity of common birds in productive compartments, and there is a strong case for having as full a range of successional stages as possible in each large block of forest.

In order to obtain the greatest diversity of bird species in any forest the greatest possible range of successional stages (open spaces inclusive) should be represented at any time, and if possible there should be no break in the availability of any particular stage (Fig. 4.2). This means that forests of the future should be more varied than those seen at present. It should be possible to walk through any forest area and see birds associated with every successional stage; from Tree Pipits in the early stages, through Willow Warblers to Goldcrests and Coal Tits in the mature forest.

The age structure of the first rotations of the new forests has been exactly the opposite of this ideal. For efficiency, large areas have been planted within a short time-span, forming large plantations of uniform age and growth stage. As Danish forestry is still dominated by planting and large scale felling, the variation in age within forests is very small compared with the national range of tree ages. As time goes on, and the forests enter the second and subsequent rotations, followed by restocking, the variation within forests will increase markedly. The forest of Hov is an extreme example of a varied forest in terms of age class distribution of trees (Fig. 1.2b).

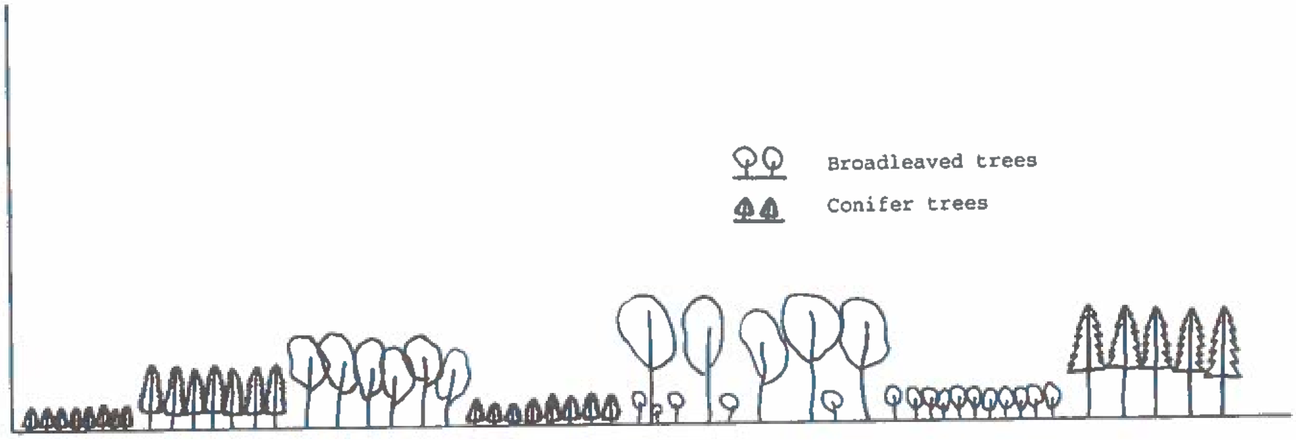


Figure 4.2. Age class diversity created in a large hypothetical production woodland together with alternating stands of broadleaves and conifers encourage a high bird richness. Abbreviations refer to plant names in Appendix II.

The forester can adjust both the age at which trees are felled, and the size of the areas felled. At felling, boundaries can be effectively remodelled. The area felled is influenced most strongly by the need to find a windfirm edge. Although simple in theory, in practice restructuring is a considerable challenge to the forest manager's skill if he is not to suffer economic costs: varying age class in particular is a demanding balancing act. The point at which it is most profitable to fell can be quite clearly defined and although economic penalties five years either side of the optimum are slight, beyond that they climb rapidly. However, with careful planning most stands can be felled within five years of the economic optimum and still leave significant age class differences.

The open space of restocks will always be the most significant area of early successional stages within the forest, but permanent open spaces like areas for conservation in and around the forest can be important for birds (e.g. Nightjars and Woodlarks). Forest edges are proven to be highly valuable for both plants and insects and on their turn for birds (Anderson and Carter 1988).

Broadleaved trees within coniferous plantations will bring in new bird species (section 3.2.2). Birch, for example, is valuable for birds; its soft wood makes it a suitable nesting tree for hole-cutting birds and its aphids are of special importance to newly arrived spring migrants like Willow Warbler. Mixed conifer-deciduous forests had a more diverse passerine fauna than did pure conifer or pure deciduous stands (section 3.2.3). Therefore, getting broadleaves into forest blocks and alternating areas with stands of different ages are the most obvious ways of trying to improve the forest for birds (Fig. 4.2).

However, all measures cannot be fulfilled in every site. Soil and climate often confine the range of forest types to a very small series. In general rich soils and a warm, humid but not too wet climate give way to the richest forests. Broadleaved regeneration in coniferous forests indicates a rich soil and can be used for increasing the structural richness and the proportion of broadleaved trees in the forest.

4.2 New horizons

While the wildlife within existing forests remains important, the greater issue in the relationship between forestry and birds for the next few decades is likely to be the effects of afforestation. Agricultural change in Europe is already affecting the Danish forestry scene. Large areas of arable land are to be taken out of production to reduce agricultural surpluses and more land is becoming available for forestry.

