Restoration of oak forests: soil characteristics and light availability and their relation to early plant colonization patterns

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Summary

- Recently established broadleaf plantations on former arable land initially do not contain a characteristic ground layer species community with forest herbs. They are therefore dependent on colonization processes. However due to former land use, environmental conditions in these plantations differ from continuously forested land. This study aimed to analyze some of the environmental conditions found in young secondary woodlands and investigates their importance for establishment of ground layer species.

- Ground layer species communities of 36 broadleaf woodlands in Southern Sweden were analyzed in reference to their land use history. 18 recently established oak plantations on former arable land were compared to 18 adjacent old woodlands with long broadleaf forest continuity. Community ordination analysis was used to investigate the importance of differing environmental conditions between recent and old woodlands for the formation of the present ground layer species communities.

- Soil properties and light conditions were found to be significantly different between recent and old woodlands. In community ordination, the factor accounting for land use history was found to be most influential for the explanation of the observed differences in species community structures. However soil properties also seem to be an important factor influencing the colonization process.

- Even young plantations of 20 years in age can provide suitable growing conditions for typical forest species. However a precondition seems to be a high dispersal ability of woodland species. Light and soil conditions in woodlands were found to be suitable to explain a large part of the variation in herb layer community structure. However further research is needed to be able to set the investigated factors in relation to other factors influencing the colonization process.

1. Introduction

The present cover and distribution of forests in Europe is primarily a result of human land cultivation. Nearly all forest land has once been converted to arable fields, or the forest characteristics have been significantly changed through forest grazing or harvesting of timber and non-timber goods. To account for historic traits when denoting forests in Europe, division in primary and secondary woodlands was proposed by Rackham (1980) and by Peterken & Game (1984).

Among foresters it is common sense that forests have a long memory. And indeed signs of former treatment and land use can persist for hundreds if not thousands of years under the canopy of secondary forests (Dupouey et al. 2002; Vellend, 2003). These signs can be obvious such as stone walls and open grown veteran trees or more hidden in the form of changed soil characteristics or species composition of the ground vegetation. After people became aware of their impact, the question appeared if secondary forests will ever loose their memory and return to the state of primary forests (Flinn & Vellend, 2005).

Numerous studies have focused on species compositions of the ground layer where the majority of plant diversity in temperate forests lies. Differences between secondary forests and forests with long habitat continuity were found and investigations started to look at the factors controlling the recovering process (Peterken & Game, 1984). The generally very low dispersal ability of typical forest herbs was identified as a major factor controlling recolonisation of secondary forests and was thereafter intensively studied (e.g. Brunet & von Oheimb, 1998; Dzwonko & Loster, 1992; Matlack, 1994).

Besides dispersal the importance of germination and species establishment after dispersal has been stated. Forest herbs therefore provide an ideal study object due to their life traits which exclude the recovery from persistent seed banks on former arable land (Flinn & Vellend, 2005). Additionally to the depletion of forest herbs, cultivation has been found to change soil properties considerably (Dupouey et al. 2002; Falkengren-Grerup et al. 2006; Koerner et al. 1997).

The following study was intended to elucidate some of the environmental conditions found in young secondary woodlands and investigates their importance for establishment of ground layer species. Therefore ground layer species compositions in young oak plantations were compared to those in adjacent old woodlands with long forest continuity. It was hypothesized that due to land use history, differences in soil properties of the top soil in terms of pH, organic matter content and phosphorus content exist between old and recent woodlands. It was further predicted, that these differing environmental conditions are a major factor controlling the abundance of typical forest species in recently afforested sites.

A distinctive feature of this study is given by the age of the investigated recently established plantations, which date back to the beginning of the 1990's when a change in agricultural and forestry policy in Sweden promoted the establishment of broadleaf woodlands. This resulted in several large scale afforestation projects and now provides a unique opportunity to study the succession of ground layer species composition in young secondary forests.

2. Study site description

The study was conducted in Skåne, the southernmost province of Sweden. The study area falls within the nemoral vegetation zone where deciduous hardwood forests on district and eutric cambisols dominate (Falkengren-Grerup et al. 2006). The climatic conditions in this area show an annual range of mean monthly temperatures from -2°C in January to +17°C in July and an annual precipitation of 550 – 800 mm.

2.1 Site selection

Recently established broadleaf plantations directly adjacent to old woodlands in Skåne were localised using satellite images. Applying local knowledge of the forest landscapes in Skåne, a number of study sites were considered for further investigation. Field visits were then made to assess the suitability of the suggested sites and to assign sample plot locations. It appeared that the most suitable pairs of stands of reasonable size and similar characteristics were situated on land of one of four large estates in Skåne: Näsbyholm, Övedskloster, Skabersjö and Trolleholm (Fig. 1).

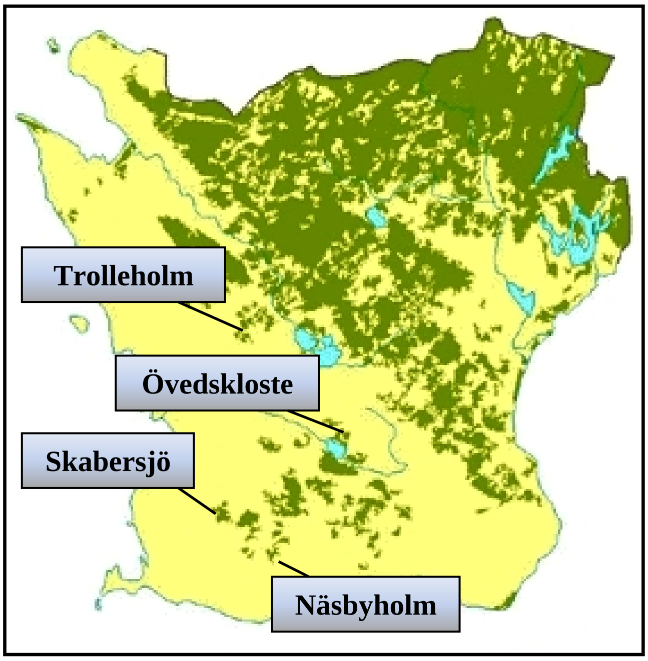

Figure 1: Map showing forestland in Skåne (green areas) and the location of the four study areas. Source: www.sna.se

The main criterion for site selection was the difference in site history. Recently established oak (*Quercus robur*) plantations (age between 15 and 20 years) were all planted respectively sown on former arable land. It appeared that due to intensive agriculture in the past a number of adjacent older woodlands were also used as arable land or for grazing during some years. This was particularly evident on the estate land of Skabersjö. There it was not possible to solely select ancient woodland sites (continuous forest cover since the years 1812 to 1820 (Brunet, 1994)) as reference for the abundance of species and for expected soil properties prior to land conversion.

Additional parameters which were taken into account when selecting study sites were:

- structural homogeneity of the stands
- ideally oak as dominating canopy tree species
- the structure of the ecotone (walls, ditches and roads) in order to minimise plant migration restrictions
- similar topography of the pair of stands.

After field assessment a total of 18 pairs of woodlands were found to sufficiently comply with the above described criteria. An overview of the characteristics of the chosen sites is depicted in table 1. The study sites are labelled with reference to their location on one of the four estates in Skåne. The seven pairs labelled “Oev” at the beginning are situated on the estate land of Övedskloster, all sites labelled with “Sk” are part of the Skabersjö estate land, the site “Ra” forms the only study site in Trolleholm and “Tä” the only site in Näsbyholm.

Table 1: Description of the selected 18 pairs of woodlands. Depicted are main characteristics of forest stands, the ecotone and the regeneration method of the recently established plantations.

