# Secondary succession in plant and bird communities from meadow to deciduous forest on a delta plain in lake Øyeren, SE Norway

Nils Valland

Dr.scient.-avhandling
Institutt for naturforvaltning
Norges landbrukshøgskole

## FORORD

Sommaren 1976 gjekk Institutt for naturforvaltning i gang med utarbeiding av ein skjøtselsplan for Nordre Øyeren Naturreservat etter oppdrag frå Fylkesmannen i Oslo og Akershus og Miljøverndepartementet. Under arbeidet med denne vart underteikna interessert i gjengroingsdynamikken på dei kulturbetinga opne områda i deltaet. Som høgskole-stipendiat gjorde eg frå 1977 studiet av sekundære suksesjonar til hovudarbeidet i den vitskaplege avhandlinga for dr. scient.-graden ved Norges landbrukshøgskole (NLH). Eit mindre omfangsrikt arbeid om konsekvensane av desse suksesjonane for skjøtselen og forvaltninga av naturreservatet vert også lagt fram. Dosent Sigmund Hus, Institutt for naturforvaltning, NLH har vore min hovudvegleiar. Eg er han stor takk skuldig for råd, støtte og oppmuntring både fagleg og menneskeleg under dei forskjellige fasane av arbeidet. Vil elles retta ein takk til førsteamanuensis Olav Hogstad, Zoologisk institutt, Universitetet i Trondheim for vegleiing i den ornitologiske delen av arbeidet. Takk også til førsteamanuensis Kåre A. Lye, Botanisk institutt, NLH for hjelp i dei innleiande fasane av prosjektet og med artsbestemming av mosane. Yngve Kvebæk, Nordre Øyeren Fuglestasjon og vit. ass. Ottar Krohn, NLH var til stor hjelp ved fugleregistreringane i 1977. Else-Margrethe Huse har maskinskrive eit preliminært utkast til avhandling, medan den ferdige avhandlinga er skrive av Randi Martin. Til desse og mange andre som har ytt meg hjelp, vil eg retta ein varm takk. Den heilhjarta støtta frå kona mi, Inger Anne, har vore ein vesentleg føresetnad for gjennomføringa av prosjektet. Undersøkingane har vore finansielt støtta av Miljøverndepartementet og Norges Landbruksvitskaplege Forskningsråd.

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Nils Valland

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SAMANDRAG

Målet med dette arbeidet var å granska framsette hypotesar om "forventa trendar" og kor generelt dei gjeld i eit økosystem som gjennomgår suksesjon. Det vart utført ved å samanlikna utviklinga av parametrar for struktur og tettleik/biomasse i plante- og fuglesamfunn i 4 stadier av ein sekundær suksesjon. Studieområdet var ein deltaflate i innsjøen Øyeren i Søraust-Noreg. Det første stadiet var ei open, slått og av og til brend våteng, det andre stadiet ei 10 års gjengrodd eng med spreidde buskar, det tredje ein 35 år gamal oreskog og det fjerde ein oreskog på minst 70 år. Forekomsten og tettleiken hjå artene i plantesamfunna vart estimert ved jamt fordelte prøveflater på 2 $m^2$. Fuglesamfunna vart målt ved hjelp av kartmetoden.

Av dei forskjellige vekstformer dominerte fleirårige graminoider tidleg i suksesjonen, medan buskar og tre var dei dominerande i mellom- og seine stadier. Mosane var eit monaleg vekstform-innslag i yngre stadier, særleg etter 10 års gjengroing. Dekningsgraden av blomsterplanter var omtrent konstant gjennom heile suksesjonen, medan bregnene dominerte urteskiktet i skogfasane.

Den floristiske diversiteten (art/areal regresjonsindeks) var størst i dei intermediære stadier av suksesjonen, medan det første og det siste stadiet hadde ein floristisk diversitet av omlag same storleik. Men artstettleiken var høgare i den opne enga enn i klimaks-oreskogen. Den floristiske diversiteten av karplanter var monaleg lågare i slåtte-enga enn i klimaksstadiet. Endringsgraden av floristisk diversitet var størst i dei tidlege fasane av suksesjonen.

Truleg er den relativt låge floristiske diversiteten i den opne fuktegna forårsaka av høg frekvens av forstyrring eller

populasjonsreduksjonar, som hindrar potensielle kolonistar (t.d. buskarter) å restituera seg etter slått og brenning. Den floristiske diversiteten på feltet er sannsynlegvis i ein dynamisk balanse mellom artsreduserande og -fremmande effektar av skjøtselen. Populasjonsreduksjonar hjå dominante arter hindrar konkurranselikevekt og tillet såleis underlegne arter (t.d. somme av moseartene) å koeksistera. Den artsfremmande effekten av at skjøtselsforstyrringa opphøyrer, er truleg hovudforklaringa på den relativt høge floristiske diversiteten i dei intermediære stadier. Effekten av dette er større enn den forventa motsette trend når samfunnet gradvis nærmar seg konkurransejamvekt. I sluttstadiet av suksesjonen er truleg plantesamfunnet nærare denne likevekta. Dei dominante konkurrentane har meir effektivt monopolisert hovudressursane og har såleis redusert talet på koeksisterande arter og dermed deir floristiske diversitet. Indikasjonar på denne aukande interspesifikke konkurransen (truleg om lys) ser ein av det faktum at dekningsgrad-estimata av feltskiktet i aukande grad er negativt korrelert med dekningsgraden av buskar frå den unge til den eldre oreskogen.

Diversiteten av artenes dekningsproporsjon (Shannons indeks) minka litt, men ikkje signifikant, gjennom suksesjonen. Dette indikerer, saman med eit høgare dominansnivå av dei to hovudartene, at ein aukande del av dei totale ressursane vert delt mellom færre arter ettersom suksesjonen skrid fram. Den romlege heterogenitet auka i dei suksessive stadia, men dei ulike parametrane auka i avtakande grad. Lauvverksdiversitet og vegetasjonssjiktdiversitet, mål på den fysiognomiske kompleksitet av lauvverkssjikt, var nært korrelert med den totale vegetasjonstettleik eller tettleiken av busk- og tresjikt.

Av fuglesamfunna som hekka på desse suksesjonsstadia, dominerte Charadrii-gruppa i den opne enga. I buskhabitatet var Emberizidae og Sylviinae dei største taksonomiske gruppene. Skogstadia var dominert av arter som høyrer til Sylviinae, Turdinae og Fringillidae. Fugleartsdiversiteten (Shannons indeks) synte ein retningsbestemt, jamn auke frå stadium ein til fire. Diversitetsauken var størst i dei tidlege fasane og jamna seg så ut i dei seinare skogsstadia. Samstundes minka dominansen av dei to mest frekvente artene gjennom suksesjonen. Diversitet og dominans i fuglesamfunna var negativt korrelert. Jamnleikskomponenten av diversiteten var berre litt høgare i dei slutta skogshabitata enn i dei opne, tidlegare suksesjonsstadia.

Tettleiken av busk- og tresjikta var den habitatfaktoren som best forutsa fugleartsdiversiteten. Indeksane av romleg heterogenitet, t.d. lauvverksdiversitet og vegetasjonssjiktdiversitet, forklarte noko mindre av fugleartsdiversiteten. Korkje plantediversitetsindeksar, vårflaumvariasjonen eller nokon andre habitatfaktorar auka signifikant forklaringa av variasjonen i fugleartsdiversiteten i tillegg til lauvverkstettleiken eller -diversiteten.

Artstettleiken (antal arter/areal) synte ein annan trend i auken enn artsdiversiteten. Artstettleiken var forskjellig i alle stadier, men synte riktignok berre liten skilnad mellom dei intermidiære stadier. I klimaksfasen var artstettleiken 75 % høgre enn i føregåande stadium. Til trass for ulike utviklingsforlaup var dei to indeksane av diversitet i fuglesamfunna korrelerte. Artstettleiken var lineært korrelert med tettleiken av fuglesamfunnet, medan artsdiversiteten var korrelert med logaritmen (naturlege) til samfunnstettleiken. Av dei forskjellige habitatfaktorane, var det tettleiken av busk- og tresjiktet som best forutsa artstettleiken. Som for artsdiversiteten, forklarte ingen av dei tidlegare nevnte habitatfaktorane signifikant meir av artstettleiken enn busk- og tresjikttettleiken åleine.

Den strukturelle kompleksiteten av habitatet, her målt som lauvverksdiversitet eller vegetasjonssjiktdiversitet, og lauvverkstettleik, er truleg grove estimat av ressursspennvidda eller nisjerom/nisjevolum. Denne faktoren er sannsynlegvis vesentleg for å bestemma fugleartsdiversitet, saman med nisjebreidde og nisjeoverlapping.

Diversiteten i dei seine suksjonsstadia med oreskogshabitat i denne studien er lågare enn i andre lauvskogar med liknande strukturell diversitet. Data frå denne suksesjonen, samanlikna med andre lauvskogsgradientar, peikar antan på at nisjerommet er overestimert av indeksar basert på lauvverkets tettleik og diversitet eller at andre faktorar reduserer antal koeksisterande arter og deira relative tettleik. Desse faktorane kan vera miljømessige (variabilitet) og/eller indre faktorar i fuglesamfunnet (interspesifikk konkurranse, predasjon) som verkar inn på artenes ressursbruk ved å auka nisjebreidda og/eller minka nisjeoverlappinga.

Oreskogar er karakterisert av ein relativt låg fugleartsdiversitet samanlikna med andre lauvskogar, bortsett frå subalpin bjørkeskog som har omlag same diversitet. Produktiviteten i oreskogane er høg. Andre lauvskogar har berre 10 til 40 % av fuglesamfunnstettleiken til oreskogane. Dette faktum indikerer at ressursdiversiteten i oreskogar er låg, og lågare enn forventa av estimat av lauvverkets diversitet og tettleik. Volumet av forekommande og tilgjengelege ressursar må imidlertid vera stort.

Sjølv om fuglediversiteten i denne studien er sterkt korrelert med dei habitatfaktorane som er freistnader på å måla ressursspennvidda, er det likevel konkludert med at desse faktorane er unøyaktige mål for ei vidare gruppe hekkehabitat enn dei som finst i denne suksesjonen.

Tettleiken av fuglesamfunnet auka omtrent lineært gjennom suksesjonen, frå omlag 120 par/km$^2$ i pionerstadiet til omlag 3000 par/km$^2$ i klimaksoreskogen. Tettleiken av busk- og tresjikta vart vurdert å vera den habitatfaktoren som synte sterkast samvariasjon med samfunnstettleiken, men forholdet mellom desse var ikkje lineært. Logaritmen til samfunnstettleiken var lineær og sterkt korrelert med tettleiken av busk- og tresjikt. Dette indikerer anten at tettleiken av fuglar er bestemt av faktorar i tillegg til fødeproduktivitet innan feltet (dersom det er linearitet mellom lauvverksestimata og tilgjengelege fôderessursar) eller at somme arter er delvis avhengige av fødetilgang utanfor hekkehabitatet (t.d. Turdus pilaris og Columba palumbus).

Tettleiken av alle reirplasseringsgrupper auka gjennom suksesjonen. Arter med reir i busk- og tresjikta auka mest dersom ein samanlikna ung og gamal oreskog. Tettleiken av desse artene synte eksponensiell vekst gjennom suksesjonen. Busk- og tresjikttettleiken var den habitatfaktoren som forklarte mest av denne tettleiksveksten, faktoren var nært korrelert med logaritmen til tettleiken til busk- og tre-hekkande arter.

Tilveksten i fødesøksgrupper reflekterte tilveksten av fysiognomiske grupper av planter i habitata ettersom suksesjonen skreid fram. Skilnaden mellom dei tre første stadia var uttalt, men mellom dei to skogshabitata var skilnaden liten. Tettleiken av arter som finn føde i lauvverk i busk og tresjikt aukar mindre i høve til ein gitt auke i tettleiken av busk- og tresjikta enn tettleiken av arter som byggjer reir i desse sjikta. Dette kan indikera at føderessursane (om dei er lineært korrelert med lauvverkstettleik) er ein viktigare regulerande faktor enn mengda av tilgjengelege reirplassar (om lauvverkstettleik er ein god indikator på mengda av desse).

Artsomsetjinga var høgare i plantesamfunna enn i fuglesamfunna av di artstalet er høgare. Graden av artsutskiftning for begge samfunn var høgast i dei tidlege suksesjonsfasane og avtok jamt mot klimaks. Nedgangen i artsomsetjing var parallell når ein samanlikna plante- og fuglesamfunna i suksesjonen. Denne kongruente trend var den mest slåande av dei forskjellige samfunnseigenskapane som vart undersøkt i denne økosystem-utviklinga. Det er indikasjonar på at suksesjonsrate-utviklinga er uavhengig av diversitetsnivået i dei sukessive samfunna. Når ein samanliknar med andre sekundære suksesjonar, syner data frå denne studien at suksesjonsrate-nedgangen er relativt høg (eller at det er relativt kort tid før artssamansetjinga i klimakssamfunnet er nådd). Det er truleg at nedgangen i artsomsetjing er delvis bestemt av produktiviteten i området.

Den vesle auken i somme parametrar for fuglesamfunnsstabilitet (likskap i populasjonsstorleiken frå år til år eller samfunnsstabilitet) i dei seine suksesjonsstadier skuldast truleg tilfeldige variasjonar. I det store og heile fell stabiliteten i dei suksessive samfunna innan rammene for fuglesamfunnsstabilitet for denne delen av det sørlege Skandinavia. Stabiliteten er sannsynlegvis mest bestemt av klimavariasjon frå år til år.

Det er konkludert med at data frå denne studien ikkje støttar hypotesar om parallelle trendar i utviklinga av samfunnsstruktur (artsrikdom, diversitet, jamnleik, dominans) på produsent- og sekundært konsumentnivå i økosystem som gjennomgår suksesjon. Maksimal diversitet vart nådd tidlegare i plantesamfunnet enn i fuglesamfunnet i suksesjonen. Dette mønsteret kunne ein venta sidan plantesamfunnets fysiognomiske struktur er viktigare enn artsdiversiteten for fuglane, og den største strukturelle diversitet vert nådd seinare enn den største plantediversiteten.

Tettleiks- og biomasse-estimata av plante- og fuglesamfunna synte større grad av samanfallande trendar enn struktur-parametrane gjennom suksesjonen. Desse økosystemparametrane var såleis relativt meir i samsvar med dei foreslåtte "forventa trendar". Men sjølv om utviklingsretninga i grove drag var samanfallande for lauvverksdekninga eller -tettleiken og fugletettleik eller -biomasse, var ikkje endringsgraden i samsvar med teorien. Maksimal auke i parametrane for plantesamfunnet var tidleg, medan den største auken i fuglesamfunnet fanst seint i suksesjonen.

SUMMARY

The aim of the present study was to examine proposed hypothesises of "trends to be expected" and their generality in an ecosystem undergoing succession. It was performed by comparing the development of some parameters of the structure and the density/biomass of plant and bird communities in 4 stages of a secondary succession. The study area was a delta plain in lake Øyeren, SE Norway, the first stage was an open, wet, mown and occationally burned meadow, the second a 10 year old abandoned meadow with scattered shrubs, the third a 35 year old alder forest and the fourth an alder forest of not less than 70 years. The species' occurence and abundance of the plant communities were sampled by regularly distributed 2 $m^2$ quadrats. The bird communities were sampled by the territory mapping method.

Of the various forms perennial graminoids were dominating early in the succession, while shrubs and trees predominated the intermediate and late stages. The mosses were a considerable growth form in the early stages, especially about 10 years after abandonement. In the herb layer, the cover of the forbs was almost constant throughout the entire succession, while the ferns dominated in the forest stages.

The floristic diversity (species/area regression index) was found to be highest in the intermediate stages of the succession and noteworthy, the initial and final stages had a floristic diversity of similar magnitude. The species density, however, was higher in the open meadow than in the climax alder forest. When considering the vascular plants only, the floristic diversity of the mown meadow was considerably lower than of the climax stage. The rate of change in the floristic diversity was highest in the early stages of the succession.

It is assumed that the relatively low floristic diversity in the initial plant community is caused by high frequency of disturbance or population reductions, preventing some potensial colonists (e.g. shrub species) to recover after mowing or burning. The floristic diversity on the site is probably in a dynamic balance between the species-depressing effects and the species-promoting effects of the management. The population reductions of the dominants prevent competitive equilibrium and is thus allowing inferior species (e.g. some of the moss species) to coexist. The species-promoting effect of release from management disturbance is probably the major explanation of the relative high floristic diversity in the intermediate stages. The effect is greater than the expected opposite trend when the community is gradually approaching competitive equilibrium. In the final stage the plant community most probably is closer to this equilibrium. The dominant competitors have more efficiently monopolized the major resources and thus reduced the number of coexisting species and the floristic diversity. Indications of this increasing interspecific competition (probably for light) in the forest stages is given by the fact that the cover estimates of the herb layer was increasingly negatively correlated to the cover of shrubs.

The diversity of the species cover proportion (Shannon's index) was slightly, but not significantly, decreasing throughout the succession. It indicates, together with the higher level of dominance by the two major species, that an increasing amount of the total resources is shared by fewer species as the succession proceeds.

The spatial heterogenity was increasing in the successive stages but the different parameters were increasing at a decreasing rate. The foliage height and vegetation strata diversity, measures of the physiognomic complexity of foliage strata, were closely correlated to the density of the total vegetation or the density of shrubs and trees in the studied sites.

In the bird communities breeding on these successive stages, the **Charadrii-group** predominated in the open meadow. In the shrub habitat **Emberizidae** and **Sylviinae** were the major taxonomical groups. The forest stages were dominated of species belonging to Sylviinae, Turdinae and Fringillidae. The bird species diversity (Shannon's index) showed a directional, smooth increase from stage one through four. The increment was highest in the early stages and levelled off in the later forest habitats. Simultanously, the dominance of the two most common species decreased during the succession. The diversity and the dominance in the bird communities were negatively correlated. The evenness component of diversity was only slightly higher in the closed forest habitats than in the open, early successional stages.

The density of the shrub and tree layers was found to be the best predictor of bird species diversity. The indices of spatial heterogenity, e.g. foliage height diversity and vegetation strata diversity, explained somewhat less of the variation in bird species diversity. Neither plant diversity indices, spring flood variability nor any other habitat factors provided significant increase in the explanation of bird species diversity in addition to the indices of foliage density or diversity.

The species richness (number of species/area) exhibited a different pattern of increase than the species diversity. The species richness differed among all the stages, however, in the intermediate stages only minor. In the climax, the species density was 75 % higher than in the precedent. In spite of different courses of trends, the two indices of bird community diversity were correlated.

The species richness was linearily correlated to the bird community density, while the species diversity was correlated to its natural logarithm. Of the various habitat factors, the density of the shrub and tree layers gave the best prediction of bird species richness. As for bird species diversity, none of the other factors mentioned previously added further significant explanation of the species richness variation. The structural complexity of the habitat, here measured as foliage height diversity and vegetation strata diversity, and foliage density, are assumed to be rough estimates of the resource span or niche space. This factor is believed to be a major determinant of bird species diversity, together with nich breadth and overlap.

The diversity of the late successional alder forest habitats in the present study is lower than of other deciduous forests of similiar structural diversity. The data from this succession, compared with other deciduous forest gradients, suggest either that the niche space is over-estimated by the foliage diversity and density indices or that other factors reduce the number and relative abundance of coexsisting species. These factors could be environmental (unpredictability) and/or intrinsic bird community factors (interspecific competition, predation) influencing the species' resource utilation by increasing the breadth and/or decreasing the overlap. Alder forests are characterized by a relatively low species diversity compared to other deciduous forests, except subalpine birch forests which have diversity of the same magnitude. The productivity of the alder forests is high. Other deciduous forests have only 10 to 40 % of the bird community density of alder forests. This matter of fact indicates that the resource diversity in alder forests is low, and lower than expected from the estimates of foliage diversity and density. The volume of the occuring and available resources, however, must be considerable. In spite of a close fit of bird diversity to the habitat factors attempting to be estimates of the resource span in the present succession, it is nevertheless concluded that these factors are inaccurate measures for a wider group of breeding habitats.

The bird community density was found to increase almost linearily throughout the succession, from about 120 pairs/km$^2$ in the pioneer stage to about 3 000 pairs/km$^2$ in the climax alder forest. The density of the shrub and tree layer was considered to be the best predictor of bird community density, but the relationship was non-linear. The natural logarithm of the community density was linearily and closely correlated to the shrub and tree foliage density. This suggests either that the density is determined by factors supplementary to food productivity within the plot, (if there is linearity between the foliage estimates and food resources available) or that some species are partly dependent on food access outside the breeding habitat (e.g. Turdus pilaris and Columba palumbus.

The density of all breeding site groups was increasing throughout the succession. Species breeding in the shrub and tree strata were increasing most when comparing the young and the old alder forest. The combined density of these groups was found to exhibit exponential growth during the succession. The shrub and tree density gave the best prediction of shrub and tree breeders' density, however, in a non-linear way. The natural logarithm of the population density of species with nests in shrubs and trees was closely correlated to the density of the shrub and tree layer.

The addition of guilds (feeding site) reflects the addition of plant physiognomic forms in·the habitats as the succession proceeds. The difference between the three first stages was pronounced, but between the two last stages it was only minor.

The density of shrub and tree foliage feeders was found to increase less to a given increase in density of shrub and tree foliage than the density of species breeding in those strata. This may suggest that food resources (if linearily related to foliage density) is a more important regulating factor than breeding site availability (if foliage density is a good indicator of nesting site quantity).

The species turnover was higher in the plant communities than in the bird communities, due to the higher species number. The rate of species replacement for both communities was highest in the early stages and decreased gently towards climax. The decline in species turnover was found to be parallell when comparing the plant and bird communities in the succession. This congruency in trend was the most striking of the various community attributes considered in the present ecosystem development. It indicates that the succession rate development is independent of the diversity level of the successive communities.

When comparing with other secondary successions, data from the present one show that the succession rate decrement is relatively high (or the duration before the climax species composition is achieved is relatively short). It is assumed that the species turnover decline is partly determined by site productivity.

The slight increase in some parameters of bird community stability (year-to-year population persistence or community stabibility) in the late successional stages was assumed to be accidential. The overall level of stability in the successive communities fell within the ranges of bird community stability for this part of southern Scandinavia. The stability is believed to be determined mostly by climatic predictability.

It is concluded that the present data do not support hypothesis of parallell trends in the development of community structure (species richness, diversity, evenness, dominance) at the producer and secondary consumer level in ecosystems undergoing succession. The diversity peak is reached earlier in plant than in the bird communities in the succession. This pattern was to be expected since the birds respond to the physiognomic structure of the plant community rather than to the diversity of taxa, and maximum structural diversity is achieved later than plant diversity.

The density or biomass estimates of the plant and bird communities exhibited a higher degree of congruency than the structural parameters during the succession. These aspects of the ecosystems are thus relatively more in accordance with the proposed "trends to be expected". But even if the overall direction of the development of foliage cover or density and bird density or biomass is relatively conform, the observed rate of increase is not in agreement with the theory, since the maximum increase is early in the succession in the plant communities and late in the bird communities.

# 1. INTRODUCTION

## 1.1. Aim of the study.

Succession has been one of the major ecological subjects studied and debated in the 20th century. The controversies are on views of the consept as well as on the "trends to be expected" in the development of ecosystems.

MARGALEF (1968) and ODUM (1969) summarize these trends in the attributes of ecosystems undergoing succession. Some of these are:

Increasing biomass, stabilized gross production/community respiration, decreasing net community production, increasing diversity, increasing stratification and spatial heterogenity, increasing average size of organisms, increasing niche specialition, shift from predominant selection for rapid growth (r-selection) to feedback control (K-selection), increasing longevity and complexity in life cycles and increasing stability against external pertubations.

The relative rate of change in these parameters are supposed to be high in the early stages and decrease towards climax.

Many inventigations are performed, especially during the last 20-30 years to detect the validity of these proposed changes of ecosystem properties. Apparently, as showed in the review in section 1.3 and 1.4, some of the structural characteristics of plant and bird communities undergoing successional change seems to show similar trend-developments. Congruency of alterrations of these properties indicates that the proposed hypothesis apply to the whole ecosystem. However, the excisting verifications are performed only on either one or the other of two trophic levels. The object of this study was to examine some of the succession trends mentioned previously in communities at two trophic levles in an ecosystem simultanously: Plant communities on the primary producer level and breeding bird communities on the secondary (or higher) consumer level. When considering both plants and birds in successive communities, an examination of the generality of the expectations and statements put forward by MARGALEF (1968), ODUM (1969) among others, is provided. Parallel trends in comparable community parameters would support the view that the developmental courses are ecosystem characteristics of various organization levels, whether trophical or taxonomical. The attributes investigated in this elaboration are mainly associated with the species composition and abundance structure, densities, life form or guild groups, sizes, spatial heterogenity and various aspects of stability. Attempts are made to throw light upon the relationships between the communities of the two levels, to detect the mechanisms causing the pattern observed, especially the dependence of the consumer community on the producer community.

The study attempts to answer the following specific questions:

1. Is the diversity, evenness, dominance and density/biomass of the plant and bird communities undergoing directional change during succession, if so, are they exhibiting increasing or decreasing trends?

2. In what period of the succession are these structural properties exhibiting the most rapid change?

3. How are these community characteristics related?

4. Are there similarities/differences in the trends of these structural attributes of the plant and bird communities during succession?

5. Is there an increasing spatial heterogenity?

6. Is the species composition stability of the plant and bird communities increasing or decreasing?

7. Are there differences in the relative species turnover rates between the plant and bird communities?

8. Is the stability of the population densities of the bird communities increasing?

9. What habitatfactors are accounting for the majority of the variation in diversity, guild structure and density between the bird communities?

## 1.2. Definitions and approaches to succession.

The incipient definitions and statements of the succession conceptions were arrived at through botanical studies. CLEMENTS (1916) defines succession as the universal process of directional change in vegetation, a progressive change in the species composition of the community. He compared the succession of communities to the developmental processes of organisms and considered the communities to be an organic entity. CLEMENTS' view on succession is prevalent in more recent definitions, too. MARGALEF (1963) and ODUM (1969) looks upon ecological succession as an orderly process of community development that has a directional trend and is predictable. It results from the modification of the physical environment by the community. The succession is community-controlled, but the physical environment determines the pattern, rate of change and set developmental limits.

This holistic approach to succession is contrasted by a more individualistic view (c.f. GLEASON 1917). Many ecologists argue that succession is disorderly and unpredictable and arises from directional changes in extrinsic factors as well as effects from the organisms on the environment. The steady state of species composition and ecosystem properties is questioned and succession is looked upon as a probabilistic process of species replacement. As a community process, succession must result from the underlying dynamics of individual populations. This view upon succession is recently advocated by EGLER (1954), DRURY & NISBET (1973), HORN(1974, 1975 a, b, 1976) and CONNELL & SLATYER (1977).

Primary successions are the term on sites not previously occupied by vegetation. If the site is previously occupied, the succession is called secondary. Autogenic successions, where the changes are brought about by the action of the plants themselves on the habitat, are distinguised from allogenic succession, where the changes are brought about by external factors (TANSLEY 1935). The succession is progressive if the new vegetation type that develops on an area is more complex than the type it replaces (MC CORMICK 1968 in WALDEMARSON JENSÉN 1979). The most important characteristic of a progressive succession is an increasing productivity, and in a retrogressive succession decreasing productivity (WHITTAKER 1953). CLEMENTS' (1916, 1936) idea was that the biotic community was an integrated superorganism, and that it developed through a succession to a single end point, the climatic climax. The biotic reactions cause the succession, the plants and animals of the pioneer stages alter the environment and thus favour a new set of species. This process recurs until the climax is reached. Retrogression is impossible in this view, unless disturbances as fire, grazing or erosion occur. The succession culiminates in a stabilized ecosystem where maximum biomass and symbiotic functions between organisms are maintained(MARGALEF 1963, ODUM 1969).

A climax is the final or stable community in a successional series, it is self-perpetuating and in equilibrium with the physical and biotic environment (PHILLIPS 1934-1935). The climax is relatively stable compared with the successional stages that led up to it,the changes in the climax community are fluctuations around a mean, whereas changes during succession are directional (WHITTAKER 1975 a).

CLEMENTS' (op.cit.) monoclimax hypothesis suggests that within a region there is only one end point of the succession, and that the communities of the region will reach this climax stage. The overall determining factor is the climate. Observations are numerous of communities in apparantly equilibrium, but not in the climax stage according to the monoclimax theory. These are regarded as exceptions and a lot of climax categories are proposed: e.g. sub-, dis-, pre-, post-climax. These communities are determined by topografic, edaphic or biotic factors.

The idea in the polyclimax theory (TANSLEY 1939) is that many different climax communities may be recognized in a given area, these climaxes are controlled by soil moisture, nutrients, animal activity or other factors.

In the climax-pattern hypothesis (WHITTAKER 1953) it is emphasized that the communities are adapted to the whole set of environmental factors, climate, soil, fire, wind and biotic factors. This theory allows a continuity of climax types, varying gradually along environmental gradients. The climax is considered to be a steady-state community with its constituent populations in dynamic balance with the environmental gradients.

## 1.3. Plant successions

Some of the general statements of successional progress have been traced through empirical investigations to detect their generality. From the extensive literature on secondary plant successions, only papers treating community properties related to abundance structure (i.e. species richness, diversity, evenness, dominance), reproductive strategies and stability, will be mentioned in the following review. In the temperate region, many elaborations on the theme are performed on stages in successional gradients from old-fields to deciduous forests in the eastern regions of the New World.

### Diversity

Species diversity increases with successional sequence (WHITTAKER

1965, MONK 1967, BAZZAZ 1975, NICHOLSON & MONK 1974, 1975, MELLINGER & MC NAUGHTON 1975). WHITTAKER studied communities in Great Smoky Mountains, Tennessee. The age of the cove forests was 150-400 years (climax) (WHITTAKER 1975 c). MONK made investigations on 162 deciduous forest stands of different age in north central Florida. NICHOLSON & MONK's data refer to 51 seral communities from zero to 200 years of age in the Georgia Piedmont, the terminal stage beeing a hardwood community. The more short-range study by MELLINGER & MC NAUGHTON on former hayfields in central New York, ranged from 4 to 36 years after abandonement. A similar time span (40 years) was covered by BAZZAZ's investigations on old-fields in Illinois, the final stage beeing a deciduous forest.

The diversity development with age exhibits varying courses and time of maximum peaks in different successions. Species diversity of vascular plant strata and major growth form groups increase rapidly initially following their establishment, then increase at a decreasing rate such that diversity increments during late succession are not significant. Richness (number of species) tends to increase indefinitely with time while information content (H' = Shannons diversity index) tends to level off (NICHOLSON & MONK 1974, 1975). In many temperate successions ending with a closed forest canopy, plant diversity often stabilizes or decreases in the later stages of successions (MARGALEF 1968, LOUCKS 1970, AUCLAIR & GOFF 1971, SHAFI & YARRANTON 1973, NICHOLSON & MONK 1975, WHITTAKER 1975 a, b, c). Maximum diversity appears late in the succession, often in the late shrub and early tree stage, but before the canopy of the climax forest has fully closed. This pattern is common in boreal, mixed coniferous forests in Ontario (PIELOU 1966, SHAFI & YARRANTON op.cit.), in intermediate forests in the Great Lake District (AUCLAIR & GOFF 1971) and in more southern deciduous forests (WHITTAKER 1975 c), in Brookhaven, New York . The overall trend of monotonically increasing diversity is interrupted by temporal opposite trends even in early successional stages. A diversity peak often occurs in the stage when shrubs are invading, followed by a decline when shrubs overtop the herbs (BAZZAZ 1975, NICHOLSON & MONK 1975, TRAMER 1975, WHITTAKER 1975 c).

Evenness and dominance.

The evenness or equitability undergoes rapid increase in the initial stages of secondary successions, reaches an early peak and then stabilizes (NICHOLSON & MONK 1974). However, many authors have noted a strong terminal decline, probably due to monopolistic tendencies of one or more regional climax dominants (LOUCKS 1970, AUCLAIR & GOFF 1971, SHAFI & YARRANTON 1973). This tendency is more pronounced in northern parts of the temperate zone than in southern (NICHOLSON & MONK op.cit.). The absolute and relative dominance decreased in the communities during the time span of 36 years after abandonement in the successional study of MELLINGER & MC NAUGHTON (1975).

The many contradictory statements and generalizations on diversity - succession found in the literature are not surprising. The three commonly used diversity measures, number of species, equitability and information content (Shannon's index) may behave different under certain conditions (ODUM 1969). Data that span the entire successional sequence are rare, and critical ages are often represented by minimal numbers of samples (SHAFI & YARRANTON 1973, NICHOLSON & MONK 1974), thus sample-dependent diversity indices being considerably influenced (HURLBERT 1971). In many cases, successionaly unrelated sites are involved: i.e. data from floristically different areas and varying site types are pooled (NICHOLSON & MONK op.cit.).

Reproductive strategies

Low-saturated, short-lived, herbaceous plants dominate early successional communities, while tall, long-lived, woody plants dominate later successional communities (PICKETT 1976). The species composition in a successional series is related to different selection strategy hypothesis, r- and K-selection

(MAC ARTHUR & WILSON 1967, SANDERS 1968, PIANKA 1970). In early stages, where the communities are physically controlled, the selection pressure is towards r-strategy (rapid development, high innate capacity of increase in numbers, early reproduction, small body size and single reproduction). In later successional stages, with biologically accomodated communities, selection is towards K-strategy (slower development, greater competitive ability, delayed reproduction, larger body size and repeated reproduction).

In succession, the sequence of annuals and biennals, followed by perennials is evident. There is a gradual change in contribution of morphological types, perennial monocots, perennial herbaceous dicots, perennial shrub dicots (KEEVER 1950, BAZZAZ 1968, DAYTON 1975, MELLINGER & MC NAUGHTON 1975, WHITTAKER 1975 c).

Stability

Increasing ecosystem stability is one of the major features of succession, and a theme of continuing controversies, of which some are attributed to the diversity of stability-definitions. Stability is the ability of a system to maintain or return to its ground state ofter an external pertubation (MAC ARTHUR 1955). Another definition: Stability is the persistance of a stable species combination through time(MARGALEF 1968). Although few, some investigations are carried out to test the hypothesis.

On the basis of community models and field investigations HORN (1975a) concluded that the dynamic stability decrease with time in a forest succession. If a late stage is disturbed, the rereneration must pass through a long series of changes before the late stage is regained. But when an early shrub phase is disturbed, a few years later the phase is reestablished. In a fertilizer pertubation experiment on old-field communities of 6 and 17 years, the effects on total net aboveground productivity and species diversity were much more pronounced on the youngest stage (MELLINGER & MC NAUGHTON 1975). When contrasting this increasing stability trend with the findings of HORN (op.cit.), the difference in age of the successional stages and the magnitude and severeness of the pertubations must be kept in mind.

## 1.4. Bird successions.

It is often assumed that birds and other animals are largely passive elements in plant successions. All organisms are, however, integral part of the ecosystem, and there are welldocumented cases where vertebrate animals have influenced and even controlled plant succession (grazing, dispersal of seeds). Probably the most important direct effect of birds on plant successions is the dispersal and/or destruction of seeds, especially in the intermediate stages of succession (JOHNSTON & ODUM 1956, HAGAR 1960). The structure of the bird community is known to be dependent on the physiognomic structure of the habitat (MAC ARTHUR & MAC ARTHUR 1961, KARR & ROTH 1971, WILLSON 1974). The plant succession thus provide a gradually more complex habitat for the bird community, the latter more or less reflecting the heterogenity.

In the temperate region, estimates of breeding bird communities in successional stages are numerous. The varyity of site type, origin, timerange and geographical location is considerable. Several investigations are made in oldfield successions with deciduous forest climaxes (ODUM 1950, JOHNSTON & ODUM 1956, ZIMMERMAN & TATSCHL 1975), in regions with a coniferous forest climax, the successions originating after burning or clearfelling (HAGAR 1960, MARTIN 1960, HAAPANEN 1965), on stripmined land closing up in a deciduous forest (KARR 1968), in oakforest successions, evolving after abandonement or cutting (FERRY & FROCHOT 1970, HOPE JONES 1972), and in an oak-hornbeam succession following a clearfelling (GŁOWACINSKI 1972, 1975).

### Diversity

The general pattern of bird species diversity is increase through the successional stages to the climax community (HAAPANEN op.cit., KARR op.cit., KRICHER 1972, HOPE JONES op.cit., GŁOWACINSKI op.cit., ZIMMERMAN & TATSCHL op.cit., VÄISÄNEN & JÄRVINEN 1977, a, b, DES GRANGES 1980). In most of the studied bird successions, the rate of increment is high in the initial stages and then leveling off towards the mature forest. Some authors report maximum diversity in the terminal stage (JOHNSTON & ODUM 1956, HAAPANEN 1965, KARR 1968, HOPE JONES 1972) while others have found the highest diversity in younger forest stages and a slight decline towards climax (MARTIN 1960, FERRY & FROCHOT 1970, GŁOWACINSKI 1975, ZIMMERMAN & TATSCHL 1975). Several studies have revealed a temporate diversity-peak in the shrub-stage (JOHNSTON & ODUM, MARTIN, HAAPANEN, GŁOWACINSKI op.cit.).