5 References

Anderson, S.H. & Shugart, H.H., Jr. (1974): Habitat selection of breeding birds in an east Tennessee deciduous forest. Ecology 55: 829-837.

Anderson, M.A. & Carter, C.I. (1988): Shaping ride sides to benefit wild plants and butterflies. In: Wildlife Management in Forests. Proceedings of a Discussion Meeting (D.C. Jardine). Edinburgh: Institute of Chartered Foresters.

Berkel, C.J.M. van (1979): Onderzoek naar kwantitatieve methoden voor het beschrijven van vegetatiestructuren. Stageverslag L.H. Wageningen, Plantenoecologie, RIN Leersum.

Biby, C.J., Aston, N. & Bellamy, P.E. (1989a): Effects of brodleaved trees on birds in upland conifer plantations in North Wales. Biological Conservation 49: 17-29.

Bibby, C.J., Bain, C.G. & Burges, D.J. (1989b): Bird communities of highland birchwoods. Bird Study 36: 123-133

Blondel, J., Ferry, C. & Frochot, B. (1973): Avifaune et végétation. Essai d'analyse de la diversité. Alauda 41: 63-84.

Erdelen, M. (1978): Quantitative Beziehungen zwischen Avifauna und Vegetationsstruktur. PhD thesis, Universität Köln.

Fuller, R.J. (1982): Bird habitats in Britain. Calton: T. and A.D. Poyser.

Gleason, H.A. (1992): On the relation between species and area. Ecology 3: 158-162.

Haila, Y., Järvinen, O. & Väisänen, R.A. (1980): Habitat distribution and species associations of land bird populations on the Åland Islands, SW Finland. Ann. Zool. Fennici 17: 86-105.

Hedegaard, H.M. (1992): Strategi for de danske naturskove. Skoven 24: 522-525.

Hibberd, B.G. (1985): Restructuring of plantations in Kielder forest district. Forestry 58: 119-129.

Hildén, O. (1965): Habitat selection in birds - a review. Ann. Zool. Fennici 2: 53-75.

Hurlbert, S.H. (1971): The nonconcept of species diversity: a critique and alternative parameters. Ecology 52: 577-586.

James, F.C. (1971): Ordinations of habitat relationships among breeding birds. Wilson Bulletin 83: 215--236.

James, F.C. & Warner, N.O. (1982): Relationships between temperate forest bird communities and vegetation structure. Ecology 63: 159-171.

Janse, C.J. & Kessler, J.J. (1981): Onderzoek naar de broedvogel bevolking en haar samenhang met de vegetatiestructuur in bossen op de Veluwe. Doktoraalscriptie, Leiden, RIN, Leersum. Pp.

Komdeur, J. & Vestjens, J.P.M. (1982): De relatie tussen bosstructuur en broedvogelbevolking in Nederlandse naaldbossen. Doktoraalverslag L.H. Wageningen, The Netherlands. Pp. 232.

Komdeur, J. & Vestjens, J.P.M. (1983): De betekenis van dood hout voor de avifauna. Nederlands Bosbouwtijdschrift 55: 86-90

Leslie, R. (1981): Birds of the northeast England forests. Quarterly Journal of Forestry 75: 153-158.

MacArthur, R.H. & MacArthur, J.W. (1961): On bird species diversity. Ecology 42: 594-598.

MacArthur, R.H. & Wilson, E.O. (1967): The theory of island biogeography. Princeton: Princeton University Press.

McDiarmid, R.W., Ricklefs, R.E. & Foster, M.S. (1977): Dispersal of Stemmadenia donnel-smithii (pocynaceae) by birds. Biotropica 9: 9-25.

Meltofte, H., Fjeldså, J. (1989): Fuglene i Danmark. Gyldendal, Denmark.

Moore, N.W. & Hooper, M.D. (1975): On the number of bird species in British woods. Biological Conservation 8: 239-250.

Nielsen, P.C. (1980): Skovens historie - fra natur til kultur. I: Danmarks natur, bd. 6. Skovene. Politikens Forlag.

Opdam, P. & Reijnen, R. (1978): Broedvogelinventarisatie met de karteringsmethode: een methodologisch onderzoek. Het Vogeljaar 26: 163-168.

Opdam, P. & Bladeren, G.J. van (1981): De vogelbevolking van qbeheerde en onbeheerde delen van het Forstamt Hasbruch en relatie tot de bosstructuur. RIN Leersum, The Netherlands. Pp. 71.

Opdam, P. & Schotman, A. (1986): De betekenis van structuur en beheer van bossen voor de vogelrijkdom (The role of forest structure and management for woodland birds). Nederlands bosbouwtijdschrift 58: 21-33.

Orians, G.H. & Wittenberger, J.F. (1991): Spatial and temporal scales in habitat selection. Am. Nat. Suppl 137: S29-S49.

Peet, R.K. (1974): The measurement of species diversity. Ann. Rev. of Ecol. and Sys. 5: 285-307.

Prodon, R. & Lebreton, J.D. (1981): Breeding avifauna of a Mediterranean succession: the holm and cork oak series in the eastern Pyrenees, 1. Analysis and modelling of the structural gradient. Oikos 37: 21-38.

Preston, (1960): Time and space and the variation of species. Ecology 41: 611-627

Rabenold, K.N. (1978): Foraging strategies, diversity, and seasonality in bird communities of Appalachian spruce-fir forests. Ecol. Monogr. 48: 397-424.