Study site	**Dominant canopy tree species**		**Broadleaf forest continuity** [yrs in 2010]		**Ecotone**	**Regeneration method**
	old	recent	old	recent		recent
Oev1	*Prunus, Fraxinus*	*Quercus, Betula*	200	20	forest edge	planted
Oev2	*Fraxinus, Prunus*	*Quercus, Betula*	200	20	path	planted
Oev3a	*Fagus, Fraxinus*	*Quercus, Betula*	200	20	path	planted
Oev3b	*Quercus, Fagus*	*Quercus, Betula*	200	20	path	planted
Oev4a	*Fagus, Quercus*	*Quercus, Betula*	200	20	path	planted
Oev4b	*Alnus, Fagus*	*Quercus, Betula*	200	20	path	planted
Oev4c	*Acer, Fraxinus*	*Prunus, Tilia*	200	20	forest edge	planted
Ra	*Quercus, Acer*	*Quercus*	200	20	forest edge	sown
Tä	*Acer, Fraxinus*	*Quercus*	200	17	path	sown
Sk1	*Quercus*	*Quercus*	75	18	forest edge	sown
Sk2a	*Fagus*	*Quercus*	69	18	path	sown
Sk2b	*Quercus, Carpinus*	*Quercus*	67	18	path	sown
Sk3	*Quercus, Ulmus*	*Quercus*	200	18	path	sown
Sk4	*Quercus*	*Quercus*	64	17	path	sown
Sk5	*Quercus, Acer*	*Quercus*	80	15	forest road	sown
Sk6a	*Quercus, Betula*	*Quercus*	90	20	path	planted
Sk6b	*Quercus, Fagus*	*Quercus*	82	20	path	planted
Sk7	*Quercus, Ulmus*	*Quercus*	61	19	path	sown

2.2 Skabersjö

The 1600 ha woodlands of the Skabersjö estate are part of a hilly forest landscape in southwest Skåne. As can be seen in figure 1, due to dominance of agricultural fields in the area the estates woodlands are partly fragmented. In particular the woodlands in the eastern part of the estate (stands Sk1, Sk2a,b; Sk3 and Sk4) form isolated forest islands in the landscape.

The current topography with an altitudinal range between 25 m – 75 m a.s.l. was formed by glacial morainic deposits upon early Tertiary limestone (Brunet, 2007). Differences in soils must be referred to human activities in this area and to a lesser extent also to variations in topography as there are no major climatic or geologic variations. Due to the objective of the estate managers to considerably reduce the area of agricultural land, large afforestation projects with broadleaf trees, especially oak, were realised in the past 20 years. Today there are around 260 ha oak forests on the estate land.

2.3 Övedskloster

The privately owned estate of Övedskloster lies in the southern centre of Skåne and is situated at the north-eastern lakeside of the Vombsjö. The hilly landscape with an altitudinal range between 25 – 100 m a.s.l. was formed by glacial moraines. The forest area comprises today about 1600 ha and belongs to the areas in Skåne with the highest biodiversity values.

For the same reason as on other estates a number of large scale broadleaf plantations adding up to more than 40 ha on former arable land were realised in Övedskloster at the beginning of the 1990s. Today broadleaf forests account for about 750 ha whereof the majority is stocked with beech. However most of the recent afforestations are plantings of oak in mixture with birch or alder. Hunting has since long been a major interest for the estate owners, resulting in a high wildlife density and diversity.

2.4 Trolleholm and Näsbyholm

Trolleholm, an estate comprising about 5000 hectares of land whereof 2000 hectares are forests, is situated north-west of central Skåne. Therewith it forms the northernmost site in this study. Dominating broadleaf tree species on the older forest land of the estate is beech, but many new stands planted with oak have been established during the past 20 years. The estate land is part of a hilly forest landscape ranging from 75 – 125m a.s.l.

The forest land of Näsbyholm, situated in south-west Skåne forms the southernmost study site. The estate land ranges from 50 – 75m a.s.l. and agricultural land use is slightly more pronounced in the landscape. The forests of the estate form one of the southernmost larger patches of broadleaf forests in Sweden.

3. Data sampling

The data collection and field work was divided in two periods. The first data collection in spring was conducted from the 12th to the 24th of April 2010. The second field work period fell within the weeks from the 28th of June to the 12th of July 2010.

3.1 Canopy cover and stand characteristics

Forest stand characteristics of the study plots such as basal area, trees per hectare and canopy cover estimates were used as indirect parameters for light availability on the forest floor. The diameter of trees in the sample plots were measured with a calliper. In old woodlands a complete measurement of all trees exceeding 7 cm in diameter was carried out whereas in young and homogenous oak plantations a circular plot with a radius of 5,64 m was established in the centre of each sample plot. Hence all trees standing in the 100 m^2 circular plot exceeding 7 cm in diameter were recorded. Mean diameters and basal area were separately calculated for each tree species. In summer the vertical projection of tree canopy (canopy cover) above each 1 m^2 subplot was estimated.

3.2 Soil sampling

In April 2010 soil samples of the top 5 cm excluding litter layer were taken in each sample plot. Five soil samples taken from the corners and the centre of each sample plot were pooled to one bulk sample of 960 cm^3. Material passing a 4 mm sieve was used for the analysis of soil pH, exchangeable phosphorus and organic matter.
Soil chemical properties were analysed at the laboratories for Plant Ecology and Systematics at the University of Lund. The exchangeable phosphorus content was analysed using 10g of sieved soil which was then extracted for 30 min in a 100 ml solution of 0,02 M Na_2SO_4 and 0,05 M NaF. The solution was filtered (over a Munktell filter with a pore size of 5 – 6 µm) and the filtrate analysed for phosphorus using Flow Injection Analysis (FIA). For determination of soil pH, again 10g of sieved soil were extracted in deionised water and after

sedimentation of the soil particles the pH (H_2O) measured in the supernatants. Loss on ignition and associated weight differences were used to determine organic matter of the soil samples.

3.3 Vegetation inventory

A vegetation inventory of all vascular plants in the ground layer including pteridophytes was conducted in all 36 woodlands using sample plots of 20 m x 25 m. 18 plots were laid out in recently established oak or oak/birch plantations and 18 plots in adjacent older woodlands.
To avoid edge effects all plots were placed as far as possible away from woodland edges. Whenever possible, sample plots were laid out with the long side running parallel to the ecotone.
Within each sample plot the centres of 10 regularly distributed subplots of 1 m² were marked. In April 2010 vernal species of vascular plants were recorded. The cover of each species occurring in the subplots was estimated using the following 18-degree scale of percentage cover:

0,5; 1; 2; 3; 5; 8; 10; 15; 20; 25; 30; 40; 50; 60; 70; 80; 90; 100

Paper quadrates covering 1% were used to calibrate the estimates for each species. Additional transect walks were made to account for species only apparent in the 500 m² sample plot but not occurring in any of the ten subplots. These species were estimated to cover 0,05 % of the total area of the sample plot. In July sample plots were revisited and all present herb layer species recorded. Lichens and mosses were not recorded in the course of this study.

3.4 Historical data collected

Historical maps were used to identify years of forest continuity of all stands investigated in this study. Forest continuity was thereby defined as the years of continuous broadleaf canopy cover until 2010. All woodlands found to have at least 200 years of forest continuity (the age of the oldest map common to all study sites) were regarded as ancient woodland sites. For all recent woodlands the time period since planting or sowing was used.

3.5 Data analysis

The mean of ten canopy cover estimates from each of the 36 sample plots were used for further analysis. The contributing canopy cover of an occasionally occurring shrub layer, which was separately recorded was added to these cover estimates. Thus canopy cover reflects the sum of cover values of the over- and understorey.

The units of soil parameters obtained from the laboratories in Lund were not transformed. Thus soil pH measured in water solution, total phosphorus in µg/g dry weight (d.w.) and organic matter content in percentage were used in following analyses. The analyses of vegetation data were based upon means of species cover percentage values for each of the 36 sample plots. For species present at both sampling occasions in spring and in summer the data set with higher cover values for each species was taken into account.