Evenness

The equitability or evenness of the species are often found to be highest in the climax community (JOHNSTON & ODUM 1956, HAAPANEN 1965, KARR 1968, HOPE JONES 1972, ZIMMERMAN & TATSCHL 1975). The picture is not clear, however, as there are registrated equitability decrements in the medium stages (JOHNSTON & ODUM, HAAPANEN, KARR op.cit.), temporal peaks in the shrub-stage (JOHNSTON & ODUM op.cit.) or a decreasing equitability throughout the succession ofter the shrub-phase (GŁOWACINSKI 1975).

Density

In the above referred studies, maximum density of the bird community is reported for the terminal stage of the sere, with two exceptions (c.f. JOHNSTON & ODUM 1956, HAAPANEN 1965). In some investigations the density, as diversity and equitability, exhibits an increase in the shrub-stage, followed by a decline (JOHNSTON & ODUM op.cit., HAAPANEN op.cit., FERRY & FROCHOT 1970, GŁOWACINSKI 1975).

Body size

The hypothesis of increasing average body size during the succession if only partly supported by explorations. KARR (1968) found that the average body weight of the birds in the first stage of the succession was high (57.5 g), that the weight dropped in the second stage (45.9 g) and increased to the climax stage (59.7 g). FERRY & FROCHOT (1970) found that the mean size of the breeding birds increased with the age of the succession, but was maximum at the sub-climax stage. WILLSON (1974), however, reports that the average body weight of all individuals in the communities did not change from the very early shrub stage to full forest (42.8-44.1 g). The birds of the initial grassland stage were noticably heavier (65 g).

## 2. STUDY AREA

This investigation is performed in Nordre Øyeren Nature Reserve, in the delta of the river Glåma's inlet to lake Øyeren (Fig. 1), (59°53'N - 11°09'E), 25 km east of Oslo. This wetland is the biggest Scandinavian lacustrine delta, and an important bird migration locality (NORDERHAUG 1973), with importance to botanical and hydrobiologic sciences (BOMAN 1974). It is situated in the boreo-nemoral vegetation zone (SJØRS 1967). The altitude is 101.34 m above sea level (regulated lake-level in summer).. In the delta the soil is dominated by the silt fraction (0.06-0.006 mm) by 50 %, fine-grained sand (0.2-0.06 mm) comprises 30 % and 20 % is fine-grained silt (0.006-0.002 mm) or clay (<0.002 mm). The mean annual precipitation in the district is about 750 mm and the mean annual temperature is 4.3°C (Gardermoen). The mean temperature for june-august is 14.6°C (Gardermoen).

The shape and position of the study plots within the area are presented in Fig. 1 and other data in Table I. The numbers on the plots are arranged along a successional gradient.

Table I. Data about the study plots

| Plot symbol | I | II | III | IV |
|---|---|---|---|---|
| Habitat | Mowed wet meadow | Shrub-grown meadow | Young Alnus-forest | Old, mature Alnus-forest |
| Age (years) | 1 | 10 | 35[1)] | >70 |
| Size (ha) | 32 | 11.5 | 12.5 | 8.5 |
| Mean height[2)] (m) | 0.5 | 0.7 | 1.4 | 1.6 |

1) Tree stand
2) Above regulated lake surface level in summer

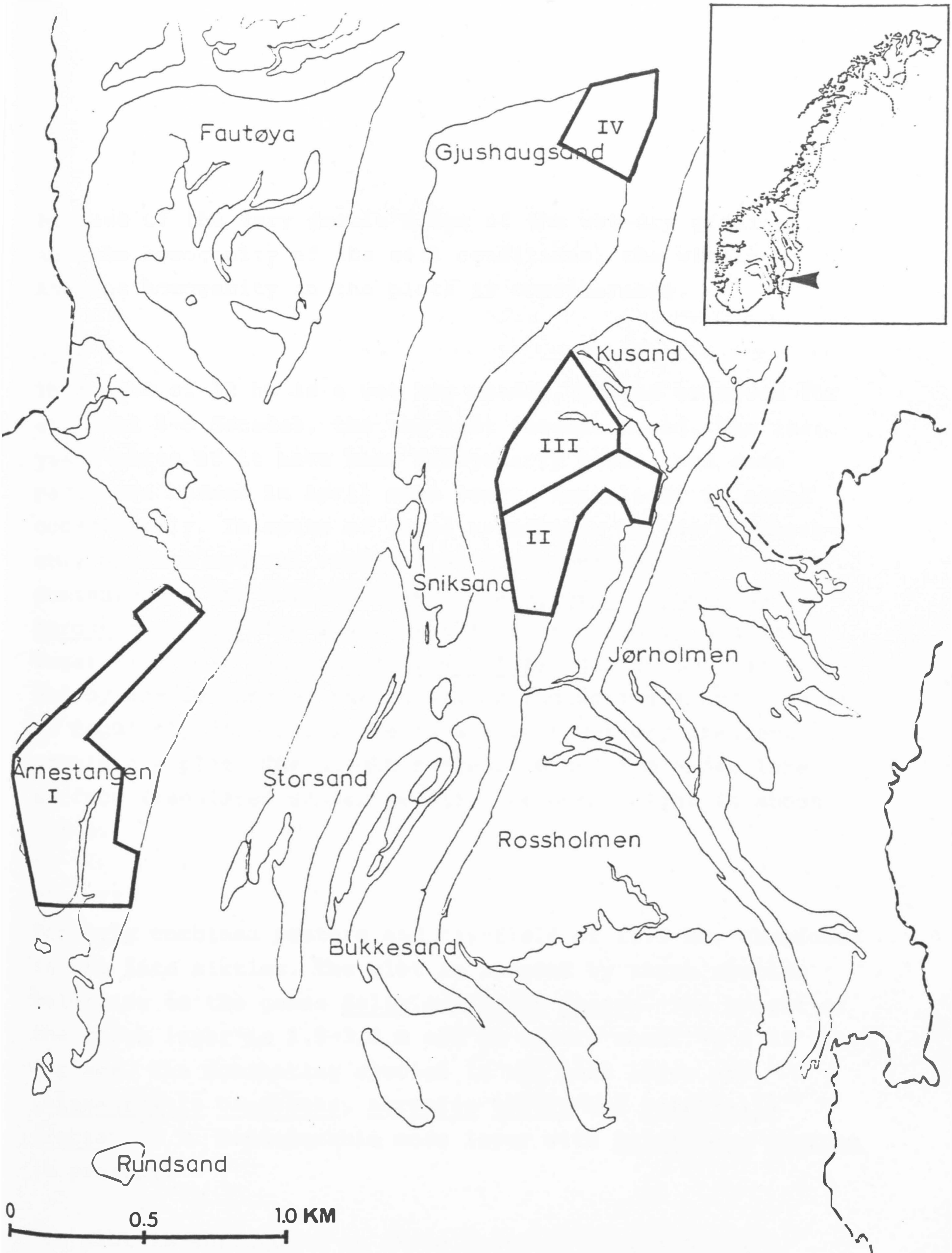


Fig. 1. Map of the delta in lake Øyeren with the positions of the study plots

Because of the very gentle slope of the wet-dry gradient, and the homogenity of the soil conditions, the within-habitat homogenity in the plots is considerable.

Plot I

This plot of 32 ha is a wet hay meadow, grazed or mowed for at least 6-8 decades, the two last decades mowed. The last years parts of it have been irregularly mowed, and some parts are burned in April some years, fertilizer is added occasionally. In spite of these treatments it has a remarkably uniform natural vegetation. Fysiognomically it is dominated by the grass species Calamagrostis canescens and Agrostis tenuis. The study plot is surrounded by a swamp vegetation belt (Equisetum fluviatile) against the lake-side and by arable land on the other. In the spring inundation it is regularly flooded. There is a slight wet-dry gradient within the plot. The height range is 0.2-0.8 m above lake surface (regulated summer level), the mean height is about 0.5 m.

Plot II

Formerly combined pasture and hay-field of 11.5 ha, abandoned in the late sixties. The plot is invaded by shrub species belonging to the genus Salix,and Alnus incana. The height of the shrub layer is 1.5-3.0 m and it covers about 40 % of the surface. The dominating species in the herb layer are Calamagrostis canescens, Agrostis tenuis and Potentilla erecta. A considerable moss layer with Polytricum commune is present.

The plot is surrounded on three sides by Alnus-incana-forests or -borders and on the fourth side by Equisetum fluviatile-svamp in an open lagune. The height range above regulated summer water-level is 0.2-1.2, the mean height is 0.7 m, the slope of the gradient is equal to that of plot I. The zonal pattern in vegetation, however, is more pronounced than in the preceding plot. A wetter Calamagrostis canescens-facies and a drier Agrostis tenuis/Potentilla erecta-facies exists. This difference between plot I and II is probably caused by the height-difference and the management.

Plot III
A young forest of 12.5 ha dominated by Alnus incana, belonging to the Alno (incanae)-Prunetum association (KIELLAND-LUND 1971). The forest was grazed for decades until the middle of the fifties and was clear-cutted in 1943-44. In the present tree stand height, age and dimensions are relatively uniform, heights about 11-12 m. The shrub layer is relatively poorly developed. The common species are Salix caprea, Prunus padus, Rhamnus frangula and Sambucus racemosa. This forest has a dense and luxuriant herb layer dominated by the fern Athyrium filix-femina.

The plot is adjacent to plot II on one side, borders an open meadow on the second and the river on the third. The mean height of the plot is 1.4 m above lake surface, the upper and lower limits being 1.7 m and 1.2 m respectively. This plot is occasionally flooded in the spring, last time in 1967, and the deposits of the suspended load in the river affect the species composition in the herb and moss layer.

Plot IV
An old forest of 8.5 ha, the same phytososiologic associa-

tion as that of the preceding plot. The forest has been subjected to restricted selection felling for fire-wood purposes up to WW II. Airphotos from 1947 show that about 10 % of the forest stand had low, dense regrowth in small patches.

Since 1945 no management has been carried out. The oldest Alnus incana-trees are about 50 years. The height of the stand is 13-14 m. The forest is structurally very heterogen, with a dense tre and shrub layer. The shrub species are mainly Prunus padus, Sambucus racemosa, Salix caprea and Rhamnus frangula, mentioned in falling abundance sequence. The herb layer is poorly developed compared to plot III, the dominating species are Athyrium filix-femina and Dryopteris carthusiana.

Considering the structure of the forest and the physiologic life-span and generation turnover in Alnus incana, the plot is in a climax stage, or at least a subclimax.

On two sides the plot is surrounded by younger Alnus incana-stands, partly mingled with Betula pubescens/verrucosa trees. The other sides are bordering the river. The height interval of the plot is 1.2-1.9, mean height 1.6 m above river/lake surface. As the precedent plot, it is occasionally flooded.

Successional connections between plots

The succession pattern and sequence is interpreted on the basis of historical recordings, air photographs (1937, 1947 and 1956) and vegetation mapping (VALLAND 1978). The main differences between the plots are caused by different management regimes or time intervals from abandonement. As in plot I and II, the time-factor in plot III and IV is isolated. The differences in soil humidity due to height differences between plot I/II and III/IV, are probably not of considerable magnitude to the question of potential climax association on plot I and II. Elsewhere in the delta, the Alno-(incanae)-Prunetum association is present on similar height levels.

There is a discontinuity in the succession between plot II and III, since the latter has developed recently from clearcutting (sucker-orginated tree stand) and not abandoned pasture or hayfield (seed-orginated tree stand). On an air photo from 1937 plot III is a forest, but the origin, age or height is indeterminable on the photo. The present stand is now a stage in a secondary succession following clearcutting of an Alno-(incanae)-Prunetum-forest. The floristic composistion of plot III could be different if the forest originated from a former pasture/hayfield, a relatively higher proportion of Salix-species in the tree layer would be expected. The herb and moss layer are assumed to be less affected, since the species in these layers are in the shade-tolerant group. The importance of the discontinuity on the bird habitat development through succession is assumed to be minor, since the bird primarily respond to the structure and not the species in the habitat.

# 3. MATERIAL AND METHODS

## 3.1 Plant communities

### 3.1.1 Sampling

In order to investigate the species composition and the abundance of the species in the communities, a systematic or regular sampling technique was employed. The grid system of the bird mapping was used to locate the quadrats. The transect lines, where the quadrats were sampled, were chosen at random. Every 25 m a quadrat of 2 m x 1 m size was sampled. About 30 quadrats (25 in plot I and 32 in plot III) were sampled in each study plot. In each quadrat the cover values of the respective species were recorded. Cover is the proportion (in percent) of the ground occupied by a perpendicular projection of the aerial parts of the individuals of the species under consideration (GREIG-SMITH 1964).

To avoid summarizing difficulties, a linear scale was used, from 1 to 100 % cover. For species with low cover values (<1 %), additional informations as 1c (common), 1s (sparse) and 1r (rare) were recorded. This subdivision was not used in any quantitative calculations. The moss species were collected for later species indentification under mikroscope. The cover values and heights of the main vegetation layers were recorded, ground (moss), field (herb), shrub (<4.5 m) and tree layer respectively.

The field work was done mostly in August and September, the plants cover and biomass were fairly stable throughout the period from July. The nomenclature of the hepaticae mosses follow ARNELL (1956), the musci follow NYHOLM (1954-1969). The notation of the vascular taxa is in accordance with LID

(1974). In the vegetation tables, the species are arranged in growth form sequences, mosses, herbs and shrubs/trees, the consecutive order within these groups follows ARNELL (1956), NYHOLM (1954-1969) and LID (1974). The quadrat number sequence in the tables is arranged in the sampling order.

Randomized and systematic sampling are equally objective (DAUBENMIRE 1968). As he points out, the only disadvantage in systematic sampling seems to be the likelihood of error if the vegetation show some spatial periodicity. Patterns of regular periodicity were, however, not detectable in the habitats studied here. Plant populations depart more or less from randomness, tending to be clumped or contagiously distributed (GREIG-SMITH 1964). A grid of regularly distributed samples across the vegetation tend to give a better variation estimate than do randomized samples (MUELLER-DOMBOIS & ELLENBERG 1974). The systematic sampling technique is convenient when the aim of the investigation is to determine the average composition and structure of a stand (DAUBENMIRE 1968). The cover value parameter was preferred due to the difficulties of counting individuals in plant populations, the individual concept may be somewhat more indefinite in plants than in animals. Cover as a quantitative measure, has the advantage that all plant life forms, from mosses to trees, can be evaluated by the same parameter and are thus comparable (MUELLER-DOMBOIS & ELLENBERG 1974). Cover estimates are of greater ecological significance than density, because cover gives a closer measure of plant biomass than does the number of individuals (DAUBENMIRE 1968).

For obtaining the smallest sample area with a maximum number of species of a community, the species-area curve is the best tool.

The minimum-area idea is primarily connected to the homogenity-consept of European phytosociologic studies where the quadrat numbers generally are few and the quadrat sites are subjectively selected (KERSHAW 1973, MUELLER-DOMBOIS & ELLENBERG 1974). Since the aim and methods of this investigations are not classical sociologic, special pre-investigation were not performed to estimate the minimum quadratsize. The species-area curve cannot define the sample size needed for accurate estimation of species density or cover (MUELLER-DOMBOIS & ELLENBERG 1974). As they pointed out there are two types of sample quadrats, the large minimal area quadrat, used for sampling a representative species composition in reccuring plant assemblages, and the small quadrat, size-determined by height and spacing of species individuals used for quantitative analysis of individuals or cover per species.

The quadratsize for the field layer in the present investigation follows NICHOLSON & MONK's (1974, 1975) and BAZZAZ's (1975) studies of secondary plant successions. Their shrub and tree layer quadrat size of 16 $m^2$ and 100 $m^2$ respectively was considered unnecessary for the purpose of this study. They counted number of individuals of the species, i.e. density, while this study use the cover value parameter. The latter is assumed to be less affected by sample size than density, due to the spatial extensivity of the crown foliage of the shrub and tree individuals.

### 3.1.2. Calculations

Species indices

The constancy, C, is the proportion, in percent, of the quadrats where a certain species occurs.

The average cover value, CV, in percent, is the sum cover values of a certain species in all quadrats in the plot divided by the number of quadrats.

The cover proportion, CP, in percent, is the sum cover values of a species in all quadrats divided by the total sum of cover values of all species in the plot. This index is considered to be an estimate of the foliage proportion of a species or an approximation of the proportion of the total photosynthetic biomass in the plot.

Community indices

Life forms and strata cover. The cover estimates of the major life forms according to BEARD (1978) and cover estimates of different vegetation layers were calculated.

Floristic diversity
The species/area curve is of interest because it indicates an important community property, the species diversity in relation to increasing size of area (MUELLER-DOMBOIS & ELLENBERG 1974). Species-area curves are most useful in comparing diversities between habitats or between samples of different size. Classical diversity measures compare diversity based on a single sample size, whereas species-area curves permit the comparison of the entire distribution

of the species number with area. Species-area curves can also be used to "factor out" the effect of area on diversity, so that the effects of other variables on species number can be determined (CONNOR & MC COY 1979). GLEASON (1922) suggested that the species-area relationship is exponential: $S = \log k + z \log A$
(a species/log area regression model) where S is the number of species, log k is the intercept, z is the slope and A is the area. This species/log area model is commonly employed in botanical studies (CONNOR & MC COY op.cit.), and has an advantage since it permits the use of the statistical techniques of linear regression. Comparisons between two or more bivariate distributions of species number and area, are most adequately performed by regression analysis (CONNOR & MC COY 1979).

To obtain species-area curves in the present study, the cumulative number of species was counted per added quadrat. Since the quadrat-sequence in the tables was arranged in sampling number order, the quadrats were not independent. The presupposition of independent variables for the statistical treatment would not be obliged. To meet this requirement, the sequence of quadrats was randomized (c.f. PIELOU 1966). Due to the differences between quadrats in species number, the curve of species on quadratnumber is considerably affected by the sequence and exhibit plateau courses. To obtain a smooth course and reduce the variance, the cumulative number of species per added quadrat was counted in 5 randomizations and the curves were based on the mean. In estimating the regression line of cumulative number of species on log number of quadrats (natural logarithm) the number of species on the first quadrat was deleted.

Floristic diversity index (FD)

This index is the regression coeffisient (FD = $b_1$ = slope) in the simple linear regression of number of species (y) on log number of quadrats (x)

$$y = b_0 + b_1 \cdot x$$

where $b_0$ is the number of species on one quadrat. This index is calculated for all plant species and vascular plants respectively. Comparisons of floristic diversity between plots are performed by testing hypothesis of the slope, $b_1$, by simple linear regression techniques.

Plant species cover proportion diversity (PPD)

(MAC ARTHUR & MAC ARTHUR 1961). This index is calculated with Shannon's formula, $H' = -\Sigma pi \ln pi$, pi refers to the total leaf cover value of the i'th species, expressed as a proportion of the total leaf cover value of all species, i.e. the cover proportion of the i'th species.

Plant species evenness (PJ')

(TRAMER 1969, PIELOU 1975). This index is a measure of the equitability component of species diversity and hence an index of the dominance structure in the community. PJ' = PPD/ln S where PPD is the plant species cover proportion diversity and S the total number of species in the sampled quadrats.

Plant species dominance (PD)
(MC NAUGHTON 1967)
This index is the cover proportion of the two most abundant species ($CP_1+CP_2$), measured as the total cover value of these species in all quadrats divided by the total cover value of all species.

Succession rate

Numbers of methods for comparing communities are available, based on qualitative or quantitative data (HORN 1966, SOUTHWOOD 1966, MUELLER-DOMBOIS & ELLENBERG 1974).

Species turnover (STJ)
This index is derived from Jaccard's similarity formula (SOUTHWOOD 1966) and is a qualitative index based on presence and absence of species.

$$STJ = 100 - \frac{100 \cdot c}{a+b+c}$$

The notation a and b are the number of species present exclusively either in community A or B, respectively. The species number present in both is denoted c. When the species turnover is small, the index is close to 100.

Community turnover (CTH')
This index is quantitative and based on Shannon's diversity index, H', (MAC ARTHUR et. al. 1966, CODY 1970, GŁOWACINSKI & JÄRVINEN 1975). The index measures the difference between the H'-value of the combined community ($H'_{A+B}$) and the average of the two communities considered separately.

$$CTH' = 100 \left( H'_{A+B} - \frac{H'_A + H'_B}{2} \right)$$

To obtain estimates of succession rates, the turnover-indices are divided by the succession time (in years). The rates are denoted $SR_J$ and $SR_H$, respectively.

## 3.2. Habitat structure

### 3.2.1. Sampling

Some aspects of the habitat structure were estimated through the vegetation analysis (the systematic quadrat-sampling), e.g. cover and height of vegetation strata. To obtain estimates of other structure parameters in the habitats (e.g. heterogenity, density, spatial distributions and foliage profiles), additional sampling was required.

The vertical foliage density is by several previous authors called cover (MAC ARTHUR & MAC ARTHUR 1961, KARR 1968, KARR & ROTH 1971, RØV 1975). but in this study vegetation parameters estimated by the following method are denoted density to distinguish them from the horizontal cover value estimates resulting from the quadrat sampling. The vegetation density sampling paralleled the quadrat sampling, using the grid system of the bird territory mapping, the line transects chosen at random. At points, 2 m apart, the presence of vegetation was recorded continually in the vertical plane, without any predetermined intervals. The presence of vegetation was estimated by counting foliage contacts with a 6 m long vertical stick or indirect "touches" with its imaginal elongation. The height above ground level was noted as well as the species for each contact. The number of sample points range from about 340 to 390 in each plot.

EMLEN (1967) proposed a method of measuring presence - absence of vegetational layers by use of simple optimal instruments, from which the present method is derived. MAC ARTHUR & HORN (1969) described a similar method as EMLEN (op.cit.) for estimating vertical foliage profiles, they developed the method for use of somewhat more refined instruments. Methods with more or less corresponding techniques to the present have been employed in several bird-habitat studies (KARR 1968, KARR & ROTH 1971, RØV 1975).

3.2.2. Calculations

The data collected have been stratified in different height intervals to construct vertical foliage profiles and different habitat density and heterogenity indices. Due to the different number of sample points in the four plots, the vertical foliage profiles are calculated per 100 sample points, to do the plot-estimates comparable. When calculating the different vegetation density and diversity indices, the number of sample points with foliage contacts within a height interval, is counted. The indices are thus a measure of presence or absence of foliage in particular height strata. The vegetation density of a stratum is thus the number of sample points with presence of leaves or branches divided by the total number of sampled points.

Foliage height diversity (FHD)

(MAC ARTHUR & MAC ARTHUR 1961). Shannon's diversity index, $H' = - \Sigma pi \ln pi$, is used where pi is estimated by the i'th layer's proportion of the total vegetation, pi = ni/N where ni is the number of points with foliage contacts in the i'th layer and N is the total number of sample points with foliage contacts in all layers. The following height intervals are used: 0-0.6 m, 0.6-6.0 m and > 6.0 m.

Vegetation strata diversity I (VSD I)

(RØV 1975). Shannon's diversity index, H', calculated as the preceding index, but with following layers: a) Herb layer, with all non-woody plants above ground layer (mosses and lichens excluded). b) Shrub layer, with all woody plants growing less than 3 m above ground level. c) Tree layer, with all woody plants above 3 m.

Vegetation strata diversity II (VSD II)

Shannon's diversity index, H', calculated where pi is the number of sample points with foliage contacts in the i'th layer divided by the total number of sample points analysed. The layers are identical with the layers in VSD I. This is not a purely vertical stratification index as the two preceding indices, since it takes into account the vegetation density in the horizontal plane.

Vegetation density index (VD)

(KARR & ROTH 1971). This index is defined as the sum of density estimates for individual vertical vegetation layers. $VD = \Sigma pi$, where pi is the number of sample points with foliage contacts in the i'th layer divided by the total number of sample points. The vegetation layers are the same as in the vegetation strata diversity indices (VSD).

Vegetation cover index (VC)

This index is the sum of the mean cover values for the vegetation layers in the three precedent indices. $VC = \Sigma pi$ where pi is the mean horizontal projected cover value of all the plants growing in the i'th layer. The index is based on cover estimates

## 3.3 Bird communities

### 3.3.1 Composition

The population densities of the bird species were determined by the territory mapping method (ENEMAR 1959). The field work and territory evaluation prosedure were performed largely according to the recommandations of the International Bird Cencus Committee (SVENSSON 1970). The study plots were divided into a grid system with squares of different size. Plot I had 100 x 100 m squares, in plot II through IV the squares measured 50 x 50 m. In plot III and IV, the grid coordinates were marked by a plate with a coordinate code. Additionally, along one of the axis in plot III and IV (survey route) every 25 m was marked, due to the dense vegetation. All coordinates in plot II, III and IV were marked by crepe paper. The scale of the visit maps was 1:5000 in plot I, 1:1667 in plot II and 1:1000 in plot III and IV.

Since strong wind, rainfall and low temperatures are considered to have bad impact on the mapping efficiency (ENEMAR 1959, JOENSEN 1965, HOGSTAD 1967), censuses were not performed under such weather conditions. In a few cases a slight rain shower passed the plot during the census. The total number of visits in the plots were 10-12 each year. The song activity reaches a peak after sunrise (HOGSTAD 1967), consequently the majority of censuses were carried out in the mornings. But due to the different diurnal song activity peaks of the species, about 40 % of the censuses were done in the evenings. The time interval when most of the morning and evening censuses were performed and the mean cencus time duration are presented in Table II. On average, the evening censuses are made faster than in the mornings in the forest habitats. The evening duration is only 77 % of the morning duration, no difference exist in the open habitats.

Table II. The span of censuses and mean census duration (min.)

| Plot | I | II | III | IV |
|---|---|---|---|---|
| Morning | 0530-0900 | 0430-0730 | 0300-0700 | 0300-0730 |
| Mean time, min. | 86 | 96 | 156 | 177 |
| Evening | 1700-2000 | 1700-2000 | 1800-2030 | 1800-2100 |
| Mean time, min. | 86 | 96 | 126 | 126 |

The census were carried out during the period 12.5-21.6 1977 in plot III and IV, 22.5-14.6 1978 in plot I and II, 5.5-14.6 1978 in plot III and IV and 13.6-21.6 1979 in plot I and II.

The number of visits in the different time intervals are presented in Table III. Efforts were made to carry out the censuses in periods with high song activity expectancy. The guidlines of cencus timing given by SLAGSVOLD (1977), depending on weather conditions and phenology,were paid attention to in the 1978 census of the forest habitats. The difference between 1977 and 1978 is not considered to be decisive, since the relatively higher amount of late censuses in 1977 coincided with the relatively late arrival of the latest migrants this year, compared to 1978.

Table III. Number of visits in census periods.

| Year | 1977 | | 1978 | | | | 1979 | |
|---|---|---|---|---|---|---|---|---|
| | | | Plot | | | | | |
| Period | III | IV | I | II | III | IV | I | II |
| 5.5-19.5 | 2 | 3 | | | 6 | 4 | | |
| 20.5-31.5 | 3 | 2 | 3 | 6 | 2 | 3 | | |
| 1.6-10.6 | 2 | 3 | 5 | 3 | 2 | 2 | | |
| 11.6-21.6 | 5 | 4 | 1 | 2 | 1 | 2 | 10 | 10 |
| Total | 12 | 12 | 10 | 11 | 11 | 11 | 10 | 10 |

As DYRCZ & TOMIAŁOJC (1974) points out, the main problem in quantitative studies of bird populations in marshland, is the marked influences of the water level oscillations on the distribution of breeding pairs and the time of breeding. High water level cause a part of the breeding population to nest in suboptimal habitats, locally high aggregations of breeding birds occur, birds starting early suffer high brood losses, or breeding is delayed.

Because of the low height level of plot I and II, the spring flooding disturbed the optimal census timing in these open habitats. The census in 1978 and 1979 in these plots was performed after the flooding, the census starting-time coincided with the date when maximum 25 % of the plot's area were submergent, c.f. Fig. 2. The spatial distribution of territories held before the flooding was disturbed, and reorganization and reoccupying of the habitats started immediately as the plot surface gradually emerged from the withdrawing water. Since the species accumulated in the study area during the flooding and thus all were present after culimination, it was assumed a quick settling of the

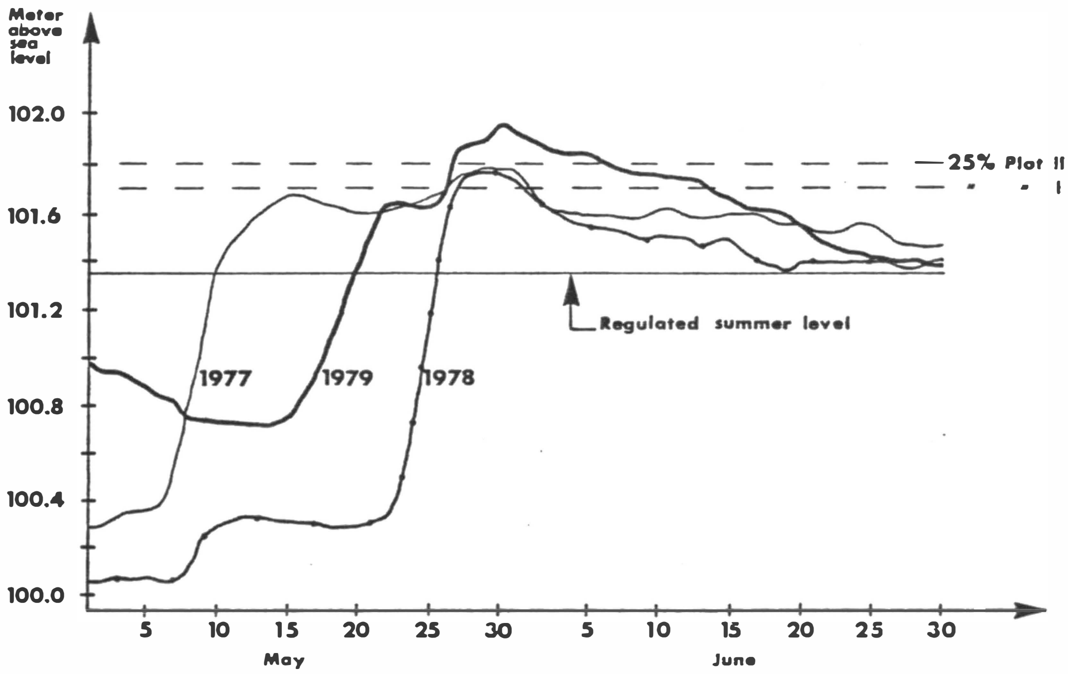


Fig. 2. Spring flooding course in 1977, 1978 and 1979 in lake Øyeren, measured as mean daily water level at Mørkfoss (Source: Norwegian Water Resources and Electricity Board) and the water level of 25 % submergence of plot I and II.

habitats. The somewhat compressed census period in these habitats has probably not influenced the census efficiency considerably.

The mapping method was outlined primarily for estimating passerine populations in forest plots, by recording territorial behaviour (especially vocalizing) in males.

However, the method is used in numbers of investigations in a variety of open-habitat types, with considerable proportions of the communities comprising non-passerines, e.g. alpine meadows, bogs and heaths (ALM et. al. 1965, 1966, MOKSNES 1972, 1973, LIEN et. al. 1974), wetland habitats (marshes, bogs, peats, mosses, wet meadows) (FREMMING & SLAGSVOLD 1968, DYRCZ et. al. 1972, BELL et. al. 1973, DIEHL 1974, DYRCZ & TOMIAŁOJC 1974, JENSEN 1974, MOKSNES 1977, references in LARSEN & MØLLER 1978, SVENSSON 1978) and farmland (SNOW 1965, WILLIAMSON 1967, c.f. LARSEN & MØLLER 1978). Open habitat breeders, especially the waders, differ from the passerines in behaviour, having otherwise or weaker territorial utterings. Due to these differences, the accurancy of the method is affected. Nest-searching and recording of anxious or aggressive behavior from the breeding couple is thus a matter of necessity to reduce the bias in detecting territories (MOKSNES 1972, 1973, 1977, DYRCZ et. al. 1972, DYRCZ & TOMIAŁOJC 1974, LARSSON 1976, SVENSSON 1978). During the breeding cycle, many of the wader species have highest detectability immediately after hatching (HAKALA 1971).

Special attention was given to the Charadrii-group during the censuses in plot I. The complete absence of shrubs and trees in the habitat faciliated visual observations of the birds. Philomachus pugnax and Numenius arquata often leave the nest site on long distances from the observer, causing difficulties in determining the exaxt nest location (ALM et. al. 1965, MOKSNES 1973, DYRCZ & TOMIAŁOJC 1974). Due to these circumstances, much emphasis was not given to nest-searching in addition to the observations and searching during the censuses. For Vanellus vanellus, the aggressive behaviour close to the nest site, nest findings and simultanous visual contacts were the most important mapping criteria. The counting of male Philomachus pugnax on the lek, give only a rough estimate of the population density in the study area, due to the polygamy of this species. The number of breeding "pairs" in this species are thus based on females. During incubation Philomachus pugnax females leave the nest only if the observer is very close (HAKALA 1971). Repeated break cover of females on the same plot were the most important recording for this species. For Numenius arquata, nest findings, repeated break cover from the same spot and repeated simultanous visual recordings of birds were regarded as the main territory-detecting recordings. Good density estimations of Gallinago gallinago are difficult to obtain by the mapping method (FREMMING & SLAGSVOLD 1968, MOKSNES 1973, DYRCZ & TOMIAŁOJC 1974, LARSSON 1976). For this species SVENSSON (1978) recommend censuses in twilight. The aerial display and repeated break cover on the same spot were the criteria used in the mapping in this study.

Alauda arvensis reflect the borders of the territory only when flying close to the ground (DYRCZ & TOMIAŁOJC 1974), territory mapping by recordings of singing males are thus difficult, and SNOW (1965) reports of great variability between observers when censusing the same population. In the present study, the singing males were recorded and the clusters evaluated in the standard way. The number of singing males was remarkably stable form one survey to another, and the number of contemporary contacts between two or more adjacent birds was considerable. The standard territory registration requirements of the mapping method were thus far exceeded. SNOW (1965), HAUKIOJA (1968) and JENSEN (1974) report more or less severe underestimation of Emberiza schoeniclus-populations by the standard mapping method, while BELL et. al. (1973), however, found that 7 surveys of the method detected 92 % of an assumed known (ringed) population. In the present study, the recommandations of SVENSSON (1970) are followed in the evaluation procedure for this species.

The total amount of time used in the field work during the 10 visits in plot I was 27 min./ha, and the walking velocity averages 40 m/min. The field work intensity increase with increasing bird population densities. In plot II, 83 min./ha were used and the average walking velocity was 28 m/min. In the forest plots, the corresponding figures were 108 min./ha and 22 m/min., 204 min./ha and 12 m/min., in plot III and IV respectively. In these plots the time spent on surveys or speed of penetration, is in accordance with recommended or reported intensities in studies of comparable community densities. 30-40 m/min. are recommended by HOGSTAD (1967), 25 m/min. by SLAGSVOLD (1969) for spruce forests. For deciduous forests 18-20 m/min. were used by ENEMAR (1959), 26 m/min. by JOENSEN (1965) and 105-120 min./ha by RØV (1975) with densities of 850, 1336 and 1038 pairs/km$^2$ respectively. TOMIAŁOJC & PROFUS (1977) used 180 min./ha on plots with a density of 1152 pairs/km$^2$ and SÆTHER (1980a) had a walking velocity of 13.3 m/min. in a Alnus incana-forest with 4023 pairs/km$^2$. The velocity-retarding effect of dense shrub vegetation and the time used in numerous breaks when jotting down the observations in relatively dense populations, are the main factors causing slower speed of penetration in high-density communities (JOENSEN 1965, RØV 1975).

The high species densities in the forest plots forced accurate locations of the birds when mapping. To obtain cross-bearings of singing males, rather rapid movement was convenient. However, the speed was sufficiently low to permit putting down contacts. At the grid point, the observer waited a couple of minutes to be able to record contemporary contacts or cross-bearings. Before the leafing of the shrub layer, a special nest-searching survey of about 3 and 5 hours in plot III and IV respectively, was performed in order to locate nests of Turdus pilaris and Fringilla coelebs. The number of territories are based on the criteria of SVENSSON (1970) for most of the species in plot II, III and IV. The population of Turdus pilaris was determined by nest-findings alone. When analyzing the species maps, the detection of territories was considerably faciliated by the simultanous contacts, being especially numerous in the abundant species. The relative importance of contemporary contacts versus the other criteria is high in dense communities due to the high territory-packing.