Rotenberry, J.T. & Wiens, J.A. (1980): Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61: 1228-1250.

Sas Institute Inc. (1988): SAS/STAT' User's Guide, Release 6.03 Edition. Cary, NC: SAS Institute Inc. Pp. 1028.

Shannon, C.E. & Weaver, W. (1949): The mathematical theory of communication. University of Illinois Press, Urbana.

Smith, K.G. 1977: Distribution of summer birds along a forest moisture gradient in an Ozark watershed. Ecology 58: 810-819.

Spindler, M. & Kessel, B. (1980): Avian populations and habitat use in interior Alaska taiga. Syesis 13: 61-104.

Steele, R.C. (1972): Wildlife conservation in woodlands. London: HMSO.

Teixera, R.M. (1977): Kwantitatieve inventarisatietechnieken. Het Vogeljaar 25: 30-36.

Tomialojc, L. (1979): The combined version of the mapping method. In: Bird census work and nature conservation, Vogelerfassung und Naturschutz (H. Oelke): 92-106.

Wiens, J.A. (1989): The ecology of Bird Communities 1. Foundations and Patterns. Cambridge University Press, Cambridge.

Wiens, J.A. & Rotenberry, J.T. (1981): Censusing and the evaluation of avian habitat occupancy. Studies in Avian Biology 6: 552-533.

Williams, C.B. (1964): Patterns in the balance of nature. London, Ac. Press.

Woolhouse, M.E.J. (1983): The theory and practice of the species-area effect, applied to the breeding birds of British woods. Biological Conservation 27: 315-332.

Worperfect Corporation (1990): Wordperfect Corporation, Version 5.1. USA.

Yapp, W.B. (1979): Specific diversity in woodland birds. Field studies 5: 45-58.

Appendices

Appendix I. English, scientific and Danish names of birds mentioned in the text.

Species name:	Scientific name:	Danish name:
Goshawk	*Accipiter gentilis*	Duehøg
Black Grouse	*Tetrao tetrix*	Urfugl
Wood Pigeon	*Columba palumbus*	Ringdue
Snipe	*Gallinago gallinago*	Dobbeltbekkasin
Woodcock	*Scolopax rusticola*	Skovsneppe
Nightjar	*Caprimulgus europaeus*	Natravn
Green Woodpecker	*Picus viridis*	Grønspætte
Black Woodpecker	*Dryocopus martius*	Sortspætte
Great-spotted Woodpecker	*Dendrocopus major*	Stor Flagspætte
Red-backed Shrike	*Lanius collurio*	Rødrygget Tornskade
Woodlark	*Lullula arborea*	Hedelærke
Tree Pipit	*Anthus trivialis*	Skovpiber
White Wagtail	*Motacilla alba*	Hvid Vipstjert
Wren	*Troglodytes troglodytes*	Gærdesmutte
Dunnock	*Prunella modularis*	Jernspurv
Whitethroat	*Sylvia communis*	Tornsanger
Lesser Whitethroat	*Sylvia curruca*	Gærdesanger
Garden Warbler	*Sylvia borin*	Havesanger
Blackcap	*Sylvia atricapilla*	Munk
Icterine Warbler	*Hippolais icterina*	Gulbug
Willow Warbler	*Phylloscopus trochilus*	Løvsanger
Wood Warbler	*Phylloscopus sibilatrix*	Skovsanger
Chiffchaff	*Phylloscopus collybita*	Gransanger
Grasshopper Warbler	*Locustella naevia*	Græshoppesanger
Goldcrest	*Regulus regulus*	Fuglekonge
Spotted Flycatcher	*Muscicapa striata*	Grå Fluesnapper
Pied Flycatcher	*Ficedula hypoleuca*	Broget Fluesnapper
Blackbird	*Turdus merula*	Solsort
Song Trush	*Turdus philomelos*	Sangdrossel
Mistle Thrush	*Turdus viscivorus*	Misteldrossel
Robin	*Erithacus rubecula*	Rødhals
Redstart	*Phoenicurus phoenicurus*	Rødstjert
Coal Tit	*Parus ater*	Sortmejse
Marsh Tit	*Parus palustris*	Sumpmejse
Great Tit	*Parus major*	Musvit
Blue Tit	*Parus caeruleus*	Blåmejse
Crested Tit	*Parus cristatus*	Topmejse
Long-tailed Tit	*Aegithalos caudatus*	Halemejse
Nuthatch	*Sitta europaea*	Spætmejse
Treecreeper	*Certhia familiaris*	Træløber
Chaffinch	*Fringilla coelebs*	Bogfinke
Greenfinch	*Carduelis chloris*	Grønirisk
Linnet	*Carduelis cannabina*	Tornirisk
Redpoll	*Carduelis flammea*	Gråsisken
Bullfinch	*Pyrrhula pyrrhula*	Dompap
Siskin	*Carduelis spinus*	Grønsisken
Hawfinch	*Coccothraustes coccothraustes*	Kærnebider
Yellowhammer	*Emberiza citrinella*	Gulspurv
Reed Bunting	*Emberiza schoeniclus*	Rørspurv
Whinchat	*Saxicola rubetra*	Bynkefugl
Starling	*Sturnus vulgaris*	Stær
Hooded Crow	*Corvus corone cornix*	Gråkrage
Jay	*Garrulus glandarius*	Skovskade