The nomenclature of species follows Mossberg et al. 1992. Classification into species predominantly found in forests under closed or dense canopy (typical forest species) and species found in forests as well as under open conditions followed Schmidt et al. (2003). Categorization of typical woodland species according to their diaspore dispersal was based on data published by Brunet & von Oheimb (1998) and Brunet (2007).

All statistical tests were carried out with Minitab 15. Measured variables such as soil parameters and canopy cover were tested for differences between old and recent woodlands with the paired t-test and Mann-Whitney test. The prerequisite for paired t-tests of normally distributed paired differences were tested with the Kolmogorov – Smirnov (K-S) test.

Relations between environmental variables were assessed using spearman´s rank order correlation. One-way Anova with Fisher´s post hoc test was used to compare the means of typical forest species present in three different categories of forest continuity (Dytham, 1999).

Patterns in the recorded vegetation data and investigation of the underlying factors explaining these patterns were analysed with the help of Canoco 4.5 (ter Braak & Šmilauer, 2002). The five variables used in the multivariate analysis in Canoco (pH measured in water, exchangeable phosphorus, organic matter content, canopy cover and broadleaf forest continuity) were therefore combined under the term environmental variables.

As a first step when analysing data with Canoco 4.5, unconstrained ordination with DCA was performed to investigate the total variability in species composition.

Linear regressions between sample scores on DCA-axis 1 and 2 and environmental variables were calculated to assess the relation between gradients detected in DCA and the measured variables.

Secondly, to get a better understanding about the amount of variability in species composition explained by the measured environmental variables, a constrained ordination (canonical correspondence analysis – CCA) was performed. Due to correlations between environmental variables it was necessary to test for confounding effects. This was done following the concept of variation partitioning proposed by Borcard et al. (1992). Co variation of environmental variables was thereby removed before the impact of single variables on the species variation in the ordination method was assessed.

4. Results

4.1 Forest stand characteristics and light conditions

One criterion for study site selection was homogeneity and dominant canopy tree species of the forest stands. The intention was to select preferably oak dominated stands. In total the canopy of 27 woodlands was dominated by pedunculate oak (*Quercus robur*). Dominance hereby means that oak accounted for the greatest share of total basal area of the study site. Beech (*Fagus sylvatica*), Sycamore (*Acer pseudoplatanus*), Ash (*Fraxinus excelsior*) and Alder (*Alnus glutinosa*) were dominant canopy species in the remaining old woodlands (figure 2). However oak was also present in most of these stands as a supplementary species. All recent woodlands except one were plantings of oak, in seven stands with the admixture of birch. The exception was the recent woodland Oev4c where the canopy was formed by cherry (*Prunus avium*) and lime (*Tilia cordata*). For results of canopy cover estimates and measurements of basal area and trees per hectare see Appendix 1. Even though canopy cover estimates from trees and shrubs added up to more than 100% in some of the subplots, means of canopy cover for whole study plots never reached more than 100% with a maximum value of 95% for the old woodland in Trolleholm (Ra).

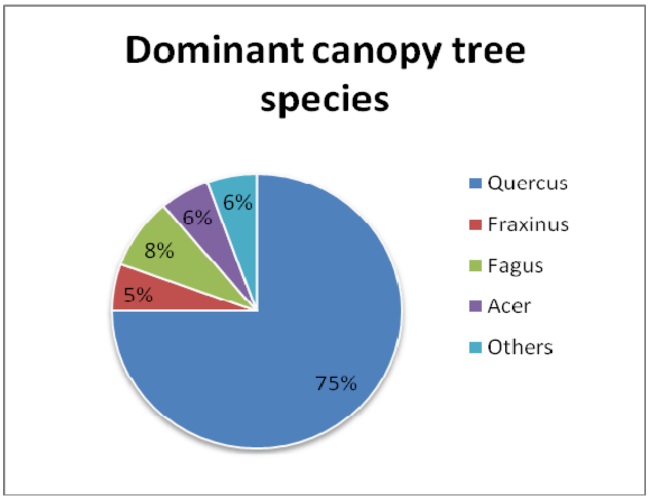

Figure 2: Dominant canopy tree species in percent of basal area at the selected 36 study sites.

A clear tendency towards higher values for canopy cover and basal area in stands on the Skabersjö estate compared to forest stands in Övedskloster was found. Differences were also found when comparing stand characteristics of old and recent woodlands. Canopy cover and basal area obtained significantly higher values in old woodlands (table 2).

Table 2: Differences in canopy cover and basal area between old and recent woodlands. Significance according to paired t-test.

	Older woodland (mean values of 18)	**Recent woodland** (mean values of 18)	**Significant at**
Canopy cover [%]	80,6	63,9	0,002
Basal area	27,2	15,6	0,001

In order to decide about the most suitable variable, when attempting to account for differences in light availability in community ordination, correlations between canopy cover, basal area and trees per hectare were calculated (data not shown). A significant correlation was found between canopy cover and basal area. The variable trees per hectare was not significantly correlated with canopy cover and revealed a significant negative correlation with basal area. In contrast to basal area, it also does not account for the size of trees measured. Hence, number of trees per hectare was not further considered as an indirect measure for light availability in this study. Due to the disregard of shrubs and small trees smaller seven centimeters in diameter when measuring basal area, only canopy cover estimates were used in final analyses.

4.2 Soil characteristics

It was decided to test collected soil samples for soil pH, exchangeable phosphorus and organic matter content. Results from soil analyses showed that the variability of soil properties between the four estates was suitable to cover a wide range of ecological gradients investigated. The range covered was for soil pH (4,5 – 6,7) for phosphorus (1,9 – 90,2 µg/g d.w.) and for organic matter content (3,2 – 21,8%). Clear trends were found when comparing pairs of study sites. Old woodlands differed from recently established plantations by having generally lower pH values, lower total phosphorus contents and higher values for organic matter content in the top five centimeters of soil (see appendix 2). The evident differences are significant for all three soil parameters tested (see table 3). The highest phosphorus content in old woodlands was found in the only ancient woodland site on the estate of Skabersjö (Sk3).

Again, correlations between soil parameters were investigated (see table 9 in section 4.5). Exchangeable phosphorus was found to be negatively correlated with pH and organic matter content.

Table 3: Differences in measured soil properties between old woodlands and recent woodlands. Significance according to paired t-test.

	Old woodland (mean values of 18)	**Recent woodland** (mean values of 18)	**Significant at**
pH (H2O)	5,6	5,9	0,019
Exchangeable phosphorus [µg/g dry weight]	23,6	39,3	0,000
Organic matter [%]	10,5	5,4	0,000

Variation of environmental variables was further investigated by looking at the variability between study site locations. Thereby old and recent woodlands on the estate of Övedskloster were found to have generally higher soil pH values, higher organic matter contents and lower exchangeable phosphorus contents compared to the nine pairs of stands on the estate of Skabersjö (Table 4). The only study site on the estate of Trolleholm (Ra) deviates from other study sites in terms of soil characteristics. The highest value for organic matter content was measured here (see also appendix 2).

Table 4: Differences between sample plots on the two estates of Skabersjö and Övedskloster. Significance according to Mann-Whitney test.

	Övedskloster (median of 7 stands)	**Skabersjö** (median of 9 stands)	**Significant at**
Soil pH old stands	6,1	5,0	0,026
Soil pH recent stands	6,2	5,7	0,001
Soil phosphorus old stands	3,1	36,8	0,004
Soil phosphorus recent stands	18,0	56,8	0,001
Organic matter old stands	11,6	8,0	0,071
Organic matter recent stands	6,9	4,0	0,001

4.3 Species distribution

Species diversity expressed as the total number of species per plot did not differ significantly between old and recent woodlands. Further insights in species compositions of sample plots were obtained by dividing the entity of recorded species in two classes. Classification into typical forest species and species found in forests as well as under open conditions revealed clear trends and different abundance patterns. A list of all 43 typical forest species identified in this study can be found in appendix 3.