Some species have low detectability and their population densities are thus more or less underestimated when strictly following the recommandations of the International Bird Census Committee. Methodical studies by several authors have determined severe underestimation (approximately 30-50 %) in the following species: Prunella modularis (ENEMAR 1959, JOENSEN 1965, SNOW 1965, HOGSTAD 1967, JÄRVINEN et. al. 1978), Sylvia communis (SNOW 1965, JENSEN 1974), Muscicapa striata (JOENSEN 1965, SNOW 1965), Parus caeruleus, P. major (SNOW 1965, MANNES & ALPERS 1975, NILSSON 1977) and Certhia familiaris (JOENSEN 1965, NILSSON 1977). Some of these authors and others (c.f. BERTHOLD 1976) have proposed correction factors to the obtained mapping estimates. In the present study multiplication factors are not used. However, the low mapping efficiency of these species are taken into consideration when analyzing the species maps. Generally, two observations are accepted as a territory in cases when the territorial behaviours and/or the spatial distributions of observations and adjacent clusters, indicate a high probability of a breeding territory. Nevertheless, the majority of the territories of these species are based on the standard criteria.

In 1977 50 % of the surveys in plot III and IV were performed by 2 other, experienced field ornithologists, in 1978 and 1979 all plots were censused by the author. The evaluation prosedure is performed by the latter for all three years. The observer variability may cause error in the results. The observer coincidence in registrations is found to be rather high,on average 75 % in a deciduous forest plot (ENEMAR 1962) and 82 % in a coniferous forest plot (HOGSTAD 1967). ENEMAR et. al. (1978) concluded in a methodical study with 4 observers (in a sub-alpine birch forest) that census data obtained from different observers were comparable. They found, as expected, decreasing difference in estimated territory numbers with increasing sample size. The coeffisient of variation between observers was linearly correlated to log number of territories. In view of these results, it is assumed that the observer variability has not caused severe bias in the number of territories in the present study.

The reliability of density estimates is questioned by several authors (c.f. BERTHOLD 1976). The density of the populations and the mapping efficiency of the species in the community are factors influencing the accurancy. In a study of the method in farmland habitats with pastures, arable land, hedges, hedgerows and small woodland strips or plots, SNOW (1965) pointed out that during 8 visits an experienced observer obtained results that, when analysed in a standard way, were on average only some 60-70 % of pairs that would be recorded if twice as many visits were made. A wet meadow habitat with patches of shrub and trees was censused by DIEHL (1974). Standard evaluation of the census results after 10 visits, recorded only 50 % of the totally number of pairs compared to 27 visits and about 70 % compared to 21 visits. An investigation was performed in a patchy marsh habitat with 9 different participants visiting the plot during one day (JENSEN 1974). Species maps after 10 surveys evaluated according to the internationally accepted rules, detected only 30 % of the total territory number. The territories reported were known from colour-ringed birds. However, the generality of this latter result is limited, partly due to the methodical shortcomings (only one day during the breeding cycle). Other studies report a considerable accurancy of the method. When comparing population estimates of nest hunting and mapping, ENEMAR et.al. (1976) found fairly good agreement for the total community in subalpine birch forest. It must be concluded that the mapping method, when the standard recommandations are applied, has a significant varying habitat-and community-specific efficiency. In the present study, the number of surveys and amount of time per survey, exceed the standard recommandations for open habitats (8 visits, SVENSSON 1970) and the simplified, revised version for bogs (5 visits, SVENSSON 1978), thus reducing the error in the estimates of plot I, the habitat with the obviously lowest mapping efficiency. The survey prosedure outlined in this chapter, and the evaluation criteria applied, are considered to reduce the inherent error in the method to give acceptable figures of the species population densities in the plots for the purpose of this study.

### 3.3.2. Calculations

Community indices

Bird species diversity (BSD)

Shannons formula (SHANNON & WEAVER 1963, PIELOU 1975) (or the information theory function) of diversity is used $H' = -\Sigma pi \ln pi$, where $pi = \frac{n_i}{N}$ is estimated by $n_i$, the number of territories of the i'th species divided by N, the total number of territories in the study plot.

Bird species evenness (BJ')

(TRAMER 1969, PIELOU 1975) is a measure of the dominance structure in the community. $BJ' = H'/\ln S$ where H' is the species diversity and S the number of species in the community.

Bird community density (BCD)
is the sum of the individual species population densities measured as number of territories per $km^2$.

Bird community biomass (BCB)
is the sum of all species population biomasses in g/ha. The bird weights are recorded from JÄRVINEN & VÄISÄNEN (1977) and OWEN & COOK (1977).

Bird species richness (BSR)
is the species density in the community, measured as the number of species per 10 ha.

Bird species dominance (BD)
(MC NAUGHTON 1967) BD = $(n_1 + n_2)/N$, where $n_1$ and $n_2$ are the number of territories of the two most abundant species in the plot, and N the total number of territories.

Ecological groups

Breeding ecology groups
The species in the four stages of succession are divided into four nest site or breeding ecology groups. The basis for the divisions is experiences from the field work and recordings from the literature, mainly JOENSEN (1965), HAAPANEN (1965) and HAFTORN (1971). Some species have nests in different sites and these species, marked 1/2, are assumed to have 50 % of the populations breeding in either nest sites.

Ground: Anas platyrhynchos, Vanellus vanellus, Philomachus pugnax, Numenius arguata, Gallinago gallinago, Alauda arvensis, Anthus trivialis, Motacilla flava, M. alba, Phylloscopus trochilus, Saxicola rubetra, Erithacus rubecula, Turdus merula ½, T. iliacus ½, Emberiza citrinella ½, E. schoeniclus.

Shrub: Prunella modularis, Acrocephalus scirpaceus, Hippolais icterina, Sylvia borin, S. atricapilla, S. communis, Turdus merula ½, T. iliacus ½, Carpodacus erythrinus, Emberiza citrinella ½.

Tree: Columba palumbus, Muscicapa striata, Turdus pilaris, Fringilla coelebs, F. montifringilla.

Hollow: Dendrocopus leucotos, D. minor, Fidecula hypoleuca, Parus montanus, P. caeruleus, P. major, Certhia familiaris.

Feeding ecology groups

The species are divided into four feeding site groups in the breeding season. Observations during the field work and recordings from the literature are the basis for the divisions. The main sources are HAAPANEN (1965), JOENSEN (1965), HAFTORN (1971), ULFSTRAND (1976) and SÆTHER (1980b) Anas platyrhynchos, Columba palumbus and Turdus pilaris are excluded from the calculations of density and biomass, due to their habits of feeding partly outside the breeding plot. Species marked ½ are assumed to feed 50 % on either of the feeding sites they occur in. Biomass calculations are based on body weights listed in JÄRVINEN & VÄISÄNEN (1977).

Ground: Vanellus vanellus, Philomachus pugnax, Gallinago gallinago, Numenius arquata, Columba palumbus, Alauda arvensis, Anthus trivialis ½, Motacilla flava ½, M. alba ½, Prunella modularis, Acrocephalus scirpaceus ½, Saxicola rubetra ½, Erithacus rubecula, Turdus pilaris, T. merula, T. iliacus, Carpodacus erythrinus, Emberiza citrinella, E. schoeniclus ½.

Air: Anthus trivialis ½, Motacilla flava ½, M. alba ½, Muscicapa striata, Fidecula hypoleuca, Saxicola rubetra ½.

Trunk: Dendrocopus leucotos, D. minor, Certhia familiaris.

Foliage,shrub: Acrocephalus scirpaceus ½, Hippolais icterina ½, Sylvia borin, S. atricapilla, S. communis, Phylloscopus trochilus ½, Parus montanus ½, P. major ½, Fringilla coelebs ½.

Foliage,tree: Hippolais icterina ½, Phylloscopus trochilus ½, Parus montanus ½, P. caeruleus, P. major ½, Fringilla coelebs ½, F. montifringilla.

Succession rate

Indices of succession rate of the bird communities are identical to the indices described for the plant communities.

Stability

Variation in the following parameters are indicies of community stability, aspects of persistence stability in time (BOTKIN & SOBEL 1975). Some of the indices (1, 3, 4, 5) are proposed by JÄRVINEN (1979).

1. Coefficient of variation of total density, in percent, C.V. (BCD). This index is suggested to measure the constancy of energy flow through the bird community. Compensatory changes in the species populations of the community reduce the magnitude of this index.

2. Coefficient of variation of species richness (total number of species S/plot size) in percent, C.V. (BSR). This index is only influenced by the variation in population density of the rare species.

3. Coefficient of variation of species diversity (H' = Shannons index) in percent, C.V. (BSD). This index is affected by the variation in number of species (S) and the distribution of species frequencies.

4. Coefficient of variation of the evenness component of species diversity ($J' = H'/\ln S$) in percent, C.V. (J'). This index measures changes in the species frequencies distribution.

5. Variance-ratio (V). This index is the sum of variances of population densities of different species in a community divided by the variance of the total community density. If V is close to 1, compensating fluctuations tend to balance parallel fluctuations in the community. If parallel fluctuations dominate, $V < 1$ and compensating fluctuations $V > 1$. This index is calculated for all species and for species comprising > 5 % of the community respectively.

6. Similarity (S). This index is a quantitative modification of the Jaccard similarity index, used by WITKOWSKI (1973, 1978). $S = w/\ a+b-w$ where w is the smaller number of individuals in the two years compared for all the species in the community, a and b is the number of individuals of the first and second year respectively.

### 3.4. Statistical methods

The statistical methods employed in this study is mostly simple linear or multiple regression analysis (CHATTERJEE & PRICE 1977). T-test of one- or two-tailed probabilities is frequently used, the test level is denoted in each case. Non-parametric tests, as Spearman rank correlation, have been added to some t-tests for comparison (c.f. SNEDECOR & COCHRAN 1967). Tests based on rank sums, e.g. the Mann-Whitney U-test (SIEGEL 1956, SOKAL & ROHLF 1969) are used.

Methods for one-way analysis of variance are employed, either F-tests (SNEDECOR & COCHRAN 1967), combined with a Newman-Keul procedure to detect significant differences between groups (SPJØTVOLL 1974), or the non-parametric Kruskal-Wallis test (SIEGEL 1956, LEHMANN 1975).

## 4. RESULTS

### 4.1. Plant communities

#### 4.1.1. Composition

The species and layer cover estimates and heights of strata in the sampled plots are listed in Appendix I, II, III and IV. The species composition, constancy, mean cover value and the relative abundance in the four successional communities are presented in Tables IV through VII.

Species

In plot I, Calmagrostis canescens is dominant, the species has 38.6 % of the total cover value of all species in all quadrats (cover proportion), and it occurs on 96 % of the quadrats, the corresponding figures for the subdominant Agrostis tenuis is 17.8 % and 92 %. Juncus filiformis makes 9.2 %, and has a constancy of 84 %. Drephanocladus polycapus constitutes 8.1 % of the cover, but has a relativly low constancy, 48 %. Carex aquatilis contributes by 6.4 % of the cover with 68 % constancy.

Table IV. Constancy (C), average cover value (CV), and cover-proportion (CP), for the plant species on 25 quadrats of 2 $m^2$, plot I, Årnestangen.

| Species | C % | CV % | CP % |
|---|---|---|---|
| Blasia pusilla | 4 | 0.04 | 0.05 |
| Scapania irrigua | 16 | 0.16 | 0.18 |
| Dicranella c.f. crispa | 4 | 0.04 | 0.05 |
| Pohlia bulbifera | 28 | 2.44 | 2.72 |
| " c.f. elongata | 4 | 0.04 | 0.05 |
| Bryum sp. | 24 | 0.40 | 0.45 |
| " tortifolium | 32 | 0.32 | 0.36 |
| Mnium pseudopunktatum | 16 | 0.16 | 0.18 |
| Drephanocladus polycapus | 48 | 7.24 | 8.08 |
| Calliergon cordifolium | 28 | 1.08 | 1.21 |
| Campylium stellatum | 20 | 0.24 | 0.27 |
| Amblystegium riparium | 16 | 2.28 | 2.55 |
| Polytrichum commune | 4 | 0.20 | 0.22 |
| | | | |
| Equisetum pratense | 36 | 1.16 | 1.30 |
| " palustre | 12 | 0.12 | 0.13 |
| " fluviatile | 52 | 0.56 | 0.63 |
| Agrostis tenuis | 92 | 15.92 | 17.78 |
| " stolonifera | 8 | 0.28 | 0.31 |
| Calamagrostis canescens | 96 | 34.60 | 38.63 |
| Deschampsia caespitosa | 8 | 0.08 | 0.09 |
| Carex acuta | 16 | 1.20 | 1.34 |
| " aquatilis | 68 | 5.76 | 6.43 |
| " leporina | 4 | 0.04 | 0.05 |
| " nigra | 4 | 0.04 | 0.05 |
| Juncus filiformis | 84 | 8.28 | 9.25 |
| Caltha palustris | 36 | 0.44 | 0.49 |
| Ranunculus repens | 12 | 0.12 | 0.13 |
| Comarum palustre | 24 | 0.64 | 0.72 |
| Potentilla erecta | 16 | 1.24 | 1.39 |
| Lysimachia thyrsiflora | 4 | 0.04 | 0.05 |
| " vulgaris | 24 | 0.24 | 0.27 |
| Mentha arvense | 4 | 0.04 | 0.05 |
| Pedicularis palustris | 76 | 2.24 | 2.50 |
| Galium palustre | 52 | 0.92 | 1.03 |
| Hieracium umbellatum | 4 | 0.04 | 0.05 |
| " vulgatum | 4 | 0.08 | 0.09 |
| | | | |
| Salix caprea | 8 | 0.84 | 0.94 |

Table V. Constancy (C), average cover value (CV), and cover proportion (CP) for the plant species on 30 quadrats of 2 $m^2$, plot II, Kusand.

| Species | C<br>% | CV<br>% | CP<br>% |
|---|---|---|---|
| Cephaloziella leucantha | 3.3 | 0.03 | 0.03 |
| Cephalozia rubella | 3.3 | 0.03 | 0.03 |
| Ceratodon purpureus | 10.0 | 0.10 | 0.08 |
| Brachythecium starkei | 13.3 | 0.13 | 0.10 |
| Polytrichum commune | 86.7 | 53.37 | 39.81 |
| | | | |
| Equisetum pratense | 46.7 | 0.70 | 0.52 |
| " fluviatile | 23.3 | 0.23 | 0.17 |
| Agrostis tenuis | 80.0 | 6.83 | 5.10 |
| " stolonifera | 3.3 | 0.03 | 0.03 |
| Calamagrostis neglecta | 3.3 | 0.03 | 0.03 |
| " canescens | 70.0 | 17.90 | 13.35 |
| Deschampsia caespitosa | 16.7 | 0.20 | 0.15 |
| Molinia caerulea | 13.3 | 2.83 | 2.11 |
| Nardus stricta | 3.3 | 0.17 | 0.12 |
| Eriophorum angustifolium | 3.3 | 0.03 | 0.03 |
| Scirpus sylvaticus | 36.7 | 1.00 | 0.75 |
| Carex acuta | 16.7 | 0.33 | 0.25 |
| " aquatilis | 13.3 | 0.17 | 0.12 |
| " leporina | 3.3 | 0.03 | 0.03 |
| " nigra | 16.7 | 0.20 | 0.15 |
| " panicea | 3.3 | 0.10 | 0.08 |
| Juncus filiformis | 96.7 | 1.40 | 1.04 |
| Luzula multiflora | 6.7 | 0.07 | 0.05 |
| Rumex acetosa | 43.3 | 0.50 | 0.37 |
| Stellaria graminea | 13.3 | 0.13 | 0.10 |
| Ranunculus acris | 20.0 | 0.20 | 0.15 |
| Comarum palustre | 40.0 | 0.40 | 0.30 |
| Potentilla erecta | 73.3 | 5.80 | 4.33 |
| Lysimachia vulgaris | 23.3 | 1.93 | 1.44 |
| Mentha arvense | 10.0 | 0.10 | 0.08 |
| Pedicularis palustris | 3.3 | 0.03 | 0.03 |
| Galium palustre | 20.0 | 0.20 | 0.15 |
| Achillea ptarmica | 3.3 | 0.03 | 0.03 |
| Leodonton autumnalis | 20.0 | 0.53 | 0.40 |
| Hieracium umbellatum | 13.3 | 0.13 | 0.10 |
| | | | |
| Salix caprea | 83.3 | 21.76 | 16.24 |
| " cinerea | 36.3 | 4.33 | 3.23 |
| " aurita | 3.3 | 1.00 | 0.75 |
| " pentandra | 10.0 | 0.23 | 0.17 |
| Populus tremula | 3.3 | 0.03 | 0.03 |
| Alnus incana | 10.0 | 5.70 | 4.25 |
| Betula verrucosa | 16.7 | 4.83 | 3.61 |
| " pubescens | 10.0 | 0.20 | 0.15 |
| Rhamnus frangula | 3.3 | 0.03 | 0.03 |

Table VI. Constancy (C), average cover value (CV), and cover proportion (CP), for the plant species on 32 quadrats of 2 $m^2$, plot III, Kusand.

| Species | C % | CV % | CP % |
|---|---|---|---|
| Ciriphyllum piliferum | 3.1 | 0.03 | 0.02 |
| Brachythecium velutinum | 21.9 | 0.34 | 0.23 |
| " salebrosum | 65.6 | 1.66 | 1.11 |
| | | | |
| Matteuccia struthiopteris | 9.4 | 1.72 | 1.15 |
| Athyrium filix-femina | 96.9 | 42.66 | 28.56 |
| Thelypteris phegopteris | 6.3 | 0.41 | 0.27 |
| Gymnocarpium dryopteris | 3.1 | 0.03 | 0.02 |
| Dryopteris carthusiana | 84.4 | 11.50 | 7.70 |
| Phalaris arundinacea | 6.3 | 0.19 | 0.13 |
| Agrostis tenuis | 3.1 | 0.03 | 0.02 |
| Calamagrostis canescens | 15.6 | 0.50 | 0.34 |
| Deschampsia caespitosa | 12.5 | 0.50 | 0.34 |
| Scirpus sylvaticus | 3.1 | 0.06 | 0.04 |
| Carex leporina | 12.5 | 0.38 | 0.25 |
| Paris quadrifolia | 25.0 | 0.25 | 0.17 |
| Maianthenum bifolium | 3.1 | 0.31 | 0.21 |
| Humulus lupulus | 3.1 | 0.09 | 0.06 |
| Rumex acetosa | 3.1 | 0.06 | 0.04 |
| Stellaria graminea | 3.1 | 0.03 | 0.02 |
| " nemorum | 21.9 | 1.03 | 0.69 |
| Viola riviniana | 25.0 | 1.38 | 0.92 |
| Ribes rubrum | 9.4 | 0.28 | 0.19 |
| Rubus idaeus | 68.8 | 5.06 | 3.39 |
| Filipendula ulmaria | 9.4 | 0.16 | 0.11 |
| Oxalis acetosella | 9.4 | 0.63 | 0.42 |
| Angelica sylvestris | 31.3 | 0.50 | 0.34 |
| Lysimachia thyrsiflora | 6.3 | 0.09 | 0.06 |
| " vulgaris | 9.4 | 0.34 | 0.23 |
| Trientalis europaea | 18.8 | 0.25 | 0.17 |
| Galium palustre | 18.8 | 0.19 | 0.13 |
| | | | |
| Picea abies | 6.3 | 0.09 | 0.06 |
| Salix caprea | 12.5 | 4.38 | 2.93 |
| " cinerea | 3.1 | 0.16 | 0.11 |
| Alnus incana | 93.8 | 48.91 | 32.74 |
| Betula pubescens | 3.1 | 2.19 | 1.46 |
| Sorbus aucuparia | 25.0 | 1.44 | 0.96 |
| Prunus padus | 62.5 | 7.34 | 4.92 |
| Rhamnus frangula | 37.5 | 6.78 | 4.54 |
| Sambucus racemosa | 40.6 | 7.44 | 4.98 |

Table VII. Constancy (C), average cover value (CV), and cover proportion (CP) for the plant species on 30 quadrats of 2 $m^2$, plot IV, Gjushaugsand.

| Species | C % | CV % | CP % |
|---|---|---|---|
| Mnium rugicum | 10.0 | 0.10 | 0.05 |
| Ciriphyllum piliferum | 63.3 | 2.57 | 1.35 |
| Brachythecium velutinum | 76.7 | 2.00 | 1.05 |
| Athrichum undulatum | 16.7 | 0.33 | 0.18 |
| | | | |
| Athyrium filix-femina | 73.3 | 17.67 | 9.26 |
| Thelypteris phegopteris | 6.7 | 0.83 | 0.44 |
| Dryopteris carthusiana | 96.7 | 17.50 | 9.17 |
| Phalaris arundinacea | 13.3 | 0.17 | 0.09 |
| Calamagrostis canescens | 3.3 | 0.33 | 0.18 |
| Carex leporina | 13.3 | 0.40 | 0.21 |
| " elongata | 6.7 | 0.23 | 0.12 |
| Paris quadrifolia | 10.0 | 0.10 | 0.05 |
| Humulus lupulus | 3.3 | 0.33 | 0.18 |
| Stellaria nemorum | 40.0 | 1.87 | 0.98 |
| Ribes nigrum | 3.3 | 0.50 | 0.26 |
| " rubrum | 6.6 | 0.20 | 0.11 |
| Rubus idaeus | 30.0 | 4.10 | 2.15 |
| Filipendula ulmaria | 16.7 | 0.57 | 2.97 |
| Oxalis acetosella | 36.7 | 1.67 | 0.87 |
| Angelica sylvestris | 23.3 | 0.26 | 0.14 |
| Lysimachia vulgaris | 6.7 | 0.06 | 0.04 |
| Valeriana sambucifolia | 3.3 | 0.33 | 0.18 |
| | | | |
| Salix caprea | 20.0 | 7.16 | 3.76 |
| " daphnoides | 3.3 | 2.00 | 1.05 |
| Alnus incana | 96.7 | 66.70 | 34.95 |
| Betula verrucosa | 6.7 | 1.00 | 0.52 |
| " pubescens | 3.3 | 0.03 | 0.02 |
| Sorbus aucuparia | 20.0 | 0.60 | 0.31 |
| Prunus padus | 100.0 | 45.70 | 23.94 |
| Rhamnus frangula | 36.7 | 4.97 | 2.60 |
| Fraxinus exelsior | 13.3 | 0.40 | 0.21 |
| Sambucus racemosa | 33.3 | 9.37 | 4.91 |
| Viburnum opulus | 26.7 | 0.80 | 0.42 |

In plot II, the moss Polytrichum commune dominates the cover proportion with 39.8 %, it occurs on 86.7 % of the quadrats. Salix caprea comprises 16.2 % of the total cover and has a constancy of 83.3 %. Calamagrostis canescens' percentage of the cover is 13.4 and it is registrated on 70 % of the sampled quadrats. Estimates of Agrostis tenuis and Potentilla erecta make 5.1 % and 4.3 % of the cover, respectively, and have a constancy of 80 % and 73.3 %. Alnus incana comprises 4.3 % of the cover, but occurs only on 10 % of the quadrats, thus exhibiting a considerable non-uniform distribution.

In the young forest plot (III), Alnus incana is the dominant species with 32.7 % of the total cover, the constancy of the species is 93.8 %. The fern Athyrium filix-femina is sub-dominant, the corresponding figures are 28.6 % and 96.9 %. Dryopteris carthusiana comprises 7.7 % of the total cover, and has a relatively high constancy, 84.4 %. Sambucus racemosa, Prunus padus and Rhamnus frangula are the dominant shrub species, their cover proportion is 5.0 %, 4.9 % and 4.5 % respectively. Prunus padus occurs most regularly of the shrub species, it has a constancy of 62.5 %, the others about 40 %.

In the final stage, plot IV, still Alnus incana predominantes with 34.9 % of the cover, and a constancy of 96.7 %. The cover proportion of Prunus padus has increased considerably, this species has 23.9 % and it is registrated on all quadrats. The overall pattern in the plot is that Alnus incana forms the overstory and Prunus padus the shrub layer. But on a few small patches in the forest, Prunus padus is the canophy-forming species. Under the dense crowns of the latter, the shrub and field layer are poorly developed. Athyrium filix-femina and Dryopteris carthusiana are still dominating the herb layer, they contribute by 9.3 % and 9.2 % to the total cover of the plot, their constancy is 73.3 % and 96.7 %, respectively. The cover proportion of the subdominant shrub species, Sambucus racemosa, is not to any great extent different from the preceding seral stage.

When sampling cover estimates for species in the shrub and tree layer with small quadrats, the probability of error is present, especially when the species are non-uniformly distributed. KORSMO's (pers. comm.) species cover estimates in these layers in 10 quadrats of 200-400 $m^2$ in plot III and IV, confirm the expectation that the error in average cover values estimated by many small-sized quadrats is satisfactorily low in these uniform plots.

Layers

The development of different vegetational strata during the succession is illustrated in Fig. 3, estimates of cover given in Table VIII. The cover values are the mean cover of the layers and are thus not affected by the species overlapping cover within the layer. The total cover increases from 72 % in the initial stage to about 96 %

Table VIII. Mean cover values and heights of vegetation layers in successional stages.

| | | Plot | | | |
|---|---|---|---|---|---|
| | | I | II | III | IV |
| Number of quadrats | | 25 | 30 | 32 | 30 |
| Mean cover of ground layer, | % | 13.7 | 52.6 | 2.0 | 4.4 |
| " " " field " | " | 67.2 | 38.0 | 56.7 | 42.5 |
| " " " shrub " | " | 0.8 | 37.2 | 29.5 | 53.7 |
| " " " tree " | " | | | 51.7 | 85.0 |
| " total cover | " | 72.2 | 86.3 | 85.3 | 95.7 |
| " height of field layer, | m | 0.5 | 0.6 | 1.0 | 0.8 |
| " " " shrub " | " | 1.1 | 2.0 | 3.2 | 3.2 |
| " " " tree " | " | | | 10.9 | 12.8 |

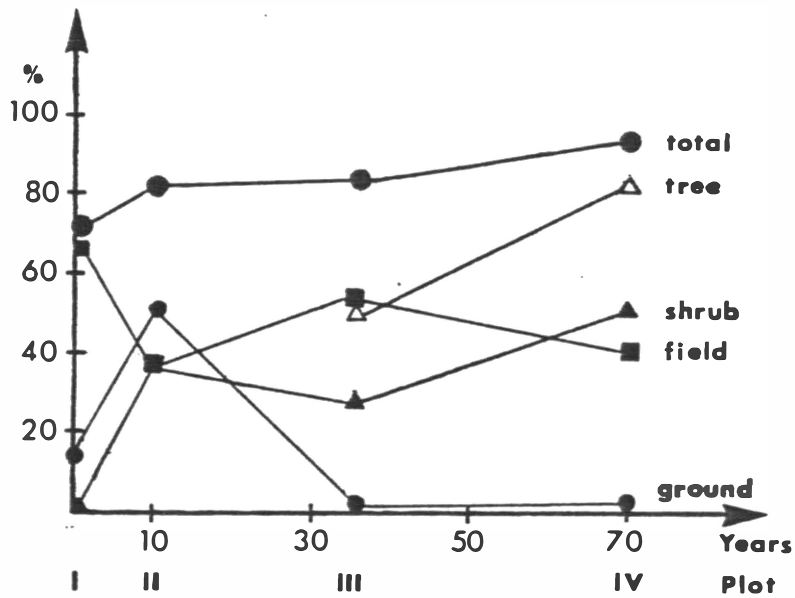


Fig. 3. Mean cover values (%) of different vegetation layers in successional stages.

in the final stage. The increase of cover in the ground layer (mosses) from 13.7 % to 52.6 % 10 years after abandonement is considerable. The mosses cover only 2 % and 4.4 % of the surface in plot III and IV respectively. The field layer (herbs) development is resiprocal to the moss layer in the initial stages of the succession, ranging from 67.2 % cover to 38 %. The decrement of the herb layer from 56.7 % cover in plot III to 42.5 in the final stage is noteworthy, as well as the coinciding increment of the shrub layer from 29.5 % to 53.7 % cover. The tree cover in the final stage is considerably higher than in the preceding stage, the cover in plot III is 51.7 % and in plot IV 85 %, an increment of about 33 %. The average tree height is about 2 m higher in the final stage.

Growth forms

Consideration of relative contributions of growth forms to community total cover through succession, provides insight into competitive interplay between plant groups. The cover values of species in major growth forms are summarized (Table IX and Fig. 4). The herbs comprise 82.7 % of the total cover values initially, but their percentage disminishes as the other growth forms establish themselves after abandonement, the percentage is 31.5, 45.9 and 24.7 in plot II, III and IV, respectively. The forbs' total cover is fairly stable throughout the succession, varying from 6 % cover in the initial stage to about 10 % in the three later stages. The relative amount, however, decreases monotonously from 6.7 % in plot I to 5.2 % in plot IV. The graminoids are dominants within the herb group in the first two stages, the ferns dominate in the two last ones. The former's amount of total cover is 75.9 % in plot I and 24.1 % in plot II, the latter comprises 37.7 % in plot III and

Table IX. Total cover values of the species in major growth forms during succession.

| Plot / Growth form | I | II | III | IV |
|---|---|---|---|---|
| Mosses | 14.64 | 53.66 | 2.03 | 5.00 |
| Ferns | | | 56.32 | 36.00 |
| Graminoids | 68.04 | 32.25 | 1.66 | 1.23 |
| Forbs | 6.04 | 9.98 | 10.65 | 9.89 |
| Herbs total | 74.08 | 42.23 | 68.63 | 47.12 |
| Shrubs and trees | 0.84 | 38.11 | 78.73 | 138.73 |
| Total | 89.56 | 134.00 | 149.39 | 190.85 |

18.9 % in the final stage. Changes in relative contribution of woody species are resiprocal to the herbs. 10 years after abandonement shrubs are 28.4 % of total cover, the corresponding figures for shrubs and trees in the two final stages are 52.7 % and 72.7 %.

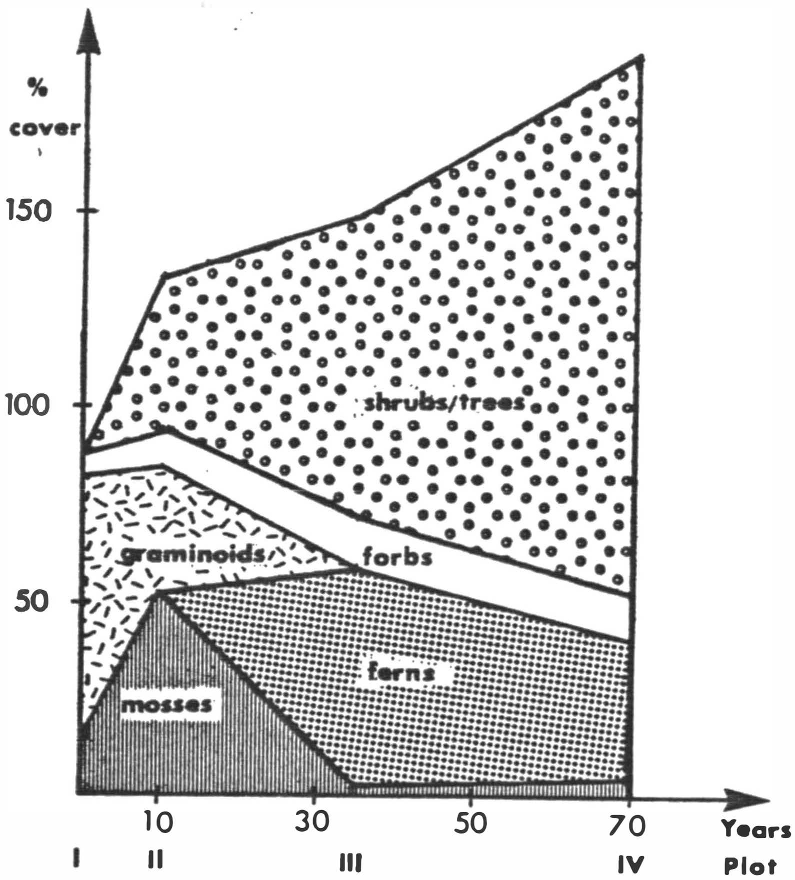


Fig. 4. Total cover value of the species in major growth forms during succession.

The moss cover proportion is considerable in the first stages of the succession, the importance is minor in the plots of late stages. In plot I the mosses comprise 16.4 % of the total cover, and not less than 40 % in plot II. The increment is caused by Polytrichum commune, demonstrating the competitive ability of this species in early successional stages.

Competition

The competition between species in different growth forms is partly recognized when considering cover values of different vegetational layers. The species of a particular growth form are prevalent occuring in a specific layer, but among the woody species exceptions are numerous, since many species occur in two strata. In Table X the correlation coefficients between cover values of vegetational layers are listed. The cover estimates are the cover of the layer, not the overlapping-influenced estimates when cover of all the species in the layer are combined. No significant negative correlation between the moss and herb layer exists in the initial stage. The correlation coefficient between these two layers is negative, r = -0.626, highly significant, 10 years after abandonement. The influences of the invading shrubs are not significant detrimental to the herb layer cover in this stage, the correlation is negative, but weak. In a multiple regression of the herb layer cover on the moss and shrub layer cover as independent variables 1 and 2, respectively, the shrub layer cover added no significant increase in the explanation of the herb layer cover variation. The negative correlations between the cover of the herb and the shrub layer in the two late successional stages suggest a competition between species in these two growth forms, between the ferns and the woody species of the shrub. The correlation coefficients of r = -0.505 and

Table X. Correlation coefficients between cover values of vegetation layers (in 2 $m^2$ quadrats). *** and ** denotes the significance level of $P < 0.001$ and $P < 0.01$ respectively, n = number of quadrats.

| Plot | n | Layer | FC | SC | TC |
|---|---|---|---|---|---|
| I | 25 | GC | -0.091 | | |
| II | 30 | " | -0.626*** | | |
| II | 30 | FC | | -0.216 | |
| III | 32 | " | | -0.505** | -0.097 |
| III | 32 | SC | | | -0.170 |
| IV | 30 | FC | | -0.648*** | |
| IV | 30 | SC | | | 0.194 |

Abbreviations:
GC = ground (moss) layer cover
FC = field (herbs) " "
SC = shrub " "
TC = tree " "

r = -0.648, both significant, in plot III and IV respectively, further suggest an increasing competition between species of these categories with successional age. Significant negative association exists neither between the herb and the tree layer nor between the shrub and tree layer. Adding the tree layer cover to the shrub layer cover in a mulitple regression of the herb layer as dependent variable, no significant additional amount of variation in the latter was explained. The decrease in cover value of the herb species and the decreasing proportion of herbs in the two latest successional stages are thus primarily accounted for by the increase of the shrub layer species.

## Spatial distribution

Correlation between constancy and cover proportion of the species in a commnuity is a rough measure of the uniformity or spatial distribution of the species throughout the plot.

When considering the species comprising more than 1 % of the total cover value, the correlation coefficient is for plot I, r = 0.706 ($P < 0.01$), for plot II, r = 0.463 ($P < 0.15$), for plot III, r = 0.697 ($P < 0.02$) and for plot IV, r = 0.674 ($P < 0.02$). Clearly, the distribution of the common plant species are most uniform in plot I. The correlation between constancy and cover proportion is somewhat weaker in the two final stages, indicating a relatively more uneven species distribution. The correlation on plot II is weak and not significant. The species in this community thus display a irregular, patchy spatial distribution, as indeed observed in the shrub species. The mosaic pattern most likely reflect the dispersion strategy of the species.

### 4.1.2. Diversity

#### Floristic diversity

The relation between number of species and number of quadrats is tabulated in Table XI and illustrated in Fig. 5. The overall coarse of the curves is increased at a decreasing rate. When comparing the plots, however, it is evident from the slope and plateauning levels, that the species richness differ. However, visually it is difficult to distinguish some of these curves from each other satisfactorily. The regression equations of cumulative number of species on log number of quadrats, together with the coefficient of determination ($R^2$) are listed in Table XII. The floristic diversity indices (FD), literally the slopes ($b_1$), are tested for differences. When considering all species, the diversity indices are different, except for plot I and IV. The significance level in a two-tailed t-test for plot II and III, $P < 0.005$, is the weakest, the other significance levels are considerably smaller ($P < 0.0001$).

The corresponding tests for the indices of the vascular species confirm the expectation that all the indices differ, highly significant.

Even if the floristic diversity ($b_1$ in Table XII) is not different in stage I and IV, the species density ($b_0$ = intercept in Table XII) is significantly higher in plot I ($P < 0.007$ in a one-tailed t-test).