Appendix II. Abbreviations of plant names used (see Fig. 1.2 and Fig. 2.3).

abbr:	scientific name:	species name:	
		Danish:	English:
Acs	*Acer sp.*	Ahorn/Løn	Sycamore/Norway Maple
Ag	*Alnus glutinosa*	Rødel	Common Alder
As	*Abies sp.*	Ædelgran sp.	Fir sp.
Bs	*Betula sp.*	Birk sp.	Birch sp.
Cav	*Corylus avellana*	Hassel	Hazel
Co	*Crataegus oxyacantha*	Hvidtjørn	Hawthorn
Cv	*Calluna vulgaris*	Hedelyng	Heather
Db		Kvasbunke	Piles of dead branches
Ds	*Dryopteris sp.*	Bregne sp.	Bracken sp.
Dw		Død træ	Dead wood
Fe	*Fraxinus excelsior*	Ask	Ash
Fs	*Fagus sylvatica*	Bøg	Beech
Gr		Græsser	Grasses
He		Urter	Herbs
Lp	*Lonicera periclymenum*	Alm. gedeblad	Honeysuckle
Ls	*Larix sp.*	Lærk sp.	Larch sp.
Mg	*Myrica gale*	Porse	Bog Myrtle
Pa	*Picea abies*	Rødgran	Norway Spruce
Pi	*Prunus domestica*	Kræge	-
Pim	*Pinus mugo*	Bjergfyr	Mountain Pine
Pis	*Picea sitchensis*	Sitkagran	Sitka Spruce
Pm	*Pseudotsuga menziesii*	Douglasgran	Douglas Fir
Pn	*Pinus nigra*	Østrigsk fyr	Austrian Pine
Prs	*Prunus spinosa*	Slåen	Blackthorn
Ps	*Pinus sylvestris*	Skovfyr	Scottish Pine
Psp	*Prunus sp.*	Hæg sp.	Cherry sp.
Pt	*Populus tremula*	Bævreasp	Aspen
Qp	*Querqus petrea*	Vintereg	Sessile Oak
Qr	*Querqus robur*	Stilkeg	Pedunculate Oak
Rf	*Rhamnus frangula*	Tørst	Alder Buckthorn
Rfr	*Rubus fruticosus*	Brombær	Bramble
Ri	*Rubus idaeus*	Hindbær	Raspberry
Rs	*Rosa sp.*	Rose sp.	Rose sp.
Sa	*Sorbus aucuparia*	Alm. røn	Rowan
Sn	*Sambucus nigra*	Hyld	Common Elder
Ss	*Salix sp.*	Pil sp.	Willow sp.
Us	*Ulmus sp.*	Elm sp.	Elm sp.

Appendix III. The values of forest structure parameters for the forest types (see Table 2.3).

Forest	1. H(t)	2. H(lg)	3. De(t)	4. Di(t)	5. σ(di)	6. V(di)	7. diam(t)	8. σ(diam)	9. V(diam)
I.1	0.68	0	0	1.83	1.25	68.31	0.73	0.32	43.84
I.2	2.21	0	0	1.94	1.58	81.44	2.19	1.29	58.9
I.3	7.76	1.86	0	1.71	0.83	48.54	10.25	4.64	45.27
I.4	11.4	5.13	0	2.32	0.96	41.38	12.9	2.94	22.79
I.5	14.13	5.95	0	2.4	1.12	46.67	16.53	4.64	28.07
I.6	11.71	7.13	2.5	1.93	0.97	50.26	13.43	6.27	46.69
I.7	20.6	9.5	0	3.64	1.93	53.02	23	7.51	32.65
I.8	17.19	8.55	1.3	4.35	2.41	55.4	21.84	9.44	43.22
I.9	13.47	7.99	10	3.29	1.7	51.67	20.81	9.1	43.73
II.1	7.88	1.97	0	2.86	1.01	35.31	10.23	2.96	28.93
II.2	10.79	3.23	1.3	2.97	1.2	40.4	11.36	5.99	52.73
II.3	19.04	4.45	0	3.36	1.51	44.94	20.41	9.32	45.66
II.4	22.26	8.08	0	5.63	2.49	44.23	37.9	19.53	51.53
III.1	1.85	0.49	8.8	2.19	1.48	67.58	3.27	5.08	155.35
III.2	2.68	0.92	5	1.88	1.5	79.78	3.89	5.26	135.22
III.3	14.76	3.6	8.8	5.1	2.68	52.55	26.65	10.92	40.98
III.4	15.24	3.15	8.8	4.93	2.3	46.53	28.4	13.7	48.24
IV.1	17.03	8.93	5	3.92	1.87	47.7	22.65	7.89	34.83
IV.2	14.73	2.31	0	4	2.03	50.75	19.2	3.39	17.66
IV.3	0.81	0	0	4.47	7.22	161.52	6.06	12.76	210.56
IV.4	21.63	4.41	0	7.1	3.56	50.14	41.79	18.5	44.27
IV.5	1.46	0.06	0	1.59	0.61	38.36	1.73	0.64	36.99
V.1	19	8.66	1.25	3.82	2.55	66.75	23.28	8.73	37.5
V.2	14.21	4.4	0	5.12	3.86	75.34	26.21	19.67	75.05