Table 5: Differences in species diversity of all recorded species and of recorded typical forest species between old woodlands and recent woodlands. Significance according to paired t-test.

	Old woodlands (mean values of 18)	**Recent woodlands** (mean values of 18)	**Significant at**
Number of species /plot	35,7	32,7	0,343
Number of typical forest species/plot	13,8	6,7	0,000
Sum % cover of forest species/plot	53,7	7,1	0,000

The primary interest in differences between old and recent woodlands was tested by concentrating on typical forest species only. Thus, old woodlands contained in average twice as many forest species as recent woodlands. The difference became even more pronounced when the sum of cover values of forest species per plot were compared (table 5).

A clear trend was discovered when frequencies of woodland species for each of the two woodland categories were calculated. A list of the most common species with a frequency > 19% in all 36 plots including categories for diaspore dispersal is depicted in table 6.

Table 6: Typical forest species with a frequency in all study plots > 19%.

	Frequency of typical forest species [%]		**Diaspore dispersal**
	old	recent	
Brachypodium sylvaticum	55,6	44,4	Adhesive
Circaea lutetiana	50,0	55,6	Adhesive
Elymus caninus	44,4	33,3	Adhesive
Festuca gigantea	66,7	66,7	Adhesive
Milium effusum	88,9	33,3	Adhesive
Poa nemoralis	83,3	83,3	Adhesive
Anemone nemorosa	66,7	5,6	Ants
Anemone ranunculoides	38,9	5,6	Ants
Carex sylvatica	27,8	16,7	Ants
Gagea lutea	44,4	5,6	Ants
Lamiastrum galeobdolon	38,9	5,6	Ants
Melica uniflora	50,0	0,0	Ants
Mercurialis perennis	61,1	0,0	Ants
Viola riviniana/reichenbachiana	44,4	5,6	Ants
Athyrium filix-femina	27,8	22,2	Wind
Dryopteris filix-mas	44,4	61,1	Wind
Dryopteris carthusiana	27,8	16,7	Wind
Adoxa moschatellina	16,7	22,2	Ingested
Oxalis acetosella	38,9	0,0	Auto
Impatiens parviflora	44,4	33,3	None
Moehringia trinervia	38,9	55,6	None
Stachys sylvatica	50,0	33,3	None
Stellaria holostea	38,9	11,1	None
Stellaria nemorum	72,2	5,6	None

In general frequencies of woodland species were higher in old woodlands. This difference was particularly pronounced for ant dispersed species (table 7). Wind dispersed forest species and species dispersed via adhesive seeds were more frequently found in recent woodlands.

Table 7: Differences in mean frequencies of typical woodland species separated according to their dispersal type. Significance according to paired t-test.

	Frequency old woodlands [%]	Frequency recent woodlands [%]	Significant at
Adhesive (mean of 7)	58,7	45,2	0,136
Ants (mean of 11)	37,4	3,7	0,000
All forest species (mean of 43)	32,2	15,5	0,000

Besides the 43 typical forest species a number of species occurring in forests as well as under open conditions were recorded. Comparison of their frequencies did not reveal distinctive patterns as found within forest species (table 8). An exceptional observation was the restricted occurrence of *Aegopodium podagraria* in old woodlands. Also noticeable is the abundant occurrence of *Epilobium montanum*, *Galium aparine, Geum urbanum, Poa trivialis, Taraxacum officinale* and *Urtica dioica* in recent woodlands.

Table 8: List of species found in forests as well as under open conditions with a frequency in all study plots > 19%.

	Frequency old woodlands [%]	Frequency recent woodlands [%]
Aegopodium podagraria	38,9	0,0
Alliaria petiolata	22,2	16,7
Deschampsia cespitosa	38,9	50,0
Epilobium montanum	33,3	94,4
Equisetum arvense	0,0	44,4
Fragaria vesca	16,7	44,4
Galeopsis spec.	44,4	27,8
Galium aparine	88,9	94,4
Geranium robertianum	33,3	27,8
Geum urbanum	77,8	94,4
Glechoma hederacea	33,3	16,7
Juncus effusus	16,7	33,3
Lapsana communis	27,8	27,8
Mycelis muralis	16,7	27,8
Poa trivialis	55,6	100,0
Ranunculus ficaria	72,2	44,4
Ranunculus repens	33,3	50,0
Silene dioica	50,0	11,1
Taraxacum spp.	38,9	100,0
Urtica dioica	83,3	100,0
Veronica chamaedrys	16,7	50,0
Vicia sepium	27,8	11,1

Mean cover values of typical forest species were also separately investigated for each pair of stands (appendix 4). In seven out of 18 pairs significant differences in the mean cover of forest species were found. In one site the mean cover was higher in the recent woodland than in the adjacent secondary woodland (Sk 6a). In all other old woodland sites forest species covered a larger area than in the paired recent woodland. The highest cover value of typical forest species in recent woodlands was found in the northernmost study site in Trolleholm (Ra).

4.4 Relation between forest species diversity and forest continuity.

Additionally to the detected higher frequencies and cover values of typical forest species in old woodlands, total number of forest species was plotted against years of forest continuity. A rise in the number of typical forest species with increasing forest continuity was found (figure 3).

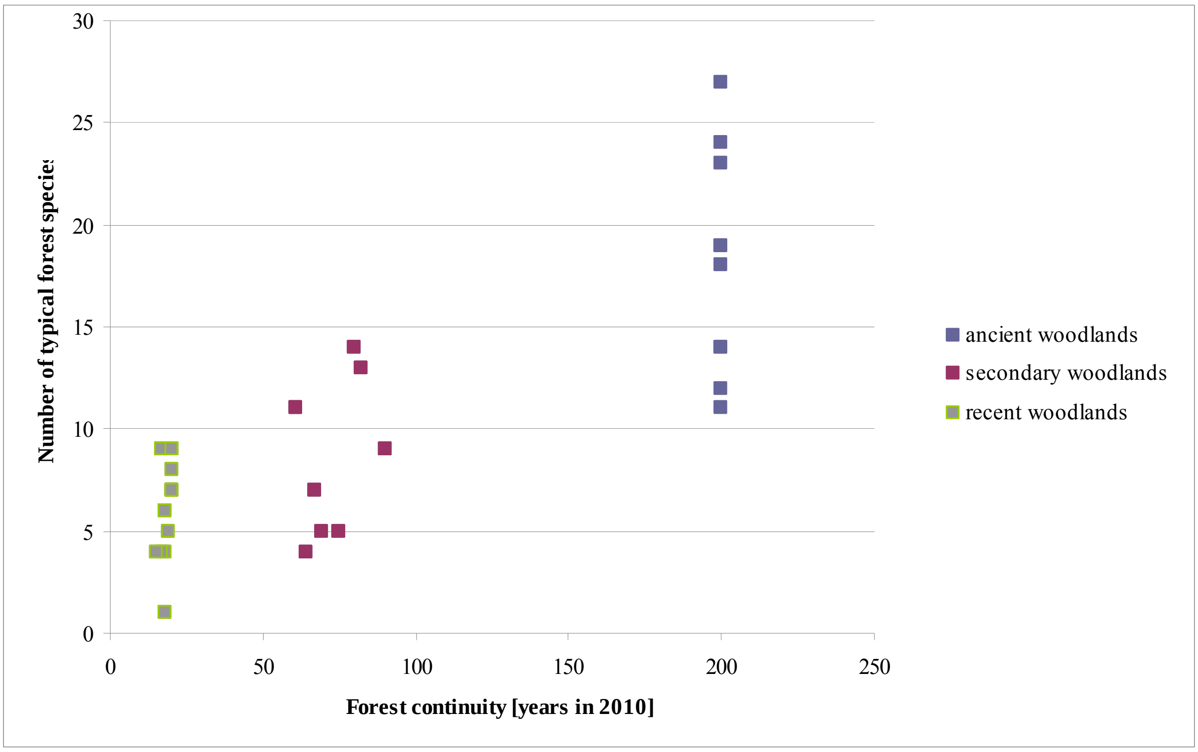

Figure 3: Scattergraph showing the number of typical forest species found within the woodlands in three forest continuity classes. Significant differences between means of forest continuity classes were tested with one-way Anova (R^2 = 77,49 ; P-value: 0,000).

