Vegetation-environment interactions in a boreo-nemoral forest in east central Sweden

Master´s thesis 20 p.
(examensarbete)

by

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2001 Rapport 2001:13

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ISSN 1403-997X

Abstract

The purposes of this study were to describe the vegetation, and to find out how vegetation and environment interact in a boreo-nemoral forest in east central Sweden, and to use the species data set to evaluate a newly produced and earlier not evaluated species composition prediction model. The importance of different environmental variables on the species composition and variation was investigated and analysed using multivariate methods. The most important variables for the species composition in this area were tree crown cover, shade and soil moisture. However, much of the variation was not explained by the environmental variables used in this study. Ellenberg indicator indices for pH, nitrogen content, light and soil moisture gave a low correlation to measured values. The prediction model failed to predict the species composition in the area.

Introduction

Species occur within a given range, i.e. in a limited number of habitats, and they generally have an environmental optimum where they peak in abundance (ter Braak & Prentice, 1988). For example pH has been shown to be an important variable for species composition in several studies (e.g. Økland, 1993).

Main threats to biodiversity in Swedish forests are 1) land use and 2) air pollutions. Modern land use has changed the natural conditions for biodiversity in several ways. The proportion of different forest types has been altered, for example marsh lands, ancient forest and decidiuos forest have decreased. The structure of the forest has also changed by a decrease in amount of dead wood, large trees and hollow trees with wood mould. Another important factor that has decreased is the number of forest fires, which is important for the natural dynamic of the boreal forest. Air pollution has caused several reactions in the forest ecosystem, for example soil acidification, accumulation of heavy metals and increased access to nutrients. This has had a negative impact on soil-dwelling organisms and vegetation. (Naturvårdsverket, 1999)

The Swedish Environmental Protection agency has developed Environmental Quality Criteria (EQC), which is a tool to improve environmental planning and management. The criteria are designed to enable local and regional authorities and others to make an accurate assessment of environmental quality on the basis of available data (Naturvårdsverket, 1999). These criteria are used to compare an investigation area with what is considered to be the “natural” i.e. “comperative” state of a forest.

The work presented in this paper is a basic study of the plant community at the forest estate of Krusenberg, which belongs to the Swedish University of Agricultural Sciences. Species and environmental data were collected for analysis of species diversity and how presence and abundance of species varies with changes in environmental variables, i.e. how species composition changes along environmental gradients.

Before this study the knowledge of the vegetation and environment at the forest estate of Krusenberg (except for data about tree stands and wood production) consisted of inventories of areas valuable for nature conservation, made by the Uppsala community, the latest report from 1997 (Park&Natur Uppsala, 1997). The Swedish University of Agricultural Sciences has, after its acquisition of the estate in 1996, also evaluated the forest to find areas valuable from a conservatory point of view (SLU, 1999). This evaluation was based on the earlier work of Uppsala community and the resulting report placed three areas, of 2.8, 0.6 and 2.6 ha respectively, within the limits of the investigation area of the present study. One question addressed later in the discussion is if it is possible to find areas valuable for conservatory purposes with the inventory method used in this study.

Multivariate methods

Ordination is used to reduce the dimensionality of a data matrix by extracting axes, also called coenclines. Økland (1990a) explained the basic principles of ordination by for example stating that since "in all terrestrial systems, the number of complex-gradients with major impact on the vegetation is low" it is possible to order sample plots and species modes of all data sets along coenclines. These coenclines can be seen as hypothetical environmental variables, constructed to fit the species data in the best possible way to a particular statistical model of how species abundance varies along gradients (ter Braak & Prentice, 1988). In other words ordination provides an opportunity to test the impact specific environmental variables have on species composition and the joint effects of environmental variables on vegetation may be sorted out.

Pearson (1901) invented principal component analysis (PCA), and it was the first ordination method to be applied to a vegetation data set (Goodall, 1954). Correspondence analysis (CA) and detrended correspondence analysis (DCA) provides a non-linear rescaling of the ordination axes in units of mean standard deviation of species turnover so called S.D. units (Hill, 1979). In DCA the S.D. unit has been shown to be a reliable estimate of diversity for unidimensional gradients (Økland, 1986). Canonical correspondence analysis (CCA) is a constrained version of DCA, which is used to test hypothesis about the species - environment relationship. Still it is not certain that the environmental variables that are the most important for species composition are found with the CCA method, since they can be hidden in for example noise or by interactions between variables (Økland, 1990a).

PCA is not recommended for analysis of vegetation data, since it assumes linear relationship between variables and their underlying gradients, but it can be an effective tool to describe the interrelationships between measured environmental variables and their grouping into complex-gradients. Some adjustments may have to be made to the environmental variables to make them comparable and with equal weight (Økland, 1990a).

Biological indicators

Another way of approaching the interaction between species and environment is to try to predict environmental variables from the species composition in an area. Provided that the relationships between species and environmental variables are known, the environmental conditions at a site can be estimated from the species composition. The base for using this method is that the species composition is a good predictor of environmental conditions. These predictions can be made using for example the indicator values provided by Ellenberg et al. (1991). The Ellenberg indicator values indicate species ecological optima in Central Europe and include most vascular plants, mosses and lichens in this area (Ellenberg et al. 1991). This approach could be used in environmental monitoring, when for example equipment and analyse methods are not available. In this study, some environmental variables were estimated with Ellenberg indicator values and then compared with the observed values.

Prediciton model
The second part of this work is the first evaluation of a model for prediction of species composition. This type of model can be used to shorten the time spent on describing vegetation in forest areas. The only inventory necessary in this case is that of environmental variables.

The model is constructed with its base in The National Survey of Forest Soils and Vegetation (Ståndortskarteringen, SK), which is a long-term inventory of permanent sample plots of the Swedish National Forest Inventory (NFI). The sample plots of the NFI are laid out objectively and systematically, covering the whole country every year, except for the high mountain area in the NW. Thus, forming a good statistical representation of Sweden, the plots give a good base for environmental monitoring. The SK inventory, in very brief terms, includes descriptions of the soil and vegetation, and a general site description.

This study aims to describe the vegetation and the environmental condition at the forest estate of Krusenberg. The interaction between species and environment will be analysed, with the intention to try to find out what environmental variables are most important for the species composition. Species composition and Ellenberg indicator values will be used to see if the environmental condition can be estimated. A brief evaluation, according to the EQC, of the natural state of the forest estate will be made. Finally the possibility to predict species composition by using environmental data and a new prediction model will be evaluated.

The investigation area

The investigation area is situated within the forest estate of Krusenberg, owned by the Swedish Agricultural University, in Uppsala, Sweden. Krusenberg is situated approximately 12 kilometres south of Uppsala, and is 832 ha in size of which 510 ha is forestland. The investigation area consists of 266 ha forestland.

The area is located below the highest coastline and the bedrock mainly consists of gneissic rock. Morainic deposits are sparse, and the soil layer is very thin in many places. There are scattered outcrops of the bedrock, however mostly covered by a thin layer of lichens and mosses. The investigation area is situated in a rather flat landscape, and lies within the altitude interval of 35-60 meters.

Climatic data from the nearest weather station, Ultuna, shows that mean rainfall was 527 mm per year during the period 1961- 1990. Highest monthly mean temperature was 16,3 (July) and the lowest - 4.6 (February). Mean number of days per year with frost was 149.

The investigation area lies within the boreonemoral phytogeographical region and the forest mainly consists of normal production forest. Parts of the investigation area are recently logged, others where logged 10-20 years ago, and therefore have a dense population of young trees. Other parts consist of mature forest, which soon will be suitable for logging. The area has got both dry and rocky parts where *Pinus sylvestris* is the dominating tree species and moister parts with a thicker soil layer where *Picea abies* dominates the tree layer.

Humans have used the area since it was brought above sea level, after the latest glaciation. However the way of use has changed over time. During the 19th century to the beginning of the 20th century, the forest was most likely subject to wood gathering as well as grassing by cattle. This caused a more open structure than today, when it is only used for wood production. After the main reorganisation of farm boundaries in 1894, the way of using the land started to change, and when the 1920's was over the common forest grassing also had seen its last days in this area (Ahlberg et al. 2000).