Forest	10. H(s)	11. S/are	12. Cov(l)	13. Cov(dw)	14. Cov(b)	15. Cov(h)	16. Cov(s)	17. Cov(t)	18. Cov(hst)
I.1	0.25	0.63	4	2	8	62	14	8	84
I.2	0	0	0	6	10	54	0	38	92
I.3	0	3.44	74	0	0	46	0	92	138
I.4	0	0	80	42	0	16	0	76	92
I.5	0	0	94	8	6	4	0	92	96
I.6	0	0	90	4	0	10	0	90	100
I.7	0	2.81	52	22	10	40	0	68	108
I.8	1.1	50.31	32	18	2	57	44	53	154
I.9	0.79	24.69	54	8	0	23	65	80	168
II.1	0	1.88	94	0	6	20	0	98	118
II.2	0	0	97	23	1	15	0	91	106
II.3	0.25	16.25	95	10	2	48	6	91	145
II.4	0	0	95	5	0	68	0	92	160
III.1	0	0	12	0	0	89	0	48	137
III.2	0	0	40	1	0	62	0	60	122
III.3	3	0	13	6	0	84	1	79	164
III.4	3	0.63	52	30	0	47	2	95	144
IV.1	0	0	0	2	0	96	0	78	174
IV.2	0.25	7.19	64	0	0	66	2	84	152
IV.3	0.38	0	36	6.5	3.2	61.3	33.8	6.5	101.6
IV.4	0	15	88	1	0	43	7	90	140
IV.5	0	58.44	35	2.6	0	44.7	31.6	26.3	102.6
V.1	1.19	6.25	48	20	6	45	16	69	130
V.2	1.18	18.61	56	6	4	52	16	72.7	140.7

Forest	19. FHD(hst)	20. SD(h)	21. SD(s)	22. SD(t)	23. SD(hst)	24. Het(h)	25. Het(s)	26. Het(t)	27. Het(hst)
I.1	0.747	0.44	0.45	0	0.89	2.423	1.613	1	5.036
I.2	0.678	0.25	-	0	0.25	2.258	0	2.382	4.64
I.3	0.637	0.69	-	0.15	0.84	2.083	0	1.519	3.602
I.4	0.462	0.69	-	0	0.69	1.929	0	2.004	3.933
I.5	0.173	0.69	-	0.21	0.9	0.845	0	1.415	2.26
I.6	0.325	0.95	0	0.67	1.62	1.519	0	1.279	2.798
I.7	0.659	0.46	0	0.09	0.55	1.881	0	2.083	3.964
I.8	1.093	0.94	1.34	1.06	3.34	2.191	2.275	2.439	6.905
I.9	0.993	0.79	0.92	1.12	2.83	1.886	2.219	2.057	6.162
II.1	0.455	0.33	-	0.29	0.62	1.785	0.477	0.699	2.961
II.2	0.408	0.34	0	0.09	0.43	1.441	0	1.506	2.947
II.3	0.79	0.58	0.64	0.27	1.49	2.32	0.854	1.1	4.274
II.4	0.682	0.59	0	0.01	0.6	2.311	0	1.613	3.924
III.1	0.648	0.61	-	0.51	1.12	1.442	0	2.344	3.786
III.2	0.693	0.5	-	0.63	1.13	2.097	0	2.349	4.446
III.3	0.726	0.2	-	1.14	1.34	1.391	0.239	2	3.63
III.4	0.699	0.39	0	0.88	1.27	1.809	0.557	1.042	3.408
IV.1	0.688	0.41	-	0.44	0.85	1	0	2.004	3.004
IV.2	0.747	0.69	0.69	0	1.38	2.528	0.477	1.851	4.856
IV.3	0.847	0.75	0.39	0	1.14	2.161	2.337	1.114	5.612
IV.4	0.796	0.95	0.57	0.15	1.67	2.258	1.95	1.671	5.879
IV.5	1.074	0.88	1.21	0.76	2.85	2.22	0.845	1.929	4.994
V.1	0.961	0.9	0.73	0.74	2.37	2.184	1.663	2.052	5.899
V.2	0.956	1.26	1.772	1.202	4.234	2.245	1.827	1.851	5.923

