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Shedding Light on Bidstrup's Changing Plant Community: the connection between understorey vegetation, light and former land-use from 1998 to 2022

Masteroppgave i Natural Resources Management

Veileder: Bente Jessen Graae

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Norges teknisk-naturvitenskapelige universitet
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Kunnskap for en bedre verden

ABSTRACT

Modern forests are often situated on soil affected by human intervention, with most European forests having been transformed into agricultural fields or plains for husbandry grazing at some point. In Denmark most forests are former fields or plains, with only 2-3% of forested areas consisting of ancient stands with continuity of more than 250 years. Because forest plant diversity is dependent on the amount and quality of available resources, such as light and soil nutrients, this thesis has investigated whether such resources and former land-use influence the understorey plant composition. A comparative analysis of 28 forest stands consisting of ancient forests, former fields and former plains has been performed in Bidstrup, Denmark, in which data on species frequencies from 2022 is compared with data on frequencies in the same stands from 1998. The analysis considers relationships between understorey vegetation, light and land-use histories by applying non-metric multidimensional scaling (NMDS) to 1998 and 2022 datasets. The analysis demonstrates that light is the most important environmental variable on stand composition, and the forest stands have darkened significantly during the previous two decades. No significant effect of land-use histories on the composition of the understorey vegetation could be identified.

OPPSUMMERING

Moderne skoger er ofte plassert på områder som er sterkt påvirket av menneskelig inngrep, og de fleste europeiske skoger har tidligere vært brukt som jordbruksområder eller slettelandskap som beitemark. I Danmark er de fleste skoger tidligere årke eller sletter, og kun 2-3% av skogsområdene består av gammelskog med kontinuitet på over 250 år. Siden skogplanters diversitet og mangfold avhenger av tilgjengeligheten av ressurser som lys og næring, har denne masteroppgaven undersøkt om slike ressurser og tidligere arealbruk påvirker sammensetningen av vegetasjon på skogbunnen. Analysen ble gjort på 28 skogsområder med ulik tidligere arealbruk (gammelskog, tidligere åkre, tidligere sletter) i Bidstrup, Danmark. Data om artsfrekvenser fra 2022 ble sammenlignet med frekvenser fra de samme bestandene fra 1998. Analysen undersøker sammenhengene mellom komposisjonen av skogbunnsvegetasjon, lys og tidligere arealbruk ved å bruke ikke-metrisk multidimensjonal skaleringsmetode (non-metric multidimensional scaling, NMDS) på datasett fra 1998 og 2022. Analysen viser at lys er den viktigste miljøvariabelen som påvirker sammensetningen av skogsområdenes plantebestand, og skogsområdene har blitt signifikant mørkere de siste to tiårene. Tidligere arealbruk hadde ingen signifikant effekt på sammensetningen av skogbunnsvegetasjonen.

ACKNOWLEDGMENT

Five years of studies are coming to an end, including more than a year of working on this project, and it has been quite a ride. I have learned (and cried) a lot, and I am grateful for all the people who have supported me these past years. For this project, I would like to extend a special thanks to my supervisors Bente Jessen Graae and Hans Henrik Bruun for their academic advice and guidance, both in the setup of the project, feedback on my writing, and help in coding in R. I also thank you both for being cool people 😎

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1 INTRODUCTION

1.1 Forest ecosystems

Forest ecosystems are complex and dynamic systems, essential for the survival of many living organisms (Watson et al., 2018). In addition to providing habitats for thousands of species, forests provide several ecosystem services for humans, including the regulation of Earth's climate, purification of water and air, the production of raw resources, and otherwise contribute to human well-being and recreation (Mori et al., 2017). Understanding the structure, function and dynamics of forest ecosystems is critical to conserve and manage them in sustainable ways.

Forests are areas covered by trees with multiple layers of undergrowth which are composed of a variety of species (OED, 2021). The layers of the forest are separated into three zones: tree canopy layer, sub-canopy layer (small trees and bushes), and understorey layer (Peña-Claros, 2003). The understorey layer is defined here as less than 2 m tall, containing shrubs, herbaceous plants and graminoids.

Many factors influence the diversity of understorey plants. Canopy density is the main determiner of how much light is available to drive photosynthesis in the understorey vegetation, influencing the species of plants and diversity (Hill, 1979). In general, dark forests have lower biodiversity than light forests, but can nonetheless act as a refuge for uncommon and rare species (Szymura and Szymura, 2011).

1.2 Plant diversity and a healthy ecosystem

Plant diversity plays a crucial role in maintaining the health and stability of a forest ecosystem (Cadotte et al., 2012). Having a diverse array of plant species helps to support a variety of wildlife (Paillet et al., 2010), reduce the impact of pests and diseases by lowering the density of susceptible plants (Jactel et al., 2021), and increase the resilience of the ecosystem to environmental stressors such as drought, fire, erosion, and climate change (Brookhuis and Hein, 2016; CPF, 2008). In addition to the direct benefits which plant diversity provides, a diverse forest is less likely to suffer from large-scale infestations of pests or disease because there is a greater chance that some species will be resistant.

The conservation of biodiversity in natural landscapes is important to ensure that healthy ecosystems are able to survive in the long term (Morton and Hill, 2014). Ancient forests with high continuity are particularly important in this respect, as their environmental variables have had sufficient time to develop variation in structure, including in nutrients and pH (Petersen, 1994), available light from canopy density (Depauw et al., 2020), and exposed soils for easy recruitment (Hermy et al., 1999). The combination of heterogeneous structure and long continuity means that ancient forests tend to have a higher diversity of plant species than recently forested areas, both in the number of ramets and in the soil seed bank which remains dormant until more favorable conditions emerge (Eriksson, 1996; Hermy and Verheyen, 2007; Peterken and Game, 1984). These forests work as a refuge, especially for species which have a low rate of dispersion. *Anemone nemorosa* and *Stellaria holostea* are common species in ancient European forests which disperse slowly because they use rhizomes and clonal growth as dispersal mechanisms, making it difficult to disperse into areas with low connectivity to surrounding ancient forests (Brunet and von Oheimb, 1998; Graae, 2000).

Beech (*Fagus sylvatica*) and oak (*Quercus robur*) are naturally occurring tree species which dominate many temperate forests in Northwestern Europe. The two species contrast in growth structures and branch architecture, resulting in dissimilar understorey light environments (Rohner et al., 2012). Although highly dependent on the pattern of which the trees are planted, oak generally forms a mottled, airy crown with lateral branches stretching outwards (Kint et al., 2010). This creates a less dense canopy which lets more light down to the understorey vegetation relative to tree species with steep growth angles. In contrast, beech trees are more competitive with a more upright growth form with high plasticity in branch growth in response to light, which creates a denser canopy compared to oak (Castaño-Santamaria et al., 2021; Kunstler et al., 2005). In beech forests, most of the light is absorbed by the trees, letting little light down through to the understorey. This difference in the availability of light beneath the canopy of oak- and beech-dominated forest stands heavily influences their understoreys' species composition.