The intensive forest management reached its peak in exploitation rate during the 60-80's. Changes in the Forest Management law from 1993 made the preservation of biodiversity and the traditional production goal equally important issues. The importance given to protection of biodiversity and the increased attention given to environmental issues during the 90's, made the forest industry change its management methods towards a more sustainable use of the forest resources, and to give priority to conservation (Skogsstyrelsen, 2001).

Materials and methods

All fieldwork was carried out during August and the beginning of September 2000. On the sample plots, all vascular plants were recorded, and their cover was estimated in percent of the whole plot. The environmental variables were partly the same as those used in the SK inventory. All other environmental variables in the study were recorded since they were thought to be of importance to the species distribution in the landscape.

The sample plots were separated by 150 m in a regular grid covering an area of approximately 1.6 x 1.5 km. Each plot was circular and the area was 100 m^2. The centre of each circular sample plot was permanently marked with an aluminium rod. Each sample plot position, latitude and longitude, was acquired with GPS LOWRANCE Globalnav 212, 12 channel receiver (figure 1). In some places the GPS positions are not correct because of bad reception. Altitude was acquired from topographic map (1:50000).

In total 97 plots were inventoried. Three of the plots where excluded from the data analysis. Two because they consisted of two different plant community types, wetland and forestland, and one for being all wetland deviating vastly from all other plots.

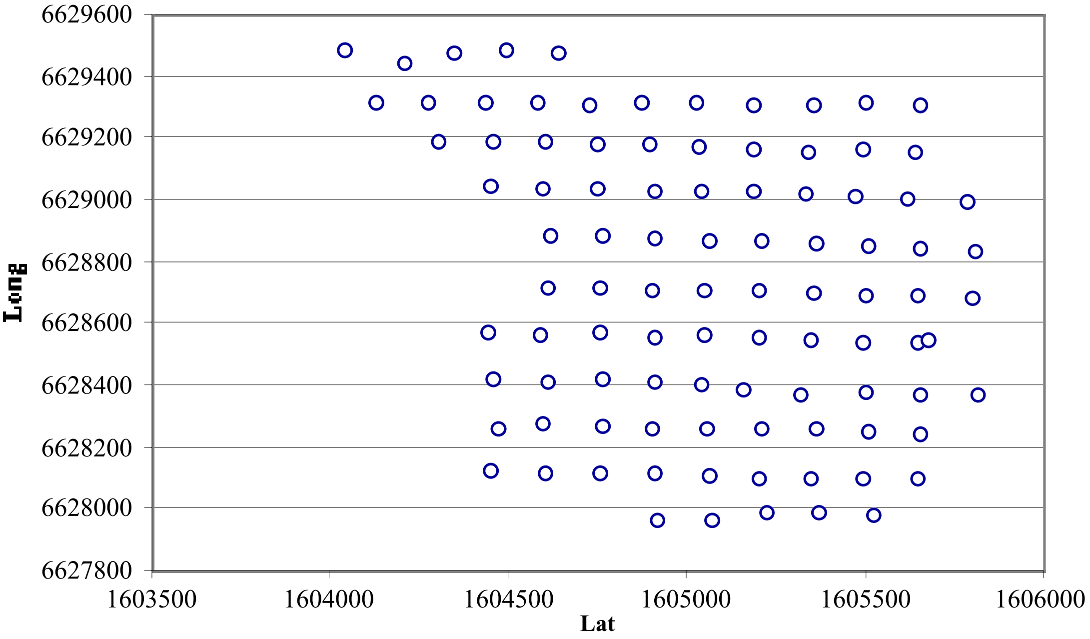

Figure 1. Sample plots latitude and longitude positions, according to GPS instrument.

Field measurements

In each plot the following variables were measured or estimated: (Words within brackets are used in figure 5.)

Vegetation:

- Presence of all vascular species encountered by the investigator was recorded and the cover was estimated in percent of the total plot area.
- The type of vegetation was estimated according to the 16-class scale used by SK (Karltun et al. 1999), for future use in the species prediction model.
- Living, standing trees where counted in three steam size categories: 1) < 5 cm, 2) > 5-<15 cm and 3) > 15 cm in diameter. *(Tree number)*
- The dominating tree height was measured using an optic instrument. *(Tree height)*
- The tree crown coverage was estimated in percent of the total plot area. *(Tree cover)*
- The number and total length of dead fallen logs were measured. *(Fallentrees)*

Environmental variables:

- Sample plot aspect was measured with a compass (400^g). The aspects where later grouped into nearest 50^g to make the data set easier to handle, resulting in six aspect classes and a class of no aspect: 1 – N, 2 – NW, 3 – NE, 4 – S, 5 – SW and 6 – W. *(N, NW, NE, S, SW, W and Noaspect)*
- Terrain shape was estimated subjectively, following a list of seven possible shapes: 1 – level, 2 – valley or concave terrace, 3 – concave valley side, 4 - level valley side, 5 – convex valley side, 6 – ridge and 7 – peak. *(Terrain1-6)*
- Surface roughness was estimated following a four-point scale: 1 – relatively even, 2 – uneven, 3 – boulder rich and 4 – cliffs and ravines. *(Surface1-4)*
- The percentage of bedrock outcrop was estimated. *(%Bedrock)*
- Soil samples were collected from the upper layer of the humus using a soil cover, diameter 10.2 cm. The soil samples where taken two meters north from the centre of the sample plot (permanent marking). The samples were bagged for later determination of pH and total nitrogen content. *(pH and Tot-N)*
- Type of humus form was estimated at the same time as taking the soil sample. The humus forms were classified according to the ten-point scale used by SK (Karltun et al. 1999). *(Humus1-10)*
- Soil class was also estimated from the soil sampling spot, and from the character of the ground surface, using a six-point scale: 1 – sediment with a high level of assortment, 2 – sediment with a low level of assortment, 3 – moraine, 4 – rock, 5 – peat and 6 – mud. *(Soil1-6)*
- Dominant soil moisture regime was estimated subjectively following a five-point ordinal scale: 1 – dry, 2 – mesic, 3 – mesic to moist, 4 – moist and 5 – wet. *(Moisture)*
- Shade was estimated subjectively following a six-point ordinal scale: 1 – no shade, 2 – slightly shaded, 3 – half shaded, 4 – partly deep shade, 5 – mostly deep shade and 6 – deep shade. *(Shade)*

Soil sample analysis

Soil samples were separated in a sieve and only the fractions of 5 mm or smaller were used for further analysis. The samples where dried at 40°C in a hot air oven until the soil felt dry by touch, approximately 24 hours, and thereafter stored in closed mugs.

For the pH analysis, 5 grams of each sample was used. 50 ml of distilled water was added and the slurry was mixed on a shaker for two hours. After letting the humus sediment over night pH was measured using a pH-meter (Dr Lange LCE 75) with electrode Mettler Toledo DG 115-SC.

The Department for soil sciences, at the Swedish University of Agricultural Sciences, performed the analysis of nitrogen content. The analysis was made through combustion of the samples and the equipment used was LECO 2000. The final value, used in the statistical analyse, was derived from the nitrogen content divided by the average loss of ignition for the whole sample set.

Analysis methods

Biodiversity indices

There are several commonly used diversity indices that describe different aspects of variability within and between communities. In this paper three of the most frequently used will be assessed.

α-diversity; or local diversity also commonly referred to as species richness, is the number of species in a small area of more or less uniform habitat (Ricklefs, 1996). It can be estimated by simply using the total number of species found within the investigation area, or more commonly the average number of species per sample plot found within the investigation area (Økland, 1990a). The latter was used in the present study.

Species inventories are almost always made through sampling and there are several methods developed to estimate the total number of species in an area. In this study first and second order Jack knife methods have been used. Both methods are based on the distribution of species in the samples. First order Jack knife estimate of total species richness (Burnham & Overton, 1979), was calculated using the following formula:

$$S_{j1} = S_{obs} + Q_1\left(\frac{m-1}{m}\right),$$

and a second order Jack knife (Smith & van Belle, 1984) by:

$$S_{j2} = S_{obs} + \left(\left(Q_1\frac{(2m-3)}{m}\right) - \left(Q_2\frac{(m-2)^2}{m(m-1)}\right)\right),$$

where $S_{j1\text{-}j2}$ = the estimated total number of species in an area, S_{obs} = total number of observed species, Q_1 = number of species occurring in one sample, Q_2 = number of species occurring in two samples and m = number of samples.