Table XI. Number of accumulated plant species per quadrate number (Mean 5 random sequences of quadrate samples).

| Quadrate no. | Plot | | | |
|---|---|---|---|---|
| | I | II | III | IV |
| 1 | 10.8 | 10.0 | 7.0 | 8.4 |
| 2 | 16.6 | 13.0 | 10.8 | 12.0 |
| 3 | 19.0 | 17.2 | 14.4 | 14.4 |
| 4 | 21.6 | 19.6 | 17.0 | 16.6 |
| 5 | 22.4 | 22.8 | 18.4 | 18.0 |
| 6 | 24.0 | 25.2 | 20.6 | 20.0 |
| 7 | 26.2 | 29.2 | 23.2 | 22.0 |
| 8 | 27.6 | 30.6 | 25.4 | 22.8 |
| 9 | 28.6 | 31.8 | 27.0 | 23.8 |
| 10 | 29.2 | 32.2 | 28.5 | 24.6 |
| 11 | 29.6 | 32.8 | 29.2 | 25.2 |
| 12 | 30.6 | 33.4 | 30.4 | 26.0 |
| 13 | 31.0 | 34.6 | 31.6 | 27.0 |
| 14 | 32.0 | 35.4 | 32.0 | 27.2 |
| 15 | 32.8 | 36.0 | 32.6 | 27.6 |
| 16 | 33.2 | 36.4 | 33.4 | 28.4 |
| 17 | 33.4 | 37.2 | 33.8 | 28.6 |
| 18 | 33.8 | 37.4 | 34.8 | 28.8 |
| 19 | 34.2 | 38.2 | 35.2 | 30.2 |
| 20 | 34.8 | 38.8 | 35.4 | 30.8 |
| 21 | 35.4 | 39.0 | 35.8 | 31.8 |
| 22 | 35.6 | 40.2 | 36.2 | 31.8 |
| 23 | 36.2 | 41.0 | 36.6 | 31.8 |
| 24 | 36.4 | 42.0 | 36.8 | 32.0 |
| 25 | 37.0 | 42.0 | 36.8 | 32.0 |
| 26 | | 42.2 | 37.6 | 32.2 |
| 27 | | 42.6 | 38.2 | 32.2 |
| 28 | | 43.2 | 38.6 | 32.2 |
| 29 | | 43.6 | 38.6 | 33.0 |
| 30 | | 44.0 | 38.8 | 33.0 |
| 31 | | | 38.8 | |
| 32 | | | 39.0 | |

Table XII. Regression equations of cumulative number of species (y) and ln number of quadrates (x), $y = b_0+b_1x$, in succesional stages. $R^2$ = coefficient of determination i.e. the proportion of the v-variation explained by x.

| | Plot | $b_0$ | $b_1$ | $R^2$ |
|---|---|---|---|---|
| All plants | I | 10.002 | 8.295 | 0.996 |
| | II | 5.233 | 11.383 | 0.992 |
| | III | 2.768 | 10.786 | 0.991 |
| | IV | 5.623 | 8.210 | 0.995 |
| Vascular plants | I | 8.492 | 4.786 | 0.994 |
| | II | 4.603 | 10.171 | 0.996 |
| | III | 3.617 | 9.837 | 0.993 |
| | IV | 3.805 | 7.547 | 0.994 |

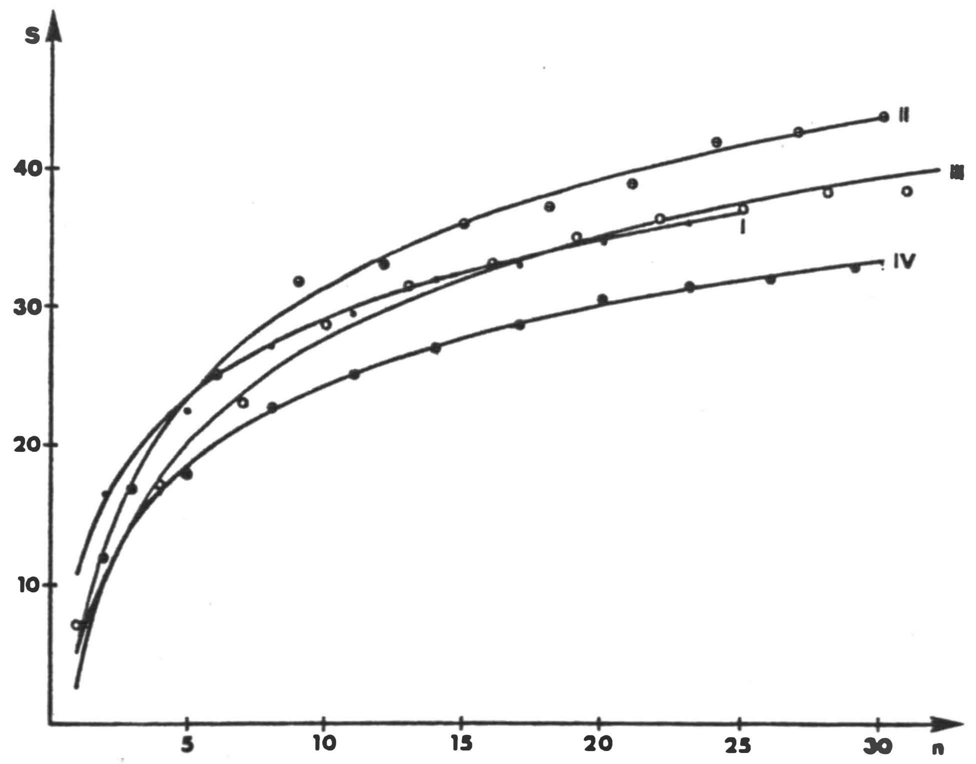


Fig. 5. Accumulated number of species (S) in relation to number of sampled quadrats (n) in four successional stages (plot I through IV). Every third point from Table XI and the fitted regression lines (Table XII) is given.

The ability of the sampling method and calculations of the floristic richness is tested when comparing predicted and independently observed number of species on a certain area. In plot II, on 100 $m^2$ in a continually transect at right angle to the wet-dry gradient, it was registrated 49 species (VALLAND 1978). The predicted number of species on 50 quadrats each 2 $m^2$ according to the regression equation is 49.76. KORSMO (pers. comm.) registrated 59 species on sample squares of 200-400 $m^2$, totally covering 1200 $m^2$, in plot III. The regression predicted number of species is 71.77, a clear overestimation. When compiling the species of KORSMO's sampling and the present study, however, the predicted number is in accordance with the observed 72.33 and 72, respectively. In plot IV, KORSMO found 58 species on sample squares of sizes equal to the preceding plot, totally 1200 $m^2$. The predicted number of species is 58.14. When compiling his data and data from the present study, the observed number is 66 and the predicted 58.54, the regression line underestimates the number of species. When considering these discrepancies, the different sampling methods must be kept in mind. KORSMO's sampling is conform to the Braun-Blanquet tradition, his work being a forest-sociologic study. The location of samples is thus chosen in homogenous, typical stands within the plot. An extention of number of sampled quadrats in the present study most likely would not change the picture. When computing regression equations on 15 quadrats, the intercept and the slope are not considerably changed. The differences between observed and predicted values must thus probably be attributed to methodical differences in site selection and ability of detecting species richness. The overall pattern is, however, a fairly good congruency in figures obtained by these three sampling methods.

The trend in the floristic diversity index (FD) throughout the succession is a relatively low diversity, but rapid increase in the initial stages, followed by an intermediate period with high floristic diversity, decreasing but at a low rate (Table XIII and Fig. 6). In the terminal stage of the succession, the floristic diversity is low, the decrement from plot III to IV is faster than in the intermediate stages.

The species density (i.e. predicted number of species per 50 and 100 $m^2$) exhibits the same overall trend-pattern as FD. However, the species density is higher in stage I than in stage IV.

Table XIII. Plant community indices in successional stages.

| | Plot | | | |
|---|---|---|---|---|
| | I | II | III | IV |
| Number of quadrats | 25 | 30 | 32 | 30 |
| Total number of species, S | 37 | 44 | 39 | 33 |
| Floristic diversity, FD I 1) | 8.295 | 11.383 | 10.786 | 8.210 |
| " " FD II 2) | 4.786 | 10.171 | 9.837 | 7.547 |
| Species per 50 $m^2$ | 36.7 | 41.9 | 37.5 | 32.1 |
| " " 100 " | 42 | 50 | 47 | 39 |
| Species cover proportion diversity PPD I 1) | 2.157 | 2.098 | 2.106 | 2.076 |
| " PPD II 2) | 1.737 | 2.348 | 2.055 | 1.981 |
| Species evenness PJ' | 0.597 | 0.554 | 5.575 | 0.619 |
| " dominance PD | 0.564 | 0.561 | 0.613 | 0.589 |

1) I = all plants
2) II = vascular plants only.

It is noteworthy that the floristic diversity in the initial stage, the mown, wet meadow, is of the same magnitude as in the climax stage, an old *Alnus incana*-forest, and that the species density is higher in the meadow than in the terminal forest stage.

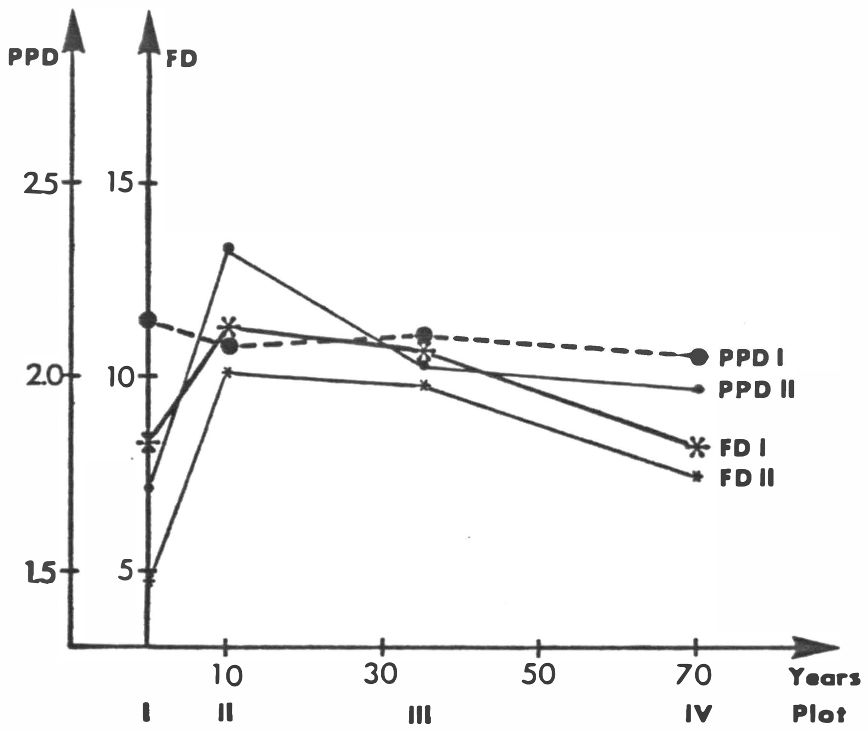


Fig. 6. Plant community diversity in successional stages.
FDI= floristic diversity all species
"II= " " vascular species
PPDI= species cover proportion diversity, all species
"II= " " " " , vascular species.

When considering the vascular plants only, the difference between the first and the last stage of succession is significant, due to the large number of moss species in the former. The floristic diversity trend in the three last stages, however, conforms to the picture for all species: a slight decline in diversity.

Species cover proportion diversity (PPD).

The cover proportion diversity appears to decline through succession, the direction of change neither is clear nor extensive (Table XIII and Fig. 6). The somewhat "unexpected" result, that this community index of diversity (PPD) on average is lower in the later stages than in the initial, is partly explained by the dominance structure in the communities. The dominance of the two most common species is higher in plot III and IV than in the preceding (Fig. 8), however, not significant ($P < 0.085$ in a one-tailed t-test). The PPD-index is relatively most influenced by the abundance of the dominant species. When calculating the index only on species > 1 % cover (CV), the index-value for plot I is reduced with 14.5 % and number of species with 67.6 %, the corresponding figures is 10.3 % and 70.5 % for plot II, 9.8 % and 64.1 for plot III, 8.6 % and 57.6 % for plot IV. Contrary to the floristic index, the cover proportion diversity index is sample-size dependent. To illustrate this relation, the PPD-index is plottet against number of quadrats in Fig. 7. It is assumed that the error in the indices for the successional stages in the present study is not serious for the actual number of quadrats the indices are based on.

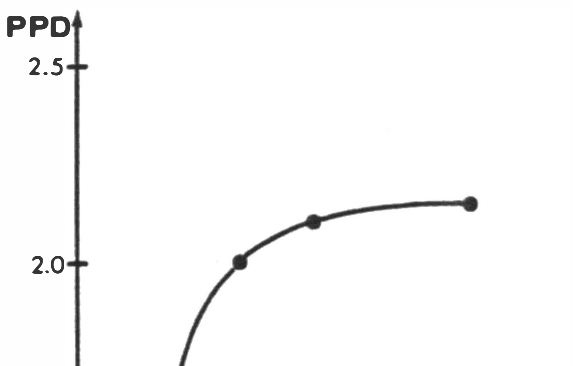


Fig. 7. Plant species cover proportion (PPD) and number of quadrats (n) in plot I.

Finally, the estimates of the plant species cover proportion diversity (PPD) do not support a clear statement of distinct directionally change during the succession, yet, the data suggest a slight decrement. The diversity index calculated for the vascular species only, exhibit a trend through the succession, to some degree congruent with the floristic diversity index (FD). Although, the decrease in the two latest stages are less pronounced.

Evenness

The evenness (PJ') of the plant communities evidently does not conform to any hypothesis of monotonously increasing evenness through the succession (Table XIII and Fig. 8). The evenness estimates of the initial and the final stage are significantly the highest, the intermediate stages appear to have the most uneven community ($P < 0.005$ in a one-tailed t-test).

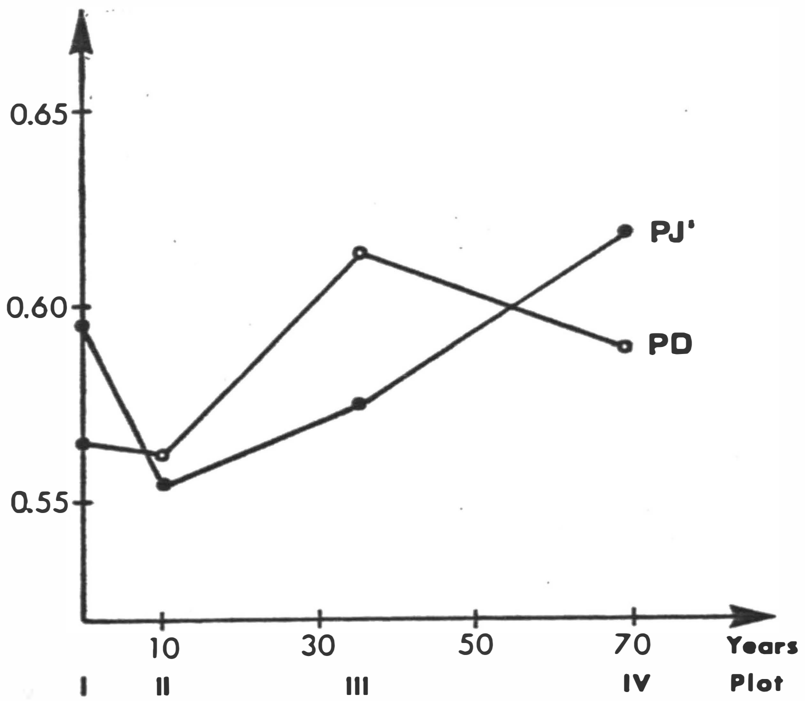


Fig. 8. Plant community dominance (PD) and evenness (PJ') in successional stages.

Evidently, the evenness is higher in the climax community than in the intermediate stages, and there is a trend of increase during the three last stages. As expected by definition of the dominance and evenness indices, their coarse of direction is inverse, but the picture is not clear in plot II.

The plant community structure indices are tested for correlations. Only two indicies are significantly correlated. Floristic diversity (FD) is weakly negatively correlated to plant species evenness (PJ') r = -0.938 ($P < 0.062$). This result is not unexpected, since both indices by definitions are considerably more affected by the rare species than the other indices. The floristic diversity index is counting species whether abundant cover or not, and the evenness component of species diversity is reduced proportionally to the logarithm of the number of sampled species. The floristic diversity of vascular plant species (FD II) is positively correlated to the vascular species cover proportion diversity (PPD II), r = 0.905, however not significantly ($P < 0.1$). The similar trend through succession in these plant diversity indices is neither significant nor positive when all plant species are considered. The relatively high moss proportion in the early successional stages is the proximate factor in the observed vascular species indices similarity, thus giving a more "expected" result. The floristic diversity index and the cover proportion species diversity are measuring different aspects of the community structure. The former is a species richness index, and the latter a species abundance index considerably affected by the dominant species (PEET 1975, KEMPTON & TAYLOR 1976) and is thus the equitability component of diversity.

## 4.2. Habitat structure

### 4.2.1. Foliage profiles

The heights and densities of foliage in the four plots are presented in Table XIV and foliage profiles of the successional stages in Fig. 10. In the initial stage, the absence of shrubs and trees forms an extremely simple habitat.

Table XIV. Vegetation density (number of sample points with vegetation contacts per 100 points) in height intervals in successional stages.

| m | Stage | | | |
|---|---|---|---|---|
| | I | II | III | IV |
| 16 | | | | 0.3 |
| 15 | | | 0.8 | 8.8 |
| 14 | | | 7.0 | 27.1 |
| 13 | | | 6.2 | 24.8 |
| 12 | | | 15.0 | 25.7 |
| 11 | | | 17.1 | 27.7 |
| 10 | | | 23.1 | 35.6 |
| 9 | | | 29.8 | 34.4 |
| 8 | | | 38.3 | 25.4 |
| 7 | | | 27.5 | 18.4 |
| 6 | | | 30.8 | 27.7 |
| 5 | | | 26.9 | 20.4 |
| 4 | | | 24.9 | 34.7 |
| 3 | | 13.2 | 29.3 | 52.2 |
| 2 | | 47.0 | 34.2 | 70.9 |
| 0.5-1 | 12.5 | 46.8 | 67.4 | 89.2 |
| < 0.5 | 87.5 | 87.0 | 40.7 | 57.7 |

Invading shrub species in plot II, thus have pronounced effects on the structural complexity, forming a mosaic pattern of shrubs and open space. 10 years after the area was abandoned, the heights of the majority of the shrubs are still below 3 m, but some of the shrub individuals are higher than 3 m. In the young

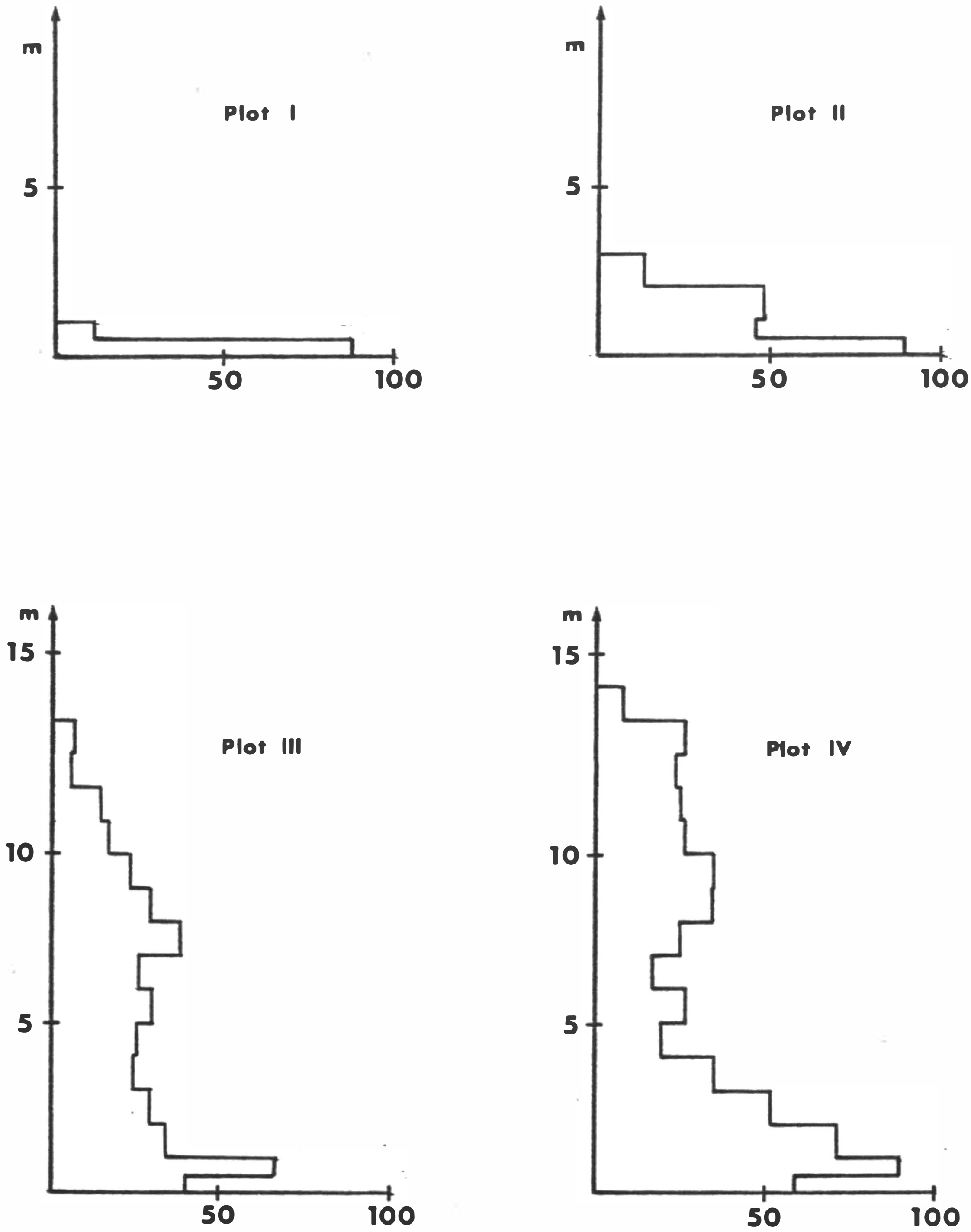


Fig. 9. Vegetation density profiles for successional stages (number of sample points with vegetation contacts per 100 sample points).

forest stage, from 1 to 7 m above ground level the foliage density is fairly uniform due to the poorly developed shrub layer. A distinct density peak appears at the 7-8 m height level and a monotonously density decline towards the top of the crown layer. The majority of the overstory tree heights are 12-13 m. The dense and luxuriant herb layer, and the crown layer form a typical di-layered habitat.

In the old forest, the foliage density profile differ. Even if the luxuriancy of the herbs are far exceeded in the precedent plot, the foliage in the 0-1 m height level is denser in plot IV, due to numerous contacts of the shrub species foliage. The shrub layer (< 4 m) is distinct and highly developed and forms a considerable amount of the foliage volume in the forest. In the height level of 4-7 m, the density is lower. The crown layer is characterized by its high density, uniformity and depth, from 8 to 13 m above ground level.

The overall pattern in development of the habitats throughout the succession is the increasing structural complexity. The simple, monolayered grassland habitat in the initial stage, develops through transition stages of a dilayered, preforest shrub habitat to a dilayered forest and finally a dense, tri-layered forest habitat.

4.2.2. Density and diversity

Density estimates obtained in the transect sampling and cover values from the quadrat sampling are presented in Tables XV and XVI respectively. The density estimates are stratified in two different ways to calculate indices foliage height diversity (FHD) and vegetation strata diversity (VSD). All habitat structure indices employed in the present study are listed in Table XVII.

Table XV. Number of sample points with foliage contacts in strata.

| Strata | Study plot I | II | III | IV |
|---|---|---|---|---|
| 0 - 0.6 m | 337 | 319 | 149 | 174 |
| 0.6 - 6.0 m | 6 | 179 | 358 | 310 |
| > 6.0 m | 0 | 0 | 309 | 296 |
| Total | 343 | 498 | 816 | 780 |
| Field | 337 | 348 | 351 | 202 |
| Shrub < 3 m | 6 | 189 | 169 | 273 |
| Tree > 3 m | 0 | 0 | 355 | 317 |
| Total | 343 | 537 | 875 | 792 |
| Total number of sample points | 343 | 355 | 386 | 343 |

Table XVI. Mean cover values in 2 $m^2$ quadrates.

| Strata | Study plot I | II | III | IV |
|---|---|---|---|---|
| Field layer | 0.675 | 0.387 | 0.571 | 0.425 |
| Shrub layer < 3 m | 0.007 | 0.363 | 0.294 | 0.537 |
| Tree layer > 3 m | 0 | 0 | 0.514 | 0.812 |
| Total | 0.682 | 0.750 | 1.379 | 1.774 |
| Number of quadrates | 28 | 31 | 33 | 28 |

The total vegetation density (TVD) growth in the succession is logarithmic, a rapid increase in the initial stages and an increase at decreasing rate in the later stages. The shrub and tree density (STD) growth in the second half of the succession is more persevering than the former, due to the decline in field layer density (herbs) a component of the total density estimate (Fig. 10).

Table XVII. Habitat structure indices

| Study plots | | I | II | III | IV |
|---|---|---|---|---|---|
| Foliage height diversity | FHD | 0.088 | 0.653 | 1.040 | 1.069 |
| Vegetation strata diversity I | VSD I | 0.088 | 0.649 | 1.050 | 1.082 |
| " " " II | VSD II | 0.088 | 0.355 | 0.525 | 0.566 |
| Total vegetation density | TVD | 1.000 | 1.512 | 2.267 | 2.309 |
| Shrub and tree layer density | STD | 0.017 | 0.532 | 1.358 | 1.720 |
| Field layer density | FLD | 0.983 | 0.980 | 0.909 | 0.589 |
| Total vegetation cover | TVC | 0.682 | 0.750 | 1.379 | 1.774 |
| Shrub and tree layer cover | STC | 0.007 | 0.363 | 0.808 | 1.349 |
| Field layer cover | FLC | 0.675 | 0.387 | 0.571 | 0.425 |

The developmental coarse of the diversity indices (FHD, VSD) follow total vegetation density to a high degree. On that account, high correlation between density and diversity estimates is expected.

All correlations between the diversity indices, between these and total density (TVD) or shrub and tree density (STD) are ranging from 1.0 to 0.92, all significant. (Table XVIII): None of the correlations between the diversity indices and the density of the field layer are significant.

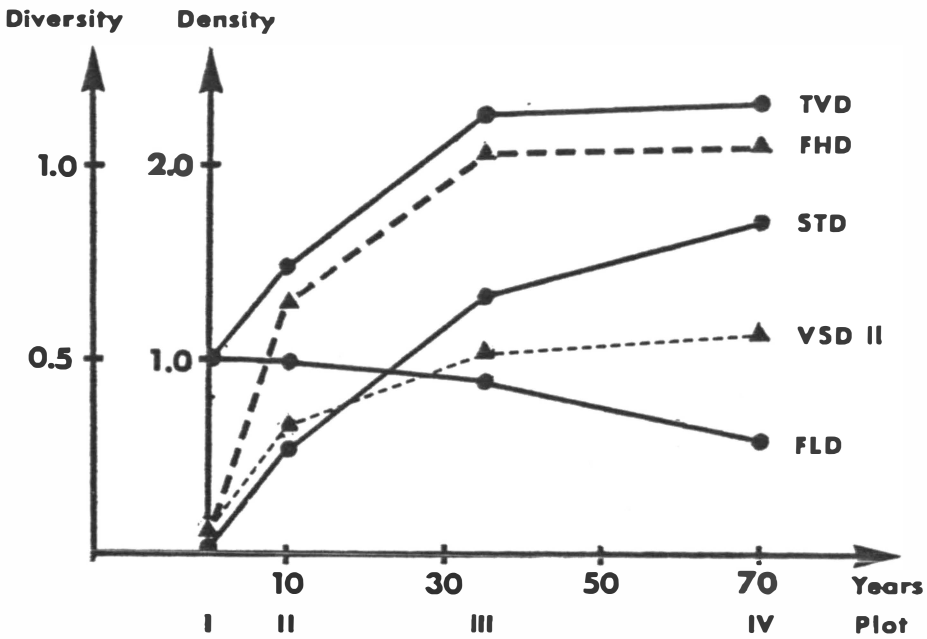


Fig. 10. Vegetation density of layers and habitat strata diversity in succession.

TVD = total vegetation density
STD = shrub and tree layer density
FLD = field layer density
FHD = foliage height diversity
VSD II vegetation strata diversity

Evidently, the vegetation stratification of 0 - 0.6 m, 0.6 - 6.0 m and > 6 m, the basis for calculation of the foliage height diversity (FHD), in the habitats of this study, caused no significant different diversity estimates compared to a stratification of herbs, shrubs < 3 m and trees > 3 m.

Table XVIII. Correlation matrix of habitat structure indices. P is the significance level.

| | FHD | | VSD I | | VSD II | |
|---|---|---|---|---|---|---|
| | r | P < | r | P < | r | P < |
| VSD I | 1.0 | | | | | |
| VSD II | 0.999 | 0.001 | 0.999 | 0.001 | | |
| TVD | 0.982 | 0.02 | 0.984 | 0.02 | 0.981 | 0.02 |
| STD | 0.956 | 0.05 | 0.920 | 0.05 | 0.964 | 0.05 |
| FLD | -0.580 | 0.36 | -0.646 | 0.36 | -0.69 | 0.32 |

These high correlations between density and diversity indices suggest that these different indices are equal in ability to measure the magnitude of habitat structure variation in the sere, the equality proportional to the correlation.

When comparing the density and the cover value estimates, the indices of the shrub and tree layers correlate closest $r = 0.98$ ($P < 0.021$). The correlation between total vegetation density (TVD) and total vegetation cover (TVC) is high ($r = 0.92$) but not significant ($P \approx 0.08$). The descrepancy is caused by the field layer component in the indices, the latter is uncorrelated ($r = 0.42$). Evidently, the field layer estimates of the cover estimate method and the density method are the least comparable.

## 4.3. Bird community

### 4.3.1. Composition

The estimates of the breeding populations densities of the stages in the successional sere are listed in Tables XIX through XXII.

Species

In the open, wet, grassland habitat in the initial stage, Alauda arvensis is the dominant species. The wader species may be considered indicator species in this habitat, since Vanellus vanellus, Philomachus pugnax and Numerius arquata are the most habitat specific species in this plot, their occurence definitely dependent on the habitat management. Motacilla flava and Emberiza schoeniclus are confined to the early seral plots. The latter is dominating the shrub habitat of plot II and has its population density maximum here. Together with Carpodacus erythrinus, it is the most typical species of this habitat. The appearance of denser and taller shrub patches within the plot meets the habitat requirements of a number of species of the warbler group:

Table XIX. Number of territories on plot I, Årnestangen, 32 ha

| Species | 1978 | 1979 | Mean |
|---|---|---|---|
| Vanellus vanellus | 3.25 | 2.50 | 2.875 |
| Philomachus pugnax | 2.50 | 2.00 | 2.250 |
| Numenius arquata | 2.00 | 2.00 | 2.000 |
| Gallinago gallinago | 1.00 | 1.00 | 1.000 |
| Alauda arvensis | 23.00 | 15.00 | 19.000 |
| Motacilla flava | 5.50 | 3.25 | 4.375 |
| Emberiza schoeniclus | 6.50 | 5.50 | 6.000 |
| Total number | 43.75 | 31.25 | 37.500 |

Table XX. Number of territories on plot II, Kusand, 11.5 ha

| Species | 1978 | 1979 | Mean |
|---|---|---|---|
| Anas platyrhynchos | 0 | 1.0 | 0.5 |
| Alauda arvensis | 0.5 | 1.0 | 0.75 |
| Motacilla alba | 1.0 | 1.0 | 1.00 |
| " flava | 3.0 | 1.0 | 2.00 |
| Acrocephalus scirpaceus | 0 | 1.0 | 0.50 |
| Hippolais icterina | 1.0 | 1.0 | 1.00 |
| Sylvia borin | 3.0 | 3.5 | 3.25 |
| " communis | 1.5 | 0 | 0.75 |
| Phylloscopus trochilus | 8.0 | 9.5 | 8.75 |
| Saxicola rubetra | 3.0 | 0 | 1.50 |
| Turdus merula | 1.0 | 0 | 0.50 |
| Carpodacus erythrinus | 3.5 | 1.0 | 2.25 |
| Emberiza citrinella | 1.0 | 1.5 | 1.25 |
| " schoeniclus | 21.0 | 21.5 | 21.25 |
| Total number | 47.5 | 43.0 | 45.25 |

Table XXI. Number of territories on plot III, Kusand, 12.5 ha

| Species | 1977 | 1978 | Mean |
|---|---|---|---|
| Columba palumbus | 3.5 | 7.0 | 5.25 |
| Dendrocopus minor | 1.0 | 1.0 | 1.00 |
| Prunella modularis | 1.0 | 1.5 | 1.25 |
| Hippolais icterina | 4.0 | 0 | 2.00 |
| Sylvia borin | 17.5 | 14.0 | 15.75 |
| " atricapilla | 35.5 | 18.5 | 27.00 |
| Phylloscopus trochilus | 32.0 | 26.5 | 29.25 |
| Fidecula hypoleuca | 2.0 | 2.0 | 2.00 |
| Erithacus rubecula | 13.5 | 17.5 | 15.50 |
| Turdus pilaris | 15.0 | 10.5 | 12.75 |
| " merula | 3.5 | 3.5 | 3.50 |
| " iliacus | 9.0 | 7.0 | 8.00 |
| Parus montanus | 1.0 | 1.0 | 1.00 |
| " caeruleus | 2.5 | 5.5 | 4.00 |
| " major | 6.0 | 8.0 | 7.00 |
| Fringilla coelebs | 42.5 | 42.0 | 42.25 |
| Total number | 189.5 | 165.5 | 177.50 |

Table XXII. Number of territories on plot IV, Gjushaugsand, 8.5 ha

| Species | 1977 | 1978 | Mean |
|---|---|---|---|
| Columba palumbus | 6.5 | 5.0 | 5.75 |
| Dendrocopus leucotos | 1.0 | 0 | 0.50 |
| " minor | 1.0 | 1.0 | 1.00 |
| Anthus trivialis | 1.0 | 0 | 0.50 |
| Prunella modularis | 2.0 | 4.5 | 3.25 |
| Hippolais icterina | 5.5 | 11.5 | 8.50 |
| Sylvia borin | 7.5 | 19.0 | 13.25 |
| " atricapilla | 25.0 | 24.5 | 24.75 |
| Phylloscopus trochilus | 24.5 | 29.5 | 27.00 |
| Fidecula hypoleuca | 3.0 | 3.5 | 3.25 |
| Muscicapa striata | 0.5 | 1.5 | 1.00 |
| Erithacus rubecula | 16.0 | 19.5 | 17.75 |
| Turdus pilaris | 52.0 | 45.0 | 48.50 |
| " merula | 4.0 | 6.5 | 5.25 |
| " iliacus | 14.0 | 24.0 | 19.00 |
| Parus montanus | 0 | 0.5 | 0.25 |
| " caeruleus | 3.0 | 12.0 | 7.50 |
| " major | 12.0 | 10.0 | 11.00 |
| Certhia familiaris | 0 | 1.0 | 0.50 |
| Fringilla coelebs | 49.0 | 59.0 | 54.00 |
| " montifringilla | 0 | 2.0 | 1.00 |
| Total number | 227.5 | 279.5 | 253.5 |

Acrocephalus scirpaceus, Hippolais icterina, Sylvia borin, S. communis and Phylloscopus trochilus. In the intermediate, young forest stage, Fringilla coelebs predominate. The warblers Sylvia borin, S. atricapilla and Phylloscopus trochilus, together with Erithacus rubecula, Turdus pilaris and T. iliacus are the species constituting the major proportion of the bird community.

Basically, these species' relative importance in the community is similar in the terminal stage. However, some differences are considerable, e.g. the amount of Turdus pilaris is just below Fringilla coelebs in plot IV. Parus *montanus*, *P. caeruleus* and *P. major* are confines to the forest habitats, as well as *Columba palumbus*, *Prunella modularis*, *Dendrocopus leucotos* and *D. minor*.

Taxonomical groups

The densities of the breeding bird populations within some major taxonomical groups in the succession are shown in Table XXIII. The warbler density is increasing at decreasing rate during the succession development (Fig. 11). The increment from the stage III to IV is 46 %. The proportion of the *Sylviinae*-group in the bird community, however, is decreasing from 41.3 % in plot III to 28.9 % in plot IV.

Table XXIII. Density of some taxonomical groups (pairs/ha)

| Study plot | I | II | III | IV |
|---|---|---|---|---|
| Charadrii | 0.254 | 0 | 0 | 0 |
| Sylviinae | 0 | 1.239 | 5.920 | 8.647 |
| Turdinae | 0 | 0.177 | 3.180 | 10.647 |
| Paridae | 0 | 0 | 0.960 | 2.206 |
| Fringillidae | 0 | 0.196 | 3.380 | 6.471 |
| Emberizidae | 0.188 | 1.957 | 0 | 0 |

When considering the *Turdinae*-group, the increase in the three later stages is at an increasing rate. The density in the young forest of plot III is only about 30 % of the older forest of plot IV. The corrensponding figures for *Turdus pilaris* alone is 17.9 %, and the other species 43.7 % in plot III, demonstrating that *Turdus pilaris* is responsible for majority of the density increment. The *Turdinae*-proportion of the community is significantly increasing from 22.5 % in plot III to 35.9 % in plot IV ($P < 0.048$ in a one-tailed t-test).