1.3 Light as a resource

Tall trees often create a tight canopy, only letting light down to the ground after it is filtered through the upper leaves (Castaño-Santamaria et al., 2021). Because trees need time to reach the height at which they form such tight canopies, forests characterized by darkness are also typically older, homogenous forests in late stages of succession; consequently, older forests are expected to be less diverse (Plue et al., 2013). For instance, the understory of a homogenous beech forest, a common forest type in Europe, is shown to contain only 5-10% relative light intensity (Gálhidy et al., 2006). The species composition is additionally affected by the availability of nutrients, as nutrient abundance drives niche differentiation, including in competition for light (Keddy, 2017).

1.4 Measuring light

Measuring the availability of light in a comparative way can be challenging. Devices for measuring available light, such as light meters, are unrepresentative of average light conditions (Englund et al., 2000). These devices only capture the light conditions of a specific point in time, which may be affected by cloud cover and other variables (Francone et al., 2014). One way to combat the time-dependency of direct light measurements could be to use an estimate of available light, e.g. by using a spherical densiometer to measure canopy openness, as done in this project (Forestry Suppliers inc, 2008). This is shown to be especially efficient in semi-closed stands of 20% or higher mean openness (Russavage et al., 2021).

The German vegetation ecologist Heinz Ellenberg (1913-1997) is best known for his work on ecological indicator values, and his book "Zeigerwerte der Gefasspflanzen Mitteleuropas" (Indicator values of central European vascular plants) (1974). This publication introduced the Ellenberg indicator values (EIV), a system which quantifies the ecological requirements that plant species need for optimal growth. It is based on their occurrence in different types of habitats. The system assigns numerical values typically between 1 and 9 to different environmental factors such as temperature, light, moisture, soil nutrients, and soil reactivity (pH), based on the optimal habitat preferences of each plant species. In recent years, values for environmental nitrogen and phosphor have also been added (Tyler et al., 2021). The values are used to characterize the ecological requirements and tolerances of each plant

species and to compare the environmental conditions of different habitats (Ellenberg, 1974). EIV provides a standardized and quick way to describe the environmental conditions of different habitats, useful when analyzing the responses of different plant species to environmental variation (Diekmann, 2003).

1.5 Anthropogenic disturbance and history of Danish forests

Causes which can alter the composition of the forest like storms, droughts, and insect outbreaks are a natural part of forest lifespan and succession (Keddy, 2017). Forests respond to such environmental disturbances and have the capacity to recover afterwards. However, the rate and extent of recovery is highly dependent on the frequency and severity of the disturbance (CPF, 2008). As anthropogenic disturbances are becoming more common, e.g., proximate husbandry, agriculture and human expansion, the subsequent increase in disturbances such as floods undermine forests' ability to recover, occasionally leading nearby forest ecosystems to transform into new ecosystems (Brookhuis and Hein, 2016; CPF, 2008).

Many European countries have cleared a majority of their forests at some point in history, often replacing them with agricultural fields, pastures, or tree plantations populated by non-native tree species (Bradshaw, 2004). Denmark is no exception, having only 14.9% (approx. 628 440 ha) of their land area covered by forests in 2020 (UN Food and Agriculture Organization, 2020). Ancient forests, characterized as areas without a break in forest continuity since their establishment (Bradshaw, 2004), are scarce, covering only 2-3% of Denmark (Ministry of environment, 2002).

In the 1700s, forest owners in Denmark were incentivized to create open, pasture-like areas within their forests to lease out for grazing, leading to one-third of all forested areas being cleared between 1770s and 1800s (Fritzboøger, 1994). The laws "Landboreformerne" and "Fredskovsforordningen" were passed in 1805 after a shortage of fuelwood during the Napoleonic Wars, mandating forests to be free of husbandry and grazing by livestock to encourage forest protection and reforestation. Logging nevertheless continued, primarily to meet the demand of Denmark's domestic market for fuelwood. Beech forests accounted for 80% of the total tree production in Denmark in the 1880s, but conifer plantations increased

in share towards the 1900s, in which non-native species like Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) were favored (Miljøministeriet, 2021; UN Food and Agriculture Organization, 2020). Conifers are dominant in production forests today, with deciduous forests accounting for 57.6% of the forest area in Denmark but only 32.7% of the nation's timber production (Statistikbanken, 2020; UN Food and Agriculture Organization, 2020).

After the introduction of the two laws of 1805, Denmark experienced a steady increase in forest cover (UN Food and Agriculture Organization, 2020). In modern times, Denmark has initiated several measures to ensure continued protection of its forests and their biodiversity, a recent notable example being "Natur- og biodiversitetspakken" (Nature and biodiversity package) from 2020 (Miljøministeriet, 2020). This allocates 888 million Danish kroner for creating new national nature parks, as well as the protection of untouched forests and threatened species. Measures like these are important to preserve the natural diversity which still remain nationally and globally.

1.6 Research questions

This thesis will analyze the composition of understorey vegetation and environmental variables from forest stands with three different forest histories, and compare these findings to the same stands' vegetation data from 1998 (Graae et al., 2003). With the collected data, the thesis will answer the following research questions:

- 1) *How has plant composition changed in the forest stands of Bidstrup between 1998 and 2022?*
- 2) *How does the observed change relate to available light?*
- 3) *What is the relationship between the observed change and land-use history?*

I expect that there will be a shift in plant species composition between the two years, due to differences in understorey light availability. This is expected to result in changes towards darker stands in 2022 compared to 1998, as forests grow darker with time. Stands of different land-use histories are expected to show differences in composition based on the difference in continuity and environmental factors. Stands of the same history should exhibit similar trends in species richness.

2 METHODS

2.1 Study sites

The study sites used in this thesis are 28 forest stands in the area of Bidstrup, located centrally on the island Zealand, Denmark N 55°49'20.93", E 12°25'47.66" (Figure 1). The geology of the area mostly consists of clayey moraine left by glaciers during the latest two ice ages (Gravesen, 2021). The high nitrogen-supply in clayey moraine makes a fertile soil foundation, providing good habitats for a high diversity of plant species (Beyer, 1994). The forest stands of Bidstrup are also home to several red listed animal species, including hazel dormouse (*Muscardinus avellanarius*) and European pine marten (*Martes martes*) (Harding, 2021). The climate in Lejre municipality is characterized by dry air and an average temperature (2011-2022) of 8.8°C, with average precipitation of 771.2 mm (DMI, 2022).

Today, the Bidstrup canopy is covered by 78% deciduous forest, with 48% of its canopy consisting of European beech (*Fagus sylvatica*) and 17% pedunculate oak (*Quercus robur*) (Harding, 2021; Kleinert, 2018). The two species differ in canopy densities, with oak producing a more open canopy with higher light penetration than beech (Rohner et al., 2012). Stands were categorized based on dominant tree species and historical land-use, leading to three categories: former agricultural fields, former plains with livestock grazing, and ancient areas that have been continuously forested for the previous 250 years. Information about previous usage and forest history were derived by Graae et al. (2003) from topographical maps from the 1820s and management plans for the Bidstrup area from 1842, found in the municipal archives of Copenhagen. All investigated forest stands consisted of trees older than 90 years old, specific age and additional information can be found in Appendix A. This resulted in the following number of forest stands:

- Six ancient beech (*Fagus sylvatica*) stands with continuous forest cover for >250 years (BA1-2, BA4-7)
- Five beech stands which were plowed agricultural fields on 1820s maps (BF1-3, BF5-6)
- Six beech stands which were plains for livestock on maps from 18th-19th century (BP1-6)
- Six ancient oak (*Quercus robur*) stands with continuous forest cover for >250 years (OA1-6)
- Five oak stands which were plains for livestock on maps from 18th-19th century (OF1-5)

Understorey plant communities were investigated during two field periods, including both spring ephemerals and summer-flowering plants, May (04th-16th) and July (11th-24th) in 2022. Figure 1 shows the 28 forests stands, color coded by dominant tree species and previous land-use.