The mean of several different cumulative observed species curves, where the order of the sample plots is randomised, is used to calculate the species-area relationship. Therefore the observed values can be non-integers, which not is expected from observed number of species.

Shannon diversity index (H’) is another way of measuring α-diversity, where the value of the index depends on the number of species and the evenness (J) of species abundance. H’ was calculated using the formula:

$$H' = -\Sigma\left(\frac{a_i}{a}\right)\log_2\left(\frac{a_i}{a}\right),$$

where a_i is the estimated abundance of species i, and a is the total estimated abundance for all species. The evenness (J) was calculated by the formula:

$$J = \frac{H'}{H_{max}} ,$$

where $H_{max} = \log_2$ (number of species).

β-diversity; or species turnover, is the degree of change in species composition along coenclines i.e. the difference in species composition from one habitat to the next (Ricklefs, 1996). In this work β-diversity was estimated by detrended correspondence analysis (DCA). The DCA ordination provides a non-linear rescaling of the ordination axes in units of mean standard deviation of species turnover, so called S.D. units (Hill, 1979). The S.D. unit has been shown to be a reliable estimate of diversity for unidimensional gradients (Økland, 1986). When running DCA to estimate β-diversity the option of downweighting of rare species was used, as recommended by Eilertsen et al. (1990). This means all species with frequencies below 20% of the maximum frequency are downweighted in proportion to their frequency. This is motivated by the fact that species with low abundance and low frequency strongly influences the chi-square measure of dissimilarity in the data set (Eilertsen et al. 1990).

Ellenberg indicator values

The formula used for calculating a mean Ellenberg indicator value for a plot, weighed by species cover is:

$$z = \frac{(\Sigma\, yu)}{(\Sigma\, y)} ,$$

where y is the species abundance, u the species indicator value relative to an environmental gradient.

In this study weighted mean of light, pH, moisture and nitrogen content was calculated for all sample plots using the indicator values by Ellenberg et al. (1991). Species without an Ellenberg index were disregarded. The calculated mean values where then tested against the measured environmental values to see if there where any correlation. Both shade and tree crown cover was used as an indicator of light.

Classification

Classification of species and sites was made using two-way indicator species analysis, run by the computer program TWINSPAN (Hill, 1979). The basic idea is that a characteristic species combination (or at least a group of differentiated species) should gather samples containing these species into clusters of similar samples (Økland, 1990a).

These clusters are formed according to similarities in species composition. By looking at how the environmental variables in sample plots vary in and between these clusters, conclusions of what environmental variables are important for species distribution can be drawn.

The program TWINSPAN was run with the following options; 7 pseudospecies cut levels, and the cut levels chosen were 0.00, 1.00, 2.00, 5.00, 10.00, 20.00, and 50.00, the minimum group size was five plots per division, maximum number of indicator species was seven and maximum level of division was six.

Ordination

Which ordination methods to choose depend on the number of species having their optima within the data set (ter Braak & Prentice, 1988). Species in data sets with low β-diversity respond more or less linear to the main gradients, whilst in data sets with higher β-diversity the species show a more unimodal response to the underlying gradient (e.g. Økland, 1990a). Thus if the community variation (β-diversity) is within a narrow range, the linear ordination method PCA is appropriate. If the community variation is over a wider range, non-linear ordination methods – including DCA and CCA – are appropriate (ter Braak & Prentice, 1988).

β-diversity, or species turnover, which was estimated by the length of the first DCA axis, was estimated to be 2.6. This is not very long, but neither is it short enough to assume that the species response is linear to the main gradients (Jongman et al. 1995). Thus, in this study multivariate methods assuming unimodal response were used to study species composition. CCA was used to describe species-environment relationships. PCA was used to describe relationships among environmental variables.

The statistical package CANOCO 3.15 (ter Braak, 1997) was used for all calculations of ordination values, and the statistical program JMP version 3.1 was used for all correlation calculations.

A distribution-free Monte Carlo simulation test, included in the CANOCO package, was used to test the significance of the environmental variables in CCA. The variation in species composition explained by the environmental variables was compared with the variation explained by each of 99 permutations of the variables. Variables significantly influencing the species distribution were selected and kept in the analysis; this process is called forward selection. For each new environmental variable to be tested by the forward selection procedure, α was Bonferroni corrected to α/n, where n is variable number.

Environmental quality criteria

Methods and criteria for assessment of forest environmental quality are described in a report from The Swedish Environmental Protection agency (Naturvårdsverket, 1999). The report can be used as a manual. The assessment involves two aspects: 1) an appraisal of whether the recorded state may have any adverse effects on the environment or our health, 2) an appraisal of the extent to which the recorded state deviates from a "comparative value". In most cases the comparative value represents an estimate of a "natural" state. The results of both appraisals are expressed on a scale of 1-5.

The amount of dead wood can be used as an indicator of the natural value of a forest area since good correlation exists between this factor and species diversity (Naturvårdsverket, 1990). Many species are dependent on dead wood, lying as well as standing, and therefore it is an important component for biodiversity in boreal forests. Many species included in the Swedish red-list of threatened species, depend on this type of natural elements. The reason they are endangered in the first place is that the modern forest industry has changed the natural state of the forests so they contain less dead wood, old trees and deciduous trees than what is natural (Artdatabanken, 2000). It is important however to have in mind that areas with dead trees do not automatically host red-list species.

The model for prediction of species composition

The newly developed model for prediction of species composition was evaluated for the first time in this study. The model aims to predict the species composition from some environmental variables. The model is based on presence/absence data for 166 species in 9135 plots investigated by the SK during 1993-96. The species list is restricted to species in the field layer.

The model has two parts. The first part consists of reference tables with probabilities of occurrence. There is one table for each of the nine considered environmental variables; latitude, longitude, altitude, vegetation type, tree height, soil type, humus type, pH and soil moisture. Each environmental variable was divided into sections, forming 5-10 classes. After forming classes, the probability that a species is present in a class was calculated as the share of presences in that class in relation to all presences of the species. For example if *Deschampsia flexuosa* had 5 presences in plots in the class comprising soil pH between 4.25 and 4.75, and 149 presences in total, the probability for that species occurring in a plot with soil pH between 4.25 and 4.75 is $5/149 \approx 0.034$. This was repeated for all 166 species and all classes (example in table 1).

Table 1. Part of a reference table with probabilities of presence for species, in different tree height classes.

Tree height:	0-5	5.1-10	10.1-15	15.1-20	20.1-25
Viola tricolor	0.007	0.000	0.007	0.003	0.000
Viola riviniana	0.111	0.133	0.128	0.177	0.252

In the second part of the model, new environmental variables are entered and categorized into the same classes as the variables in the probability tables. The probabilities of finding any of the 166 species in the new samples are then calculated from the probability tables. The tree height in plot 2 in table 2 is 24. This gives, according to column six in table 1 (= tree height

20.1-25) a probability of finding *Viola tricolor* of 0.000 while the probability of finding *Viola riviniana* is 0.252, judged from tree height solely.

Table 2. Part of database containing environmental variables from sites where the species composition should be predicted.

Plot nr	Latitude	Longitude	Altitude	Vegetation type	Tree height
1	58.1	14.89	190	4	19
2	59.6	16.71	40	2	24
3	58.8	15.1	140	1	5

In the original draft of the model, the final probability for presence of a species in a plot was calculated as the sum or the product of the presence probabilities for each of the nine reference tables. This method did not produce any interpretable results. Instead the following criteria were used: first if the presence probability for any of the 9 environmental variables was zero, the species was considered not present. Different criteria for rejecting species remaining in the model after excluding all species with one or more zero probabilities were tried. In the method first tested, all species with a presence probability higher than a pre-selected level in the most limiting environmental factor was kept. Different probability levels were tested. In the second method, the second most limiting environmental variable was used. Also here different probability levels were tested. Predicted species lists from both methods and with different probability levels, were compared with the actual species list.