Forest	28. Cov(<0,5)	29. Cov(0,5-6)	30. Cov(6-16)	31. Cov(>16)	32. Cov(0->16)	33. SD(<0,5)	34. SD(0,5-6)	35. SD(6-16)	36. SD(>16)
I.1	82	0	0	0	82	1.22	-	-	-
I.2	96	22	0	0	118	0.82	0	-	-
I.3	46	86	32	0	164	0.835	0.137	0.179	-
I.4	16	34	46	0	96	0.693	0	0	-
I.5	4	6	88	0	98	0.693	0	0.17	-
I.6	10	10	84	4	108	0.95	0.598	0.615	0
I.7	40	0	62	12	114	0.614	-	0.103	0
I.8	72	42	44	9	167	1.715	1.557	0.408	0
I.9	75	46	66	10	197	1.448	1.771	0.475	-
II.1	20	82	56	0	158	0.325	0.269	0	-
II.2	16	51	62	3	132	0.702	0.24	0.013	0
II.3	53	31	86	47	217	1.516	0.396	0.072	0.247
II.4	68	14	41	89	212	0.867	0	0	0
III.1	89	47	0	0	136	0.748	0.493	-	-
III.2	63	52	5	0	120	0.802	0.566	0	-
III.3	84	42	71	25	222	0.302	1.145	1.084	0.603
III.4	47	52	76	45	220	0.504	0.719	0.964	0.765
IV.1	96	10	42	32	180	0.416	1.056	0.325	0.234
IV.2	80	24	84	0	188	1.104	0	0	-
IV.3	65	16	0	0	81	1.445	1.089	-	-
IV.4	62	31	64	61	218	1.662	0.696	0.237	0.079
IV.5	76	34	5	0	115	1.855	1.54	-	-
V.1	50	21	59	21	151	1.416	1.202	0.552	0.337
V.2	57.1	40.7	60	21.3	179.1	1.842	1.647	1.201	0.251

Appendix III, continued ...

Forest	37. SD(0->16)	38. Het(<0,5)	39. Het(0,5-6)	40. Het(6-16)	41. Het(>16)	42. Het(0->16)	43. FHD4	44. Cov(0,5-2)	45. Cov(2-4)
I.1	1.22	1.756	0	0	0	1.756	0	0	0
I.2	0.82	0.954	2.083	0	0	3.037	0.481	22	2
I.3	1.151	2.083	1.613	2.258	0	5.954	1.014	20	44
I.4	0.693	1.929	2.337	2.161	0	6.427	1.019	2	10
I.5	0.863	0.845	1.114	1.568	0	3.527	0.398	0	2
I.6	2.163	1.519	1.863	1.785	0.845	6.012	0.758	0	4
I.7	0.717	1.881	0	2.179	1.613	5.673	0.936	0	0
I.8	3.68	2.202	2.266	2.282	1.632	8.382	1.219	39	5
I.9	3.694	2.044	2.045	2.22	0.926	7.235	1.225	36	14
II.1	0.594	1.785	2.037	2.337	0	6.159	0.97	20	60
II.2	0.955	1.658	2.133	2.133	0.557	6.481	1.064	14	33
II.3	2.231	2.301	1.982	1.896	2.151	8.33	1.32	15	14
II.4	0.867	2.311	1.305	1.849	1.515	6.98	1.226	5	8
III.1	1.241	0.982	2.243	0	0	3.225	0.645	36	15
III.2	1.368	2.044	2.232	0.98	0	5.256	0.833	19	37
III.3	3.134	1.464	2.34	2.093	1.503	7.4	1.293	7	24
III.4	2.952	1.809	2.341	1.911	2.298	8.359	1.362	11	27
IV.1	2.031	1	1.114	2.4	2.228	6.742	1.142	0	0
IV.2	1.104	2.083	2.104	1.851	0	6.038	0.986	12	14
IV.3	2.534	2.037	1.959	0	0	3.996	0.497	16	0
IV.4	2.674	2.224	2.23	2.222	2.42	9.096	1.351	22	11
IV.5	3.395	2.037	2.292	0	0	4.329	0.77	34	5
V.1	3.507	2.239	2.017	2.195	1.685	8.136	1.282	15	6
V.2	4.941	2.295	2.292	2.224	1.565	8.376	1.321	19.3	15.3

Forest	46. Cov(4-6)	47. Cov(6-8)	48. Cov(8-10)	49. Cov(10-12)	50. Cov(12-16)	51. Cov(16-20)	52. Cov(>20)	53. Cov(0->20)	54. FHD(10)	55. VM
I.1	0	0	0	0	0	0	0	0	0	41
I.2	0	0	0	0	0	0	0	24.48	0.558	85
I.3	64	26	12	6	0	0	0	173.01	1.749	357
I.4	30	42	34	8	0	0	0	127.02	1.668	259
I.5	4	20	34	42	38	0	0	140.4	1.584	358
I.6	10	26	44	0	0	0	0	84.76	1.322	173
I.7	0	12	28	28	26	10	2	106.94	1.743	304.8
I.8	2	4	12	17	24	11	0	115.22	1.75	314.5
I.9	8	11	11	30	42	9	2	164.22	1.946	447.5
II.1	70	50	26	2	0	0	0	228.97	1.705	456
II.2	38	39	28	20	18	3	0	194.06	2.058	429
II.3	16	30	51	70	74	47	15	333.32	2.129	944.5
II.4	10	5	7	19	35	61	80	231.23	1.878	1155.5
III.1	6	0	0	0	0	0	0	57.64	1.012	140.5
III.2	13	5	0	0	0	0	0	74.83	1.329	170
III.3	21	27	33	33	44	15	0	205.29	2.007	564.5
III.4	25	28	45	48	47	36	11	279.36	2.204	736.7
IV.1	10	18	16	22	24	30	2	123.14	1.691	398
IV.2	8	22	30	62	38	0	0	186.99	1.831	482
IV.3	0	0	0	0	0	0	0	16.5	0.497	56.5
IV.4	12	19	27	33	48	47	38	258.35	2.175	815.2
IV.5	3	0	0	0	5	0	0	47.77	1.004	125
V.1	6	15	31	40	34	12	5	165.28	2.048	441.5
V.2	18	19.3	32	28.7	32	20.7	9.3	195.92	2.189	526.52

Appendix IV. The values of bird parameters for the forest types (densities are in number of territories/10 ha; see Table 2.4).