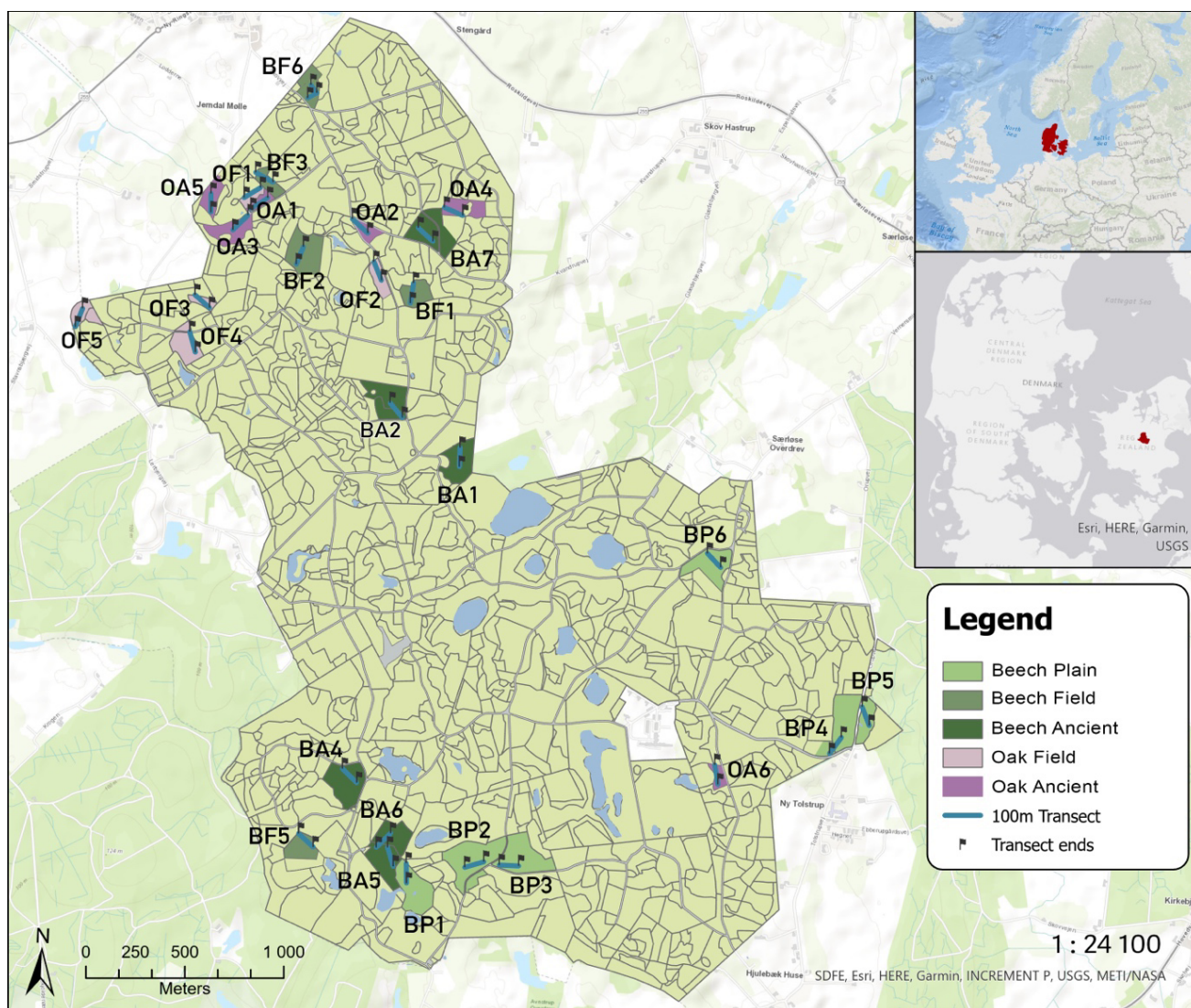


Figure 1: The map shows the location of Bidstrup forest stands in Denmark. The forest stands are color-coded by dominant tree species and land-use history. Stands dominated by beech (green) are on sites with three different land-use history (heath, field, ancient) and oak stands (purple) are on sites with two types of land-use history (field, ancient). The investigated 100m transects are marked in blue.

2.2 Field sampling

In each forest stand, a 100m transect was established at the longest continuous diagonal of the stand. Ten plots were marked at 10-meter intervals along the transect in May, with the first plot at 10m and the last at 100m (Figure 2). The same plots were used during the revisiting in July.

An area of 1m x 2m around the central point of each plot was surveyed by the use of a 0.5m x 1m aluminum frame, as shown in Figure 2A. The frame was sectioned into 10 smaller rectangles, providing a total of 40 sub-plots per plot. Vegetation analysis was done by recording absence/presence data for the different species in each subplot, resulting in species frequency data with values between 0 and 40 per plot. For a plant to be registered as present, it had to be rooted inside one of the subplots.

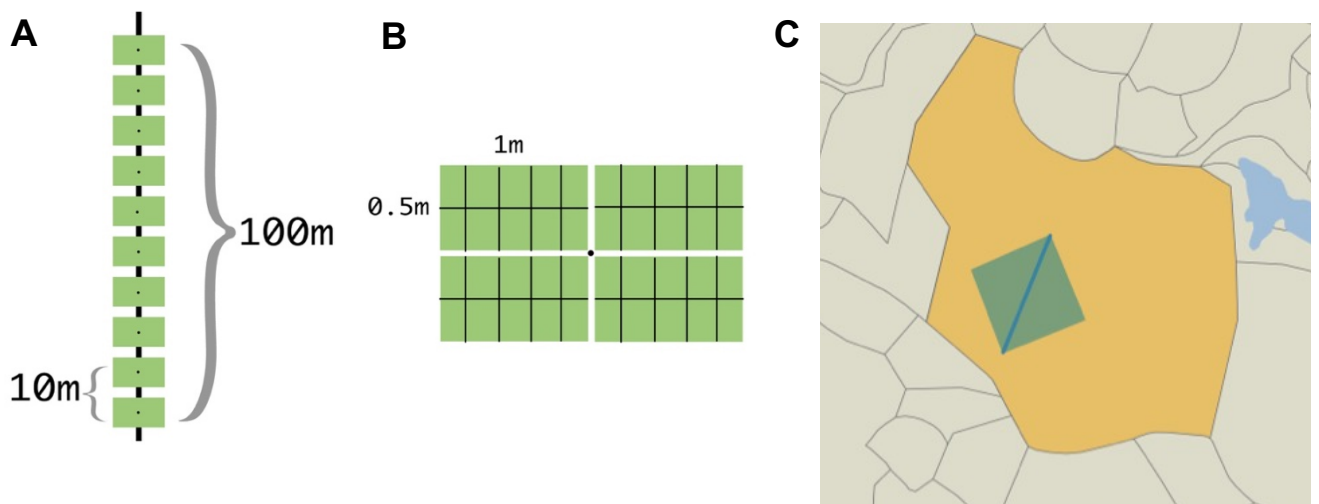


Figure 2: Schematic representation of vegetation recording design. **A)** Setup of 100m transect with 10 plots evenly distributed and **B)** setup of one plot around a center point with 40 sub-plots in total. Absence/presence data was collected for all species rooted inside the sub-plots, providing a frequency of 0-40 for each species. **C)** the area in which the supplementary species list was collected. The blue line is the transect with plots for vegetation analysis. Green marks the hectare with the transect as a diagonal and yellow marks the rest of the stand. Two people spent 15 minutes recording additional species inside the green area, and 7 minutes per additional hectare inside the yellow area.