Results

In total 137 taxa were found. The mean number of species per plot was 20.3 (sd = 7.8). Maximum number of species in one sample plot was 46 and the minimum was 7 species. Both first and second Jack order knife estimates of total species richness showed that quite a few species, except those found in this survey, grows in the investigation area. The first order Jack knife value for total number of species in the investigation area was 172.61, which means 35.61 more species than found in the inventory. According to the second order Jack knife method there were 192.36 species in the investigation area. Thus, the Jack knife estimates indicate that between 36 and 55 species were not included in the sample plots.

Many species were only present in one or very few sample plots. Of all species found, 40.43% were present in one plot only, and 72.34% were present in at the most 5% of the plots. According to Hanskis core and satellite species hypothesis (1982) most of these species are so-called satellite species, they occur in few suitable places at low abundances, for example *Polygala vulgaris, Andromeda polifolia* and *Vaccinium oxycoccos*. Rarely occurring but relatively abundant species, so-called urban species, were few and represented by for example *Eriophorum vaginatum* and *Festuca ovina*. *Goodyera repens* was the only orchid found during the inventory, it was present in nine sample plots, all dry and dominated by *Pinus sylvestris* and *Vaccinium* species. Only 13 taxa out of 137 (13.83%) were present in more than 50% of the sample plots. Out of these common species for example *Pinus sylvestris, Vaccinium myrtillus* and *Vaccinium vitis-idaea*, were found to be abundant in most of the suitable sample plots, so called core species (Hanski, 1982). Common species mostly found in small amounts, so called rural species (Hanski, 1982), were for example *Luzula pilosa* and *Sorbus aucuparia*.

The Shannon diversity index (H') varied for the different sample plots, the mean was 2.16 (sd = 0.74). The maximum was 4.19 and the minimum value was 0.21. The evenness varied likewise and its mean was 0.51 (sd = 0.15). Maximum evenness was 0.78 and the minimum was 0.06. Of the ten continuous environmental variables used in the study five were found to be significantly correlated with H' (forward stepwise regression) (figure 2 and table 3).

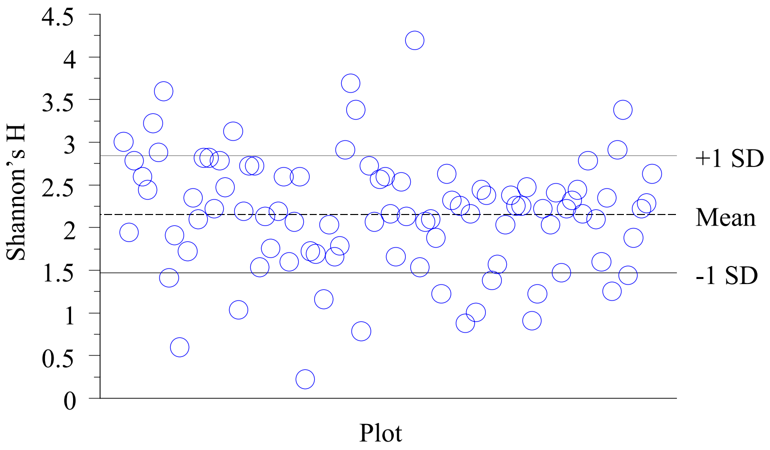

Figure 2. Shannon values plotted against sample plot numbers.

Table 3. Stepwise regression with forward selection of estimated Shannon values and continuous environmental variables.

Parameter	n	P	R^2	Slope
Nitrogen	92	0.0000	0.44	-
Moisture	94	0.0003	0.46	+
Tree size	94	0.0017	0.54	-
Tree crown c.	94	0.0023	0.35	-
Shade	94	0.0308	0.57	-
pH	94	NS	---	---
Tree height	94	NS	---	---
Tree number in plot	94	NS	---	---
%Bedrock	94	NS	---	---
Elevation	94	NS	---	---

The investigation area had quite low pH with a maximum of 6.37 and a minimum of 2.99. The mean pH for the whole area was 3.8 and the median value was 4.0. Considering the mean, the degree of acidification in the investigation area falls within the limits of class 4 according to the Environmental Quality Criteria (EQC), developed by The Swedish Environmental Protection agency.

Risk assessment tables given by the EQC was used to estimate the long-term risk of damages from continued acid depositions. There are three risk levels; small, moderate and high. These depend on the degree of acidification and the amount of sulphuric deposition. The deposition over eastern Sweden is considered to be moderate, and in combination with acidification class 4 it results in moderate risk of damages in the long-term.

The number of fallen dead tree trunks (> 10 cm in diameter) varied between 0 – 5 per sample plot (100 m^2), or 0 – 50 per ha. The mean was 9.89 trunks per ha (sd = 13.24), which falls within EQC class 5, i.e. very small amount. The number of dead lying trees (> 10 cm in diameter) considered being natural for this region is 90 per ha. Hence, the deviation from the comparative value falls within class 4, i.e. large difference. When looking at the mean for the region it is 2.2 m^3 dead wood per ha. The difference in measurement makes a comparison impossible in this case.

The nitrogen content, measured in percentage of sample weight, varied between 2.37 and 0.24. The mean was 1.24 (sd = 0.46).

Ellenberg indicator values for light, pH, moisture and nitrogen were calculated for all sample plots in this study. A linear fit was made to see if any linear correlation existed between estimated and measured values. All variables tested showed a significant linear correlation between the values estimated by Ellenberg and the measured values. The R^2 values were low for all correlations, except for tree crown cover (table 4).

Table 4. Weighed mean Ellenberg indicator values tested against measured values.

Variable	P	n	R^2 (1)	Slope
Moisture	0.0004	94	0.13	+
Nitrogen	0.02	92	0.06	-
pH	0.0044	94	0.10	+
Shade	0.0001	94	0.21	-
Tree crown cover	0.0001	94	0.39	-

The result of the TWINSPAN classification was a division of the 137 species into 28 classes and of the 94 sample plots into 22 groups (figure 3). The species classes will not be presented.

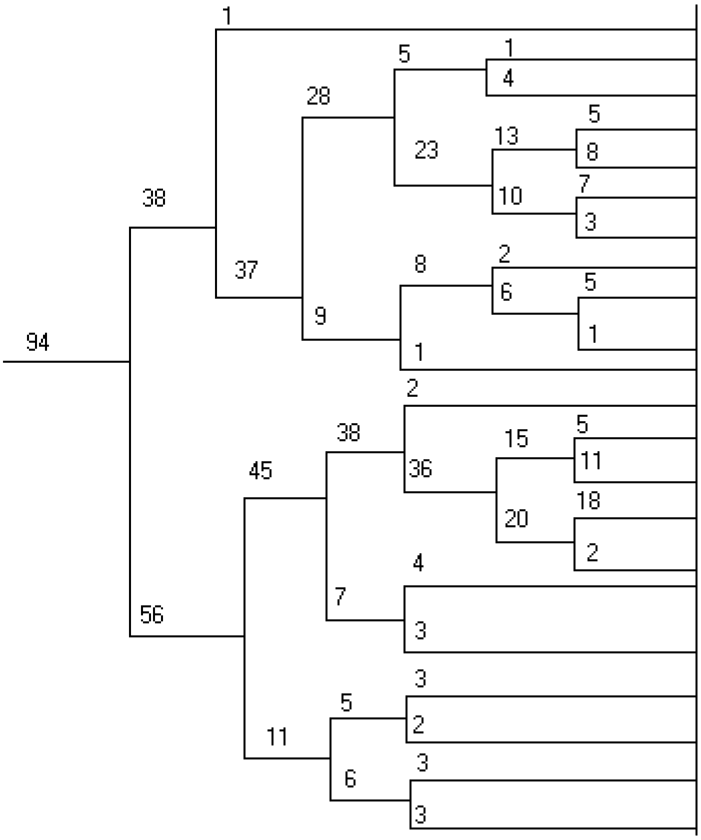

Figure 3. Visualization of a TWINSPAN classification. Figures at nodes indicate number of samples. Length of nodes are not proportional to similarity levels.