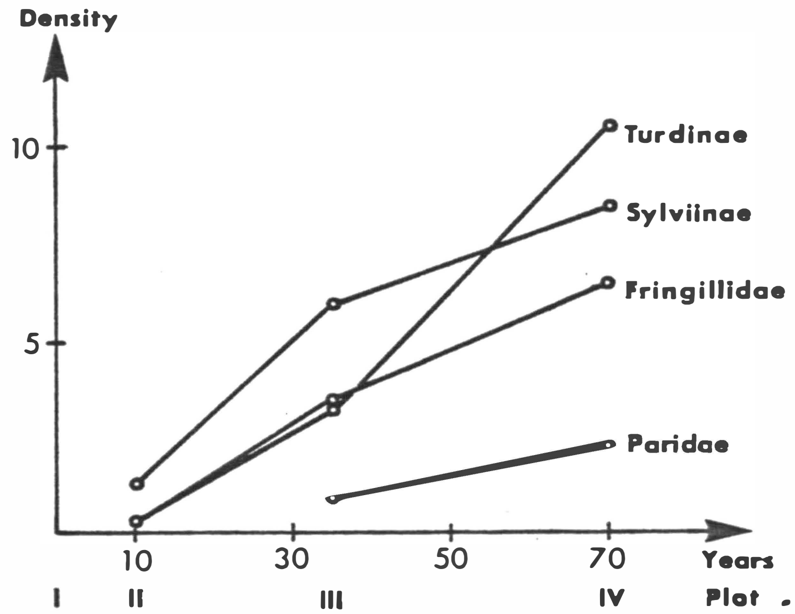


Fig. 11. Density of some taxonomical groups during succession (pairs/ha)

The density of the tits in plot IV are more than twice the density in plot III. Among the Fringillidae species, only Fringilla coelebs is present in the two last stages of the sere. The coarse of directional change are thus mainly attributed to this species. The overall pattern for the group follow largely the Sylviinae-groups. The population density of Fringilla coelebs increase about 88 % from the young to the old forest habitat.

Breeding ecology groups

The density estimates of the different nest site groups are found in Table XXIV. The density of the species breeding on the ground increase gradually with succession time (Fig. 12). The density in the two last stages are significantly higher than in the preceding ($P < 0.04$ in a one-tailed t-test). The proportion of the community, however, decrease from 100 % to 22.5 % for this group.

Table XXIV. Density (pairs/10 ha), proportions and diversity* of breeding ecology groups. Estimates for each of two investigation years

| Study plot | | I | II | III | IV |
|---|---|---|---|---|---|
| Ground | Density | 0.137<br>0.098 | 0.326<br>0.311 | 0.414<br>0.394 | 0.593<br>0.754 |
| | pi | 1.00 | 0.789<br>0.832 | 0.273<br>0.298 | 0.222<br>0.229 |
| Shrub | Density | | 0.087<br>0.063 | 0.514<br>0.313 | 0.582<br>0.900 |
| | pi | | 0.211<br>0.168 | 0.339<br>0.236 | 0.217<br>0.274 |
| Tree | Density | | | 0.488<br>0.477 | 1.266<br>1.305 |
| | pi | | | 0.322<br>0.360 | 0.473<br>0.397 |
| Hollow | Density | | | 0.100<br>0.140 | 0.236<br>0.329 |
| | pi | | | 0.066<br>0.106 | 0.088<br>0.100 |
| Diversity | | 0<br>0 | 0.515<br>0.453 | 1.265<br>1.307 | 1.234<br>1.289 |

* $H' = -\Sigma pi \ln pi$, where pi is the proportion of the i'th group


Fig. 12. Density of breeding ecology groups (pairs/10 ha) in the succession.

The shrub-breeders exhibit a steadily density-growth during the succession. The density is significantly higher in stage III and IV when contrasting stage II ($P < 0.013$ in a one-tailed t-test). Their amount of the community density is fairly stable in the three seral stages this group appear. The significant increament of birds with nest sites in trees is about 166 % from the young to the old forest habitat, ($P < 0.01$ in a one-tailed t-test), mainly due to the high breeding density of Turdus pilaris and Fringilla coelebs in the latter. The proportion of the tree-breeders in the communities is not increasing significantly. Although the density of hole-nesting species in plot III is only 42.5 % of the density in plot IV, the difference is insignificant ($P \approx 0.1$ in a one-tailed t-test).

Feeding ecology groups

The breeding densities of the broadly defined major feeding site or feeding guild groups are listed in Table XXV (Fig.13) and the corresponding biomass figures in Table XXVI. The density of species feeding on the ground is increasing throughout the successional stages, a rapid increment when contrasting plot I and II, relatively relaxed increase from II to III and a rapid increase in density between the two last stages. The picture is somewhat different when considering the biomass.

Table XXV. Density and diversity of feeding ecology groups* (pairs/ha) (two investigation years)

| Study plots | I | II | III | IV |
|---|---|---|---|---|
| Ground | 1.179<br>0.840 | 1.739<br>1.370 | 2.16<br>2.36 | 4.235<br>6.412 |
| Air | 0.086<br>0.051 | 0.304<br>0.087 | 0.16<br>0.16 | 0.471<br>0.588 |
| Trunk | | | 0.08<br>0.08 | 0.235<br>0.235 |
| Foliage, shrub | 0.102<br>0.086 | 2.087<br>2.196 | 7.66<br>5.70 | 9.177<br>11.618 |
| Foliage, tree | | | 3.62<br>3.54 | 5.706<br>8.147 |
| Diversity | 0.222<br>0.208 | 0.885<br>0.793 | 1.089<br>1.119 | 1.234<br>1.127 |

* Anas platyrhynchos, Columba palumbus and Turdus pilaris are excluded.

Table XXVI. Biomass of feeding ecology groups* (g/ha). (Two investigation years)

| Study plots | I | II | III | IV |
|---|---|---|---|---|
| Ground | 219.3<br>185.2 | 85.8<br>58.5 | 432.6<br>349.5 | 1649.3<br>1638.4 |
| Air | 7.0<br>5.1 | 11.0<br>3.3 | 2.1<br>2.1 | 13.8<br>16.4 |
| Trunk | | | 3.8<br>3.8 | 30.4<br>8.0 |
| Foliage Shrub | 3.9<br>3.3 | 64.1<br>66.0 | 282.1<br>210.7 | 342.4<br>430.4 |
| " Tree | | | 116.9<br>103.6 | 197.2<br>242.9 |

* Anas platyrhynchos, Columba palumbus and Turdus pilaris are excluded.

There is a significant decline of 64.3 % in the biomass from plot I to plot II, due to the amount of heavy birds in the former ($P < 0.05$ in a one-tailed t-test). The biomass of this guild in the young forest plot is about 93 % greater than in the initial stage. The increase from plot II to III is significant ($P < 0.04$ in a one-tailed t-test). The significant biomass difference between the two latest succession stages is even more pronounced than the density estimates, primarily caused by the heavy thrushes ($P \approx 0.0013$ in a one-tailed t-test).

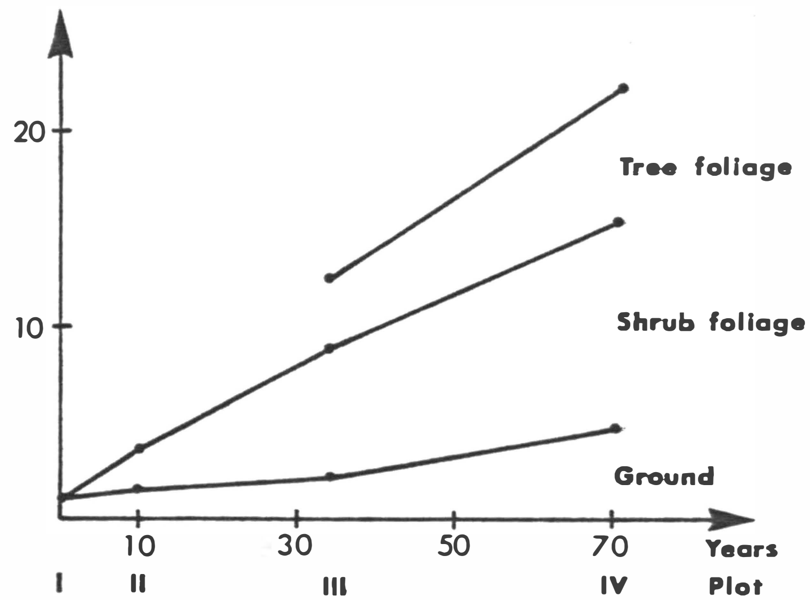


Fig. 13. Density of feeding ecology groups (pairs/ha) in the succession.

The shrub foliage feeders evince a steadily density and biomass increase during the successional stages, the growth rate slightly declining between the two last stages. The density is significantly higher when contrasting the final and the initial stages ($P < 0.01$ in a one-tailed t-test), the increase between stage I and II is significant($P \approx 0.01$), the differences between the three last stages are not significant.

The population densities of species feeding in the overstory tree strata are 93.5.% higher in the terminal stage than in the preceding, however, due to the variation, the difference is insignificant. The biomass difference is about 100 %, neither significant.

### 4.3.2. Community density

The total densities of all breeding bird populations in the successional communities are listed in Table XXVII. The mean community density in 117.2 pairs/km$^2$ in plot I, 393.5, 1420, 2982.4 pairs/km$^2$ for plot II, III and IV respectively. The directional development of density during successional stages appear linear, but when considering the corresponding biomass estimates, the growth seems rather exponential (Fig. 14).

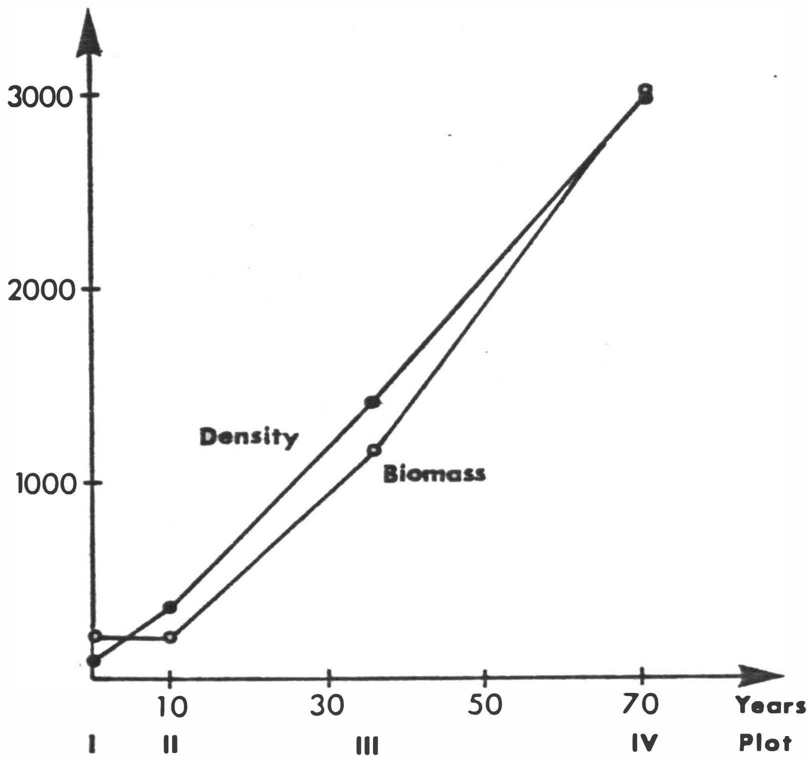


Fig. 14. Community density (pairs/km$^2$) and biomass (g/ha) in successive stages.

The density increment is 219 %, 260.9 % and 110 % between the plot I and II, II and III, III and IV respectively. The differences between stages are significant (K = 6, P = 0.014 in a one-tailed Kruskal-Wallis test, F = 178.75, P ≈ 0.0001 in a one-way analysis of variance of ln BCD).
On average the annual increase in breeding bird density is highest in the late stage (Table XXVIII, Fig. 16) the figures for the biomass increase are even more promounced.

*Table XXVII. Bird community indices.*

| Plot | | I | | | II | | | III | | | IV | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | | 1978 | 1979 | Mean | 1978 | 1979 | Mean | 1977 | 1978 | Mean | 1977 | 1978 | Mean |
| Density, | BCD[1)] | 136.7 | 97.7 | 117.2 | 413.0 | 373.9 | 393.5 | 1516.0 | 1324.0 | 1420.0 | 2676.5 | 3288.2 | 2982.4 |
| Biomass | BCB[2)] | | | 211.9 | | | 226.6 | | | 1182.0 | | | 3023.2 |
| Number of species, | S | 7 | 7 | 7 | 12 | 11 | 11.5 | 16 | 15 | 15.5 | 18 | 19 | 18.5 |
| Species richness, | BSR[3)] | 2.19 | 2.19 | 2.19 | 10.44 | 9.57 | 10.01 | 12.8 | 12.0 | 12.4 | 21.18 | 22.35 | 21.77 |
| Dominance, | BD | 0.674 | 0.656 | 0.665 | 0.611 | 0.721 | 0.666 | 0.412 | 0.414 | 0.413 | 0.444 | 0.372 | 0.408 |
| Diversity, | BSD | 1.467 | 1.558 | 1.513 | 1.859 | 1.614 | 1.737 | 2.229 | 2.274 | 2.252 | 2.28 | 2.434 | 2.357 |
| Evenness. | BJ' | 0.75 | 0.8 | 0.775 | 0.67 | 0.67 | 0.67 | 0.80 | 0.84 | 0.82 | 0.79 | 0.83 | 0.81 |
| Mean body weight, | all.(g) | | | 90.4 | | | 23.8[4)] | | | 41.6 | | | 50.7 |
| " " " | passerines | | | 30.5 | | | 18.5 | | | 27.7 | | | 39.9 |
| " clutch size | | | | 4.36 | | | 5.52 | | | 5.68 | | | 5.70 |

1) pairs/km$^2$, 2) g/ha, 3) S/10 ha, 4) Anas platyrhynchos excluded. 5) Calculated for one clutch from HAFTORN (1971). Every species contribution to the clutch size estimate is weighted by its relative abundance.

Table XXVIII. Differences between indices-values of the bird communities in succession and turnover rates, measured as growth rate in the time interval between successive stages . (Difference/t).

| | | I/II | II/III | III/IV |
|---|---|---|---|---|
| Density difference pairs/km$^2$ | $BCD_{Diff}$ | 276.3 | 1026.5 | 1562.4 |
| Turnover rate | $TR_{BCD}$ | 27.63 | 41.06 | 44.64 |
| Biomass difference kg/ha | $BCB_{Diff}$ | 0.0147 | 0.9554 | 1841.2 |
| Turnover rate | $TR_{BCB}$ | 1.47 | 38.22 | 52.61 |
| Diversity difference H' | $BSD_{Diff}$ | 0.224 | 0.515 | 0.105 |
| Turnover rate | $TR_{BSD}$ | 0.0224 | 0.0206 | 0.003 |

### 4.3.3. Community structure indices

#### Bird species diversity

The coarse of direction in the bird species diversity (BSD) development is the characteristic of the logaritmic growth, increase at a decreasing rate. (Table XXVII, Fig. 15 and 16). The diversity level in the late stages is significantly higher than in the initial stages ($U = 0$, $P = 0.028$ in a two-tailed Mann-Whitney U-test).

The hypothesis that stage I, II and III + IV equals is rejected ($K = 6.0$, $P = 0.014$ in a one-tailed Kruskal-Wallis test).

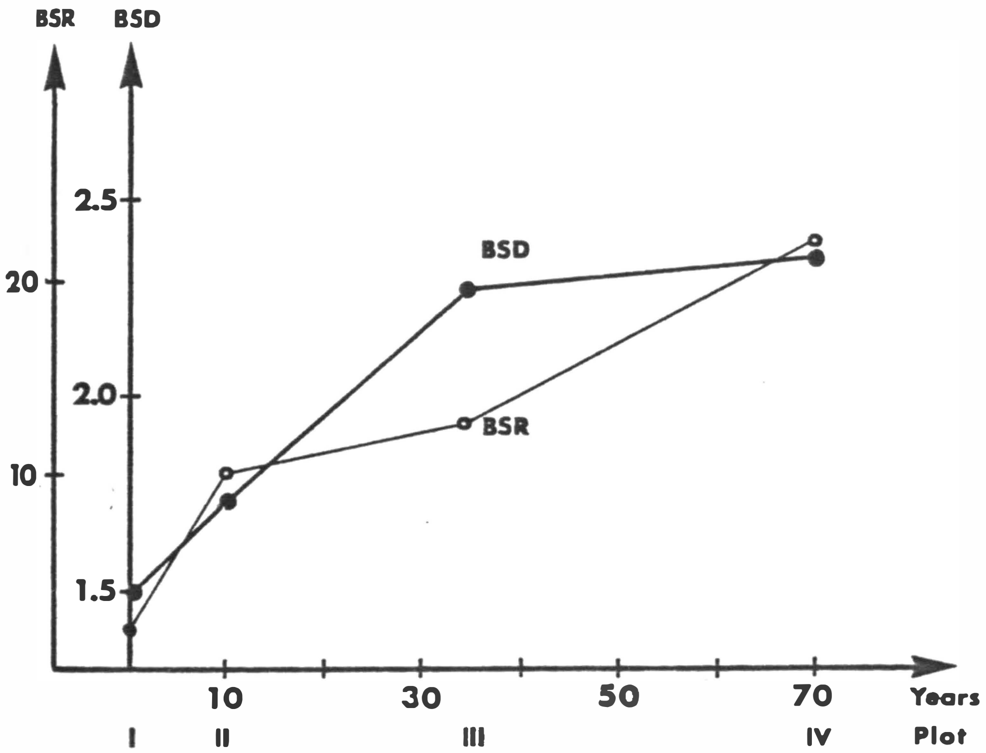


Fig. 15. Bird species diversity (BSD) and bird species richness (BSR) in successional stages.

When considering rates of increase, it is noteworthy to recognize the striking difference in successional development of bird community density (BCD) and bird species diversity (BSD), exhibiting opposite trends during the sere (Fig. 16).

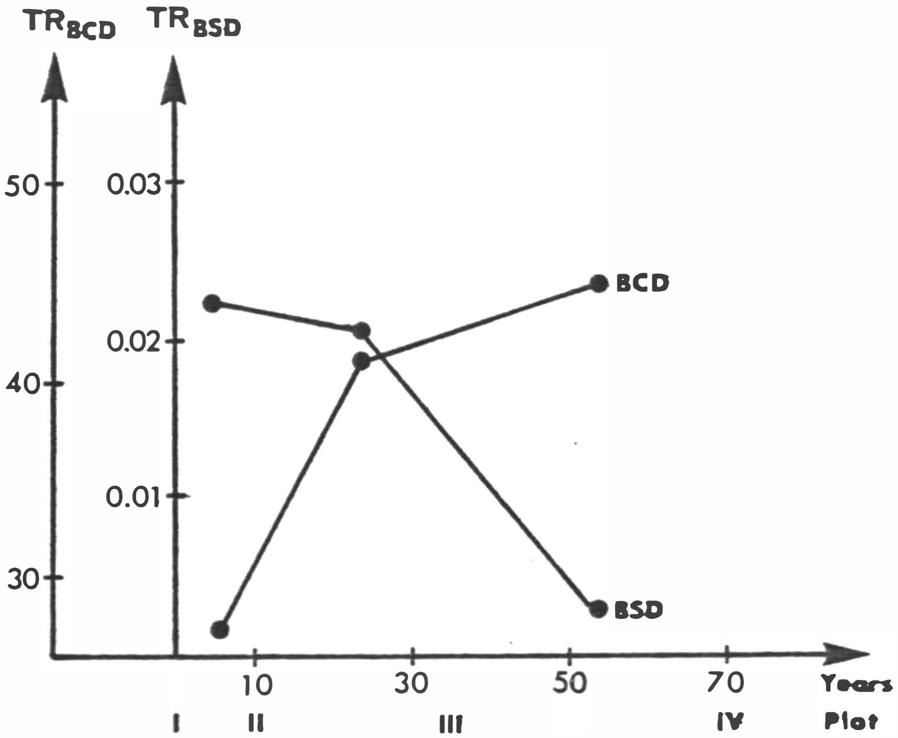


Fig. 16. Turnover-rate of bird species diversity ($TR_{BSD}$) and bird community density ($TR_{BCD}$). Plotted on the mid-range of the time interval between successive stages.

Fundamentally, the diversity (Shannon's index) of breeding and feeding site groups follow the species diversity trend, not unexpected (Tables XXIV and XXV). All these coinciding diversity trends suggests increasing niche-density, at least in the early half of the succession range studied here.

Bird species richness

The density of species (BSR) in the four successional plots is not following the smooth coarse of the species diversity (Fig. 15). In the intermediate stages, the species richness values are intermediate, and the richness in plot II and III is far exceeded in the final stage. The species richness in plot IV is 75 % higher than in plot III. The hypothesis of no differences between plot I, II + III and IV is rejected. (K = 6 , P = 0.014 in a Kruskal-Wallis test).

In an one-way analysis of variance on ln BSR, the hypothesis of no differences between stages is rejected (F = 1052, P < 0.0001) and the Newman-Keüt test detects that all differences are significant (P < 0.05).

Dominance and evenness

The dominance of the two most common species in the community is considerably higher in the early stages of the sere than in the final, the average figure (BD) for plot I and II is 0.67 and 0.41 for plot III and IV (Fig. 17). The difference is significant (U = 0, P = 0.0143 in a Mann-Whitney U-test).

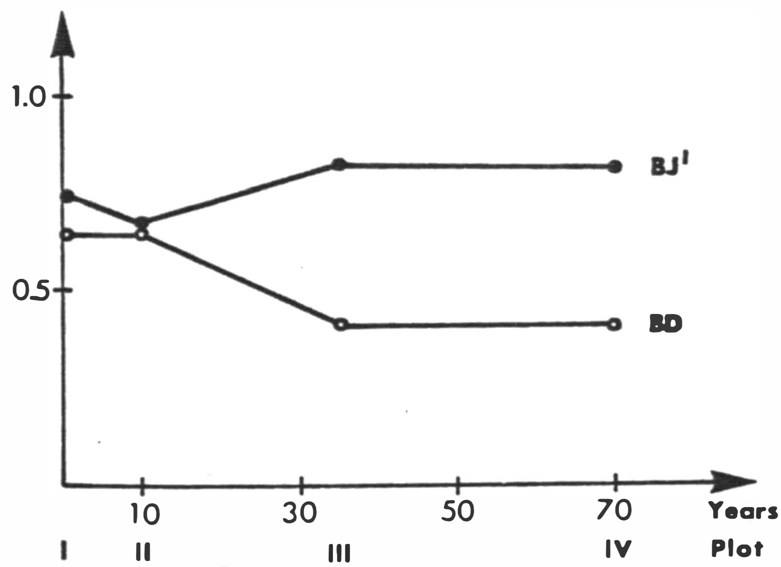


Fig. 17. Bird species dominance (BD) and bird species evenness (BJ')

Consequently, the proportions of the species in the community, exhibit a relatively more even distribution in the two forest habitats than in the open and the shrub habitat (Fig. 19). The bird species evenness (BJ') is significantly higher in the former (U = 0, P = 0.0143 in a Mann-Whitney U-test).

Body weight and clutch size

Hypothesis of increasing size of individuals during succession is only partly supported by the present study. The average size of individuals in the initial stage is 90.4 g and 50.7 g in the terminal stage, contradicting the hypothesis (Fig. 18). The amount of heavy wader species in the wet, open habitat is responsible for the observed high body weight figures. When considering passerine species only, the weights in the climax stage exceed the other stages, due to the high density of Turdus species in the former.

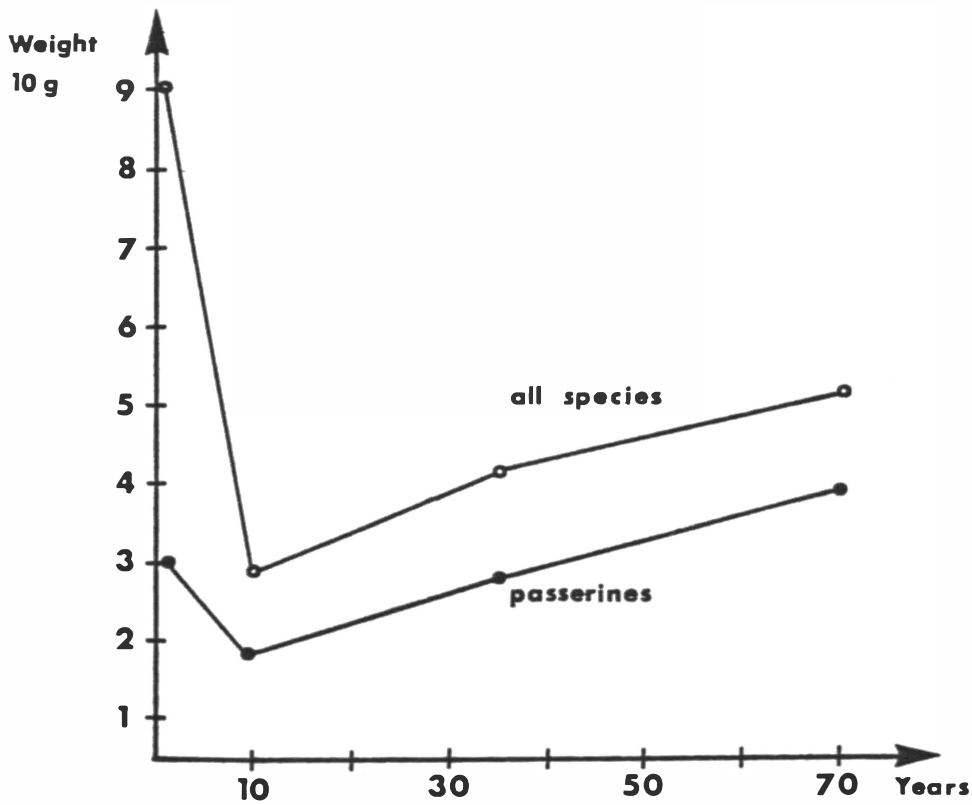


Fig. 18. Mean body weights in grams during succession (Anas platyrhynchos is deleted)

The overall trend in the three last stages in increasing average body weights in the communities. The mean clutch size is not higher in the early stages.

4.3.4. Correlations of community indices

The correlation coefficients for the bird community indices are listed in Table XXIX. The relationship between bird species diversity (BSD) and bird species dominance (BD) is significantly negative (Fig. 19).

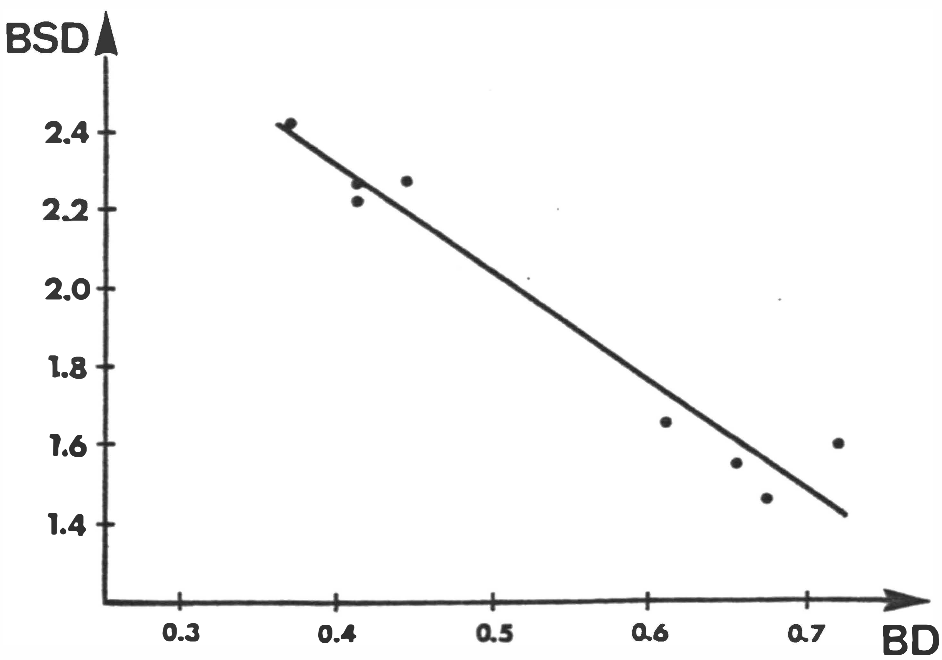


Fig. 19. Bird species diversity (BSD) in relation to bird species dominance (BD). BSD = 3.394 - 2.673 BD, $R^2$ = 0.914, $P < 0.0002$ in a two-tailed t-test

From the regression analysis of the index values of the present study nothing points to this relation beeing nonlinear. The correlation between the BSD and bird species richness (BSR) is positive and significant ($P < 0.008$). No significant correlation between BSD and bird species evenness (BJ') exists, nor between BSR and BJ'. The relations between the diversity indicies and the density of the community (BCD) is noteworthy. The relation is linear between BSR and BCD (Fig. 20). When considering the information content index, BSD, however, the relation is nonlinear. From the coefficients of determination ($R^2$) and analysis of standarized residuals, evidently the relation is curvilinear, and best fitted to a logarithmic regression model. BSD is linearly correlated to the natural logarithm of BCD (Fig. 21). Only 80.1 % of the variation in BSD is explained by BCD in a linear model, but 92.5 % in a log model.

Table XXIX. Correlation matrix for bird community indices. r = correlation coefficient in a linear regression model, $r_s$= Spearman rank correlation, *, ** and *** denotes the significance level of r in a two-tailed t-test for $P < 0.05$, $< 0.01$ and $< 0.001$ respectively.

| | BSD | BJ' | BSR | BD |
|---|---|---|---|---|
| BJ' | r = 0.6 | | | |
| BSR | r = 0.849**<br>$r_s$ = 0.97 ** | r = 0.323 | | |
| BD | r =-0.956**<br>$r_s$ =-0.81 * | r =-0.747*<br>$r_s$ =-0.714* | r = -0.777*<br>$r_s$ = -0.744* | |
| BCD | r = 0.895<br>$r_s$ = 0.952** | r = 0.57<br>$r_s$ = 0.417 | r = 0.945***<br>$r_s$ = 0.994** | r =-0.856**<br>$r_s$ =-0.833* |

Abbrevations
BSD = Species diversity
BJ' = " evenness
BSR = " richness
BD = " dominance
BCD = Community density

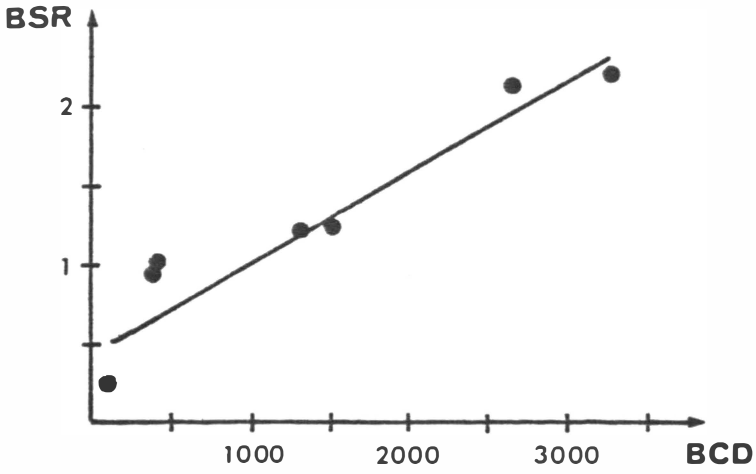


Fig. 20. Correlation between bird species richness (BSR = species/ha) and bird community density (BCD = pairs/km$^2$). BSR = 0.443 + 0.583 BCD, $R^2$ = 0.945, P < 0.0005

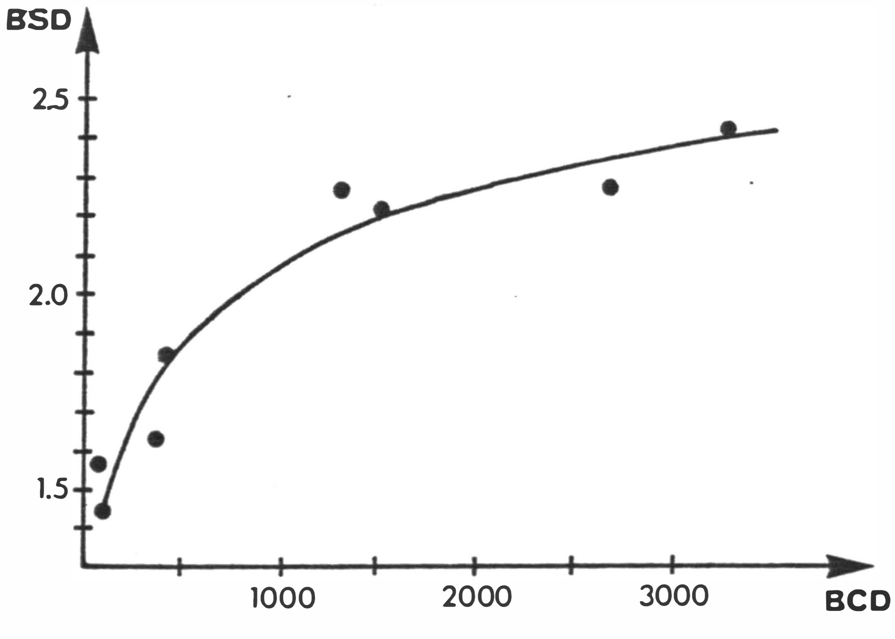


Fig. 21. Bird species diversity (BSD) in relation to bird community density (BCD = pairs/km$^2$). BSD = 0.161 + 0.278 ln BCD, $R^2$ = 0.925, P < 0.0002

### 4.3.5. Bird community and habitat relationships

Regression equations of the relations between the bird community density/diversity indices and the indices of habitat structure, are listed in Table XXX.

Community density

On assuming that the total density of the breeding bird community is determined by the available food resources and that these resources are linearly related to the density of the foliage, foliage estimates as good predictors of the density would be expected. When relating BCD to the density or cover estimates in linear regression models, the shrub and tree cover estimates (STC) give the relatively best prediction. Evaluating the ability of the cover or density indices to predict BCD by the coefficient of determination alone, total vegetation cover (TVC) is the second best, shrub and tree density (STD) third and total vegetation density (TVD) fourth.

A regression model with a transformation of the bird community density to a log scale (natural logarithm) linearly related to STD, gave a close fit (Fig. 22).

That the breeding bird community density increases exponentially with the foliage density of the shrub and tree strata, suggests either that the assumption of linear proportionality between foliage density and food density is invalid or that BCD is determined by other factors or factor combinations.

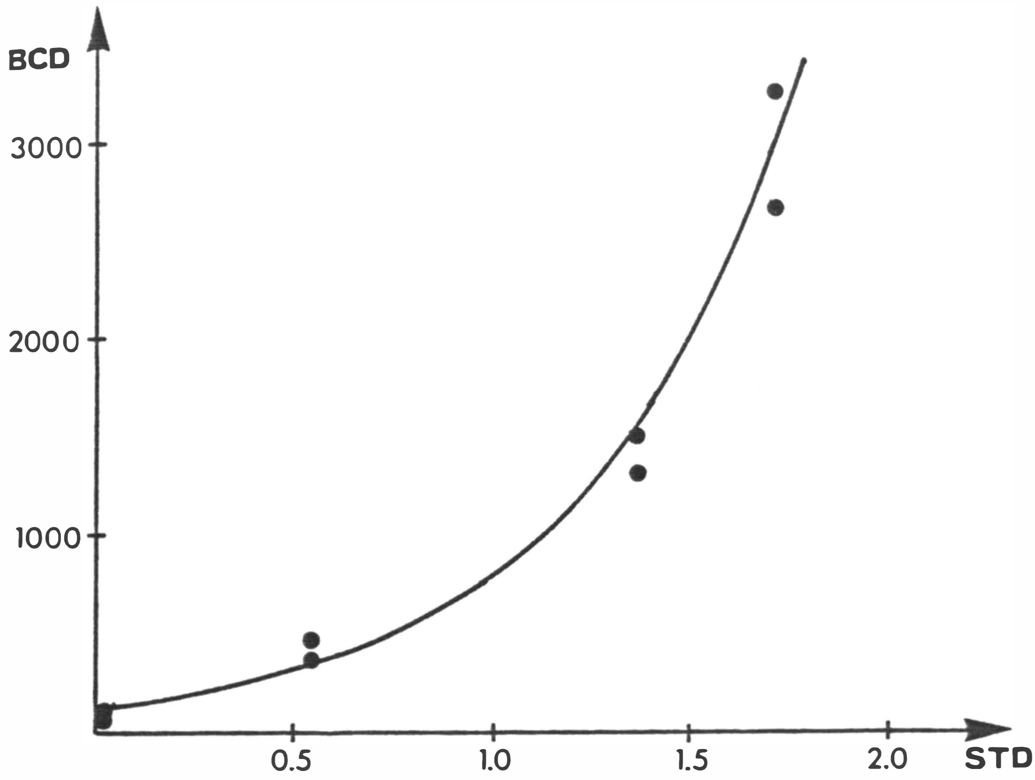


Fig. 22. Bird community density (BCD, pairs/$km^2$) in relation to shrub and tree strata density (STD). The regression equation is given in Table XXX.