The categorization of forest continuity in three classes with division of old woodlands in secondary and ancient woodlands allowed for further exploration of the relation between the two investigated variables. Class one thereby contained all recently established plantations, class two all stands with a forest continuity of 50 – 100 years (secondary woodlands) and class three contained all ancient woodlands. Findings confirmed that recent woodlands contain a significant lower number of typical forest species than ancient woodland stands. However, also secondary woodlands were found to have significantly lower numbers of typical forest species when compared to ancient woodlands. No difference in the mean number of forest species was detected between recent and secondary woodlands.

4.5 Correlation between environmental variables

To obtain more information about the relations of the investigated variables, correlations between six environmental variables were calculated. Strong correlations were found between forest continuity and measured soil properties with the strongest positive correlation between forest continuity and organic matter (table 9).

Table 9: Correlations between soil properties, stand characteristics and forest continuity tested with Spearman's rank order correlation. Positive and negative r_s values and significances of correlations are depicted.

	pH	P	C	CCo	BA
P	- 0,475**				
C	- 0,095 NS	- 0,567***			
CCo	- 0,218 NS	0,062 NS	0,163 NS		
BA	- 0,383*	0,021 NS	0,313 NS	0,442**	
FC	- 0,015 NS	- 0,573***	0,803***	0,359*	0,486**

The variables investigated were exchangeable phosphorus (P), pH in H_2O (pH), organic matter (C), canopy cover (CCo), basal area (BA) and broadleaf forest continuity (FC).

NS = not significant
* P ≤ 0,05
** P ≤ 0,01
*** P ≤ 0,001

4.6 Data analysis with CANOCO

4.6.1 Unconstrained detrended correspondence analysis (DCA)

In regression analysis following DCA in Canoco 4.5, the two most important gradients detected in DCA were found to be closely related to the five investigated environmental variables. The regression analysis revealed a strong relation between forest continuity and organic matter with sample scores on DCA-axis one (table 10). The highest r^2 values from this regression analysis were recorded for forest continuity. For sample scores on DCA-axis 2 a significant correlation was found with soil pH which was not found to be related to sample scores on DCA-axis one.

Table 10: Linear regression between sample scores on DCA-axis 1 & 2 and environmental variables.

	Axis 1 r^2	Axis 2 r^2
canopy cover	0,272***	0,012 NS
pH	0,067 NS	0,272***
Phosphorus	0,119*	0,092 NS
organic matter	0,445***	0,006 NS
forest continuity	0,728***	0,023 NS

NS = not significant
* P ≤ 0,05
** P ≤ 0,01
*** P ≤ 0,001

However the detected relation was less strong compared with linear regression scores on DCA-axis one. No relation was found between all other investigated environmental variables with the second most important gradient in the DCA. Considering the fact that the first two DCA-axes explain about 20% of the total variation in the species composition (table 12 in section 4.6.4), the measured environmental variables and their close relation to these axes seem to be suitable for explaining a considerable part of the species composition.
The decision about the constrained ordination method was primarily based upon the beta diversity in the composition of the vegetation data. Therefore the length of the longest gradient in DCA was used as an indicator (Lepš & Šmilauer, 2003). This length was found to be 3.7 which pointed towards a constrained analysis with an assumed unimodal species response.

4.6.2 Constrained Canonical Correspondence Analysis (CCA).

A distinctive pattern regarding the distribution of study sites was observed when displaying the results from CCA with CanoDraw 4.0 (ter Braak & Šmilauer, 2002). Positions of old woodlands in the ordination space were clearly separated from recent woodlands. Additionally, recent woodlands revealed a clustered distribution, whereas old woodlands were scattered farther in the ordination space. The relative abundance of species thereafter deviated strongly between old and recent woodland sites (figure 4).
The distribution of species in the ordination space supports the results from species classification and distribution investigations based on their frequencies (see section 4.3). Species previously classified as typical forest species were found to be characteristic for study sites with long forest continuity and high values for organic matter. Characteristic species with high abundance values in recent woodlands were among others *Galium aparine*, *Urtica dioica* and *Fragaria vesca.* Also some of the typical forest species, such as *Circaea lutetiana, Brachypodium sylvaticum* and *Stellaria holostea* were found to have a comparably higher relative abundance in recent woodland sites. Thereof *Brachypodium sylvaticum* and *Circaea lutetiana* are associated with high pH values and *Stellaria holostea* with high levels of phosphorus (figure 5).