Already in the second division the four clusters that were formed showed a pattern for soil moisture values. The smallest cluster consisted of one single plot, which had a moist soil condition. In the cluster containing eleven plots 5 plots were mesic, 5 were mesic-moist and 1 was moist. The largest cluster with 45 plots consisted of 40 mesic plots, 3 dry plots and 1 mesic-moist plot. The cluster with 37 plots consisted of 24 mesic plots, 12 dry plots and 1mesic-moist plot. Further division of plots formed clusters with more and more identical soil moisture values.

After the last division, the small clusters containing only 1-3 plots were most homogenous, while some of the larger clusters contained plots with large variation in environmental condition. Besides moisture condition, tree height and percentage of bedrock outcrop showed high resemblance within the final clusters.

Some resemblance was found when comparing the classification of sample plots with the distribution of sample plots according to the DCA ordination. Plots from the same clusters were mostly positioned close to each other, but several exceptions exist (figure 4).

Interactions and covariation between environmental variables are illustrated by a PCA (figure 5). Variables related to each other end up close to each other. For example in this PCA nitrogen content and elevation were positioned close together. Other parameters placed next to each other were tree height, tree cover, shade, soil moisture and pH.

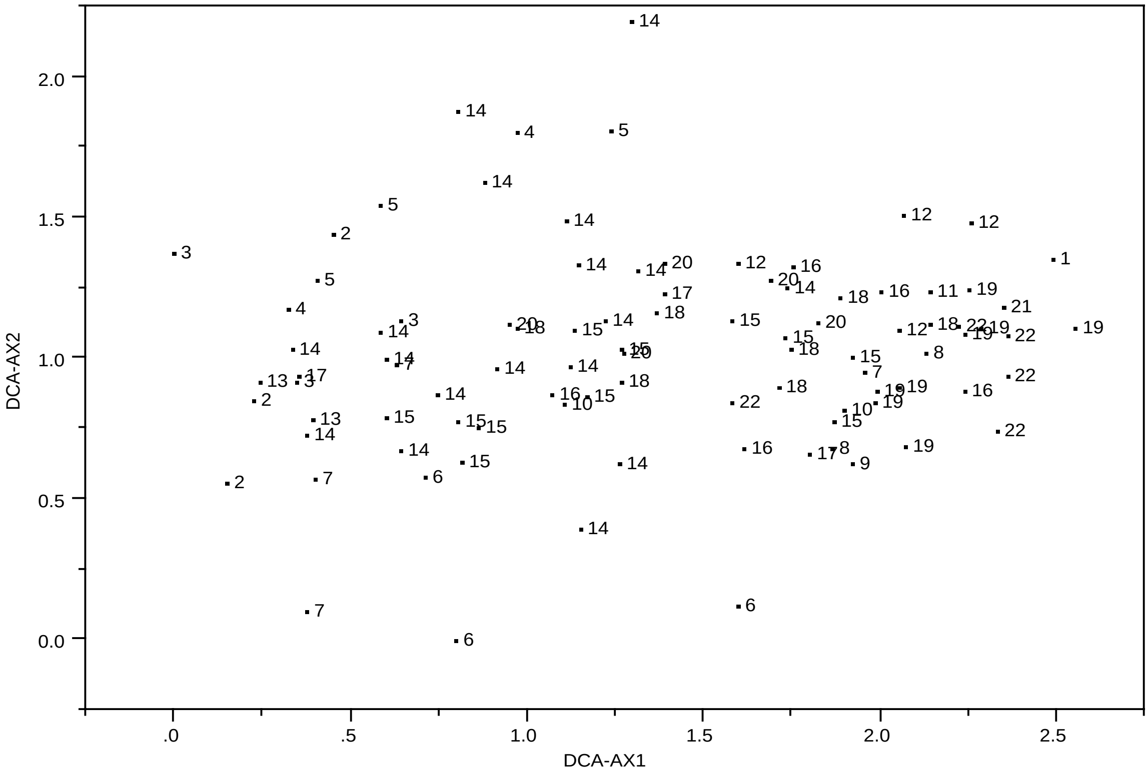

Figure 4. Sample plot DCA ordination. Numbers represent clusters according to a TWINSPAN classification. Eigenvalue of DCA axes 1 is 0.421 and of DCA axes 2 0.205.

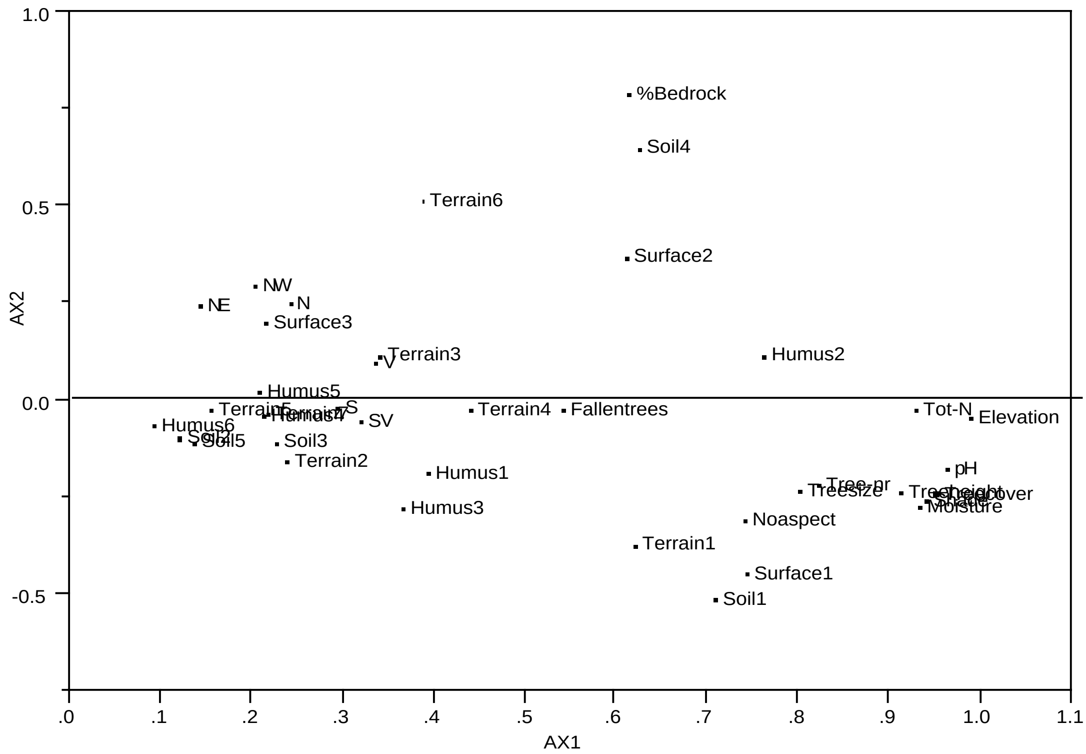

Figure 5. Relationships between the 39 environmental variables represented by a plot of the PCA result. Eigenvalue of axis 1 is 0.807 and of axis 2 0.154. Abbreviations explained on page 5, under vegetation and environmental variables.

The forward selection procedure in CCA returned three significant variables: tree height, moisture and shade. The first CCA axis was correlated to the tree height - shade coenclines and the second CCA axis to the moisture coenclines (table 5). The eigenvalues of the CCA axes show that axis 1 (Eig=0.249) explains most of the variation and axis 2 (Eig=0.116) explains some variation, while the other two axes have lower values and are not considered for further analysis.

Table 5. Significant explanatory variables from a CCA using forward selection. The values presented are the canonical coefficients for standardized variables and their corresponding approximative t-values.