Forest	56. S	57. S'	58. D	59. BSD	60. Y	61. PIE	62. E	63. DI	64. S(hob)	65. S(nhb)
I.1	2	1.33	11.84	0.636	1.8	0.444	0.92	1	0	2
I.2	20	11.3	60.86	2.584	10.475	0.905	0.86	0.3	1	19
I.3	3	2.89	35.83	1.071	2.849	0.649	0.97	0.77	0	2
I.4	7	6.64	58.46	1.764	4.821	0.793	0.91	0.5	2	5
I.5	10	6.86	67.8	1.806	4.613	0.783	0.78	0.58	2	8
I.6	7	6.37	63.75	1.647	4.199	0.762	0.85	0.65	1	6
I.7	15	9.78	73.65	2.021	5.285	0.811	0.75	0.56	4	11
I.8	19	12.33	60.23	2.494	9.288	0.896	0.85	0.35	5	14
I.9	15	9.39	60.19	2.292	7.431	0.865	0.85	0.43	4	11
II.1	9	7.92	47.89	2.119	7.718	0.87	0.96	0.35	2	7
II.2	9	6.5	21.96	2.121	7.649	0.869	0.97	0.39	2	7
II.3	9	5.79	13.41	1.852	4.792	0.791	0.84	0.59	3	6
II.4	16	9.49	25.37	2.501	9.657	0.896	0.9	0.33	5	11
III.1	17	10.95	40.67	2.595	11.473	0.917	0.92	0.3	2	15
III.2	14	9.72	52.1	2.061	4.966	0.811	0.78	0.53	3	11
III.3	22	13.69	88.18	2.75	12.142	0.918	0.89	0.3	10	12
III.4	23	13.57	79.21	2.7	12.766	0.928	0.86	0.27	11	12
IV.1	7	4.94	12.11	1.755	5.07	0.803	0.9	0.54	0	7
IV.2	30	15.91	64.16	3.103	14.761	0.922	0.91	0.24	11	19
IV.3	20	14.68	63.62	2.801	14.302	0.93	0.94	0.23	3	17
IV.4	24	13.78	101.06	2.565	9.718	0.897	0.81	0.34	8	16
IV.5	34	15.46	69.26	1.11	17.793	1	0.31	0.18	8	26
V.1	5	3.61	18.04	0.973	1.918	0.704	0.6	0.79	3	2
V.2	5	3.26	8.94	1.421	3.406	0.706	0.88	0.61	3	2

Forest	66. D(hob)	67. D(nhb)	68. D(hoc)	69. D(hbnc)	70. D(grb)	71. D(shb)	72. D(cab)	73. D(grf)	74. D(shf)	75. D(caf)
I.1	0	11.84	0	0	7.89	3.96	0	9.87	1.97	0
I.2	0.57	60.29	0	0.57	11.67	48.05	0.57	21.2	37.75	1.63
I.3	0	35.83	0	12.5	0	0	35.83	14.58	0	21.25
I.4	6.92	51.54	3.85	21.54	3.08	11.54	36.92	30	0	28.46
I.5	6.82	60.98	1.52	24.54	8.33	4.09	48.56	23.52	2.8	41.48
I.6	2.81	60.94	0	3.75	2.81	6.88	51.25	28.44	2.19	33.13
I.7	9.41	64.24	2.35	20.82	7.41	10.71	46.12	20.39	6.51	45.92
I.8	5.92	54.31	1.15	8.05	4.89	33.68	15.75	20.48	19.21	19.73
I.9	5.77	54.42	2.6	13.46	4.04	25.87	24.52	19.82	14.63	25.74
II.1	5.79	42.11	0	4.21	5.26	22.11	14.74	20.53	16.58	10.79
II.2	3.53	18.43	1.57	0	4.71	9.8	3.92	7.91	8.89	3.59
II.3	1.87	11.54	0	3.08	0.66	0.77	10.11	8.5	1.25	3
II.4	6.25	19.12	1.47	5.51	1.84	4.78	12.5	9.19	3.86	9.19
III.1	3.33	37.33	2.22	0	19.56	15.56	2.22	15.7	19.59	5.37
III.2	6.45	45.65	3.23	1.61	14.52	24.68	6.45	17.47	27.39	7.23
III.3	46.59	41.59	4.67	12.15	5.14	14.95	21.5	34.75	18.07	23.68
III.4	36.5	42.71	4.29	11.07	10.14	15.79	16.79	27.58	17.23	22.26
IV.1	0.88	11.23	0	0	3.33	7.89	0	5.79	6.05	0.26
IV.2	24.85	39.31	5.63	7.52	3.84	20.13	15.34	17.79	16.07	21.7
IV.3	5.85	57.77	0	1.28	9.04	39.57	9.15	23.51	25.21	14.89
IV.4	14.53	86.53	4.13	9.19	12.34	27.69	46.5	45.7	14.04	39.73
IV.5	16.76	52.5	3.89	6.52	6.92	23.11	22.47	25.69	15.16	23.93
V.1	3.92	14.12	1.37	12.75	1.37	0	12.75	7.39	1.01	8.07
V.2	3.53	5.41	0	4.24	0	1.18	4.24	2.51	2.16	4.27

Appendix IV, continued ...