Table XXX. Functional relationships of bird community indices and habitat structure indices, measured as simple linear regressions. $R^2$ = coefficient of determination, the proportion of the variation of Y explained by X. P is the significance level in a two-tailed t-test.

| Regression equations | | $R^2$ | P |
|---|---|---|---|
| BCD = -1.898 + 1.764 | TVD | 0.724 | < 0.01 |
| BCD = -1.554 + 2.427 | TVC | 0.939 | < 0.0001 |
| BCD = -0.157 + 2.192 | STC | 0.941 | < 0.0001 |
| BCD = -0.192 + 1.566 | STD | 0.856 | < 0.001 |
| BCD = 4.823 + 1.843 | STD | 0.986 | < 0.0001 |
| BSR = -0.198 + 3.503 | VSD II | 0.773 | < 0.01 |
| BSR = 0.308 + 0.953 | STD | 0.841 | < 0.005 |
| BSD = 1.363 + 0.844 | FHD | 0.867 | < 0.001 |
| BSD = 1.280 + 1.784 | VSD II | 0.872 | < 0.001 |
| BSD = 1.492 + 0.521 | STD | 0.945 | < 0.0001 |
| BSD = 0.838 + 0.636 | TVD | 0.937 | < 0.0001 |
| STB = 0.225 + 3.043 | STD | 0.988 | < 0.0001 |
| $STF^{1/2}$ = 0.262 + 2.225 | STD | 0.986 | < 0.0001 |
| GFD = 11.369 -10.208 | FLD | 0.885 | < 0.001 |

Abbreviations:

BCD = Bird community density
BSR = Bird species richness
BSD = Bird species diversity
STB = Shrub and tree breeders density
STF = " " " feeders density
GFD = Ground feeders density
TVD = Total vegetation density
STD = Shrub and tree layer density
TVC = Total vegetation cover
STC = Shrub and tree layer cover
VSD I = Vegetation strata diversity I
VSD II= " " " II
FHD = Foliage height diversity

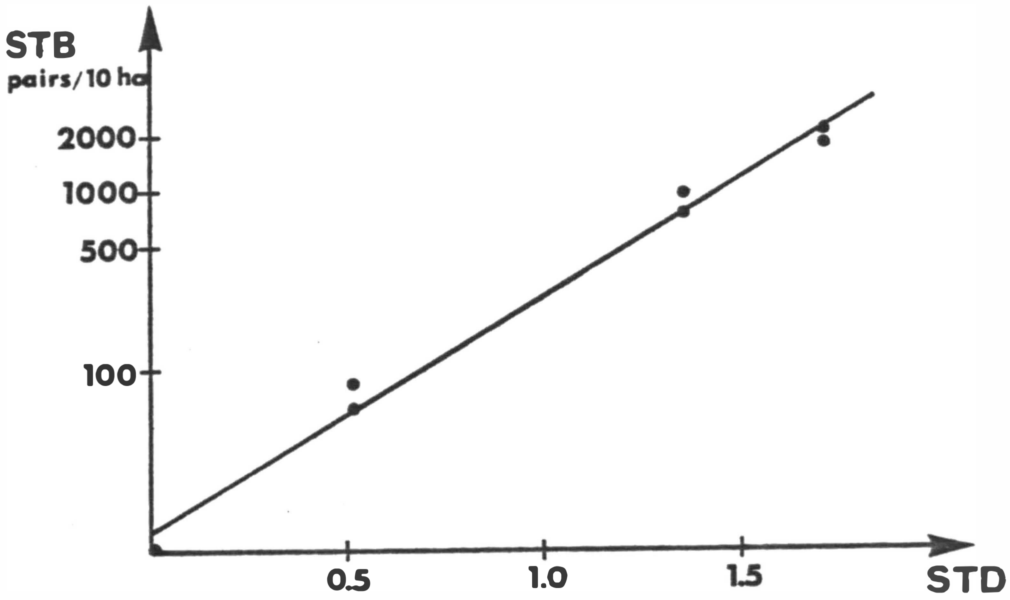


Fig. 23. The correlation between shrub and tree breeders density (STB) (ln scale) and shrub and tree density (STD). The regression equation is given in Table XXX.

Bird categories

The density of shrub and tree breeders (STB) is significantly correlated to the density of the shrub and tree layer (STD). Residual-analysis detect that this relation is non-linear. The best fit is obtained when a linear regression model between ln STB and STD is employed (Fig. 23).
Indications of the density-regulating factors are given when correlating the density of species feeding in the foliage of the shrub and tree layer (STF) to STD. Residual analysis show that this relation is neither linear. The best fit is a square root transformation of the STF-values (Fig. 24).

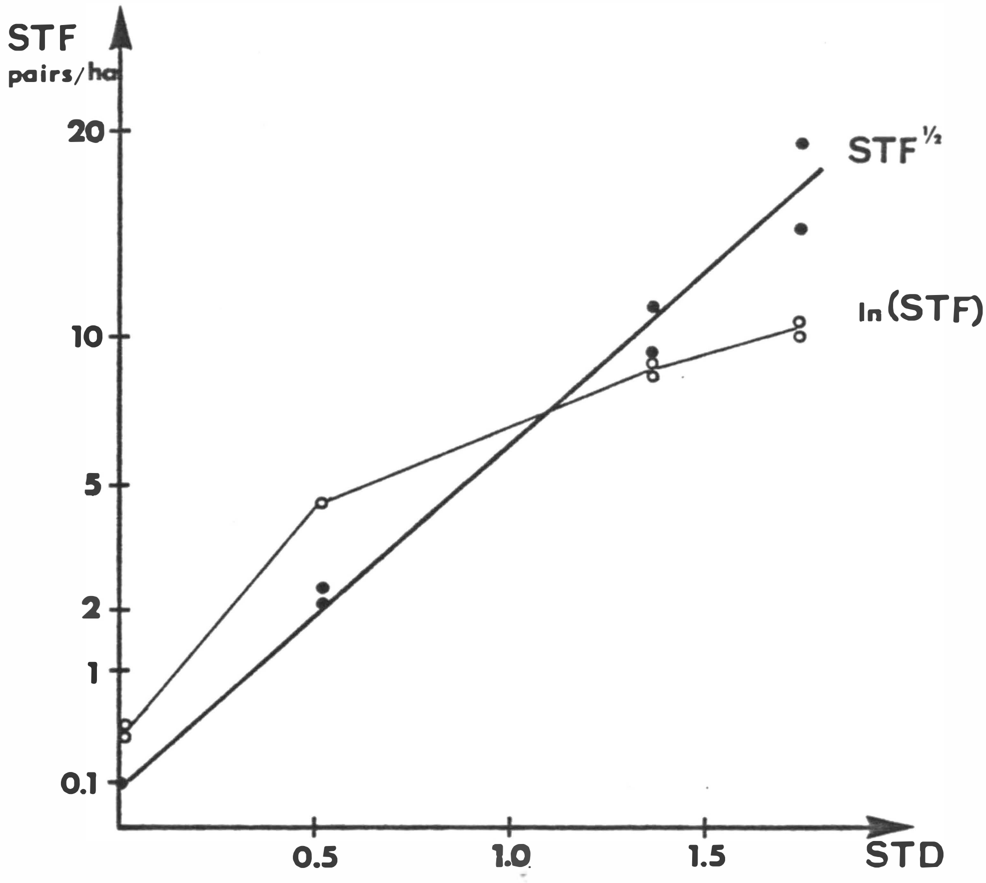


Fig. 24. Shrub and tree foliage feeders (STF) (square root scale) in relation to shrub and tree density (STD). The relation of ln STF and STD is illustrated. The regression equation is given in Table XXX.

Noteworthly is that a log transformation (natural logaritms) of STF is too "strong". When comparing ln STF and ln STB relations to STD, the latter increase indefinitely (linear) and the former at a decreasing rate (Fig. 23 and 24).

Since the foliage feeders (STF) increase at a lower rate than do shrub and tree breeders (STB) to a given increase of shrub and tree density (STD), it is an indication of that the former is relatively more "restriced" than the density of the breeding site groups. If the assumption of linear proportionality between foliage density and food resources is valid, this result

Bird species diversity (BSD)

The foliage density estimates are the best predictors of BSD (Table XXX). Shrub and tree density (STD) explain 94.5 % and total vegetation density (TVD) 93.7 %. The relationships appear linear (Fig. 25). Evidently, the density of the shrub and tree layers are the most important habitat components influencing the diversity of bird species, the latter measured as information content (Shannon). The density of the field layer adds rather decrement than increment in explanation when TVD is compared with STD alone. The vegetation strata diversity index taking into account the foliage density in the horizontal plane (VSD II), is a superior predictor of BSD to the indices of purely vertical density statification (VSD I and FHD) ($R^2$ = 0.895 versus 0.872 and 0.867, respectively). BSD and VSD II is best related in a linear regression model (Fig. 26).

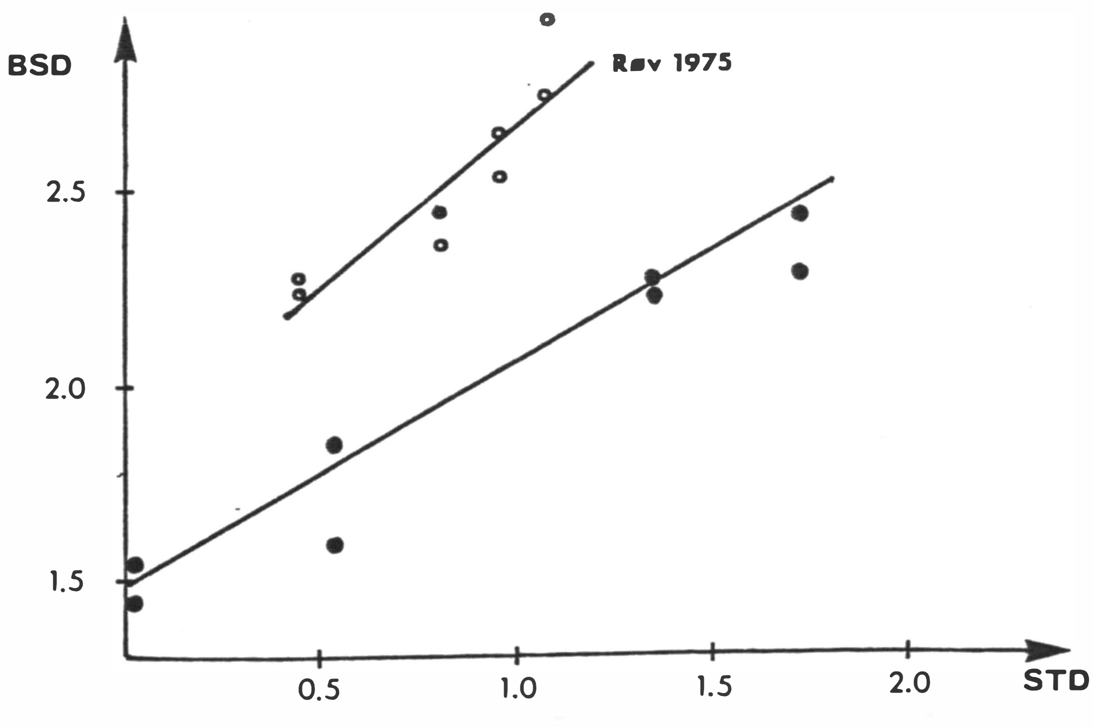


Fig. 25. Bird species diversity (BSD) in relation to shrub and tree density (STD). The regression equation is given in Table XXX. For comparison the data points and the fitted line (BSD = 1.854 + 0.81 STD) for a deciduous forest gradient (RØV 1975) is shown.

suggests that food is a relatively stronger regulating factor for species feeding in the shrub and tree layer than nest site availability is for species breeding in these layers.

Functional relationships between ground feeders and habitat factors exists. The breeding density of species feeding on the ground (GFD) within the habitat is negatively correlated ($r = -0.94$) to the density of the field layer (FLD) (c.f. Table XXX). However, GFD is not significantly correlated to the cover of field layer (FLC). GFD is positively correlated to the shrub and tree density ($r = 0.924$ between ln GFD and STD, $P \approx 0.001$).

Bird species richness (BSR)

The density of the shrub and tree layers (STD) is the best predictor of BSR (Table XXX, 84.1 % of the variation is explained by the former, whereas the strata diversity index (VSD II) account for 77.3 % of BSR-variation). All other habitat parameters are poorer predictors, when considered in simple linear regression analysis. The floristic diversity index (FD) added no significant amount of explanation of BSR to VSD II in a multiple regression model. None of the plant diversity indices are significantly related to BSR in simple linear regressions. Evidently, plant species diversity functionally is insignificant in explaining species richness in the present habitats. The foliage strata density and diversity seems to be the main assignable factors.

In a multiple regression with shrub and tree density (STD) as independent variable 1 and maximum percent of the plot flooded as variable 2 (index of uncertainty on the breeding site) the latter gave no further significant increase in the explanation of BSR. To test whether BSR was partially correlated to the density of Turdus pilaris, a multiple regression analysis with STD and density of Turdus pilaris (variable 2) was performed. The second independent variable explained further 7.8 %, however not significant ($P \approx 0.12$).

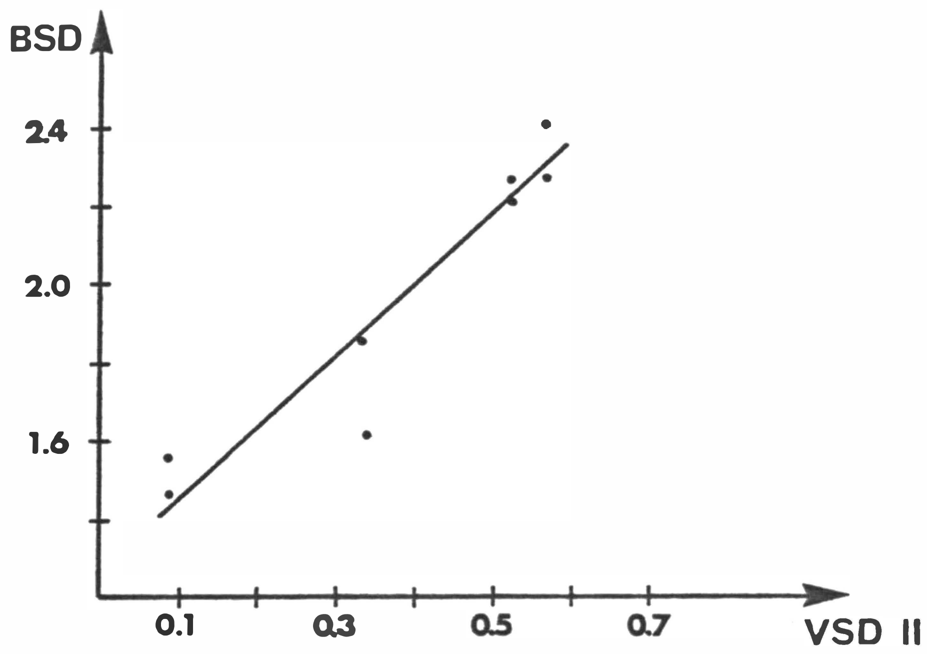


Fig. 26. Bird species diversity (BSD) correlated to vegatation strata diversity (VSD II). The regression equation is given in Table XXX.

Bird species diversity (BSD) is not affected by plant diversity in the present study. In multiple regression analysis where BSD was related to VSD II or STD as independent variable 1, and floristic diversity (FD) or plant species cover proportion diversity (PPD) as independent variable 2, the latter indices gave no significant enhancement of explanation to the bird species diversity variation. The same result was obtained when maximum per cent of the plot flooded in the spring inundation was considered as independent variable 2.

### 4.3.6. Stability

The results of the stability-analysis is presented in Table XXXI. The stability pattern is not clear in the successional stages. The indices presented here neither reveal unambigious trends of increasing stability in the communities nor decreasing stability. On average, the coeffisient of variation of the total bird community density C.V. (BCD) is smaller in the two final stages than the two first, the difference is however, not significant.

The variance ratio index, V, for the common species, have a trend of increase during the succession. In the final stage, the common species populations fluctuate relatively more compensatory than in the preceding stages. The average variance ratio for the two first stages is significantly lower than for the two last stages in the succession (P < 0.03 in a one-tailed

Table XXXI. Indices of bird community stability

| | Plot | | | |
|---|---|---|---|---|
| Index | I | II | III | IV |
| C.V. (BCD) | 23.53 | 7.03 | 9.56 | 14.50 |
| V, all species | 0.454 | 1.370 | 0.718 | 0.208 |
| V, species > 5 % | 0.454 | 0.440 | 0.505 | 1.449 |
| S | 0.714 | 0.708 | 0.748 | 0.733 |
| C.V. (BSR) | 0 | 6.15 | 4.56 | 3.80 |
| C.V. (BSD) | 4.25 | 9.98 | 1.41 | 4.62 |
| C.V. (BJ') | 4.56 | 0 | 3.45 | 3.49 |

Abbreviations:
C.V. = Coefficient of variation in percent
BCD = Bird community density
BSR = " species richness
BSD = " " diversity
BJ' = " " evenness
V = Variance kvotient
S = Similarity

t-test). This increase in variance ratio index of stability for the common species are confirmed by the similarity-based stability index (S), based on all species. The similarity in species population densities are significantly greater in the two final stages than in the two initial stages (P < 0.04 in a one-tailed t-test). The overall trend in the indices of populations density variations, give evidence, though weak, of increasing stability during the succession. The coefficients of variation for species richness (BSR) and the abundance structure of the communities, species diversity (BSD) and species evenness (BJ'), are not significantly changing directionally. Assumptions of increasing or decreasing stability in these community properties are not supported by the present study.

The similarity index of stability (S) is significantly related to bird species diversity (BSD) (Fig. 27), the stability increase with increasing diversity.

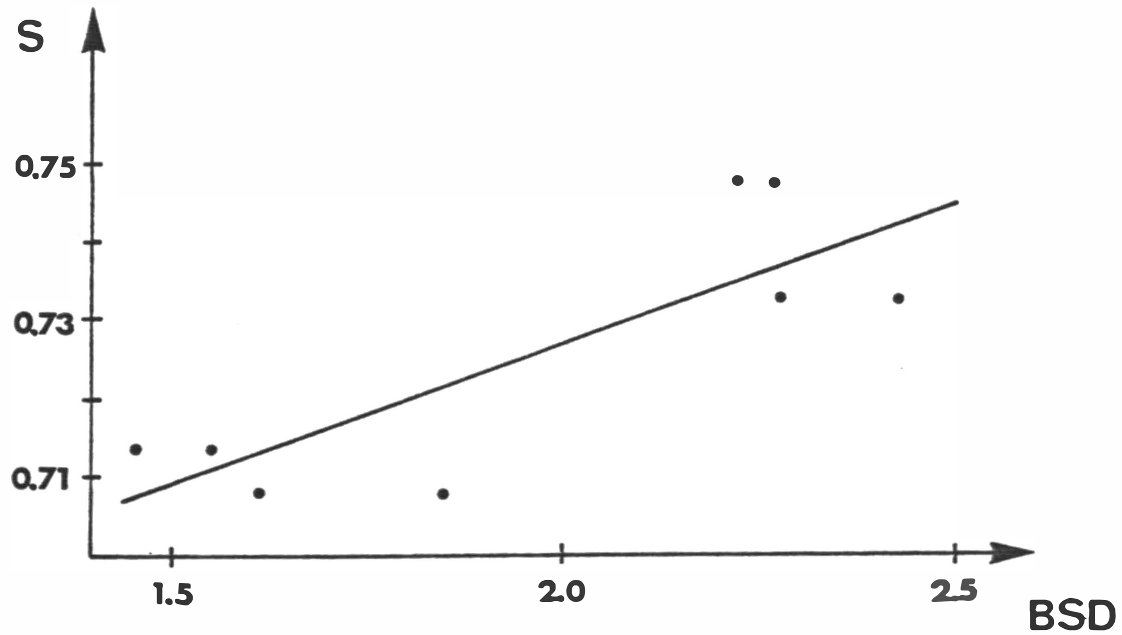


Fig. 27. Relation tetween the similarity index of stability (S) and bird species diversity (BSD). $S = 0.655 + 0.036$ BSD, $r = 0.818$, $P < 0.013$ in a two-tailed t-test.

The correlation between stability measured as the variance kvotient (V) for species > 5 % of the community and bird species diversity (BSD) is weaker, $r = 0.667$ ($P < 0.071$). When this index is related to bird species richness (BSR), however, the correlation is closer, $r = 0.88$ ($P < 0.01$).

Since the variance ratio index (V) and the similarity index (S) are mainly influenced by the common or dominant species population density fluctuations, as the Shannons diversity index is considerably affected by the dominant species (KEMPTON & TAYLOR 1976), these functional relationships between stability aspects of density and bird species diversity are not unexpected.

## 4.4. Plant and bird community similarity

### 4.4.1. Structure

If the plant and bird community structure developed simulanously throughout the succession, i.e. exhibited parallelling levels in increment or decrement of structure indices, positive correlations between diversity, evenness and dominance indices would be expected. Plant species cover proportion diversity (PPD) and bird species diversity (BSD), and their respective evenness components (PJ' and BJ') are the most relevant counterparts. Indices of species richness, floristic diversity (FD) and bird species richness (BSR) are other comparable indices.

Plant species diversity (PPD) and bird species diversity (BSD) exhibit opposite trends (though weak for PPD) during succession. BSD and PPD are significantly negatively correlated $r = -0.774$ ($P < 0.024$) or $r_s = -0.738$ ($P < 0.05$, Spearman rank correlation). This negative correlation could indicate that abundance-determinating factors operate different or opposite in the plant and bird communities during succession, this assumption is supported when considering the dominance structure of the successive communities. Plant species cover proportion dominance (PD) increase in the late stages, the opposite trend occur in bird species dominance (BD). BD and PD is significantly negatively correlated, $r = -0.879$ ($P < 0.005$).

All other indices of plant and bird community structure are tested for correlations, but none were significantly correlated. The species richness peak is reached earlier in the succession in the plant (FD) than in the bird communities (BSR), the former in the intermediate stages, the latter in the late stages. The present data do not support any hypothesis of parallel developmental coarse of diversity, equitability or dominance in the communities of two tropic levels (producer and secondary consumer) in an ecosystem undergoing succession. The precense of negative correlations or absence of parallellity rather suggest that the factors that determines the community structure act opposite, at different time intervals during the succession or that the consumers are influenced by other mechanisms than the producers.

4.4.2. Succession rate

The amount of species turnover in the plant and bird communities in the succession is presented in Table XXXII and Fig. 28. The succession rate indices are equally measuring the turnover in the communities, whether based on qualitative or quantitative data, for the plant as well as the bird communities (c.f. Fig. 28). The correlations between the SR-values are close, r = 0.998 ($P < 0.05$) for the plant succession and r = 0.993 ($P < 0.001$) in the bird succession.

When relating succession rate with time in a linear regression with ln SR in relation to time (i.e. the interval between two successive communities) the regression equations given in Table XXXIII are obtained.

For comparison, the same data for a secondary succession in oak-hornbeam habitats in southern Poland (GŁOWACINSKI & JÄRVINEN 1975) is compiled together with the present data.

Time explains 88.5 % and 83 % of the variation in plant and bird succession rate, respectively. On the basis of test of differences in the regression coefficients (slope), it is not possible to detect significant differences in the amount of succession rate decrement between plant and bird communities.

Table XXXII. Turnover and succession rates

| Indices \ Communities | | I/II | II/III | III/IV |
|---|---|---|---|---|
| STJ | plants | 54.1 | 84.3 | 52.3 |
| $SR_J$ | " | 5.41 | 3.372 | 1.494 |
| CTH' | " | 35.22 | 41.75 | 9.95 |
| $SR_{H'}$ | " | 3.522 | 1.67 | 0.284 |
| STJ | birds* | 81.25<br>80.00 | 87.5<br>87.5 | 21.05<br>21.05 |
| $SR_J$ | " | 8.125<br>8.0 | 3.5<br>3.5 | 0.602<br>0.602 |
| CTH' | " | 47.85<br>41.9 | 50.95<br>52.55 | 6.1<br>4.55 |
| $SR_{H'}$ | " | 4.785<br>4.190 | 2.038<br>2.102 | 0.174<br>0.130 |

* Calculations for two breeding seasons.

Abbreviations:

STJ = Species turnover, based on Jaccard's similarity index
$SR_J$ = Succession rate, - " -
CTH' = Community turnover, based on Shannons diversity index
$SR_{H'}$ = Succession rate, - " -

Table XXXIII. Succession rate in relation to time interval between successive stages. The succession rate values ($SR_{H'}$) are defined in text.

| | | | | |
|---|---|---|---|---|
| ln $SR_{H'}$ | (plants) | = | 2.427 - 0.097 t, | $R^2$ = 0.885 |
| ln $SR_{H'}$ | (birds) | = | 3.123 - 0.129 t, | $R^2$ = 0,83 |
| ln $SR_{H'}$ | (birds) | = | 2.443 - 0.066 t, | $R^2$ = 0.752[1] |

1) Calculated from GŁOWACINSKI & JÄRVINEN 1975

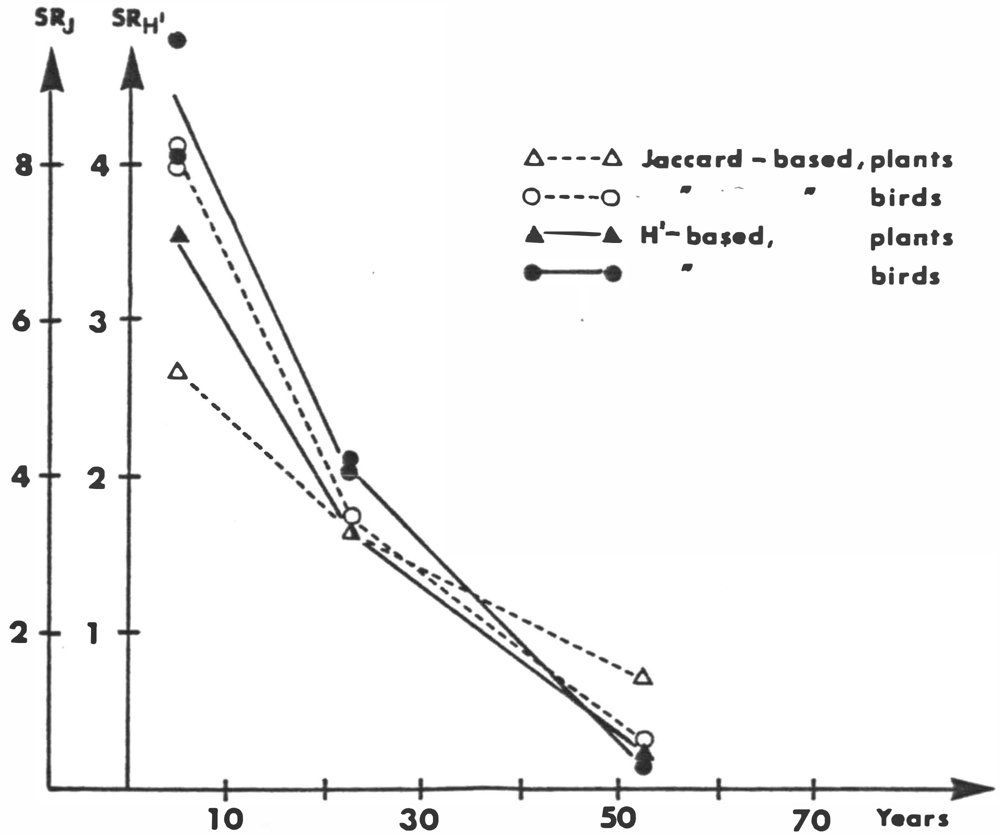


Fig. 28. Changes in turnover rates during succession. Measures are defined in text. The SR-values are plotted in the mid-time in the interval between two successive communities.

Noteworthy is the gentle, homogenous slope of decreasing succession rate in the plant succession. It confirms the expectation that the discontinuity in origion of the young forest stage (plot III) has minor impact on the species composition and relative abundance of species. It the assumption was invalid, a higher SR-value for the time interval between plot II and III would be expected. In conclusion, the relative rate of species replacement in the successive plant and bird communities is equal.

# 5. DISCUSSION

## 5.1. General hypothesis of diversity

Attempts to give probable explanations of the observed patterns in diversity-development in the present succession, lead to the current theories of factors determining species diversity in communities.

The predation hypothesis (PAINE 1966, HARPER 1969, JANZEN 1970, VAN VALEN 1974) suggests that selective predation on dominant competitors can maintain a relatively high local species diversity by preventing the dominant competitors from monopolizing the major resource. Predation keeps the prey species below carrying capasity, thus the competition is damped and new species can invade the system. A further enhancement may be promoted by a positive feedback mechanism, whereby the new species support new predatior prpulations. This hypothesis is not restricted to interacting animal communities, but it is extended to plant-herbivore systems as well. The stability and level of primary production presumably limit this process.

The competition hypothesis emphasizes that highly diverse communities arise in stable environments as a result of competition-maintained niche diversification (PIANKA 1966, 1978). Competition forces compression of niches, causing greater species packing and increasing species diversity (MAC ARTHUR & WILSON 1967, MAY & MAC ARTHUR 1972, PIANKA 1975). Interspecific competition is more intense in stable environments because these allow more species to reach carring capasity. The competition selects for increased specialization, causing reduced competition intensity. Species diversity is then increased by successful invasion of additional species. Theoretically, this mechanism is limited by the number of discrete resources available

(MAC ARTHUR 1965) or the maximum tolerable niche overlaps on continuous resources (MAC ARTHUR 1972). The ability of a species to invade a community is dependent upon the existence of a resource state where it can compete more effectively than present occupants (MAC ARTHUR 1965). This may be one of the principal mechanisms of increasing diversity in successional ecosystems (MELLINGER & MC NAUGHTON 1975).

There exists evidence that many natural ecosystems are not in competitive equilibrium (LOUCKS 1970, AUCLAIR & GOFF 1971, WIENS 1977, CONNELL 1975, 1978), but the increase and predominance of one competitor, with a correnspopnding decrease in the other, will still be expected (HUSTON 1979). Thus, competition should be inversely related to diversity. Intense competition should result in low diversity among the competing species, and high diversity would be expected in damped competitive systems (LEVINS 1968, VANDERMEER 1970, HUSTON op.cit.) In structural simple environments, competition reduces diversity through competitive exclusion. In complex environments, competition may increase diversity through increased habitat specialization (MENGE & SUTHERLAND 1976).

The non-equilibrium hypothesis of species diversity is proposed by HUSTON (1979). It assumes that most communities exist in a state of nonequilibrium where competitive equilibrium is prevented by periodic population reductions and environmental fluctuations. When competitive equilibrium is prevented, a dynamic balance may be established between the rate of competitive displacement and the frequency of population reduction, which results in a stable level of diversity. Under conditions on infrequent reductions, an increase in the population growth of competitors generally results in decreased diversity. According to this theory, diversity may be reduced by competitive displacement (or exclusion) or by frequent population reductions, preventing some of the competitors to recover. The organisms must have some minimum growth rate to recover reductions, increasing with the reduction frequency. Low growth rates of competitors and low disturbance frequencies should result in low diversity, due to the relatively long period, enough for a close approach to competitive equilibrium. Increase in the frequency of population reduction would prevent competitive equilibrium, and high diversity is expected. Further increase of the frequencies would reduce the diversity, because some competitors would be enabled to recover. Combination of high growth rates of the competitors and low frequency of population reductions would promote low diversity, due to the rapid approach to equilibrium. Diversity would increase to a maximum, followed by a decline when the disturbance frequency increases.

Following this theory, low to medium frequencies of population reductions and low to medium population growth rates should result in the highest diversity. These factors allow prolonged coexistence of competitors and provide sufficient time for compensatory factors (e.g. fluctuating environmental conditions) to operate effectively.

The hypothesis of "intermediate stress or disturbance" put forward by GRIME (1973, 1979) and CONNELL (1978) is closely related to the preceding. It suggests that moderate stress or disturbance in herbaceous vegetation cause an increase in species density by reducing the population densities of potential dominants, thus permitting subsidiary species to coexist with them.

Temporal heterogenity may affect community organization. In trophically simple communities (e.g. grasslands), physical stress (e.g. fire) creating patchiness may increase species richness (LOUCKS 1970, TAYLOR 1973, LEVIN & PAINE 1974, HORN 1975a, CONNELL 1978). These physical disturbances occur frequently enough to permit the competitive inferiour, opportunistic species to excist in the system. Physical disturbance thus changes the competitive environment from a situation where competitive exclusion would reduce the species richness to a system where disturbance-mediated competitive coexistence promotes richness.

The connection between the dynamic equilibrium hypothesis and the predation hypothesis is clear, since predation has the effect of reducing population sizes and thus preventing equilibrium and competitive displacement. Basically, the hypothesis of temporal heterogenity and intermediate disturbance are identical with and is only specialized versions of the general non-equilibrium competition hypothesis.

Environmental stability and predictability are suggested to promote species diversity (SLOBODKIN & SANDERS 1969, PIELOU 1975). Unpredictable habitats are believed to force organisms to have broad niches, resulting in lowered "niche-packing". Further are marginal populations exposed to higher extintion probabilities. However, examples are available on low-diversity communities in stable environments WHITTAKER (1966), as well as communities of high diversity in unpredictable habitats (WHITTAKER & NIERING 1965, PAINE 1966, PIANKA 1975). In the latter case the connection to the "non-equilibrium" or "temporal heterogenity" hypothesis is straight. Environmental variability might faciliate coexistence , either by continually altering the competitive abilities among the competitors or by periodically reducing population sizes and thereby the intensity of competition (c.f. PIANKA op. cit.). A relatively high degree of coexistence of competitors thus result in a relatively high species diversity.

Diversity has been positively correlated with productivity (CONNELL & ORIAS 1964, PIANKA 1966) and negatively correlated with productivity (MARGALEF 1969). Generally, the hypothesis that high productivity begets high diversity, is rejected (MARGALEF op.cit., PIELOU 1975), due to many examples of an inverse relationship between productivity and diversity (c.f. MC NAUGHTON 1968, ROSENZWEIG 1971).

The hypothesis that environmental heterogenity is a determinant of species diversity, has been one of the most appealing theories. Increased diversity in increasingly heterogen environments is to be expected (LEVIN 1974). The hypothesis is supported by a large amount of empirical evidence. The structural complexity of the habitat has been successfully correlated to species diversity in animal communities of various taxonomical groups (HUSTON 1979). However, the majority of the investigations are performed on breeding bird communities (c.f. MAC ARTHUR et.al. 1966 , CODY 1968, KARR 1968, RECHER 1969, KARR & ROTH 1971, RØV 1975).

The heterogenity is mostly based on the physical structure and physignomy of the plant community serving as substrate for the animals. Among insects, suggestions are made that the species diversity of the plant influence their diversity (MURDOCH et.al. 1972). However, even if plant species diversity or habitat heterogenity to some extent explain the diversity in animals, the question of the former still remaines unsolved. Structural complexity is regarded as an extrinsic factor (HUSTON 1979) and the hypothesis mostly confined to animal communities.

## 5. 2. Plant species diversity

When considering the present diversity trends throughout the succession in relation to the theories, elements of the different hypothesis apply to various seral stages. From the present review, evidently competition is the overall factor determining diversity. The level of diversity in the communities is influenced through factors preventing competitive equilibrium. In the total competitive environment, these factors are distinguisable in two major groups. The allogenous influences - man-made disturbances (i.e. mowing, grazing) and other external changes in the physical environment (i.e. hydrological fluctuations) and the autogenous factors (i.e. shading, nutrient levels, litter accumulation, allelopatri). The interspecific encounters acts through passive mechanisms (shading, nutrient allocation, litter accumulation) or active inhibitory strategies (release of allelopatric chemicals).