Environmental variables	CCA-axis 1		CCA-axis 2	
	Coefficient	t-value	Coefficient	t-value
Tree height	- 0.61	- 7.33	- 0.26	- 2.23
Moisture	- 0.13	- 1.45	1.07	8.60
Shade	- 0.73	- 8.32	- 0.46	- 3.72

Test of correlation between DCA axes 1 and 2 and continuous environmental variables showed that elevation (meters above see level) and percentage of bedrock outcrop where positively correlated to DCA axis 1. Shade, pH and tree height where all negatively correlated to DCA axis 1. The only variable strongly correlated to DCA axis 2 was number of trees within sample plot area, which was positively correlated to the axis. If correlations close to 0.4 are considered, elevation and tree crown coverage also has a significant positive correlation to the DCA 2 axis (table 6).

The amount of spruce was negatively correlated with DCA axis 1 (R = -0.8155, p< 0.0000) and amount of pine was positively correlated with DCA axis 1 (R=0.725).

Table 6. Correlation coefficients between 10 environmental variables, number of species and total species cover, and DCA axes 1 and 2. Only significant (p<0.05) correlations shown.

Environmental variables	DCA-axis 1		DCA-axis 2	
	Correlation	p	Correlation	p
Elevation	0.4923	0.0000	0.3268	0.0013
%Bedrock	0.4848	0.0000	---	---
Shade	- 0.4497	0.0000	0.2817	0.0059
pH	- 0.4167	0.0000	---	---
Tree height	- 0.4109	0.0000	---	---
Moisture	- 0.3393	0.0008	0.2650	0.0099
Tree crown cover	- 0.3243	0.0014	0.3245	0.0014
Species number	- 0.2723	0.0079	---	---
Total vegetation cover	- 0.2165	0.0361	0.2608	0.0111
Tree number in plot	---	---	0.4105	0.0000
Tot-N	---	---	0.2712	0.0089
Tree size	---	---	---	---

To find out which environmental variables that have the greatest influence on species richness and total cover of vegetation, correlation of continuous environmental variables and the number of species found in each sample plot and the total cover of vegetation was made. The only environmental variable positively correlated with number of species was pH, and the only negatively correlated was tot-N. Total vegetation cover was positively correlated to three variables: shade, tree crown cover and number of trees in sample plot (table 7).

Table 7. Correlation coefficients between 10 environmental variables and number of species and total vegetation cover. Only significant (p<0.05) correlations shown.

Environmental variables	Species number		Total vegetation cover	
	Correlation	p	Correlation	p
pH	0.5371	0.0000	0.2883	0.0048
Tot-N	- 0.4257	0.0000	---	---
Moisture	0.3382	0.0009	0.3595	0.0004
Elevation	- 0.3313	0.0011	---	---
%Bedrock	- 0.3192	0.0017	- 0.2965	0.0037
Shade	---	---	0.7182	0.0000
Tree crown cover	---	---	0.7930	0.0000
Tree number in plot	---	---	0.4858	0.0000
Tree size	---	---	---	---
Tree height	---	---	---	---

The prediction model

The prediction model gave different results when using different limiting variables and probability levels. Excluding only species with low probability levels always generated a wide spectrum of species, but then variation between sample plots was small. Increasing the probability levels for excluding species resulted in fewer species and higher variation between sample plots. Regardless of selecting the most limiting or second most limiting variable and various probability levels for inclusion, all results showed a poor resemblance between the true species composition and the predictions made by the model. The results were similar when using both the true complete species list and the true list limited to species included in the prediction model. A couple of examples from the runs of the prediction model can be seen in figures 6 and 7, where the predicted and true species lists have been analysed in the same DCA-analysis.

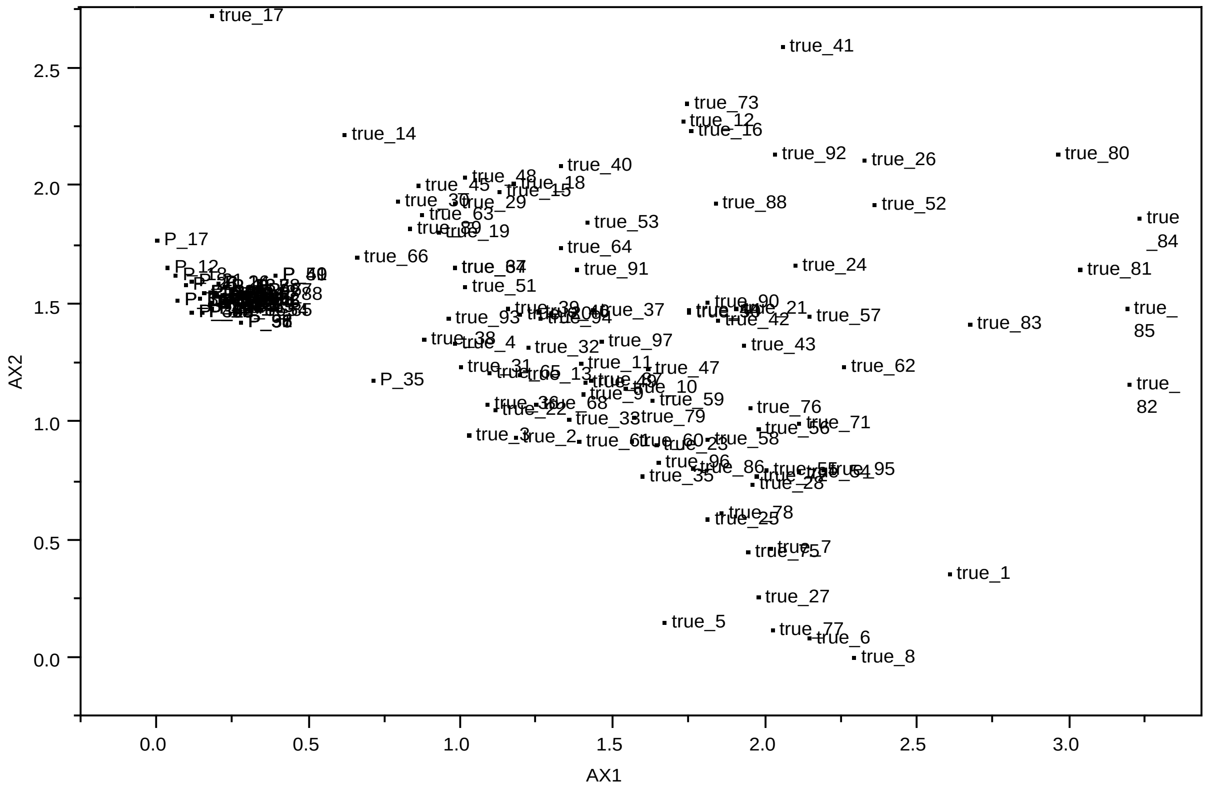

Figure 7. DCA of predicted and complete true species lists Most limiting factor and probability level >0.01. (P_nr = predicted species composition at plot nr, true_nr = species composition found in inventory at plot nr) Eigenvalues: Axis 1 = 0.538 and Axis 2 = 0.220.