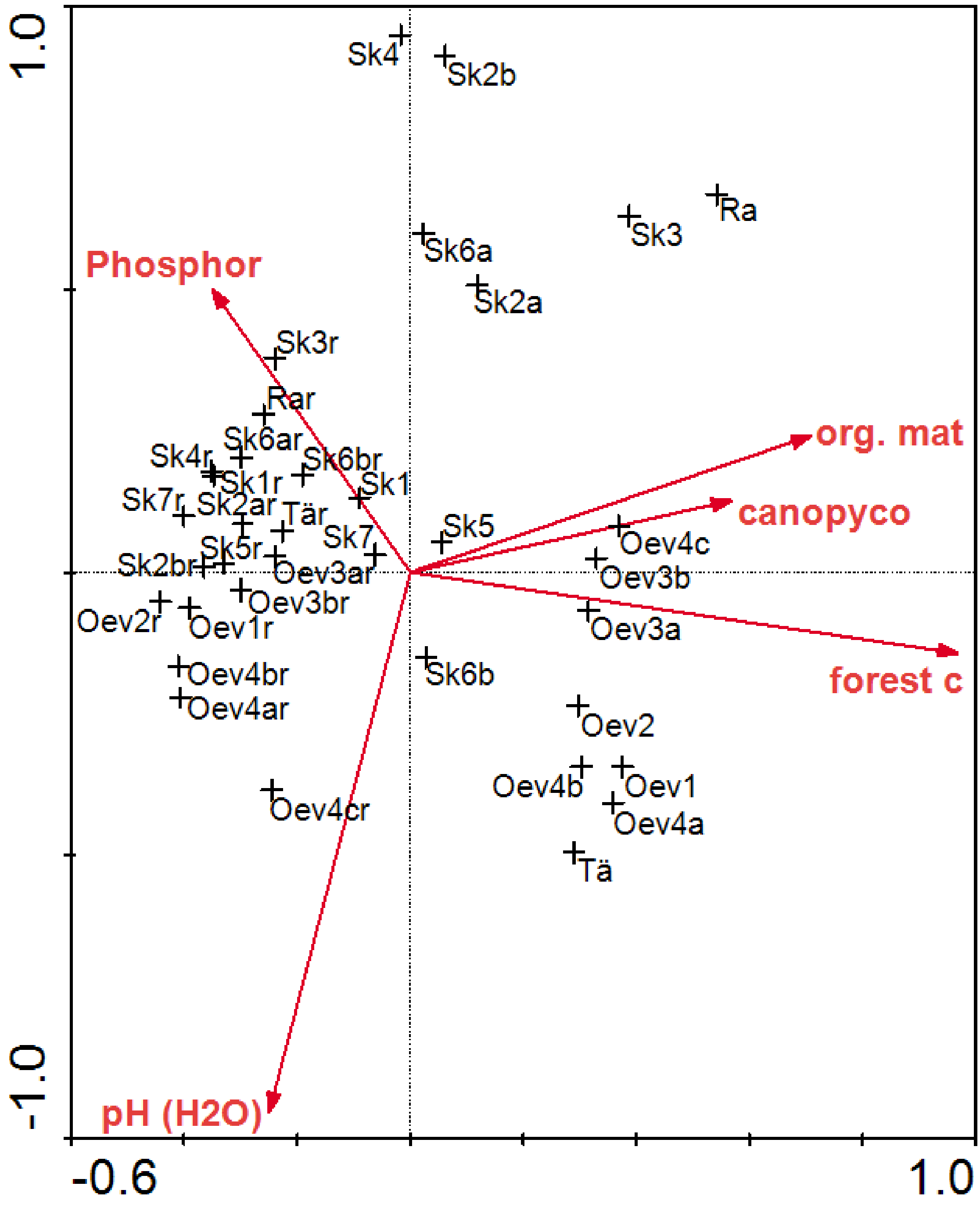

Figure 4: Biplot from CCA with study sites (marked with crosses) and environmental variables (red arrows). All 18 pairs of woodland sites are labeled according to their location and recent woodland sites are labeled with an r at the end.

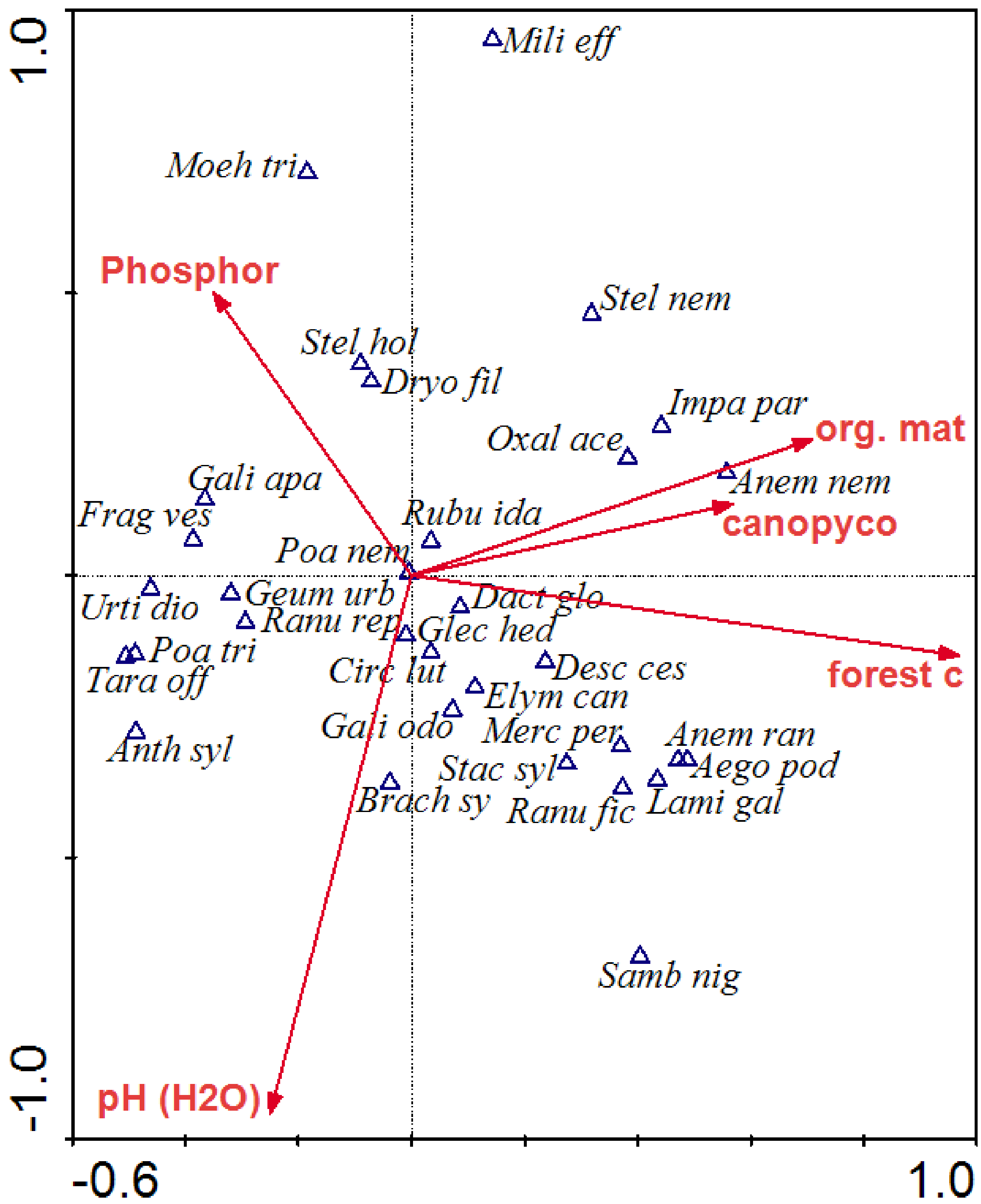

Figure 5: Biplot from CCA. Results showing the five environmental variables as arrows in the ordination space where 32 species with a weight >3% are depicted with triangle symbols. Species names are made up from the first four letters of the generic name and the first three letters of the specific name.

The sum of all canonical eigenvalues from CCA was used as a measure for the variation in species composition that could be accounted for by the environmental variables. The sum of 1.384 was then compared with the total variation (TV) obtained from DCA. Thereafter it can be assumed that the five environmental variables used accounted for about 25,3 % of the total variation (see section 4.6.3 below).

4.6.3 Relative importance of environmental variables

Additionally assessed was the relative importance of every single environmental variable on the distribution and composition of the detected vegetation pattern by following the concept of variation partitioning. In the upper part of table 11, marginal effects of the five environmental variables are depicted. The values for every single environmental variable were obtained by using the manual forward selection option in Canoco 4.5. The single most important variable thereafter was forest continuity. However as can be seen in table 9 (in section 4.5) forest continuity is closely correlated with a number of other variables used in CCA. Thus, co variations between variables were removed prior to the performance of CCA. The resulting conditional effects of each variable revealed a different order of importance (see lower part of table 11). Soil pH and forest continuity were then found to have the highest share of total variation. Canopy cover and organic matter thereafter seem to be less important for the explanation of the species community structure.

The application of Monte Carlo permutation enabled to test the dependency of the single environmental variables on the species composition. However when covariation was removed only the variables forest continuity and pH were found to significantly affect the result of the ordination.

Table 11: Relative importance of soil properties, canopy cover and forest continuity for the interpretation of the amount of variability of the species composition explained within CCA. The relative importance is expressed as percentage share of the total variation (TV) explained within DCA. Share of TV is depicted first without considering correlations between variables and secondly after removing co variation.

	Share of TV [%]	**Covariables**	**Significance of 1st CCA-axis**
TVE by CCA	25,3		0,002
pH	6,6		0,002
phosphorus (P)	4,6		0,002
organic matter (C)	7,2		0,002
canopy cover (CCo)	5		0,002
forest continuity (FC)	10,9		0,002
pH/P/C	15,8		0,002
pH	4,1	P/C/CCo/FC	0,012
phosphorus	3,4	pH/C/CCo/FC	0,082
organic matter	2,7	P/pH/CCo/FC	0,34
canopy cover	2,7	P/C/pH/FC	0,334
forest continuity	5,3	P/C/CCo/pH	0,002
pH/P/C	11,9	CCo/FC	0,002

4.6.4 Explanatory power of the first two axes in DCA and CCA.

When comparing the percentage of variance explained by only the first two ordination axes from DCA and CCA a similar picture was obtained from both analysis. This confirms that the environmental variables used in CCA are suitable to explain the main part of variability in the species composition (table 10 in section 4.6.1).