In herbaceous vegetation in fertile environments, a trend towards monoculture is often observed, due to the tendency of large herbaceous plants to suppress growth and regeneration of smaller neighbours (GRIME 1979). High species diversity in semi-natural grasslands are often associated with low levels of primary nutrients, and a decline in diversity is observed when fertiliqer is added (RORISON 1970, VAN DER MAAREL 1970, ERIKSSON et.al. 1976). Even if mowing and burning are not species-specific as management influences, in contrast to grazing, their effects are selective. The competitive environment is altered, due to the different ability of recovery of the populations of the competing species in the community. In the initial stage of the present succession, hydrologic fluctuations combined with the haymaking and irregular burning, probably are preventing competitive equilibrium, resulting in a relatively low dominance by the major plant species, high evenness and species diversity (information content). Grazing or haymaking of pastures are known to increase or maintain species diversity (HARPER 1969, 1970, VAN DER MAAREL 1970, GRIME 1973, 1979).

The opposite effect on diversity would appear if a development of dominance by species with allelopathic chemicals or other effective inhibitory methods occurred (BAZZAZ 1975, MELLINGER & MC NAUGHTON 1975). However, this mechanism is most likely not operative in the initial stage of the present succession. Temporal lowered diversity of herbs in early successional stages have partly been attributed to litter accumulation (GABRIELSON 1968 in NICHOLSON & MONK 1974). In the managed pasture, the suppressing effect of a heavy litter mat is prevented. In the second stage of the present sere it may play a role, but the influence of the litter is more than counterbalanced by other mechanisms, as far as species richness is considered.

The peak in floristic diversity in the intermediate stages of the succession conform to the predictions of the non-equilibrium hypothesis. The relatively lower species reduction frequency, compared to the disturbance in the initial stage, allow establishment of species with too low growth rates to exist in the managed pasture. The gain of species is higher than the loss of the opportunistic species promoted by the disturbance. NICHOLSON & MONK (1974) found that stable or constant environments lead to high species diversification, whereas unstable conditions lead to lowered species diversity because rare or specialized species tended to be eliminated. They concluded that the number of vascular plant species associated with various seral stages should be directly related to historical prevalence of the stage, (i.e. size and duration of existence through time). According to this view, decrements in floristic richness of the oldest stages should not be expected. LOUCKS (1970) and BAZZAZ (1975) have shown that maximum species diversity correspond to periods in which species of the shade-tolerant and shade-intolerant groups occur simultanously in the community, a result similar to the present study. LOUCKS (op. cit.) assosiated a terminal decline in the species diversity with the dominance of the community by shade-tolerant species and exclusion of the shade-intolerant species.

VAN MIEGROET (1979) points out that maximal species diversity in forest successions is not typical for the steady state equilibrium, due to homogenization, structural egalization and maximal blocking of resources.

The primary resources for which the plants compete, are light, nutrients and water, and the success in competition appears by occupation of space. Circumstantial evidence for competition in the present succession is given in the negative correlation between cover of the shrub layer and the herb layer, particularily distinct in the shrub-phase and the terminal stage. Probably the species partly are competing for light. In the forest stages, the increasing shrub species cover and decreasing herb species cover with age indicate that the shrub species are superior light-competitors. Under an increasingly dense canopy layer, the shrubs derive increasing benefits from being closest to the light source. The shading may thus be a limiing factor in the occurence and luxuriancy of herb species. The decline in floristic richness (FD) and the relatively low species cover proportion diversity (PPD) in the terminal stage most likely are caused by the dominating position of the shade-tolerators in the canopy and understory layers.

Competition for resources other than light occurs simultanously in the sere. Water as a limiting factor (WHITTAKER 1965, ODUM

1971, NICHOLSON & MONK 1975) probably is of minor importance in the present habitats, due to the high water level and the water holding and transporting capasity of the silt-dominated soil. Depletion and/or enrichment of mineral nutrients are suggested to be one of the factors affecting diversity (WHITTAKER op. cit., 1975 a, ODUM op.cit., MELLINGER & MC MAUGHTON 1975, VAN MIEGROET 1979). Generally, the nutrient stock increases with time in the succession as well as the proportion of the nutrients stored in the vegetation. In the mature stages the nutrient loss is minimal, due to the high degree of internal mineral cycling. MELLINGER & MC MAUGHTON (1975) found a lower level of phosphorous and nitrate in the 36 year old shrub-growth oldfield than in fields of 4-5 years after abandonement, the level of K was higher. They believed that much of the corresponding increase in plant community diversity was caused by local differentiation in soil properties around individual plants partly through nutrient depletions and enrichments, resulting in microgeographic heterogenity allowing penetration of new species to the community. This explanation supports the view that combinations of hypothesis of diversity-factors are relevant. The suggestion of MELLINGER & MC NAUGHTON (op. cit.) includes both competition and environmental heterogenity as cooperative factors in determining the diversity level. When extended to the climax stage of a succession, however, the effects of a lowered available provision of basic nutrients in the soil on the species diversity, are questionable. GRIME (1979) argues that the prevailing conditions in the latest stages (e.g. shading, high proportion of mineral nutrients sequestered in the plants) generate selection pressure for a relatively high ability of capturing and conserving resources.

Selection for tolerance against stress (i.e. external constraints limiting the rate of dry matter production) is proposed to be a major mechanism whereby the climax trees attain their dominance. The monopolizing of the resources by these dominants thus suppresses species diversity. Indication of such competitive exclusion occurs in several studies of climax communities (c.f. LOUCKS 1970, AUCLAIR & GOFF 1971, NICHOLSON & MONK 1974).

The difference in diversity trends between the floristic diversity (FD) and the species cover proportion diversity (PPD, information content) probably reflects the difference in effects of the diversity-determining factors upon these two community attributes. The lack of increase in species cover proportion diversity during the succession is most likely assosiated with the non-equilibrium competitive environment. This is caused by haymaking and burning, primarily affecting species abundance in the initial stage, but also with repercussions years after abandonement. The relatively high degree of species equitability (and low dominance) in the open meadow seems to balance the higher species richness in the second and third stage when compared. Water level fluctuations and the management have minor effects on the level of cover proportion diversity. Comparing the two first seral phases, however, the species spectrum is considerably displaced, containing a significant amount of competitive inferior opportunists (e.g. some of the mosses) in the meadow.

Apparantly, the impact of disturbance is heavier on species richness (FD) of the meadow community than on species abundance diversity (PPD), when comparing plot I and II. The frequency and severeness of species populations reductions in the initial stage have brougt about a floristic diversity of the similar magnitude as the competitive environment provided by the climax

## 5.3. Bird species diversity

The trend of increasing species diversity and evenness at a decreasing rate, and the decline in dominance during the succession, conform to the predictions of the succession theories as well as to the majority of previous bird community studies. However, the temporal diversity and density peak in the shrub-phase, as reported by other authors (c.f. JOHNSTON & ODUM 1956, HAAPANEN 1965, GŁOWACINSKI 1975) is not found in the present sere. To verify if the apparent smooth course of parameter development is real or accidental, a bird community at a stage between 10 and 35 years after abandonement had to be investigated.

Vegetation complexity is clearly associated with the bird community structure. The functional correlations in the present study and numerous others conform to the hypothesis of spatial heterogenity as a determinant of species diversity. Bird species diversity is found to be linearly correlated with foliage height diversity (FHD) (MAC ARTHUR & MAC ARTHUR 1961, MAC ARTHUR 1964, KARR 1968, KARR & ROTH 1971, RECHER 1969, WILLSON 1974) or vegetation strata diversity (RØV 1975).

Other investigatiors have failed to find clear correlations (e.g. BALDA 1969, PEARSON 1975, ROTH 1976) and have questioned the generality of the BSD-FHD relationship.

TOMOFF (1974) found that plant physiognomy was a better predictor of BSD in desert scrub. DES GRANGES (1980) considered the physiognomic diversity of a forest stand to be correlated to BSD.

ROTH (1976) found BSD to be more precisely predicted by habitat heterogenity than FHD.

Others have found correlations between bird species diversity indices and plant species diversity.

LOVEJOY (1972) showed that plant species diversity were closer correlated to BSD than FHD in a tropical rain forest. The number of breeding land bird species on Calefornian islands was largely accounted for by the number of native plant species in the study of POWER (1972), a similiar result was found for the number of all bird species breeding on small Hawaiian islands (AMERSON 1975).

The vegetation density and cover have been considered as important habitat dimensions influencing species diversity. Correlations between density or cover and species diversity, however, are probably not linear. KARR (1968) found a stright line relationship between bird species diversity and log percent vegetation cover, but as KARR & ROTH (1971) points out, when analyzing a broad variation of New World habitats, this cannot be generalized to different areas. Instead they suggested a sigmoid relation between species diversity and total percent plant cover, where the greatest rate of increase in diversity is over intermediate values of total percent vegetation cover. Later WILLSON (1974) found a curvilinear relationship between the two variables. RØV (1975) could not reject a hypothesis of linear correlation when considering the same indices in a deciduous forest gradient.

The data presented here, indicate a different relationship between the habitat complexity, foliage volume and species diversity than indices obtained by others. Some regression equations are given for comparison in Table XXXIV. The slope in the present study is significantly smaller than in the foliage height diversity (FHD) - bird species diversity (BSD) relationships of MAC ARTHUR & MAC ARTHUR (1961) for a wide range of open and closed deciduous forest habitats. The difference is present when comparing with the data from a secondary succession gradient on strip-mined land given by KARR (1968). The slope of the deciduous forest gradient in western Norway, obtained by RØV (1975), is

Table XXXIV. Relations between bird species diversity (BSD) and foliage height diversity (FHD), vegetation strata diversity (VSD) or density (STD) for some selected studies.

| Regression equations | P < | Source |
|---|---|---|
| BSD = 0.46 + 2.01 FHD | 0.0001 1) | MAC ARTHUR & MAC ARTHUR 1961 |
| BSD = 1.521 + 1.678 FHD | 0.001 1) | KARR 1968 |
| BSD = 0.32 + 2.15 FHD | 0.0001 1) | RØV 1975 |
| BSD = 0.10 + 2.60 VSD I 5) | 0.0001 1) | " " |
| | 0.003 2) | " " |
| BSD = 1.854 + 0.81 STD 5) | 0.021 1) | " " |
| | 0.09 2) | " " |
| | 0.0001 3) | " " |
| | 0.032 4) | " " |

1) P denotes the significance level in a t-test of the hypothesis:
$H_0$: B1 (reference) - B1 (present study) = 0 against
$H_1$: B1 (reference) > B1 (present study) (one-tailed test) where
B1 is the slope in the regression equations. The regression equations in the present study is given in Table XXX.

2) A similiar test as in 1), but the test is based on the reference data.

3) Test on differences in the intercepts.

4) Test on differences in the intercepts, based on the reference data.

5) Present notation.

significantly higher than the present, both for FHD and vegetation strata diversity (VSD I). When comparing RØV's data, using the density of the shrub and tree layer (STD) in the regression, a difference between his and the present slope is likely the case (c.f. Table XXXIX and Fig. 25). The level of BSD for his habitats is significantly higher, when evaluating the intercepts in the regression lines.

When analysing the probable causes of this lower species diversity predicted by a certain habitat heterogenity or foliage volume, compared to the references, the range of varity in types of habitats contributing to the regression lines must be emphasized. Presumably, several of the cited investigations include a wider gradient in habitat heterogenity and other major ecological factors. However, other observations supports the finding of this study that the alder forests have bird communities with lower species diversity than other deciduous forests of similiar foliage profile diversity or density. When comparing the diversity/density relationship in various deciduous forests, the alder forests is characterized by a low species diversity (BSD) and a high community density (BCD) (Fig. 29). Subalpine birch forests have BSD of the same magnitude, but with only about 10 % of BCD compared

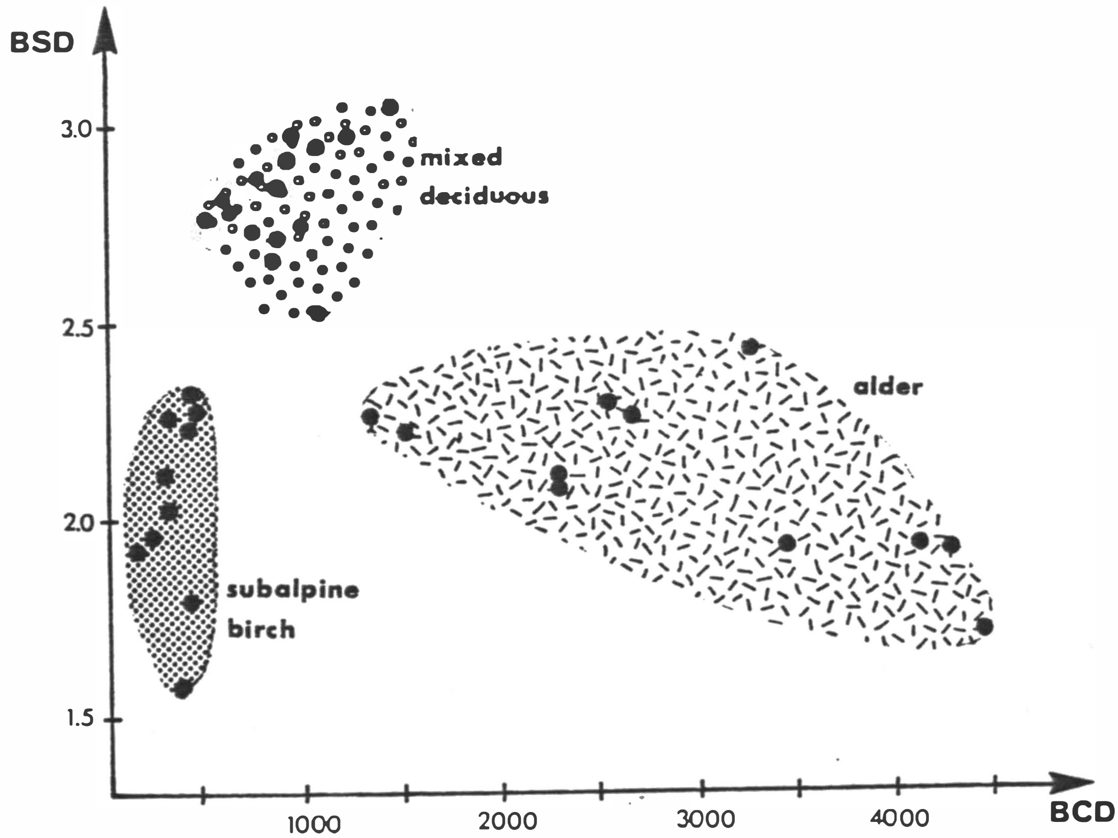


Fig. 29. Bird species diversity (BSD) and bird community density (BCD = pairs/km$^2$) in various deciduous forest habitats. The figure is compiled from the literature. The alder forest data is given in JOHANSSON (1971), MOKSNES (1974), SÆTHER (1980 a) and the present study. The data from subalpine birch forests is taken from HOGSTAD (1969), YTREBERG (1972), MOKSNES (1973) and RØV (1975). The mixed deciduous forest data is extracted from JOENSEN (1965) (beech), GŁOWACINSKI (1972, 1975) (oak-hornbeam), WILLIAMSON (1974) (oak), RØV (1975) (elm-ash) and from two studies reported by JÄRVINEN (1979) (B1, B2 in his

to the alder forests. Various other mixed deciduous forests have a considerable higher BSD($U = 0$, $P < 0.001$ in a two-tailed Mann-Whitney U-test), and a BCD of about 30-50 % of the figures from alder forests.

The correlation between diversity and density is positive for sub-alpine birch forests, $r = 0.76$ ($P < 0.01$) (HOGSTAD 1975), positive but nonsignificant for the other deciduous forests considered in Fig. 29, $r = 0.417$ ($P \approx 0.12$) and negative, $r = -0.693$ ($P < 0.03$) for the alder forests.

It is doubtful whether the majority of the variation in bird species diversity among these cited studies is accounted for by differences in foliage structure diversity or density.

The smaller BSD predicted by a given value of a habitat structure index in the forest communities of the present succession, compared to other forest habitats, reveal the shortcomings of these habitat structure parameters in predicting species diversity and challenge the generality of the hypothesis of spatial heterogenity as the major determinant of species diversity. The bird diversity of the two forest habitats in this study is not strictly in agreement with the suggestion of MAC ARTHUR (1972) that the diversity does not differ between habitats of similar structure, whether in North-America or Europe, and that diversity differences are explained by the structural differences. Formally, successful correlations between species diversity and spatial heterogenity indices, permits no definite conclusions on the latter as a primary causal factor. The habitat complexity, or vegetation structure, is more or less correlated with other mechanisms influencing species diversity (food resources, resource utilation pattern, interspecific coevolutionary forces) (KARR 1980), and might thus be looked upon as a secondary, extrinsic factor. Data from the present succession indicate that the correlations between these diversity regulators and habitat heterogenity differ among different habitats.

The discussion of relating habitat structure to breeding bird densities and community diversity is restricted by the validity of the assumption that the non-breeding season is of minor importance. FRETWELL (1972) among others have suggested that mortality factors operating outside the breeding-period, may be of the magnitude that breeding densities sometimes reflect the winter survival more than characteristics of the breeding habitat.

MAC ARTHUR's (1972) general theory of species diversity suggests that the number of species is increasing with increasing resource span (niche space), increasing niche overlaps and decreasing average species-specific proportion of resources utilized. The species number in a habitat occupied by species where the two latter factors are equal, are thus proportional to the resource span: Species diversity is according to this view proportional to the diversity of resources. CODY (1974) states that the vertical foliage estimates e.g. foliage height diversity (c.f. MAC ARTHUR & MAC ARTHUR 1961, MAC ARTHUR et.al. 1966) are approximations of the niche space in the habitats. A main question in analyzing the present diversity pattern is to what extent the diversity of resources correspond with foliage layer diversity. Data indicate that the correlation is not too close. The relatively low diversity of Alnus-forest compared to their high breeding bird densities is striking, and suggests that the diversity of resources is relatively low compared to habitats of similar foliage structure and density.

Climatic fluctuations cause increasing resource utilation proportion and hence decrease the number of species (MAC ARTHUR 1972). In more predictable environments, with seasonable stable, dependable resources, competive pressures could cause specialization of species and thereby promote greater species packing and higher diversity (KLOPFER & MAC ARTHUR 1960, LEVINS 1968, SANDERS 1969, KARR 1976). On the other hand several authors have suggested that environmental variability can enhance diversity by disrupting potential competitive dominance among species, or by providing temporal means of ecological differentiation (WHITTAKER 1975 b, WIENS 1974, 1977, CONNELL 1978).

STILES (1978) attributed higher species number in a tropical alder forest, compared to a temperate of similiar structure, to weather predictability. He assumed food resources to be more predictable as a consequence, enabling birds to evolve more specialized foraging methods, allowing more species to coexist.

The niche breadth is wider in habitats of climatic and resource uncertainty than in predictable areas (CODY 1974), and niche overlap increases with climatic predictability. In unpredictable habitats the species are of larger and more variable sizes, with relatively similar diets and forage strategies. In the more predictable habitats, however, the body sizes are smaller and the morphological similarity is more pronounced. The foraging methods are more variable.

In the present succession, the initial stages are probably more unpredictable than the later, at least when considering flooding in the breeding season. The predicted pattern of theory (large sizes, size-variability and relatively similiar foraging strategy) conforms to the bird community, at least at stage I. In the later shrub and forest stages, the individual body sizes are smaller and more similiar, and the foraging methods are probably more diverse.

The question is if morphological parameters and feeding strategy variability are good indicators of niche breadth and overlap?

Morphological similarity and niche overlap was not correlated in an analysis of niche metrics in an alder forest bird community in Central Norway (SÆTHER 1980 b). Due to the lack of such data from the present bird communities, no definite answers to the question can be given. If the indicators of niche breadth and overlap were reliable, some of the higher species diversity in the later successional bird communities could be explained by smaller niche breadth and greater niche overlap.

Another indirect way of determining the importance of niche breadth and overlap, is considering the environmental factors producing them under the assumption of significant correlations between these factors and breadth and overlap.

Climatic instability should cause fewer species to coexist due to the lesser tolerable resource utilation overlap among competing species (MAC ARTHUR 1972). Species diversity is actually lower in the habitats of highest environmental uncertainty in the present succession (plot I and II).

Evaluating the relative importance of habitat structure, a measure of niche space, and habitat unpredictability, an indirect measure of niche breadth and overlap, in determining species diversity is possible in a multiple regression. But hydrologic uncertainty, measured as maximum per cent of the plot flooded, did not significantly increase the functional explanation of bird species diversity (BSD) or species richness (BSR) in addition to what shrub and tree density (STD) or vegetation strata diversity (VSD II) explained alone. The fact that the habitats with the simplest structure simultanously are undergoing the greatest inundation, complicates the interpretation of this result. The lower diversity in the early stages could either be explained by a low foliage density (or diversity) or by an extensive flooding. The former factor is the most probable. To evaluate whether these factors are complementary or not, data sets for more years are needed.

Definite conclusions on how the niche breadth and overlap factors affect bird species diversity, however, can only be done when these niche metrics are estimated for all communities under consideration.

Relatively high dominance (or its counterpart low diversity) in a community can be related to the relative "harsness" of the environment both in shrub-grass and avian communities (WHITTAKER 1965, MC NAUGHTON & WOLF 1970). Consequently, KARR (1971) concluded that if less spatial heterogen habitats involved harsher environments, a trend for reduction of the dominance with vegetation development, would be expected. The harsher environments would involve such factors as greater diurnal and/or seasonal fluctuations, or hydrologic fluctuations. CODY (1974) found that climatic unpredictability and habitat productivity were significant contributors to the explanation of diversity in 8 habitats along a structural gradient on xeric sites. Foliage height diversity (FHD) alone explained 81 % of the bird species diversity variation, but unpredictability and resource productivity significantly increased the coeffisient of determination to 90 %. The climate variability reduced the species diversity and the productivity caused increment.

Species diversity is correlated to habitat productivity, more species can be packed into more productive habitats (MAC ARTHUR 1971). This is to be expected for two reasons. Firstly the more productive habitats provide a greater resource span. Secondly, due to the assumption that species have a more specialized diet where food is abundant, the average species utilation of the resources is reduced. These factors both enhance the number of species coexisting in the habitat (MAC ARTHUR 1972). Since no data on biomasses and spatial distribution of invertebrates, the major resource base for birds in the breeding period,are available from the present habitats, no definite conclusions can be drawn on the impact of productivity on species diversity versus other factors. However, the density/ diversity relationships in alder forests versus other deciduous forests indicate that productivity is a poor predictor of diversity.

From the review of studies of predator-prey models, STENSETH (1980) concluded that increased spatial heterogenity caused increased population stability. In the models, refuges for the prey or patchiness was operating by reducing the availibity of the prey for the predator. The number of species existing in a structural complex habitats is expected to be higher compared to a simpler. Zoo-geographical data on birds and small mammals from Fenno-Scandia support these conclusions (c.f. JÄRVINEN & VÄISÄNEN 1978, JÄRVINEN 1978, 1979). In the present succession, the community density variation in the simplest habitat is higher than in the more complex ones. Whether the relationships between predation, spatial heterogenity and population stability are operative in these habitats, as predicted from theory, cannot be rules out. But the complicating factor in analysing the pattern is that the most open and simplest habitat is the most unpredictable and hydrologically fluctuating. The terminal stage, the densest and most stratified habitat, maintain the highest species density (BSR) in the succession. The predicted relatively high stability of population densities from the predator-prey models is not found, and the actual density variation should yield a lower species number than observed, compared to the preceding stage. The relatively high species density (BSR) may nevertheless be affected by predation-restraining mechanisms, the high foliage density may provide hiding places from predators. A refuge-effect from a predator-antagonistic colony of *Turdus pilaris* (c.f. SLAGSVOLD 1979, 1980 a, b), may have influenced the density of species in the climax stage. However, to detect such effects, data from more years would be required, or data from alder forest of similiar structure but without or with smaller densities of *Turdus pilaris*.

## 5.4. Dominance-diversity and interspecific competition

In early successional stages the interspecific competition is assumed to be heavier than in intermediate or late stages (BAZZAZ 1975, WHITTAKER 1965, 1972, 1975 a). The importance and degree of interspecific competition in communities can be evaluated in dominance-diversity curves (WHITTAKER op. cit.), where the relative abundance of a species in a log scale is plotted against it's rank of abundance in the community. The "broken-stick" species abundance distribution is expected when ecological homogenous groups of species apportion among themselves a fixed amount of a governing resource at random (MAC ARTHUR 1960). The resulting relatively uniform distribution appears flat-sigmoid when plotted in the dominance-diversity diagram (WHITTAKER 1972, MAY 1975 ). A straight line plot reflects a geometric series distribution, arrived at when the community ecology is dominated by a single factor. The division of the niche volume is organized hierarcial, i.e. the dominant species pre-emts a specific proportion, the next a specific proportion of the remainder and so on (WHITTAKER 1972, MAY 1975 ). Simple plant communities in harsh environments, often conform to this pattern. Logseries distribution is often found for unstable bird communities (STENSETH 1979). When many independent factors interplay, the pattern of relative abundance usually follows a lognormal distribution. The factors are compounded multiplicatively rather then additively (WHITTAKER 1972, MAY 1975 ). The log relative abundance-species ranking plot of a lognormal distribution is sigmoid. The relative evenness of communities exhibiting a "broken-stic" distribution is highest, the geometric series distribution shows lowest and lognormal shows intermediate evenness when communities are compared (MAY 1975 ). Stable bird communities conform to the lognormal species abundance distribution (STENSETH 1979). In Fig. 30 the dominance-diversity or relative abundance curves for the successional plant and bird communities are presented. The overall pattern for the plant communities is an approach from a distribution relatively most like a geometric series in the two initial stages to a curve course relatively closer to a lognormal distribution in the two later stages. However, the pattern is

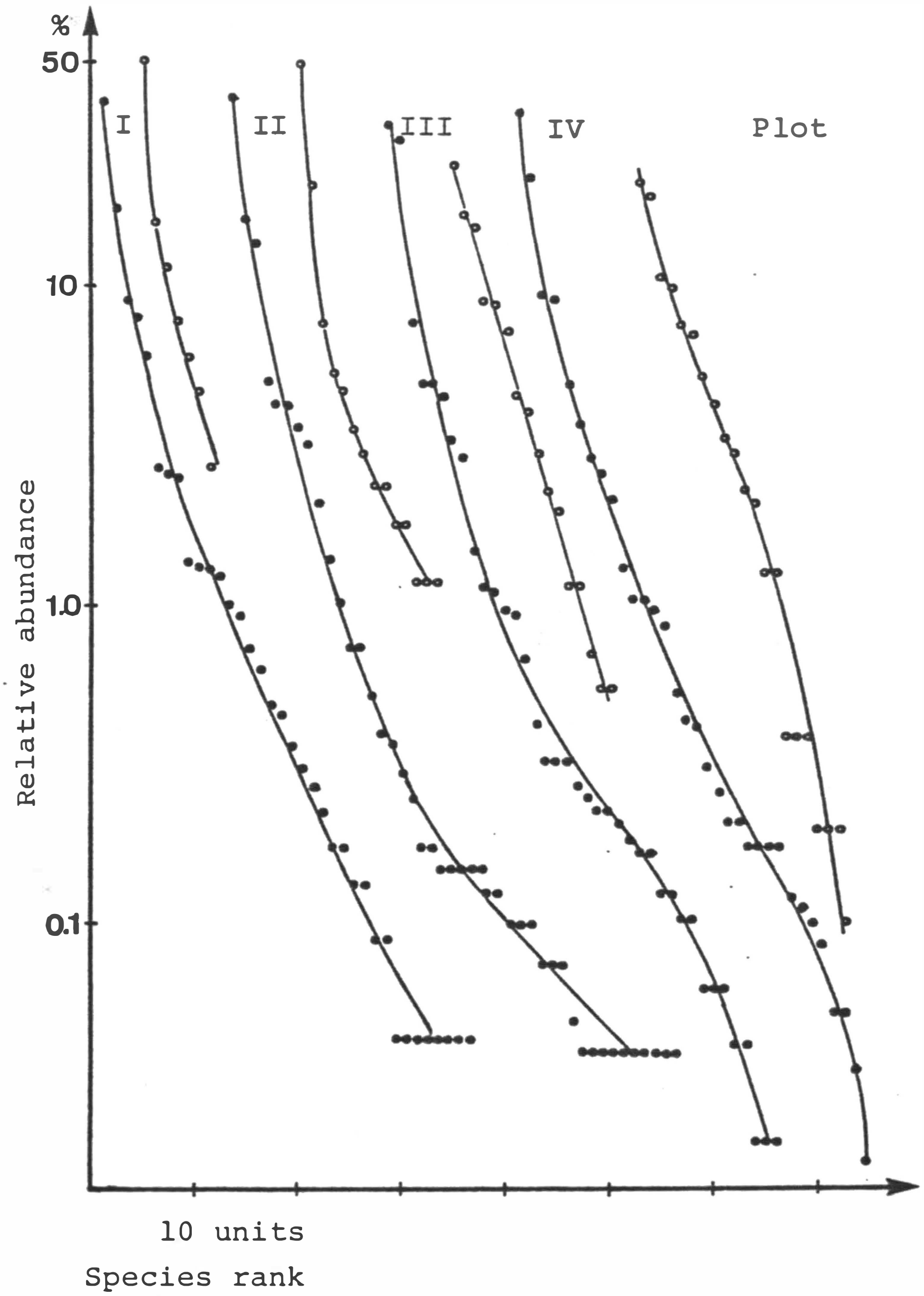


Fig. 30. Relative abundance curves for plants and birds in successional stages. For plants the cover proportion (CP) is employed (●), for the birds relative breeding density (o). The points represent a species, plotted on a log scale (ordinate) versus rank no., the most abundant species first and the least species last in the sequence (abscissa). The curves are fitted to the points by eye.

neither clear nor unequivocal. The slope of the curves is almost identical when considering species comprising more than 0.5 % of the communities. The bird communities' distributions exhibit in their essential features approximately the same pattern as the preceding, but a lognormal-like distribution appears only in the terminal stage. The slope angle of the two forest habitat distributions indicates a relatively higher bird species evenness in the late stages compared to the initial in accordance with the evenness indices. The parallellity in dominance-diversity of the communities in the wet meadow and shrub meadow habitats (I and II) is considerable. The slope is steep for the most common species, the dominants, and levels off for the rarer species. The present dominance-diversity curves are rather inconclusive as indicators of interspecific competition and community stability. Only the curves for the bird communities (particular the climax stage) may suggest a decreasing rate of interspecific competition in determining the structure of the communities along the successional gradient. Among birds, several authors have found increasing interspecific competition with decreasing structural complexity in the habitats, resulting from increased interspecific territoriality (ORIANS & WILLSON 1964, WASILEWSKI 1967, CODY 1968, 1974).

## 5.5. Bird community density

The community density estimates of the present study conform to mapping method data obtained in comparable habitats elsewhere. The density of the initial stage falls within the range of variation of the figures from 13 Central-European wet meadow communities, compiles by LARSEN & MØLLER (1978). The mean density of the studies they referred was 126 pairs/$km^2$ $\pm$ 22 (S.D.). In the later stages, the bird community density is close to the estimates in Alnus-forests in Central-Norway, 2306 pair/km$^2$ found by MOKSNES (1974) and 3429-4443 pairs/km$^2$ by SÆTHER (1980 a). Figures from South-Sweden, 1140-2500 pairs/km$^2$ (JOHANSSON 1971) are of the same magnitude. These cited densities are not strictly comparable, due to some methodical differences (e.g. census timing, species composition), however, they give satisfactorily basis for contrasting other forest habitats (see Fig. 29). The densities of the present study are a further supportion of MOKSNES' (1974) statement that the Alnus-forests sustain the densest bird communities of any North-European forest habitats. Even compared with some tropical forests (KARR 1976), the densities are higher.

Bird densities are, at least partly, correlated to habitat productivity (OELKE 1968, MAC ARTHUR 1971, VON HAARTMANN 1971, MURDOCH et.al. 1972). To support the energy demands of the high bird density of the later stages of the present succession, the production of food for the birds in the breeding period must be considerable. If there exists a linearity between density of the foliage and available food densities, the latter factor explains the majority of the variation in bird density along the successional gradient. Evidence exists that food resources have major impacts on bird densities, e.g. in the study of HOLMES & STURGES (1975) in a northern hardwood ecosystem. The change in total number of breeding birds during five consecutive summers reflected the varying abundance of a defoliating caterpillar population.

The higher densities in a more productive habitat are not only caused by higher food supply, but the vegetation densities often tends to be higher in productive areas and thus providing better hiding places from predators and reducing the number of intraspecific interactions (MAC ARTHUR 1971). Predation is known to reduce combined population densities (FRETWELL 1972, TOMIAŁOJC & PROFUS 1977). The communal mobbing of predators in colonies of Turdus pilars, seems to be an effective defence strategy. The species affect presence and density of other species in the community (SLAGSVOLD 1979, 1980 b). Nests of these species are safer from egg predation when buildt within a *Turdus pilaris* colony (SLAGSVOLD 1980 a). The density of some species increased considerably when the *Turdus pilaris*-density was increased experimentally (SLAGSVOLD 1980 b). The high breeding density of the other species in the climax stage of the present succession, may be partially explained by the dense *Turdus pilaris*-colony nesting there. However, to detect such mechanisms, removal experiments of the species would be required.

5.6. Succession rate and stability.

Ecosystem stability can be considered as a relatively steady-state equilibrium of the species composition (MARGALEF 1968, ODUM 1969, HORN 1974), or constancy in the sense of ORIANS (1975), lack of change in some parameter (e.g. taxonomic composition) of a system. Stability, in the simple sense of "absence of change" increases as succession proceeds (HORN 1975 a,b, WHITTAKER 1975 a). This kind of stability is gradually achieved towards climax in the present succession, as would be expected.

The congruency in trends of declining succession rate between the present plant and bird communities indicates that the species composition stability is a property of general application in an ecosystem undergoing succession. Evidently, it is independent of the species diversity level and trends in the component plant and bird communities, since these exhibit different trends and succession rate does not. As WHITTAKER (1975 b) points out, even if the component communities is linked by sharing species, each community may be partly self-regulated. Thus increased diversity of the community does not imply increased species stability.

When considering factors affecting the succession rate decrement, or how rapidly a climax species composition is attained, both climatic and soil factors are proposed (SHUGART & HETT 1973, GŁOWACINSKI & JÄRVINEN 1975). SHUGART & HETT found that species turnover in plant successions decreased more rapidly on mesic than on xeric sites. When contrasting succession rates in secondary bird successions, GŁOWACINSKI & JÄRVINEN (op.cit.) found a more rapid decrement in a southern, Polish oak-hornbeam succession than in northern, Finnish spruce and pine successions (HAAPANEN 1965). They believed the differences to reflect climate and soil factors. In the oak-hornbeam forest succession studied by GŁOWACINSKI (1972, 1975), the succession rate decreased monotonously throughout the succession (GŁOWACINSKI & JÄRVINEN 1975). The decrement in succession rate of birds in the present study is higher than in that succession (c.f. Table XXXIII), the difference in slopes is significant ($P < 0.05$ in a one-tailed t-test).

In spite of the more northern latitude of the present site, the decline in species turnover is more rapid, and it may suggest that soil humidity and productivity is relatively more important than climate. The climax may be looked upon as a relative notion (GŁOWACINSKI & JÄRVINEN 1975). It might be considered as a stage where the species replacement is smaller than a certain proportion of the maximum turnover in the foregoing successional stages.

Other definitions of stability emphasize the ability of a system to resist external pertubations (MAC ARTHUR 1955), resilience sensu HOLLING (1973), inertia sensu ORIANS (1975), or how fast a pertubated system returns to it's former state, elasticity sensu ORIANS (op.cit.). It is often assumed that high species diversity promote system stability (by offering alternate pathways of energy flow in webs) (MAC ARTHUR 1955). The hypothesis is that species diversity stabilizes community functional properties by compensating interactions of co-occuring species to environmental fluctuations, the cause may be a compensating fluctuations of species populations' abundance (MC NAUGHTON 1977). On the other hand may high diversity imply complexity of species interactions and when these relationships are ravelled by disturbance, it is reasonable that they are less easily constituted than in simpler, less diverse communities (WHITTAKER 1975 b). In model ecosystems, increasing diversity tends to reduce rather than increase stability (MAY 1973, PIMM 1979), apparently in contrast to many natural ecosystems where diversity seems to be correlated with stability (CONNELL & ORIAS 1964, ORIANS 1975).

A predictable environment may permit a relatively complex and delicately balanced ecosystem with high species diversity to excist. An unpredictable environment is more likely to demand a structurally simple, robust ecosystem with low diversity (MAY 1976). If diversity and community stability are positively correlated, the correlation could be explained by the effect of environmental stability. High community stability is thus the result of the stability of the environment. A stable community permits, but is not caused by high diversity. The possible tendency of high diversity to lessen community stability and hence have the opposite effect of environmental stability, has probably a weaker effect then environmental predictability (PIELOU 1975).