A supplementary species list was collected in the part of the forest which the transect did not cover, see Figure 2C. Two people spent 15 minutes walking around in the square which the transect was the diagonal of, and 7 minutes in each hectare outside the transect. Hence, in a forest stand of 4 hectares, 15 minutes were spent in the hectare with the transect, and 21 minutes in the rest of the forest. All observed species were recorded as either “within transect” or “outside transect”.

In July, canopy density was measured using a spherical densiometer as a proxy for available light in the understorey during the optimum growth season. The measurement was recorded directly after each plot, facing the end of the transect. The densiometer was read in a horizontal position in accordance to the instruction manual (Forestry Suppliers inc, 2008), described in Figure 3. The number of open quadrants were converted to a percentage of canopy density, providing information about the openness of the stand. An average of each plot’s canopy openness was used as the value for the forest stand. In addition to the vegetation frequency data, supplementary species list, and canopy density, soil samples were collected in plots 1, 5 and 10 for each forest stand. This was used to extract bulk density measurements of soil nitrogen (N), soil carbon (C), and carbon:nitrogen (CN) ratio. Methods are described in the master thesis of T. Solhus (2023).



Figure 3: Illustration of the method for measuring canopy openness with a densiometer. Each of the 24 squares can be divided into four quadrants, here represented by circles. White circles are covered by vegetation, while red dot represents quadrants without canopy cover. The uncovered quadrants are counted, here providing a measurement of 6 out of 96 uncovered squares, which can be converted to percentage canopy openness via the equation $\#uncovered\ squares * 1.04 = 6,24\%$ canopy openness.

2.3 Dataset from 1998

The locations in 2022 and the method of establishing a 100m transect on the longest diagonal of the forest stand is based on the methods and locations of Graae et al. (2003). The forest stands selected fulfilled two main criteria: they were established on an area with known land-use history, and they were at least 70 years old. The data collected in 1998 in Graae et al. (2003) was obtained in order to compare understorey plant composition from the two years. This included frequency data for 30 forests and soil data from the locations in 1998, with values for pH and moisture. The 1998-dataset included data from two forests, BA3 and BF4, which could not be examined in 2022, and therefore excluded in the analysis.

2.4 Data processing

All frequency data was digitalized in August and September 2022 using Excel (version 16.72). Small plant individuals that were observed in May but could not be identified to the species level and were no longer present in July were excluded from the dataset, as they were

presumed perished. For instance, a small ramet of *Betula sp.* in BF3 that could only be determined to genus in May and was no longer present in July is presumed to have died. Details about which species and locations this is relevant for can be seen in Appendix B. All species were categorized into one of six functional groups: fern, herb, shrub, tree, graminoid or vine. These groups would later be used to categorize the species in visual representations of the data. To avoid plants being recorded twice (once in spring, once in summer), only the highest frequency of each species for each plot was kept when merging the two field seasons into one dataset. The merging was done in R with the “summarize(max)” code from the dplyr-package (Wickham et al., 2023).

Ellenberg Indicator Values (EIV) for light, moisture, soil reactivity (pH), nitrogen, phosphorous and salinity were extracted from Tyler et al. (2021) for all species. Due to EIV being species-specific, an average value was calculated for observed plants that could only be determined to genus, based on the potential species it could correspond to, and rounded to the nearest whole number. Details about which species and genus this process was done for, is shown in Appendix C.

2.5 Analysis

All data analysis was done in R version 3.3.0, and RStudio version 2022.12.0+353. To explore similarities among the different forest habitats, a non-metric multidimensional scaling (NMDS) analysis using Bray-Curtis distance was employed (Borcard et al., 2018; Bray and Curtis, 1957). After conducting k-selection, an NMDS with three dimensions was found to have the highest accuracy and lowest stress. The NMDS was generated using the vegan package, plots were created with the ggplot2 package (Oksanen et al., 2022; Wickham, 2016).

A biological indicator for the environment was created from a value for community weighted mean (CWM) of EIV for light and moisture was produced for each location, with more abundant species having a larger influence on the value (Ricotta and Moretti, 2011). These values were combined with measured measurements of canopy openness, pH, C, N, and CN-ratio, which were fitted to the model and overlaid as explanatory vectors. A correlation table was created to display the direction of correlation and the p-values between the NMDS-axes and the environmental data.

Comparison between the datasets collected in 1998 and 2022 was done by merging the two datasets to produce a new NMDS, employing the previously described method of NMDS analysis. A CWM of EIV for light, moisture, nitrogen, and pH were calculated for all locations in both 1998 and 2022, and overlaid on the NMDS as explanatory variables. Each matching location is paired and connected by arrows to illustrate changes in plant composition between 1998 and 2022.

To identify species abundance in Bidstrup, the share of forest stands in which each species was found was calculated. Species which appear in three or more stands in only the 1998-transsects or only in the 2022-transsects were marked as having disappeared or appeared. The disappeared species were checked against the 2022 supplementary list to verify their absence from the whole stands. The impact of land-use on species composition was measured with an analysis of variance (ANOVA) in which species frequencies within the land-use history categories of former fields, former plain and ancient stands were compared. Land-use history was further grouped by dominant tree species, which were also examined with an ANOVA to identify differences in composition over time, based on historic land-use.

3 RESULTS

3.1 Overall patterns of species composition in 2022

During the two field seasons in 2022, a total of 112 species were observed in the 28 forest stands. Of these, 23 species were only observed in one forest stand each. Most locations showed clear dominance by one tree species which corresponded with the categorization of beech and oak dominated forest, exceptions were some of the oak stands. Most notable is OF1 which had a high occurrence of *Caprinus betulus* with 31 observations inside the transect, three times higher than the occurrence of oak (10). Other oak forest, including OF3 and OA6, had high occurrence of beech and sycamore maple (*Acer pseudoplatanus*).

The forest stands generally exhibited moderate states of succession, with a mix of trees in different age classes from seedlings to mature trees, and an average canopy density of 12%. The stands have been subjected to varying degrees of management, including thinning and “veteranisation”, along with natural thinning due to windfalls, see Appendix A. BA5 and BA6 are most notable with large interventions having been carried out in order to recreate open-field forests for grazing. Atypical forest structures could be observed in some stands, with infrequent trees and large, cleared footpaths for human recreation.