Table 12: Comparison of the first two axes of DCA and CCA and their explanatory power. All figures represent percentage values of total variation (TV).

	Share of TV by 1st axis	Share of TV by 2nd axis	TV by 1st and 2nd axis	TV
DCA	12,8	7,3	20,1	100
CCA	11,4	6,4	17,8	25,3

The sum of the first two axes accounted for about 18% in CCA respectively 20% in DCA of the total variation. Within CCA analysis the first and the second axis account for about 70% of the total variation explained by CCA.

5. Discussion

5.1 Methodology

All analyses of the collected vegetation data were based on estimates of percentage cover of herb layer species. Although cover estimates might not have a high precision, they are said to give a good indication about the relative importance of species in the plant community. As such, the role and importance of each species might be better reflected with cover estimates than with presence-absence data. The extra time needed for cover estimates was affordable due to small sampling units of 1 m^2.

Following the definition of Jennings et al. (1999), canopy cover was assessed as the percentage of the sample plot covered by the vertical projection of the tree canopy. Estimates were taken by vertically looking up in the tree canopy. This however reflects a high possible source of error. Bonnor (1967) found out, that only a slight angle of view different from the vertical will significantly bias the result. However the method is fast and in contrast to canopy closure measurements independent of tree height. Management interactions in the investigated forest stands also do not justify the application of expensive and time consuming canopy cover measurements. An alternative could be to carry out direct light measurements with electronic devices which could possibly deliver a more precise picture of the light regime.

All analyses with Canoco 4.5 were based on mean percentage cover values of species. This reflects a rather extreme measure due to the large number of species with low cover percentage values and low frequencies and a few species with high percentage cover values. The application of several data transformations such as transformation to an ordinal scale, log or arcsin transformation of species data prior to analyses in Canoco 4.5 and their effects on the community ordination should be investigated.

5.2 Soil and light variables and their importance in species ordination

Soil pH values and exchangeable phosphorus contents were found to be higher whereas organic matter contents were generally lower in recent woodlands than in old woodlands. Similar results were found in several other studies (e.g. De Keersmaeker et al. 2004; Koerner et al. 1997; Verheyen et al. 1999; Dzwonko & Loster, 1997 & Falkengren-Grerup et al. 2006). The hypothesis that top soil conditions differ strongly between old and recent woodlands was thereafter confirmed. With the assumption that pairs of stands had similar soil properties prior to anthropogenic influences, the detected differences in the top soil were referred to past land cultivation. It is most likely that the decision in former times, about the conversion of forest land to arable land was based on site properties; most productive sites with the best soils were converted first and less productive sites were left forested. However, some of the recent woodlands in this study were converted to arable land exceptionally late and due to the location of the investigated forestland on large estates, management goals such as sustainable timber supply and hunting have prevented clearance of broadleaf forests on fertile land. It might therefore be justifiable to assume similar soil properties in each pair of stands prior to land use change. Initially similar soil properties are further indicated by the fact that comparisons of ancient and recent woodland sites at the Skabersjö estate showed a decreasing difference of soil properties below the plugging horizon (Falkengren-Grerup et al., 2006; Valtinat et al., 2008).

Investigation of ground layer community structures with canonical correspondence analysis revealed that soil pH was the most important soil gradient for the explanation of species composition. This is in accordance with other studies (e.g. Tyler, 1989). Low pH values have been found to limit the establishment and growth of herb layer species (Falkengren-Grerup & Tyler, 1993; Brunet et al. 2000). It has therefore been hypothesized in those studies that acidification of south Swedish forest soils affects the survival and growth of acidifuge herb layer species such as *Adoxa moschatellina* or *Circaea lutetiana*. In fact, plantations adjacent to old woodlands with higher pH values were found to serve as refugees for acid sensitive forest species which are not dispersal limited (Brunet et al. 2000; Valtinat et al. 2008). Similar patterns were found in this study. Some of the typical forest species such as *Adoxa moschatellina* and *Circaea lutetiana* were found to be even more frequent in recent woodlands and according to CCA associated with high soil pH values. Due to the young age of recent woodlands in this study, it can be concluded that these species are able to access new plantations soon after establishment and find suitable conditions for establishment. On the other hand typical forest species with low dispersal ability (e.g. ant dispersed species) such as *Mercurialis perennis* and *Lamiastrum galeobdolon* never reached high frequencies in recent woodlands although they are according to CCA associated with high pH values.

Soil organic matter and canopy cover estimates were found to be less important for the explanation of the variation in species composition. In particular the strong correlations of organic matter with forest continuity and phosphorus content resulted in a large reduction of importance when co variation was removed in CCA. Another strong correlation was found in this study between the organic matter and water content in the top soil. However due to a strong temporal variation in water content it was decided not to include the parameter in CCA. However, establishment and growth of typical forest species might be favoured by the presence of a humus layer which provides a high water holding capacity, but due to the above described constraint it was not possible to further support this hypothesis. The formation of a humus layer on afforested sites will however take several decades. None of the recent woodlands in this study showed the formation of a distinctive humus layer in the first 20 years of forest land use. Only a several centimeter thick litter layer of mainly oak leaves was present in all recent woodlands.

Exchangeable phosphorus contents were not strongly correlated to sample scores on DCA axes one and two. It is thereafter less important for the explanation of the two most important gradients in DCA. Besides the direct influence of the exchangeable phosphorus content on the establishment of forest species in recent woodlands its importance might be more of an indirect control mechanism. High phosphorus contents have been considered to favour the occurrence of *Urtica dioica* therewith increasing competition for suitable germination and growing sites in recent woodlands (De Keersmaeker et al., 2004). In this study however no correlation between mean cover of *Urtica dioica* and the exchangeable phosphorus content of the 18 recent woodland sites was found (data not depicted). High phosphorus contents in recent woodlands could however also benefit other strong competitive species and further investigations should focus on the impact of phosphorus on the biotic environment in recent woodlands.

In contrast to nitrogen it is said that phosphorus is stable over a long time period due to its immobility (Koerner et al., 1997). With some exceptions, phosphorus contents gave a good indication about site history and location in this study. Clear differences were found between old and recent woodlands and also between the two large estates, where the majority of study sites were located. However the highest value of phosphorus content in old woodlands was found in the only ancient woodland site on the estate of Skabersjö (Sk3). Large differences of phosphorus contents in secondary woodlands (forest continuity 50 – 100 years) on the estate of Skabersjö might have been caused by past land use practices.

Canopy cover estimations revealed that in old woodlands light availability on the forest floor was lower compared to recent woodlands. The impact of light on the development of ground layer species communities in secondary forests can however only be assessed by taking past light levels into account. Due to the absence of a shrub layer in most of the stands investigated, light availability is very much dependent on management interactions in the overstorey. All recent woodlands in this study have been subjected to pre-commercial thinning in the past decade and some were just recently thinned which has affected canopy cover estimations in recent woodlands.

Due to the short time since recently established plantations have reached canopy closure and due to thinning operations it is most likely that in the years since establishment, light availability on the forest floor in recent woodlands was generally higher than in old woodlands. Ground layer species favored under these open conditions might have been more competitive than shade tolerant typical forest species.

A rising number of typical forest species was found with increasing broadleaf forest continuity of the study sites. Interestingly no difference was found between recent woodlands and secondary woodlands. However all secondary woodlands were situated at the estate land with the highest impact from past land use and the apparently greatest rate of fragmentation of woodlands. Percentage of forest cover in a given area and the connectivity of the landscape have been found to increase colonization success of woodland herbs (Honnay et al., 2002) The results might therefore look different if secondary woodlands on other estates were included.

Forest continuity was also used as an environmental variable for the investigation of species community structures in Canoco 4.5. It was found to be the most important variable for the explanation of the detected variation. However forest continuity deviates from other tested variables by accounting for site history and was thereafter found to be correlated to many other variables tested. It is most likely that forest continuity is also correlated to a number of variables which were not assessed in this study.