The assumption that pertubation stability is increasing during succession (ODUM 1969) is questioned by several authors (HURD et.al. 1971, HORN 1975 a, WITKOWSKI 1973, 1978) on the grounds of experimental pertubations or other observations. The degree and severeness of pertubations are important when analysing the effects. Fertilizer treatments (e.g. HURD et.al. 1971, MELLINGER & MC NAUGHTON 1975) are obviously less severe than clearfelling (c.f. HORN 1975 a). CONNELL & SLATYER (1977) considered all statements about stability of limited value unless the scales of time, space and intensity of pertubations are defined in relation to the organisms in the community.

When analysing the observed values of stability aspects in the communities in the present succession (Table XXXI), the latitudinal location of the study area must be kept in mind. The bird community stability in this transition zone between temperate and boreal regions (c.f. JÄRVINEN 1979) is of the same magnitude as the present indices, and a clear trend of increasing stability was thus not to be expected.

The lack of decrease in average clutch size (Table XXVII) during succession is an indication of that all habitats in the present succession are at the same position on the r-K selection pressure gradient, and that the fluctuations from year to year thus would be expected to be of the same magnitude. The majority of the species in the communities of the region where Nordre Øyeren is located, are more or less r-strategists, at least when compared to more southern temperate forests and tropical habitats.

The slightly higher stability level in the late successional stages and the correlation between the similarity index of stability and diversity is probably a coincidence, as well as the more compensating fluctuations among the common species in the climax stage.

JÄRVINEN (1979) defines, as this study, stability as year to year persistence of community structure (density, species number, diversity, evenness among others). Estimated geograhpical gradients in the stability indices for these community parameters showed that bird communities in northern Scandinavia were relatively more unstable than the rest of Scandinavia and Central Europe. JÄRVINEN (1979) concluded that considerable evidence supported the hypothesis that this trend was mainly caused by environmental (climatic) unpredictability.

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Appendix I. Vegetation analysis on plot I, Arnestangen: Quadrat size (2x1)m²

| Quadrat no. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date 1978 | 26.7 | - | - | - | - | - | 24.8 | - | - | - | - | - | - | - | - | 25.8 | - | - | - | - | - | - | - | - | - |
| Cover ground layer % | 5 | 2 | 1 | 1 | 2 | 40 | 1 | 20 | 10 | 10 | 10 | 10 | 10 | 60 | 15 | 5 | 10 | 15 | 20 | 60 | 15 | 1 | 5 | 5 | 10 |
| " field " " | 60 | 60 | 70 | 60 | 40 | 50 | 90 | 70 | 80 | 90 | 60 | 80 | 95 | 60 | 40 | 60 | 80 | 60 | 50 | 40 | 70 | 60 | 95 | 60 | 100 |
| " shrub " " | | | | | | | | | 20 | | | | | | 1 | | | | | | | | | | |
| Total cover " | 60 | 60 | 70 | 60 | 40 | 60 | 90 | 70 | 95 | 90 | 70 | 80 | 95 | 90 | 50 | 60 | 80 | 60 | 60 | 80 | 70 | 60 | 95 | 60 | 100 |
| Height field layer m | 0.5 | 0.4 | 0.5 | 0.5 | 0.5 | 0.4 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.4 | 0.4 | 0.4 | 0.5 | 0.7 | 0.6 | 0.5 | 0.4 | 0.3 | 0.4 | 0.4 | 0.6 | 0.5 | 0.5 |
| " shrub " " | | | | | | | | | 1.1 | | | | | | | | | | | | | | | | |
| *Blasia pusilla* | | | | | | | | | | | | | | | | | | | | | | | 1r | | |
| *Scapania irrigua* | | | | 1s | | | | | 1r | | | | | | | | | | 1r | | | 1c | | | |
| *Dicranella* c. f. *crispa* | | | | | | | | 1c | | | | | | | | | | | | | | | | | |
| *Pohlia bulbifera* | | | | | | | 1r | 20 | 5 | 10 | 10 | 10 | 5 | | | | | | | | | | | | |
| " c. f. *elongata* | | | | | | | | | | 1r | | | | | | | | | | | | | | | |
| *Bryum* sp. | 5 | 1c | 1s | 1s | | | | | | | | 1r | 1r | | | | | | | | | | | | |
| " *tortifolium* | | | | | | 1r | | | | | | | | | | 1r | 1c | 1c | 1s | | 1s | | 1c | 1c | |
| *Mnium pseudopunktatum* | | | | | | | | | | | | | | | | 1r | 1c | 1r | 1s | | | | | | |
| *Drepanocladus polycarpus* | | | | | | | | | | | | | | 60 | 10 | 2 | 1r | 1r | 20 | 60 | 15 | 1c | 5 | 5 | 1c |
| *Calliergon cordifolium* | | | | | | 1r | | | | | | | 1r | | 1r | 3 | 10 | 10 | 1s | | | | | | |
| *Campylium stellatum* | | 2 | 1s | 1s | | | | | | | | | | | | | | | | | 1r | | | 1r | |
| *Amblystegium riparium* | | | | | 2 | 40 | | | | | | | 5 | | | | | | | | | | | | 10 |
| *Polytrichum commune* | | | | | | | | | | | | | | | 5 | | | | | | | | | | |
| *Equisetum pratense* | | 10 | | 5 | 1c | | | 1c | 2 | 5 | | 3 | 1c | | | | | | | | | | | 1c | |
| " *palustre* | | | | | | | 1c | 1c | | | | | | | | | | | | | 1c | | | | |
| " *fluviatile* | | | | | 1r | 1s | | | | | | 1r | | 1c | 2 | 1c | 1o | 1c | 1c | 1o | 1c | 1c | 1r | 1r | |
| *Agrostis tenuis* | 1s | 25 | 5 | 20 | 10 | 5 | 25 | 5 | 60 | 60 | 7 | 50 | 10 | 1c | | | 1r | 1c | 1c | 1o | 5 | 15 | 5 | 5 | 80 |
| " *stolonifera* | | | | | | | | | | | | | | | 5 | 2 | | | | | | | | | |
| *Calamagrostis canescens* | 50 | 30 | 60 | 30 | 20 | 20 | 25 | 60 | 15 | 20 | 50 | 10 | 15 | 20 | 5 | | 70 | 60 | 25 | 30 | 60 | 50 | 75 | 50 | 15 |
| *Deschampsia caespitosa* | | | | | | | 1c | | | | | | | 1r | | | | | | | | | | | |
| *Carex acuta* | | | | | | | | | | | | | | | | 10 | 5 | 5 | 10 | | | | | | |
| " *aquatilis* | | | | | | | 20 | 1c | 1c | 1s | | 2 | 1c | 5 | 20 | 50 | 5 | | 15 | 1c | 5 | 1c | 5 | 10 | 1c |
| " *leporina* | | | | | | | | | | 1c | | | | | | | | | | | | | | | |
| " *nigra* | 1r | | | | | | | | | | | | | | | | | | | | | | | | |
| *Juncus filiformis* | 1s | 1s | 10 | 10 | 20 | 25 | 1c | 1c | 1c | 5 | 5 | 15 | 70 | 20 | | | | | 1c | 10 | 3 | 1c | 1c | 1c | 5 |
| *Caltha palustris* | | | | | 1r | 3 | | | | | | 1s | | 1s | 1s | 1c | 1r | 1s | 1c | | | | | | |
| *Ranunculus repens* | | | | | | | | | | | | | | | | 1c | | | | | | 1r | 1r | | |
| *Comarum palustre* | | | 1r | 1r | 1c | 2 | 10 | | | | | | | | | | | | | | | | | 1c | |
| *Potentilla erecta* | 5 | | | | | | 10 | 1r | 15 | | | | | | | | | | | | | | | | |
| *Lysimachia thyrsiflora* | | | | | | 1r | | | | | | | | | | | | | | | | | | | |
| " *vulgaris* | | | | | | | | 1c | 1c | | | | | | | 1r | | 1r | | | 1c | | | 1r | |
| *Mentha arvense* | | | | | | | | | | | | | | | | | | | | | | 1c | | | |
| *Pedicularis palustris* | | 1s | 1r | | 1s | 5 | | | | | 1r | 5 | 1c | 1c | 3 | 1c | 1r | 5 | 5 | 7 | 1r | 1r | 10 | 1r | 5 |
| *Galium palustre* | | | 1r | | | 3 | | | | | | | | 3 | 3 | 1c | 1c | 5 | 1c | 1s | 1r | 1r | 1r | 1r | |
| *Hieracium umbellatum* | | 1s | | | | | | | | 2 | | | | | | | | | | | | | | | |
| " *vulgatum* | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Salix caprea* | | | | | | | | | 20 | | | | | | 1r | | | | | | | | | | |

Appendix II. Vegetation analysis on plot II, Kusand: Quadrat size (2x1)m$^2$

| Quadrat no. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date 1978 | 28.8 | - | - | - | - | - | - | - | - | 29.8 | - | - | - | - | - | - | - | 30.8 | - | - | - | - | - | - | - | - | - | - | - | - |
| Cover ground layer % | 1 | 1 | 5 | 1 | 80 | 75 | 90 | 50 | 60 | | 80 | 70 | 95 | 80 | 95 | 95 | 30 | | 5 | 2 | 3 | 90 | 90 | 90 | 90 | 70 | 50 | 10 | 80 | 90 |
| " field " " | 45 | 30 | 30 | 65 | 20 | 20 | 20 | 45 | 40 | 50 | 40 | 30 | 15 | 50 | 5 | 15 | 40 | 80 | 50 | 50 | 60 | 15 | 30 | 50 | 50 | 15 | 35 | 75 | 60 | 10 |
| " shrub " " | 50 | 50 | 75 | 15 | 60 | 60 | 25 | 1 | 90 | 10 | 15 | 10 | 10 | 15 | 10 | 75 | 75 | | 15 | 40 | 15 | 10 | 50 | 20 | 70 | 70 | 60 | 25 | 60 | 15 |
| Total cover " | 70 | 80 | 95 | 80 | 95 | 100 | 95 | 90 | 100 | 50 | 80 | 80 | 95 | 95 | 95 | 95 | 85 | 80 | 60 | 65 | 70 | 95 | 95 | 95 | 100 | 80 | 100 | 80 | 100 | 90 |
| Height field layer m | 0.3 | 0.4 | 0.2 | 0.4 | 0.5 | 0.4 | 0.5 | 0.8 | 0.7 | 0.6 | 1.0 | 0.7 | 0.4 | 0.4 | 0.4 | 0.5 | 0.6 | 0.6 | 0.7 | 0.5 | 0.5 | 0.8 | 0.6 | 0.8 | 0.9 | 0.4 | 0.4 | 0.4 | 0.9 | 0.6 |
| " shrub " " | 3 | 2.8 | 4.3 | 1.5 | 1.7 | 2.8 | 2.4 | 0.5 | 2.9 | 1.8 | 1.7 | 1.6 | 1.0 | 1.6 | 1.6 | 2.4 | 2.8 | | 1.8 | 1.7 | 1.2 | 1.4 | 1.3 | 1.8 | 2.0 | 2.0 | 2.9 | 2.8 | 3.5 | 1.2 |
| *Cephaloziella leucantha* | | | | 1r | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Cephalozia rubella* | | | | 1r | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Ceratodon purpureus* | 1s | 1s | | 1s | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Brachythecium starkei* | | | | | | | | | | | | | | | | | | | 1r | 1c | 1c | | | 1r | | | | | | |
| *Polytrichum commune* | 1r | | 5 | | 95 | 75 | 90 | 50 | 60 | | 80 | 70 | 95 | 80 | 95 | 95 | 30 | | 5 | 2 | 3 | 90 | 90 | 90 | 90 | 80 | 50 | 10 | 80 | 90 |
| *Equisetum pratense* | 1r | 1r | 1r | 2 | 2 | 1c | 1c | 1c | 1c | | | | 1r | | | 1r | 2 | | | | | | | | | 5 | | | | 1r |
| " *fluviatile* | | | 1r | | 1r | | | | | | | | | | | | | | | | | 1r | 1c | 1c | | 1r | | | | 1r |
| *Agrostis tenuis* | 5 | 1c | 1c | 20 | 5 | 5 | 5 | 1c | 1c | 1c | | 2 | 1r | 20 | 1c | 2 | 15 | | 1c | 1r | | | | | 1s | 5 | 30 | 60 | 20 | 1c |
| " *stolonifera* | | | 1r | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Calamagrostis neglecta* | | | | | | | | | | | | | 1s | | | | | | | | | | | | | | | | | |
| " *canescens* | 1s | | | 1r | | | 2 | | | 50 | 40 | 25 | 10 | | 1c | | 5 | 80 | 50 | 50 | 60 | 15 | 25 | 50 | 20 | 1c | 1c | | 40 | 10 |
| *Deschampsia caespitosa* | | | | 1c | 1c | 1c | | | | | | | | 2 | 1c | | | | | | | | | | | | | | | |
| *Molinia caerulea* | | | | | | 15 | 10 | 30 | 30 | | | | | | | | | | | | | | | | | | | | | |
| *Nardus stricta* | | | | | | | | 5 | | | | | | | | | | | | | | | | | | | | | | |
| *Eriophorum angustifolium* | | | | | | | | | | | | 1c | | | | | | | | | | | | | | | | | | |
| *Scirpus sylvaticus* | | 1c | 5 | 5 | 2 | | | | 1c | | | | | 2 | 2 | 1c | | | | | | | 5 | | 1c | | 5 | | | |
| *Carex acuta* | 2 | 3 | 2 | 1c | | | | | | | | | | | | | | 2 | | | | | | | | | | | | |
| " *aquatilis* | | | | | | | | | | | | | | | | | | 2 | | 1c | | 1s | | | | | | | | 1s |
| " *leporina* | | | | | | | 1r | | | | | | | | | | | | | | | | | | | | | | | |
| " *nigra* | | | | | | | | 1c | | | | 1c | | 2 | 1c | 1c | | | | | | | | | | | | | | |
| " *panicea* | | | | | | | | | 3 | | | | | | | | | | | | | | | | | | | | | |
| *Juncus filiformis* | 1c | 2 | 1c | 1c | 1c | 1c | 1c | 1c | 1c | 5 | 1c | 5 | 2 | 3 | 1c | 1c | | 1c | 1c | 1c | 1c | 1c | 1c | 1c | 1c | 1c | 1c | 1c | 2 | 1c |
| *Luzula multiflora* | | | | | | | | 1c | | | | | | | | | | | | | | | | | | 1c | | | | |
| *Rumex acetosa* | 1r | 1c | 1c | 1c | 1c | | 1s | 1s | 1c | | | | | 1r | 1r | 1r | 3 | | | | | | | | | | | 1r | | |
| *Stellaria graminea* | | 1c | | | | | | | | | 1r | | | 1r | | | 1r | | | | | | | | | | | | | |
| *Ranunculus acris* | | | | | | | | | | | | | 1r | | | 1s | | | | | 1r | 1s | | 1s | 1s | | | | | |
| *Comarum palustre* | | | | | 1c | | | | | 1r | 1c | 1r | | | | | | 1s | 1s | 1s | | | 1r | 1c | 1c | | | 1c | | 1c |
| *Potentilla erecta* | 40 | 30 | 15 | 30 | 5 | 1s | 5 | 10 | 5 | | | 1c | 3 | 5 | 3 | 10 | 1c | | | | | 1r | 3 | 1r | 1r | 1c | 2 | | 1c | |
| *Lysimachia vulgaris* | | | | | 10 | | | | | | | | | | 1s | | 10 | | | | | | | | 25 | | 1c | 10 | 1r | |
| *Mentha arvense* | | | | | | | | | | | | 1s | 1r | | | | | | | | | | | | | | | 1r | | |
| *Pedicularis palustris* | | | | | | | | | | 1r | | | | | | | | | | | | | | | | | | | | |
| *Galium palustre* | | | | | | | | | | 1s | | 1r | | | | | 1r | | | | | | | 1r | | 1c | 1c | | | |
| *Achillea ptarmica* | | | | 1r | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Leontodon autumnalis* | | | | | | 1r | | | | | | | | 5 | 1r | 3 | | | | | | | | | | 5 | | | | |
| *Hieracium umbellatum* | | | | 1r | | | | 1c | | | | | | 1c | | | | | | | | | 1r | | | | | | | |
| *Salix caprea* | 50 | 25 | 10 | 5 | 55 | | 5 | | | 10 | 5 | 10 | 10 | 15 | 3 | 75 | 75 | | 15 | 10 | 15 | 10 | 25 | 10 | 70 | 70 | 60 | 5 | | 10 |
| " *cinerea* | | 10 | | | | | 20 | | | | 10 | 1c | 1r | | 7 | | | | | | 1r | | 25 | 10 | | | | | 50 | 5 |
| " *aurita* | | | | | | | | | | | | | | | | | | | | 30 | | | | | | | | | | |
| " *pentandra* | | | | | 5 | | | | | | | | | | 1c | | | | | | | | | 1r | | | | | | |
| *Populus tremula* | 1r | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Alnus incana* | | | 1r | | | 80 | | | 90 | | | | | | | | | | | | | | | | | | | | | |
| *Betula verrucosa* | | 15 | 70 | 10 | | | | | | | | | | | | | | | | | | | | | | | | 20 | 30 | |
| " *pubescens* | | | | 2 | 1c | | | | | | | | | | | | | | | | | | | | | | | 3 | | |
| *Rhamnus frangula* | | | | | | | | 1c | | | | | | | | | | | | | | | | | | | | | | |

Appendix III. Vegetation analysis on plot III, Kusand: Quadrat size $(2x1)m^2$

| Quadrat no. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date 1978 | 11.9 | - | - | - | - | - | - | - | - | 12.9 | - | - | - | - | - | - |
| Cover ground layer % | 1c | 10 | 1c | 3 | 1c | 2 | 1c | 1c | 1r | 1c | 1c | 1s | | 1r | 3 | 1s |
| " field " " | 40 | 60 | 75 | 60 | 60 | 60 | 50 | 40 | 50 | 65 | 70 | 85 | 80 | 50 | 70 | 25 |
| " shrub " " | 50 | 10 | 10 | 25 | 15 | 50 | 40 | 20 | 15 | 20 | 20 | 30 | | 50 | 15 | 75 |
| " tree " " | 60 | 30 | 60 | 70 | 65 | 70 | 40 | 60 | 65 | 60 | 80 | 60 | 70 | 40 | 10 | 30 |
| Total cover " | 80 | 75 | 90 | 95 | 85 | 90 | 75 | 75 | 85 | 90 | 95 | 95 | 95 | 90 | 80 | 80 |
| Height field layer m | 1.1 | 1.0 | 1.2 | 0.9 | 1.1 | 0.8 | 0.7 | 0.7 | 0.9 | 0.9 | 1.1 | 1.2 | 1.1 | 0.9 | 1.0 | 0.7 |
| " shrub " " | 4.0 | 4.0 | 3.5 | 2.5 | 3.5 | 2.5 | 3.0 | 4.0 | 4.5 | 4.2 | 3.8 | 2.5 | | 3.3 | 4.5 | 2.8 |
| " tree " " | 10 | 8.5 | 9 | 11 | 7.5 | 11 | 12 | 7.5 | 14 | 11 | 11 | 11 | 15 | 12 | 9 | 12 |
| *Cirriphyllum piliferum* | 1c | | | | | | | | | | | | | | | |
| *Brachythecium velutinum* | | | | | | | | | | | | | | 1r | 1r | |
| " *salebrosum* | | 10 | 1c | 3 | 1c | 2 | 1c | 1c | 1r | 1c | | 1s | | | 3 | 1s |
| *Matteuccia struthiopteris* | | | | | | | | | | | | | | | 40 | |
| *Athyrium filix-femina* | 30 | 50 | 70 | 55 | 50 | 30 | 40 | 25 | 50 | 60 | 55 | 60 | 80 | 5 | 10 | |
| *Thelypteris phegopteris* | | | | 3 | | | | | | | | | 10 | | | |
| *Gymnocarpium dryopteris* | | | | | | | | | | | | | | | | |
| *Dryopteris carthusiana* | | 10 | 5 | | 5 | 30 | | 15 | 2 | 5 | 10 | 15 | 5 | 50 | 30 | 20 |
| *Phalaris arundinacea* | | | | | | | | | | 5 | 1c | | | | | |
| *Agrostis tenuis* | 1r | | | | | | | | | | | | | | | |
| *Calamagrostis canescens* | | | | | | | | | | | | | | | 10 | |
| *Deschampsia caespitosa* | | | | | | | | | | | | | | 5 | | |
| *Scirpus sylvaticus* | | | | | | | | | | | | | | | | |
| *Carex leporina* | | 5 | | | | 1c | | | | 5 | | | | | | |
| *Paris quadrifolia* | | | 1r | | 1s | | | 1c | | 1s | | | | | | |
| *Maianthemum bifolium* | | 10 | | | | | | | | | | | | | | |
| *Humulus lupulus* | | | | | | | | | | | | | | | | |
| *Rumex acetosa* | 2 | | | | | | | | | | | | | | | |
| *Stellaria graminea* | 1r | | | | | | | | | | | | | | | |
| " *nemorum* | | 1s | 1c | 5 | 1c | 5 | | | | | | | | 10 | | |
| *Viola riviniana* | 10 | | | | | | | | | | 1c | | | | 3 | |
| *Ribes rubrum* | | | | | | | | | 1c | | | | | | | |
| *Rubus idaeus* | | | | 2 | 1c | 3 | 5 | 1c | 1c | | 5 | 2 | 16 | 15 | 15 | 5 |
| *Filipendula ulmaria* | | | | | | | | | | 1c | 1c | | | | | |
| *Oxalis acetosella* | | | | | | | | 5 | | | | | | | | |
| *Angelica sylvestris* | 1s | | | | | 1c | 1c | 1c | | 1c | 5 | 1c | | | | |
| *Lysimachia thyrsiflora* | 2 | | | | | | | | 1c | | | | | | | |
| " *vulgaris* | | | | | | | | | | | | | | | | |
| *Trientalis europaea* | | | | | 1c | | | | | | | 1s | | 1c | | 1c |
| *Galium palustre* | | | | | | | | | 1s | | | | | 1r | | |
| *Picea abies* | | | | | | | | 2 | | 1s | | | | | | |
| *Salix caprea* | 10 | | | | 15 | | | | | | | | | | | |
| " *cinerea* | | | | | | | | | | | | | | | | |
| *Alnus incana* | 50 | 30 | 60 | 70 | 55 | 70 | 60 | 60 | 70 | 60 | 80 | 60 | | 45 | 20 | 30 |
| *Betula pubescens* | | | | | | | | | | | | | 70 | | | |
| *Sorbus aucuparia* | | | | | | 10 | 3 | 10 | | | 1c | | | | | |
| *Prunus padus* | | 5 | | 2 | | 15 | 20 | | 10 | | 1c | 10 | | 10 | 10 | 2 |
| *Rhamnus frangula* | 50 | 3 | | | | 3 | 1c | 10 | | 10 | | 5 | | 10 | | |
| *Sambucus racemosa* | | | 5 | 25 | 5 | 30 | | | 1c | 3 | | | | | 1c | 75 |

| Quadrat no. | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date 1978 | - | - | - | - | - | 14.9 | - | 18.9 | - | - | - | - | - | - | - | - |
| Cover ground layer % | 1c | | | 1c | 1c | 1c | 10 | 15 | 1s | | | 1c | 1c | 1c | 1s | 1c |
| " field " " | 70 | 75 | 75 | 50 | 60 | 50 | 40 | 15 | 60 | 80 | 60 | 30 | 60 | 40 | 60 | 50 |
| " shrub " " | 50 | 35 | 50 | 50 | 40 | 25 | 60 | 45 | 5 | 5 | 3 | 60 | 20 | 20 | 15 | 15 |
| " tree " " | 25 | 25 | 15 | 80 | 50 | 50 | 25 | 75 | 20 | 70 | 30 | 60 | 60 | 70 | 85 | 45 |
| Total cover " | 80 | 95 | 85 | 95 | 95 | 75 | 95 | 95 | 70 | 95 | 80 | 75 | 80 | 80 | 95 | 65 |
| Height field layer m | 1.3 | 1.4 | 1.5 | 1.1 | 1.1 | 1.3 | 1.1 | 0.9 | 1.3 | 1.2 | 1.0 | 0.9 | 1.0 | 0.9 | 1.2 | 0.9 |
| " shrub " " | 3.8 | 3.7 | 2.8 | 3.5 | 3.5 | 3 | 2.8 | 3.8 | 3.3 | 3.5 | 2.8 | 3.5 | 1.1 | 3.0 | 3.9 | 2.7 |
| " tree " " | 11 | 12 | 13 | 9 | 19 | 9 | 9 | 8.5 | 13 | 14 | 13 | 12 | 10 | 12 | 12 | 12 |
| *Cirriphyllum piliferum* | | | | | | | | | | | | | | | | |
| *Brachythecium velutinum* | 1c | | | | | | | 5 | 1s | | | | | | 1s | 1s |
| " *salebrosum* | | | | 1c | 1c | 1c | 10 | 10 | | | | 1c | 1c | 1c | | 1c |
| *Matteuccia struthiopteris* | | | 10 | | | | | | 5 | | | | | | | |
| *Athyrium filix-femina* | 70 | 75 | 75 | 35 | 40 | 25 | 10 | 15 | 50 | 80 | 50, | 20 | 50 | 20 | 50 | 30 |
| *Thelypteris phegopteris* | | | | | | | | | | | | | | | | |
| *Gymnocarpium dryopteris* | | | | | | | | | | | | | 1c | | | |
| *Dryopteris carthusiana* | 10 | 10 | 5 | 15 | 30 | 10 | 10 | | 10 | 10 | 10 | | 10 | 20 | 15 | 1c |
| *Phalaris arundinacea* | | | | | | | | | | | | | | | | |
| *Agrostis tenuis* | | | | | | | | | | | | | | | | |
| *Calamagrostis canescens* | 1s | | | | | 3 | 1c | | | | | 1c | | | | |
| *Deschampsia caespitosa* | | | | | | 5 | 5 | | | | | | | | | 1c |
| *Scirpus sylvaticus* | | | | | | 2 | | | | | | | | | | |
| *Carex leporina* | | | | | | | | 1c | | | | | | | | |
| *Paris quadrifolia* | 1s | | | | | | 1c | | | | | | 1c | | 1s | |
| *Maianthemum bifolium* | | | | | | | | | | | | | | | | |
| *Humulus lupulus* | | | | | | | 3 | | | | | | | | | |
| *Rumex acetosa* | | | | | | | | | | | | | | | | |
| *Stellaria graminea* | | | | | | | | | | | | | | | | |
| " *nemorum* | | | | | | | | | | 10 | | | | | | |
| *Viola riviniana* | 15 | | | | 1c | | 10 | | | | | | | | | 1s |
| *Ribes rubrum* | | | | | | 3 | | | | | | | | | | 5 |
| *Rubus idaeus* | | | 10 | | 5 | 15 | 25 | | 1c | | | 5 | 20 | 5 | 10 | 10 |
| *Filipendula ulmaria* | | | | | | | | | | | | | | | 3 | |
| *Oxalis acetosella* | | | | | | | | | | | | | 10 | 5 | | |
| *Angelica sylvestris* | 1c | 3 | | | | | | | | | | | | | 1c | |
| *Lysimachia thyrsiflora* | | | | | | | | | | | | | | | | |
| " *vulgaris* | | | | 1c | | 5 | 5 | | | | | | | | | |
| *Trientalis europaea* | 1c | | | | | | | | | | | | 3 | | | |
| *Galium palustre* | 1c | | | 1r | | 1r | | 1c | | | | | | | | |
| *Picea abies* | | | | | | | | | | | | | | | | |
| *Salix caprea* | | | | 20 | | | | 85 | | | | | | | | |
| " *cinerea* | | 5 | | | | | | | | | | | | | | |
| *Alnus incana* | 50 | 30 | 20 | 85 | 50 | 55 | 15 | | 25 | 70 | 30 | 50 | 60 | 70 | 90 | 45 |
| *Betula pubescens* | | | | | | | | | | | | | | | | |
| *Sorbus aucuparia* | | | 1c | | | | 1c | | | | | 10 | | 10 | | |
| *Prunus padus* | 1c | 3 | | | | 10 | 60 | 5 | | | | 40 | 1c | 15 | 5 | 10 |
| *Rhamnus frangula* | | | | | 40 | 10 | 40 | 25 | | | | | | | | |
| *Sambucus racemosa* | | 30 | 40 | | | | | 3 | | | | 10 | | | | 10 |

Appendix IV. Vegetation analysis on plot IV, Gjushaugsand: Quadrat size $(2x1)m^2$

| Quadrat no. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date 1978 | 20.9 | - | - | - | - | - | - | - | - | - | 25.9 | - | - | - | - | - | 28.9 | - | - | - | - | - | - | - | - | 29.9 | - | - | - | - |
| Cover ground layer % | 2 | 1s | 5 | 1r | 1s | 1s | 1s | | 1r | 1c | 1c | 5 | 10 | 10 | 3 | 3 | 3 | | 15 | 20 | 1r | 1c | 5 | 30 | 5 | 2 | 1c | 1c | 2 | 1c |
| " field " " | 50 | 60 | 10 | 70 | 10 | 20 | 40 | 60 | 20 | 25 | 20 | 60 | 70 | 70 | 60 | 60 | 60 | 30 | 60 | 40 | 60 | 20 | 80 | 40 | 70 | 10 | 25 | 15 | 30 | 30 |
| " shrub " " | 50 | 5 | 60 | 20 | 65 | 50 | 30 | 60 | 70 | 70 | 90 | 50 | 40 | 50 | 20 | 40 | 40 | 70 | 40 | 80 | 50 | 70 | 10 | 60 | 80 | 90 | 60 | 90 | 50 | 50 |
| " tree " " | 80 | 50 | 60 | 50 | 80 | 60 | 80 | 80 | 80 | 80 | 50 | 95 | 95 | 90 | 100 | 80 | 85 | 100 | 85 | 80 | 95 | 95 | 80 | 50 | 90. | 95 | 85 | 100 | 100 | 85 |
| Total cover " | 95 | 75 | 85 | 90 | 95 | 80 | 85 | 100 | 100 | 100 | 100 | 100 | 100 | 95 | 100 | 95 | 95 | 100 | 95 | 100 | 100 | 100 | 100 | 95 | 100 | 100 | 95 | 100 | 100 | 95 |
| Height field layer m | 0.7 | 0.7 | 0.6 | 1.3 | 0.5 | 0.7 | 0.8 | 0.8 | 0.4 | 0.7 | 0.6 | 1.1 | 1.1 | 0.9 | 0.8 | 0.7 | 0.9 | 1.1 | 0.9 | 0.9 | 0.9 | 0.7 | 0.9 | 1.0 | 0.8 | 0.5 | 0.8 | 0.8 | 0.5 | 0.4 |
| " shrub " " | 3.5 | 1.6 | 3.5 | 2.8 | 3.8 | 3.3 | 3.5 | 2.5 | 3.5 | 2.8 | 4.2 | 3.7 | 2.5 | 4.5 | 2.8 | 2.5 | 3.7 | 3.8 | 4.0 | 3.0 | 3.6 | 3.8 | 1.3 | 2.7 | 3.3 | 3.8 | 2.5 | 2.7 | 2.5 | 3.8 |
| " tree " " | 7 | 12 | 12 | 12 | 15 | 15 | 16 | 16 | 12 | 14 | 9 | 13 | 15 | 15 | 12 | 9 | 12 | 12 | 11 | 12 | 15 | 14 | 13 | 14 | 13 | 12 | 13 | 14 | 14 | 14 |
| *Mnium rugicum* | | | | | | | | | | | | | 1c | | | 1c | | | | | | | | | | 1c | | | | |
| *Cirriphyllum piliferum* | 1c | | 1c | | | | 1s | | | 1r | 1o | 1c | 10 | 10 | 3 | 5 | 3 | | 10 | 10 | | 1c | 5 | 10 | 2 | | 1r | | 1o | |
| *Brachythecium velutinum* | | 1s | 5 | 1r | 1s | 1s | 1s | | 1r | 1r | | 5 | | | | 1s | 1c | | 5 | 10 | 1r | 1o | 1c | 15 | 3 | 1o | 1c | 1c | 1c | 1c |
| *Atrichum undulatum* | 2 | | 1c | | | | | | | | | | | | | | 1r | | | | | | | 5 | 1c | | | | | |
| *Athyrium filix-femina* | | 30 | 5 | 60 | 5 | | | 40 | | 5 | | 40 | 25 | 40 | | 30 | 50 | 5 | 5 | 20 | 40 | 5 | 40 | 30 | 30 | | 10 | 10 | | 5 |
| *Thelypteris phegopteris* | | | | | | | | | | | | 15 | 10 | | | | | | | | | | | | | | | | | |
| *Dryopteris carthusiana* | | 30 | 5 | 10 | 5 | 20 | 40 | 20 | 20 | 20 | 10 | 5 | 15 | 20 | 40 | 30 | 5 | 30 | 50 | 20 | 5 | 15 | 5 | 10 | 30 | 10 | 15 | 5 | 25 | 10 |
| *Phalaris arundinacea* | 1c | | | | | | | | | | | | | | | | | 1c | | | | | 2 | | | | | | 1c | |
| *Calamagrostis canescens* | | | | | | | | | | | | | | | | | | | 10 | | | | | | | | | | | |
| *Carex leporina* | | | | 5 | | | | | | 1r | | | | | | 5 | | | | | | | | 1c | | | | | | |
| " *elongata* | | | | | | | | | | | | | | | | 5 | | | | | | | | 2 | | | | | | |
| *Paris quadrifolia* | 1c | | | | | | | 1s | | | | | | | | | | | | | | | | | | | 1c | | | |
| *Humulus lupulus* | | | | | | | | | | | | | 10 | | | | | | | | | | | | | | | | | |
| *Stellaria nemorum* | | | | | | | | | 1c | | | | 15 | 5 | 15 | | | 1r | 1r | | 5 | | 5 | 1c | | | | 3 | 3 | 1c |
| *Ribes nigrum* | | | | | | | | | | | | | | | | | | | | | | | | | 15 | | | | | |
| " *rubrum* | | | 1c | | | | | | | | | | | | | | | | | | | | | | | | | 5 | | |
| *Rubus idaeus* | 30 | 3 | | | | | | | | | 10 | 10 | | | 10 | | | | 5 | | | | 40 | | 5 | | | | | 10 |
| *Filipendula ulmaria* | | 5 | 5 | 3 | | | | | | | | 1r | | 3 | | | | | | | | | | | | | | | | |
| *Oxalis acetosella* | | | | | | | | | | | 2 | | 5 | 10 | | | 5 | | | 3 | | 1c | 5 | | | 3 | 3 | | 3 | 10 |
| *Angelica sylvestris* | 2 | | | 1c | | | | | | | 1c | 1c | | | 1c | | | | | 1r | | | 1o | | | | | | | |
| *Lysimachia vulgaris* | | | 1c | | | | | | 1c | | | | | | | | | | | | | | | | | | | | | |
| *Valeriana sambucifolia* | | | | | | | | | | | | | 10 | | | | | | | | | | | | | | | | | |
| *Salix caprea* | | 5 | 30 | | | 10 | | | | | | | | | | | 20 | | 70 | | 80 | | | | | | | | | |
| " *daphnoides* | | | | | | | | | | | | | | | | | | | | 60 | | | | | | | | | | |
| *Alnus incana* | 80 | 50 | 60 | 50 | 80 | 60 | 75 | 85 | 45 | 80 | 50 | 95 | 80 | 80 | 20 | 10 | 85 | 95 | 35 | 15 | 80 | 95 | 80 | 50 | 90 | 95 | 85 | 98 | 98 | |
| *Betula verrucosa* | | | | | | | | | | | | | | | | | | | | 20 | | | | | 10 | | | | | |
| " *pubescens* | | | | | | | | | | | | | | | | | | | | 1c | | | | | | | | | | |
| *Sorbus aucuparia* | | | | | | | | | | | 3 | | | | | | | 1c | | | | 1c | 5 | | | 5 | | | | 3 |
| *Prunus padus* | 40 | 1c | 15 | 10 | 60 | 20 | 50 | 30 | 60 | 60 | 95 | 40 | 70 | 50 | 95 | 70 | 20 | 35 | 10 | 80 | 50 | 70 | 10 | 60 | 10 | 90 | 60 | 50 | 20 | 40 |
| *Rhamnus frangula* | | | | | | | 1c | | 40 | 20 | 1c | | | | | | | 30 | | 5 | | 1c | | 1c | 15 | | | | 20 | 15 |
| *Fraxinus excelsior* | 1c | 5 | 5 | | | 1c | | | | | | | | | | | | | | | | | | | | | | | | |
| *Sambucus racemosa* | | | 15 | 10 | | 25 | | | | | | | 20 | 40 | | 40 | | | | | | | 1o | | 70 | | | 50 | 10 | |
| *Viburnum opulus* | | | | | | 5 | 5 | 1c | 1c | | | | 5 | | | | 1s | | 5 | | 1c | | | | | | | | | |