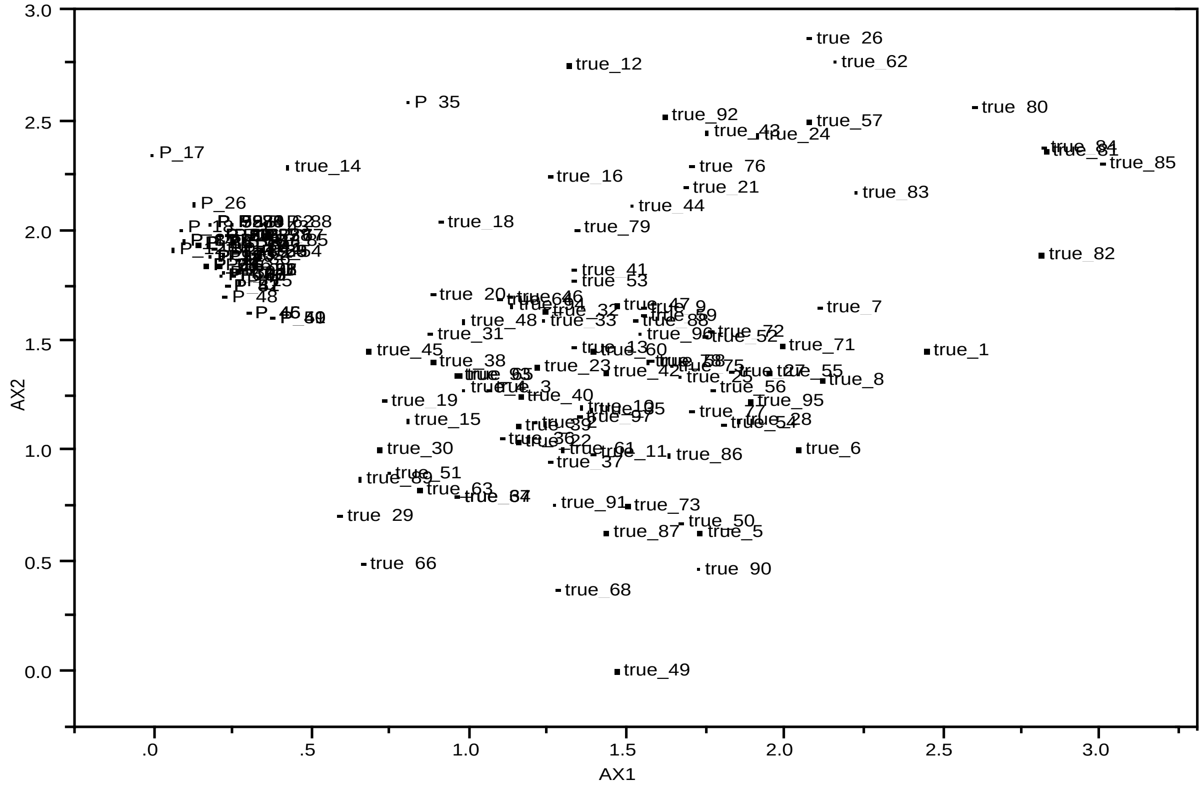

Figure 8. DCA of predicted and true species lists, limited to species included in the prediction model. Most limiting factor and probability level >0.01. (P_nr = predicted species composition at plot nr, true_nr = species composition found in inventory at plot nr) Eigenvalues Axis 1 = 0.444 and Axis 2 = 0.171.

Discussion

DIVERSITY

The species diversity in the area was quite low, but an evident variation along some underlying gradients was found, which will be discussed later on. The mean number of species per sample plot (20.3, sd 7.8) seems low considering the plot size being $100m^2$. However, comparing this study with an inventory of 129 plots similar in size and shape in 1999, (Grandin, 2001) mean number of vascular species was 22.6 (sd 12.0), no major difference is found. As for maximum and minimum number of species in one sample plot, maximum was slightly lower in this study (46 in comparison to 52), and minimum was higher (7 in comparison to 4).

Species richness estimates partly depends on where the sample plots are positioned and how many of all species in the area are represented in the sample plots. As indicated by the Jack knife tests, quite a few species in the investigation area where growing outside the sample plots and were therefore never represented in this study. To consider is also the total plot size which was only 0.94 ha while the investigation area was 266 ha in total. Whether species rich or species poor plots are sampled is also determined by chance.

When discussing species richness, it is important to have in mind that the total sample plot size affects the number of species found. As larger area is sampled more individuals are included, and the probability to find rare species increase. Therefore diversity cannot be compared between investigations not using the same sample intensity, if only looking at number of species found. Another problem associated with comparison of species richness is that not all species found should contribute equally to the estimate of diversity since their functional role in the community, to some extent, vary in proportion to their abundance (Ricklefs, 1996).

The sample plot with the highest species number had more than twice as many species as the mean. The high species number can be attributed to the fact that the plot was situated in a quite recently logged area, and hosted species from different successional stages. The plot also had a varied micro topology, and varied hydrological conditions with both dry parts and moister parts, which made it possible for species with different requirements to grow in there. Plots with few species were characterised by boulder rich ground with shallow soil and therefore quite dry conditions.

Another way, of measuring α-diversity, avoiding the problem of unequal contribution to diversity mentioned above, is to use Shannon's diversity index (H'). In H' the contribution of each species is weighted by its relative abundance. Rare species contribute less to the value of the diversity index than what common species do. The value of the index depends on the evenness (J) of species abundance i.e. the evenness of abundance in a community (dominance relationship) (Ricklefs, 1996).

The Shannon diversity index values where quite low (mean 2.16) but not much lower than what has been recorded for similar forest areas by the Swedish environmental surveillance. In the report of vegetational surveillance for 1993-94 the average H' values for forests characterised by *Vaccinium myrtillus – Picea abies* varied between 2.18 – 3.80 ($\log_2$) (Naturvårdsverket, 1993). In both the present study and the study cited above, the variation was found to partly depended on successional stage. High H' was found in areas logged some years ago, as a consequence of immigration of early successional species and species normally not found in forest areas e.g. *Andromeda polifolia*.

Environmental variables most important for species diversity were in this study: tree crown cover, nitrogen content, moisture, tree stem diameter and shade. They all turned out to be significantly correlated to the Shannon index value. Since the Shannon index is a diversity index these variables were considered to be most important to the diversity. This is similar to results from other studies, for example Pitkänen (2000) found site fertility and tree crown cover to be important factors affecting diversity.

Even though the Shannon index is a popular tool among ecologists, several scientists have questioned its relevance for ecology studies. An example is Alatalos comment from 1981, that "the diversity and evenness concepts have not produced much useful information in ecological studies" (Økland, 1990a). Despite this I find the index to be a useful tool for comparison species diversity between studies, since it accounts for the different weight of common and rare species to the diversity.

Most species found in the inventory were ordinary forest species belonging to the *Vaccinio-Piceetea* phytosociological community, for example *Vaccinium myrtillus, Vaccinium vitis-idaea* and *Deschampsia flexuosa*. Grassland species (*Polygala vulgaris)* and wetland species *(Andromeda polifolia* and *Vaccinium oxycoccos)* were found in small amounts in some sample plots. In this study, as in the earlier cited by Grandin (2001), there are few core species and many satellite species. This is a characteristic pattern in ecosystems affected by a high level of disturbance, such as modern forestry (Collins & Glenn, 1990).

ENVIRONMENTAL VARIABLES

In earlier studies it has been generally accepted that nitrogen content and pH is higher on step, south to west facing slopes (e.g. Økland, 1990b). Later studies, including the present study, on the other hand show no correlation between slope and aspect and nutrient content (Økland & Eilertsen, 1993). Considering the small variation in elevation and lack of steep slopes in the investigation area this seems natural. However nitrogen content and elevation above see level were placed very close to each other in the PCA, which might indicate a relationship similar to that described in earlier studies. It may also be pure random coincidence, or both variables could be correlated to a third unknown variable.

The probability of drying out is determined by topographic position, soil depth and soil texture (Kuusipalo, 1985). Soil moisture determines the productivity of a site (cf. the decrease in tree cover along the gradient), and soil moisture deficiency strongly reduces the rates of decomposition in the soil, in particular the N mineralization rates (Økland & Eilertsen, 1993). Hence, soil moisture is an important factor for what species can grow in an area. This was also found in the present study where the moisture coencline represented the CCA axis 2, which indicates that soil moisture strongly influence species composition.

That the moisture gradient was found to be an important factor for species composition is in accordance with the common interpretation of corresponding variation in vegetation and environmental variables governed primarily by the macro-scale topography, which in turn, determines the broad-scale soil moisture conditions (e.g. Kuusipalo 1985, van Cleve & Yarie, 1986). However, moisture conditions in different types of forest vary from different precipitation conditions, and the moisture gradient has not been found to be significant in all studies (Økland & Eilertsen, 1993). During this study the sampling was made during a period of no rain, following a very rainy summer, which make me consider the moisture conditions to be quite normal/optimal for all the different soil and forest types in the investigation area. The conditions were considered to be neither moister, nor drier than normal. Investigation of the different aspects of the soil moisture gradient in boreal forests is still urgently needed. This is also the case for investigation of different methods of measuring soil moisture (Økland, 1990b).