There are large variations in the number of species and observations of abundance between locations. Figure 4 shows the accumulated abundance of plant individuals and Figure 5 shows the species richness for each location, both sorted into functional groups. The average accumulated abundance is 517 observations, with a range of 125 to 2362 observations, and the average species richness is 23 with a range of 12 to 61. BA5 is the location with highest species richness and accumulated abundance, with 61 species and 2362 plant observations. This is 33% higher than OF3 which has the second highest abundance value. BF3 has the lowest species richness and accumulated abundance, with 12 species and 125 observations. The overall composition of each functional group as percentage is shown in Figure 5. The same general patterns are seen between the stands, with herb being the dominant group in most stands, followed by graminoids. Shrubs and vines are quite abundant in one location each, OA2 and BF3 respectively. The composition of BF3 is quite different from the other locations, with almost no herbs, and shrubs being the dominant group.

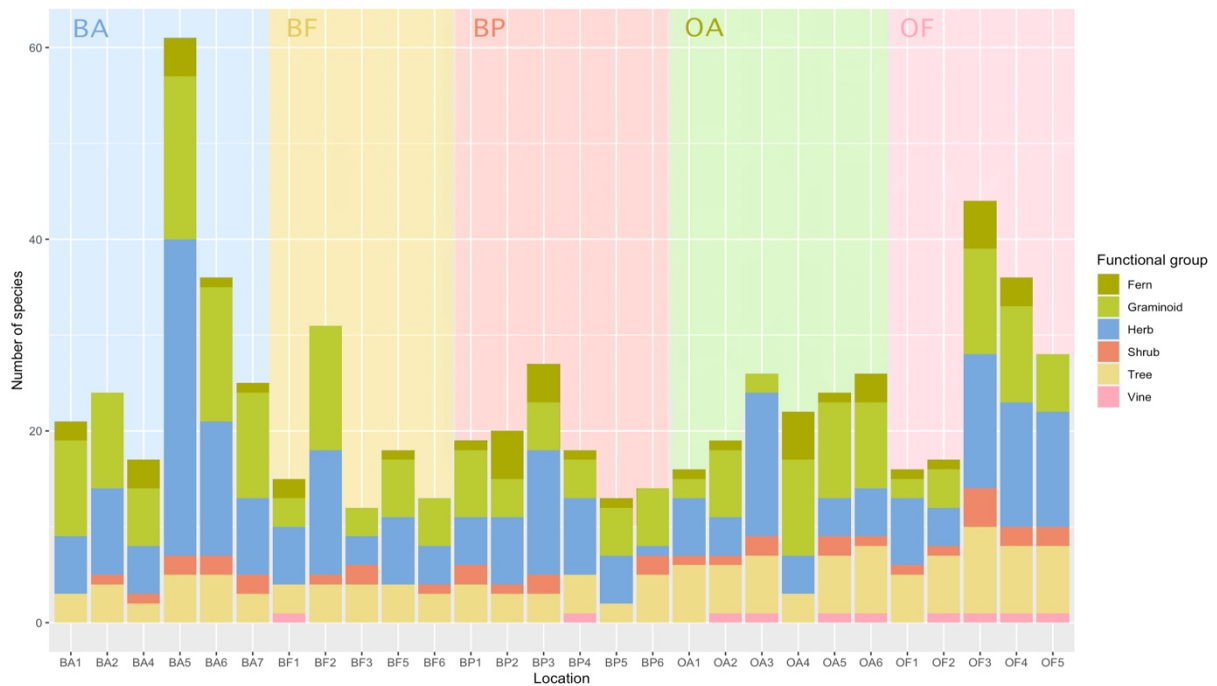


Figure 4: Accumulated plant functional group abundance for each of the 28 forest stands dominated by different tree species (beech and oak) and situated on sites with different former land-use (ancient, field, or plain). Values ranges from 125 (BF3) to 2362 (BA5), with an average of 517.

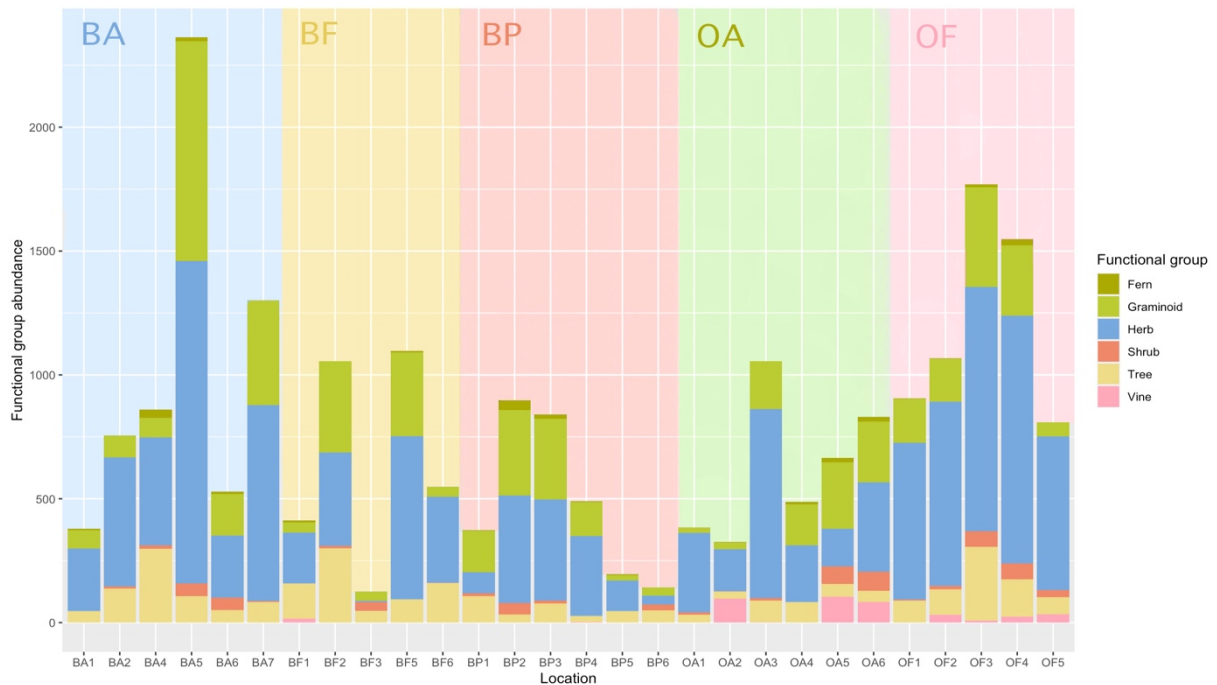


Figure 5: Accumulated number of species found in each location, divided into functional groups. The range of values go from 12 (BF3) to 61 (BA5), with the average number of species in each location being 23.