Forest	76. D(aif)	77. D(stf)	78. D(cp)	79. D(wp)	80. D(pm)	81. D(pa)	82. D(tt)	83. D(tp)	84. D(tm)	85. D(er)
I.1	0	0	0	0	0	0	0	0	0	0
I.2	0.29	0	9.77	0	0	2.3		0	10.34	2.64
I.3	0	0	0	0	0	0	8.33	15	0	0
I.4	0	0	0	0	0	7.69	7.69	7.69	0	3.85
I.5	0	0	1.06	0	3.03	0	6.06	15.15	0	1.52
I.6	0	0	4.38	0	0	0	18.75	22.5	0	2.5
I.7	0	0.82	1.18	0	2.35	1.18	2.35	20.59	0.35	0
I.8	0	0.8	9.89	0	2.3	0	3.79	3.1	0.92	0.92
I.9	0	0	5.77	0	2.6	0	0.96	9.13	11.25	1.92
II.1	0	0	6.32	0	5.26	0	10.53	0	5.26	5.26
II.2	0	1.57	3.92	1.57	4.71	0	1.96	0	0	1.96
II.3	0	0.66	0.77	0	0.66	0	4.84	0	0	0
II.4	0.18	2.94	0.74	1.47	1.1	0	1.84	0	0	0.37
III.1	0	0	0	0	2.89	0	1.11	1.11	4.44	1.11
III.2	0	0	0	0	1.61	0	3.23	1.61	20.97	1.61
III.3	1.87	9.81	0	4.67	1.87	1.87	5.61	0.93	1.87	2.8
III.4	2.5	9.64	2.5	4.29	5.64	0	3.57	0.71	0	3.21
IV.1	0	0	0.88	0	0.7	0	0	0	0	0
IV.2	0.32	8.28	4.54	4.75	2.94	1.72	1.68	0.42	1.64	1.72
IV.3	0	0	14.68	0	2.13	2.13	2.13	3.62	4.89	5.96
IV.4	0.16	1.44	5.81	0.44	5.75	5.88	19.38	14.56	0	3.06
IV.5	0.19	4.28	5.39	2.33	3.52	3	7	5.06	1.36	2.41
V.1	0	1.57	0	0	1.37	0	0	0	0	0
V.2	0	0	0	0	0	0	0	0	0	0

Forest	86. D(sa)	87. D(sapmo)	88. D(sy)	89. D(pt)	90. D(ph)	91. D(rr)	92. D(at)	93. D(cc)	94. D(fc)	95. D(pafc)
I.1	7.89	0	2	3.95	0	0	0	0	0	0
I.2	1.72	9.77	19	5.17	10.34	1.72	0.57	0.57	0	10.34
I.3	0	0	2	0	0	0	12.5	0	0	0
I.4	0	0	5	0	0	0	27.69	0	6.15	0
I.5	0	1.06	8	1.52	0	1.06	34.92	0	10.61	0
I.6	0	0	6	0	0	0	9.38	0	5.63	0
I.7	0	0	11	6.24	2.12	0	30.94	1.18	10.12	2.12
I.8	0	6.67	14	13.33	7.82	6.09	10.92	1.95	2.87	7.82
I.9	0	2.88	11	12.5	5.67	2.88	16.35	0.77	2.88	5.67
II.1	0	6.32	7	0	10.53	6.32	4.21	0	0	10.53
II.2	0	5.88	7	0	0	3.92	0	1.96	0	0
II.3	0	0.77	6	0	0	0.77	3.08	0.44	0	0
II.4	0	0.74	11	2.94	1.47	0.74	5.51	2.21	0	1.47
III.1	3.33	3.33	15	0	4.44	0	0	1.11	0	4.44
III.2	4.84	0	11	1.61	20.97	0	1.61	1.61	0	20.97
III.3	1.87	0	12	8.41	2.8	0	13.08	14.25	0.93	2.8
III.4	0.71	2.5	12	9.57	3.43	2.5	11.79	10.43	0.71	3.43
IV.1	1.75	3.51	7	2.98	0	0	0	0	0	0.53
IV.2	0	4.92	19	2.39	1.18	4.33	8.49	8.19	0.97	9.24
IV.3	0.64	8.3	17	3.83	0.53	6.17	5.32	3.19	4.04	8.09
IV.4	0	3.94	16	10.69	9.24	3.94	21.13	1.25	11.94	1.69
IV.5	0.25	4.69	26	5.25	8.09	3.83	11.05	4.47	4.53	5.82
V.1	0	0	2	0	1.69	0	12.75	0.98	0	0
V.2	0	0	2	0	5.82	0	4.24	1.18	0	1.18

National Environmental Research Institute

The National Environmental Research Institute - NERI - is a research institute of the Ministry of the Environment. NERI's tasks are primarily to do research, collect data and give advice on problems related to the environment and Nature.

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