Some authors suggest that the critical factor for plant growth and vegetation differentiation in pine forests is nutrient deficiency, in particular lack of N (Økland, 1990a). For example in a study by Diekmann and Falkengren-Grerup (1998), a NH_4^+ index was highly correlated with the first DCA axis, i.e. nitrogen content was an important factor for species composition. In my data set no correlation between nitrogen content and species composition was found. The only connection between nitrogen and vegetation was the negative correlation with number of species. This supports the view that high nitrogen content favours few and nitrofilous species, whilst lower nitrogen content favours a greater diversity of species. Nitrofilous species are often strong competitors and therefore dominates on nitrogen rich soils, where for example light might be their limiting factor. On soils with low nitrogen content the growth of nitrofilous species will be limited and other species are able to compete with them, and therefore a greater diversity of species can exist (Begon et al. 1990).

In this study the tree height – shade coencline (CCA axis 1) turned out to be the most important to species composition. However, the two variables are correlated since tree height can also be said to indicate degree of shade. A possible explanation to the importance given by the tree height – shade coencline to the species composition, is that tree height can be an estimate of stand age, and therefore could indicate different succession stages. Pitkänen (2000) concluded that successional stage of the stand was one of the most important factors affecting species diversity. Brumelis and Carleton (1989) also found that successional stage influenced on species composition.

According to Økland (1993), pH is the single environmental parameter that best explains the variation along a poor-rich coencline. “Soil acidity does not influence plants directly but has a major controlling role in spruce forests through its influence on 1) the association to ion exchange sites on the humus particles, and hence on the availability of mineral nutrients, 2) the composition of soil fauna, and 3) the litter decomposition and N mineralization rates, and hence, the availability of N” (Økland, 1993). In this study CCA did not show pH as one of the important environmental parameters.

However, when using the DCA method and correlating the axes with continuous environmental variables, a different result was found. Except for tree height and shade, pH was also negatively correlated to the first DCA axis. Elevation and percentage of bedrock outcrop were also positively correlated to the first DCA axis, which was not the case in the CCA. The different results given by the methods indicate that there is variation in the species composition not explained by the variables used in this study. Differences in the application of the methods are that in CCA all variables are tested by the forward selection procedure, while in the correlation with DCA axes only continuous variables can be tested.

ELLENBERG INDICATOR VALUES

In this study, some environmental variables were estimated using Ellenberg indicator values and then compared with the observed values. All estimated variables were significantly correlated with the observed values, but only tree crown cover and Ellenberg indicator values for light showed a somewhat high degree of explanation ($R^2=0.39$). According to this result, an estimation of environmental variables from the species composition, by Ellenberg indicator values, would not give a good explanation of the true values in this area.

The moisture indicator values, considered to be ”the heart” of the Ellenberg system, have been related to values measured in the field, in several studies (e.g. Diekmann, 1995, Schaffers & Sykora, 2000). Conclusions from these studies were that moisture indicator values was correlated to groundwater level, but had the strongest correlation with soil moisture content and pF, since these parameters depend on both groundwater level and soil type. Apparently the simpler estimation of soil moisture in the present study does not give values that can be used to test the accuracy of Ellenberg indicator values.

The suitability of using Ellenberg indicator values in Central Sweden can be questioned considering that they were developed for conditions and species in Central Europe. Diekmann (1995) concluded that Ellenberg indicator values could be used in south Swedish deciduous forests, after calibration of the values according to regional deviation. In this study the original values were used. If calibrated values had been used a higher degree of explanation may have been found.

CLASSIFICATION

When looking at how the environmental variables are distributed by the classification of species composition it appears to resemble both the CCA and DCA ordination. This can be seen for example from the comparison of sample plot positions in the DCA diagram and the TWINSPAN classification of similar sample plots (figure 4). Clusters from the classification are quite widely distributed in the DCA ordination, but a pattern can still be seen. The quite poor, but existing resemblance between the two methods indicate that even though a certain pattern can be found in the vegetation community there are always scattered species occurring as a result of the fact that the nature is no categorical system but strongly influenced by random events and chance.

The TWINSPAN method has a disadvantage; it is sensitive to changes in the parameters defined for the classification. Therefore the program may have to be run with several sets of parameter values and their combinations, until the classification stabilizes, i.e. the change in parameter value does not cause change in the classification (Pitkänen, 2000). In this study the program was run only a few times and it is possible that it would have turned out slightly different if run more times.

ENVIRONMENTAL QUALITY CRITERIA:

The degree of acidification in the investigation area falls within class 4, which is named “high degree of acidification”. When taking into consideration the standard deviation, degree of acidification falls within classes 3-5, moderate – high acidification. In a study including 329 sample plots in Eastern Sweden the median pH was 4.9 (Naturvårdsverket, 1999), which is higher than the median in the present study (4.0). It thus seems that the investigation area is more acid than the normal and general state in this part of the country, which is dominated by calcium rich morain. The fact that the soil layer is shallow in many parts of the area and that bedrock surface in many places can contribute to the quite acid conditions. Another fact influencing the pH is that needle trees dominate the forest, which is known to cause acidification to the top layer of the soil (Lundmark, 1986). The acid condition could also depend on acid rain, but the level of H^+ in the rain falling over this part of the country is relatively low. However, it is not possible to say what is causing the acid conditions in the area from the results of the present study.

Conditions for high species diversity in the investigation area does not look too good, at least not for species depending on dead wood. From the amount of dead tree trunks it can be concluded that the area is poor in niches for red-list species and would not be considered of special interest for preservation of natural values. Though, during earlier inventories of the area point sources of valuable forest, from a conservatory point of view, were found. This shows that a regular grid as inventory method is not appropriate for finding high natural values, since these species rich areas often are small and occur scattered in the landscape. They have to be searched for specially, since the chance of finding them by the regular grid is small.

PREDICTION MODEL

Several authors have addressed the problem of finding a model that can successfully predict the species occurring in an area. Such model would be a very useful tool in nature conservation and landscape management, since complete species surveys are expensive projects. Still there are both theoretical and practical problems in collecting appropriate and sufficient data to be able to make good predictions (Dupré & Diekmann, 1998).

The most important questions in this first evaluation of the prediction model were if the model could predict the species composition on a smaller scale, compared to the scale on which the model is constructed, and how the probability of species occurrence should be calculated.

Suggested calculations to find the probability of occurrence were to use the sum or the product of all recorded occurrences. Another possibility was to use one of the two options that the model has got of limiting variables higher than zero, “most limiting” and “second most limiting”. When using the second most limiting variable the predicted species list will include species that would not occur if the most limiting variable was used. Consider a dry area, the probability to find a wetland species there would be very low, even though the rest of the environmental variables would give high probabilities for occurrence of the species. Therefore I decided to use the variable that gave the smallest probability of occurrence higher than zero of the species, i.e. the most limiting variable, as base for the calculation. This however can be discussed further since the resemblance of observed species composition and predicted species composition did not get better when using the most limiting variable than when using the second most limiting variable.

Another question addressed was what probability level to assign to the limiting variable. As expected, it was found that the lower probability level chosen the wider spectrum of species was selected, and the variation between predicted sample plots was small. If a higher probability level was chosen fewer species was included and a higher variation between sample plots was found. When the most limiting variable is given a low probability value many species will be included, and it is not very likely to find that specific species composition in the place in question.

The results show that there are poor over all resemblance between the true species composition, both complete and limited to the species included in the prediction model, and the different predictions made by the model. The use of different limiting factors and probability levels did not change that result. It is not possible to say if this poor resemblance depends on the scale used in this study or if it depends on other factors. More work has to be done on the prediction model to improve its function before it is revised again.

The species list used in the SK inventory is limited to include only the most common plants and a few mosses and lichen, which means many quite common species and all the rare species can never appear in the predicted species composition. In my opinion this is an important factor, which limits the model. It cannot be used as a tool in nature conservation since most species indicating high natural values are not included in the model. A suggestion for improvement of the models potential to predict the true species composition is that the species number represented in the model is enlarged. On the other hand this would complicate matters since so large inventory material probably does not exist, and would take a long time to acquire.

Acknowledgements

I would like to express my gratitude towards my supervisor Ulf Grandin for support and patience. Many thanks to Sven Bråkenhjälm for help with species identification and comments on the manuscript, and thanks to Tanja Bråkenhjälm for assistance with the pH analysis.

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