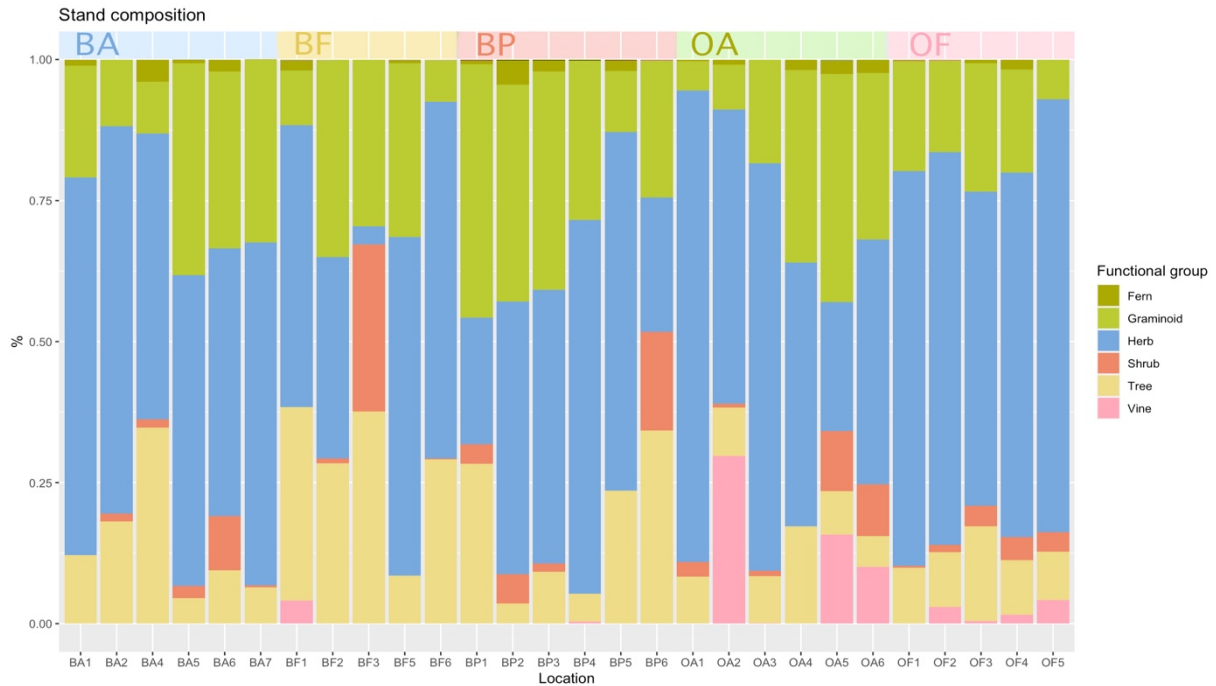


Figure 5: Stand composition by percentage proportion in each location. Species are categorized by functional group, with a general trend of herbs being the most dominating group, followed by graminoids. BF3 shows a very small percentage of herbs, but large percentage of both graminoids, shrubs and trees.

3.2 Composition in relation to environmental factors, 2022

The three dimensions of the NMDS based on the 2022 dataset are shown in Figure 6.

Explanatory variables are overlaid, which include CWM EIV for light and moisture, and measured environmental factors of canopy openness, nitrogen, carbon, CN ratio, and pH.

The length of the arrows shows the amount of influence the factor has in the NMDS and placement of location in relation to each other. Table 1 shows the influence and significance of each factor on the model and reveals significant correlations between EIV of light ($p = 0.0026$) and moisture ($p = 0.0015$) on axis 1, N ($p = 0.021$) and C ($p = 0.035$) on axis 3. Axis 2 is also correlated with EIV of light ($p = 0.0315$) but has no unique significant correlation, though pH is nearing significance ($p = 0.0676$). These five environmental factors – EIV of light, moisture, N, C and pH – are all important factors for determining the plant composition in Bidstrup forest stands, though light is the most significant variable.

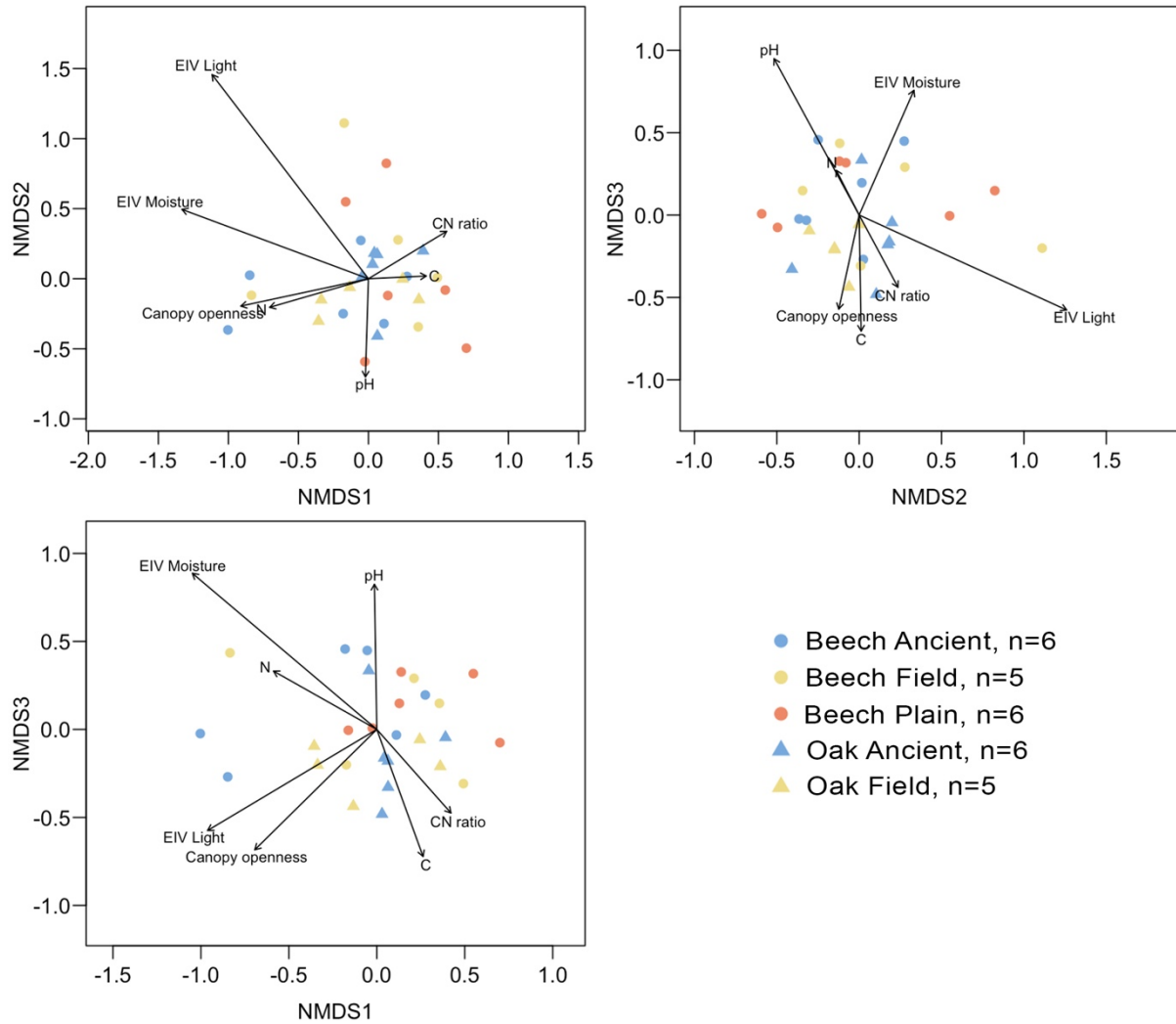


Figure 6: A non-metric multidimensional scaling (NMDS) containing three dimensions with environmental factors overlaid as explanatory variables. Length and direction of vectors show correlation of influence on plant composition. All 28 forest stands examined in 2022 are included, grouped by dominant tree species and forest history (BA = Beech Ancient, BF = Beech Field, BP = Beech Plain, OA = Oak Ancient, OF = Oak Field).