When analyzing variation of species community structures separately for each woodland site via the position of recent and old woodlands in the ordination space, it became clear that ground layer species compositions of recent woodland sites were much more similar than in old woodlands. Total number of species was found to be similar in old and recent woodlands but the pool of species in the early colonization phase of recent woodlands seems to be narrower. This more homogeneous species communities are a common phenomena in secondary woodlands and the differences to old woodlands with differing site history were found to persist for decades or even centuries (Vellend et al. 2007). The colonization process of recent woodlands in this study is still in an early phase and changes in soil properties and light conditions in combination with changes in species communities will occur. It is however difficult to predict how long this process will continue and if the investigated recent woodlands will ever totally recover from their past land use history.

The question now remains, to what extent the recovering process of recent woodlands and the formation of a distinctive forest herb layer is controlled by the soil and light conditions in recent woodlands? There is no clear answer to this question due to the high number of unknown variables influencing this process. All environmental variables in this study taken together were suitable to explain a considerable share of the variation in the vegetation data collected. However, in order to fully understand the role and importance of the differences in environmental conditions between old and recent woodlands it would be necessary to incorporate further variables such as the probability of occurrence of species and competition factors in this analysis. One possibility to account for different dispersal ability of species could be to include the probability of occurrence of species in community ordination (Hermy and Verheyen, 2007).

The young age of recent woodlands provided a unique starting point for the study of colonization processes in secondary oak plantations. This study could now serve as a starting point for a long term monitoring of processes and ground layer species community development in secondary woodlands. Further research should also focus on the incorporation of additional environmental variables such as competition factors and dispersal limitations of species.

6. Conclusion

In this study the abiotic environment (light availability and soil conditions) in recently established oak plantations and adjacent old broadleaf woodlands was investigated and significant differences between these two woodland types were found. These differences in environmental conditions were then set in relation to the present species community structure of the ground layer. Results suggest that even recently afforested sites with an age of only 20 years can provide suitable growing conditions for a number of typical forest species and can serve as refuge for acidifuge species which are not dispersal limited. However, dispersal type and ability to reach new established plantations seems to play a key role for the development of the ground layer species community in recent woodlands.

When investigating the community structure of the ground layer it was also found that the measured environmental variables were suitable for the explanation of the main compositional gradients in ground layer species communities. Hence it was possible to explain about 25 % of the total variation in the species data set with the abiotic environmental variables and the variable accounting for site history. Further investigations of relations between environmental variables and the biotic environment are needed and the incorporation of colonization capacities of species could provide substantial additional information on the probability of species occurrences.

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8. Appendix

Appendix 1: Summary of measured indirect indicators for light availability in the study plots. Shown are means of canopy cover [%], total basal area [m^2/ha] and the number of trees per hectare.

	Canopy cover		**Basal area**		**Trees/ha**	
	Old	Rec	Old	Rec	Old	Rec
Oev1	89	41,5	11,9	8,75	1060	1200
Oev2	67	36	11,3	4	500	400
Oev3a	64	74	25,4	14,8	320	1300
Oev3b	64	65	23,2	15	300	1300
Oev4a	86	42	26,6	9,2	260	1200
Oev4b	74	37,5	19,7	10,7	440	1000
Oev4c	68,5	87	17,9	14,8	200	1600
Ra	95	67	19,9	11,9	640	1400
Tä	89	85	33,2	13,2	460	2200
Sk1	90	79,5	31,2	16	360	2300
Sk2a	91,5	58,5	63,7	17,1	560	2400
Sk2b	84	56	53,6	18,2	740	2400
Sk3	83,5	90	29,6	17,1	620	2400
Sk4	73	59	28	11,6	380	2100
Sk5	86	68	34	14	720	2100
Sk6a	86	73	20,9	20	800	2500
Sk6b	82,5	79	19,4	23,1	460	2500
Sk7	77	52	19,2	18,3	380	1900

Appendix 2: Summary of measured soil parameters in the 36 study plots. Data separately depicted for old (old) and recent (rec) woodlands.

	pH (H_2O)		**P [µg/g d.w.]**		**Organic matter [%]**	
	Old	Rec	Old	Rec	Old	Rec
Oev1	6,3	6,1	2,4	17,1	11,7	6,8
Oev2	6,1	6,2	3,1	22,2	11,6	9,3
Oev3a	5,8	6,0	3,3	22,9	12,1	7,0
Oev3b	5,6	6,1	7,3	25,4	11,4	7,0
Oev4a	6,4	6,3	1,9	12,4	10,1	6,3
Oev4b	6,3	6,2	1,9	10,3	12,5	6,3
Oev4c	5,4	6,7	8,2	18,0	9,9	5,3
Ra	4,9	5,6	7,3	32,3	21,8	9,8
Tä	6,5	5,8	33,7	46,0	7,3	3,2
Sk1	5,7	5,8	74,3	90,2	6,2	4,0
Sk2a	5,0	5,7	14,9	26,8	8,4	4,1
Sk2b	4,6	5,9	36,8	44,2	15,6	3,3
Sk3	4,5	5,4	77,0	84,5	8,0	3,8
Sk4	4,5	5,6	49,7	56,8	14,5	3,4
Sk5	5,8	6,0	6,3	44,9	8,4	4,8
Sk6a	4,9	5,6	78,0	64,9	7,6	4,2
Sk6b	6,0	5,6	4,7	29,7	5,1	4,9
Sk7	5,8	5,8	14,1	58,4	6,5	3,9

Appendix 3: List of all 43 recorded typical forest species.

Adoxa moschatellina, Anemone nemorosa, Anemone ranunculoides, Athyrium filix-femina, Brachypodium sylvaticum, Bromus benekenii, Carex remota, Carex sylvatica, Chrysosplenium alternifolium, Circaea lutetiana, Convallaria majalis, Corydalis intermedia, Dryopteris carthusiana, Dryopteris filix-mas, Elymus caninus, Epipactis helleborine, Festuca gigantea, Gagea lutea, Galium odoratum, Impatiens parviflora, Lamiastrum galeobdolon, Luzula pilosa, Lysimachia nemorum, Maianthemum bifolium, Melampyrum pratense, Melica nutans, Melica uniflora, Mercurialis perennis, Milium effusum, Moehringia trinervia, Oxalis acetosella, Paris quadrifolia, Platanthera chlorantha, Poa nemoralis, Polygonatum multiflorum, Polygonatum verticillatum, Primula elatior , Pulmonaria obscura,, Stachys sylvatica, Stellaria holostea, Stellaria nemorum, Veronica montana, Viola riviniana/reichenbachiana

Appendix 4: Differences in mean cover percentage of the 43 typical forest species. The cover values are separately depicted for each pair of stands. Significances according to paired t-test.

	Mean cover of 43 forest species		**Significant at**	**N**
	old	recent		
Oev1	3,8	0,2	0,249	15
Oev2	4,1	0,1	0,043	20
Oev3a	2,9	0,2	0,072	24
Oev3b	2,2	0,1	0,048	28
Oev4a	1,8	0,3	0,016	28
Oev4b	5,8	0,4	0,044	23
Oev4c	2,1	0,3	0,018	29
Ra	2,6	2,2	0,901	21
Tä	4,9	0,5	0,063	18
Sk1	0,6	0,0	0,184	12
Sk2a	0,6	0,1	0,322	13
Sk2b	0,3	0,2	0,304	11
Sk3	5,4	0,4	0,089	18
Sk4	2,5	0,0	0,199	13
Sk5	5,1	0,1	0,231	17
Sk6a	0,6	0,9	0,047	17
Sk6b	2,1	0,1	0,016	20
Sk7	1,3	0,3	0,269	17

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