Table 1: The correlation table produces based on NMDS with data from 2022. Amount of influence which the different environmental factors have on plant composition in the understory is shown, together with p-values to show amount of correlation.

	NMDS1	p-value	NMDS2	p-value	NMDS3	p-value
Canopy openness	-0.21	0.2770	0.10	0.6168	0.29	0.1360
Mean-N	0.12	0.5443	0.07	0.7294	0.43	0.0218
Mean-C	0.30	0.1188	-0.07	0.7148	0.40	0.0346
C:N ratio	0.17	0.3803	-0.19	0.3359	0.15	0.4530
pH	-0.06	0.7736	0.35	0.0676	-0.38	0.0455
EIV, light	-0.55	0.0026	-0.41	0.0315	0.27	0.1667
EIV, moisture	-0.57	0.0015	-0.20	0.3149	-0.26	0.1892

3.3 Comparing composition of 1998 and 2022

Figure 7 shows the completed NMDS of forest stands from both 1998 and 2022 in relation to each other, with CWM EIV of light, moisture, nitrogen, and pH as overlaid explanatory values. Table 2 shows the influence and correlation of the explanatory values to each axis, with pH ($p = 0.0015$) and nitrogen ($p = 0.0355$) being correlated with NMDS1, and light ($p = 0.0000$) and moisture ($p = 0.0298$) with NMDS2. NMDS3 has no unique correlations and does not explain the observed variation in composition, as the variation is already explained by the other axes. All the tested environmental factors significantly influence the distribution of the locations in relation to each other.

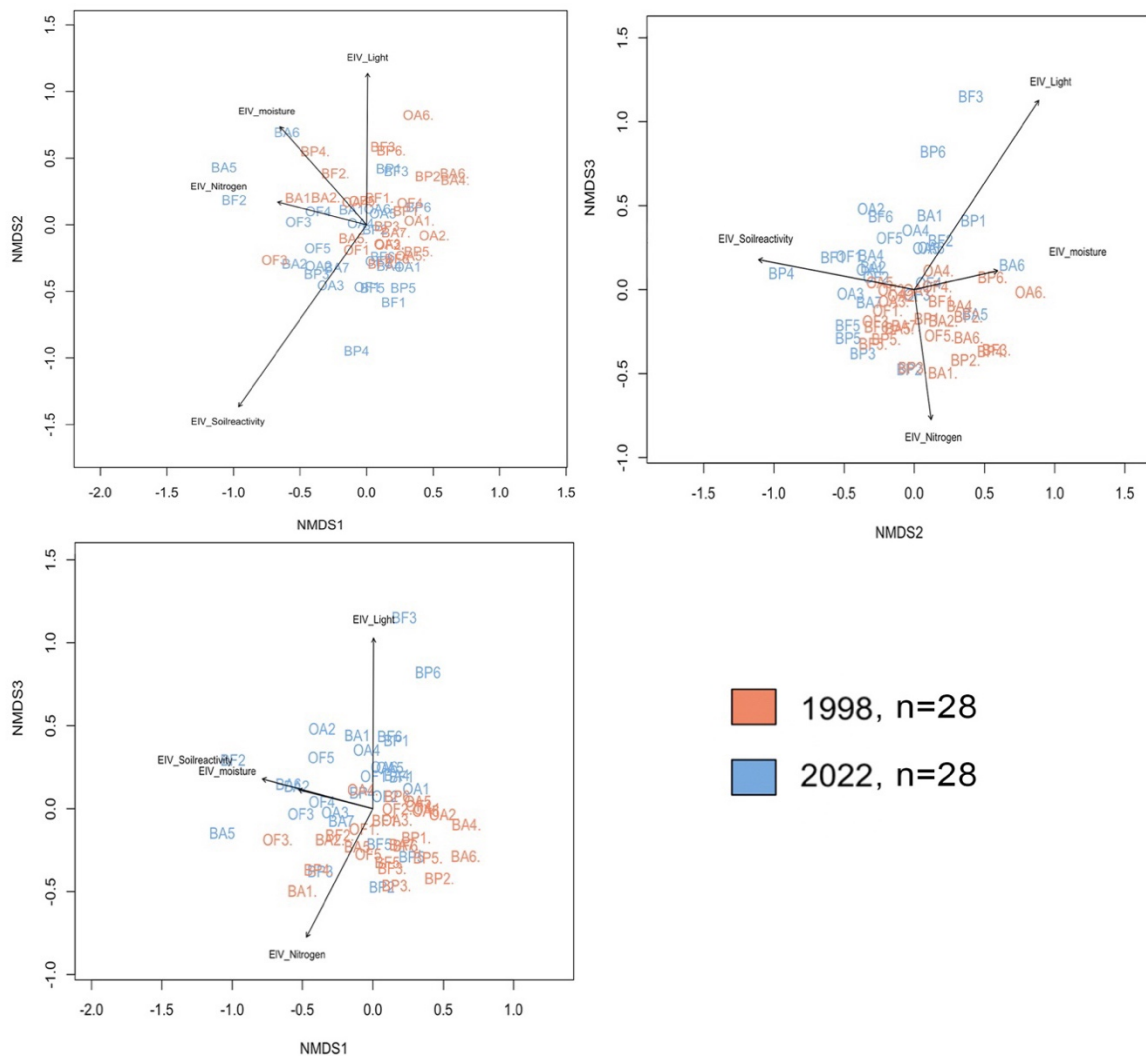


Figure 7: A non-metric multidimensional scaling (NMDS) containing three dimensions with environmental factors overlaid as explanatory variables. Length and direction of vectors show correlation of influence on plant composition. All 28 forest stands examined in 2022 are included, grouped by dominant tree species and forest history (BA = Beech Ancient, BF = Beech Field, BP = Beech Plain, OA = Oak Ancient, OF = Oak Field).

Table 2: The correlation table produces based on NMDS of data from both 1998 and 2022. The amount of influence the environmental factors have on understorey plant composition is shown, together with the p-values of correlation of the different factors.

	MDS1	p-value	MDS2	p-value	MDS3	p-value
EIV, light	0.04	0.7485	-0.54	0.0000	-0.47	0.0003
EIV, moisture	-0.17	0.1992	-0.29	0.0298	0.03	0.8188
EIV, soil reactivity	-0.41	0.0015	0.61	0.0000	-0.16	0.2537
EIV, nitrogen	-0.28	0.0355	-0.08	0.5495	0.38	0.0034

The dataset with frequencies from both years was examined for plant species with high affinity to ancient forests, defined as species which show up in >50% of ancient forests and <25% of recent forests, or in 0% of the non-ancient forest and 33% of the ancient forests (Graae, 2000). The 19 species reported in Graae (2000) showed no preference for ancient stands in our dataset, and there was no difference in their frequency between ancient and recent stands. Only one species, *Pteridium aquilinum*, met the definition's criteria when applied to the 2022 dataset as it occurred in 3 of 6 ancient beech stands and 3 of 6 ancient oak stands, but only occurred in one of each of the recent forest categories. Some species disappeared, while new ones appeared in the stands. Table 3 shows the species that appeared in three or more stands, and those that were no longer found in transect or the surrounding stand compared to 1998. New species which were observed in fewer than three locations have been excluded.

Table 3: Species which appeared or disappeared in the forest stands of Bidstrup during the period 1998-2022. Species listed in the appeared column were recorded in three or more different forests stands in 2022. The species in the disappeared column were registered in three or more locations in the 1998 transects, but not registered inside transect or in the supplementary species list for any forest stand in 2022.

Appeared	Disappeared
<i>Agrostis stolonifera</i>	<i>Carex pallescens</i>
<i>Dryopteris expansa</i>	<i>Chamerion angustifolium</i>
<i>Festuca rubra</i>	<i>Moehringia trinervia</i>
<i>Holcus lanatus</i>	<i>Stellaria media</i>
<i>Stellaria neglecta</i>	

A simplified version of the NMDS in Figure 7 is presented in Figure 8A, showing the overall change observed between 1998 and 2022 in forest stand composition. The average direction of change matches closely with the direction of pH, and in the opposite direction of light, showing the change that has happened is in line with a lower value of pH i.e., a more acidic soil, while at the same time moving into lower values of EIV of light i.e., more darkness. Running a t-test on the centroid position of the new and old datasets shows that there was a significant shift in species composition in all three axes (Figure 8B).

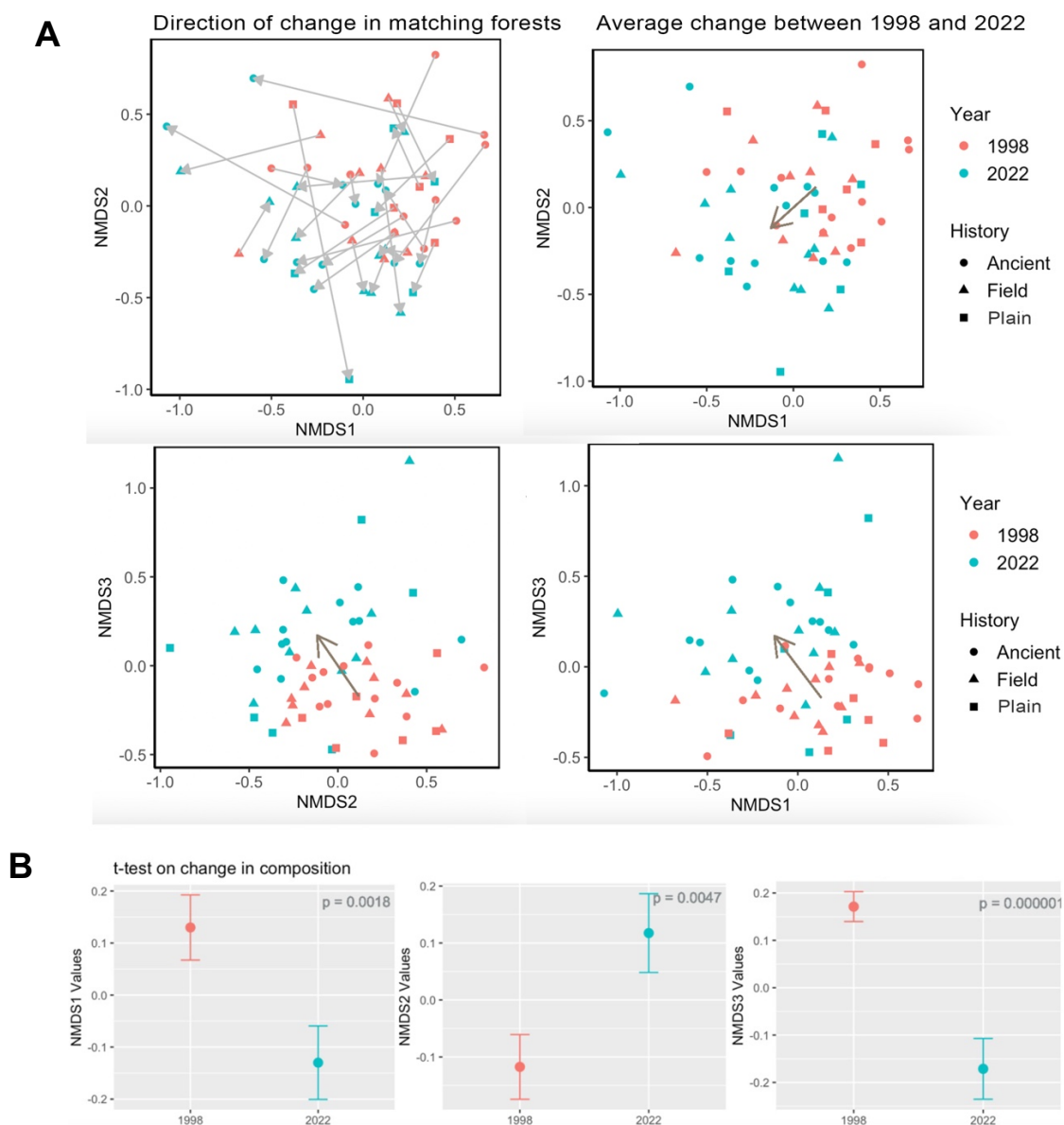


Figure 8: **A)** NMDS with three dimensions showing matching forest stand locations in 1998 (red) and 2022 (blue). Matched up locations do not show an intuitive direction of change (left), but an arrow of average position of old and new datapoints shows the overall direction of change (right). **B)** Average axes values with error bars. Top corner of each plot shows the p-value from a paired t-tests of the differences between the plant composition of the two different years. All axes show significant differences between the two years.

3.4 Effect of light

As seen in Table 1, environmental variables of EIV light and canopy openness do not have the same influence on the NMDS from 2022. Canopy openness is not significantly correlated with any NMDS axes, while EIV light shows significant correlation to NMDS1 ($p = 0.0026$) and NMDS2 ($p = 0.0315$). The first graph in Figure 6 shows higher values of light with negative values on the axes of NMDS. The length of the explanatory vector of EIV light shows the high importance of light as a determinant for forest composition in the Bidstrup forest stands.

EIV for light is also important for the change in vegetation composition which occurred between 1998 and 2022. The NMDS (Figure 7) has a vector of significant length for this environmental variable, and the corresponding correlation table (Table 2) shows significant correlation with MDS2 ($p = 0.0000$). The graph with NMDS1 and NMDS2 shows an increase in EIV values with positive NMDS2 values. When set in relation to Figure 8A, the forest stands show an average shift in composition towards more negative NMDS2 values, indicating that the forest stands have grown darker since the 1998 measurements.

3.5 Stand differences based on land-use history

The result from the ANOVA analysis of land-use with the two dominant tree species grouped together showed no significant difference between any of the land-use histories in 2022 ($p = 0.301$) (Figure 9A). No significant difference ($p = 0.291$) was shown when separated into dominant tree species and former land-use either (Figure 9B). Visual inspection of the NMDS analysis (Figure 6) backed this up, showing no clear patterns in positions or clusters with either forest history or dominant tree species. This applied to all axes.

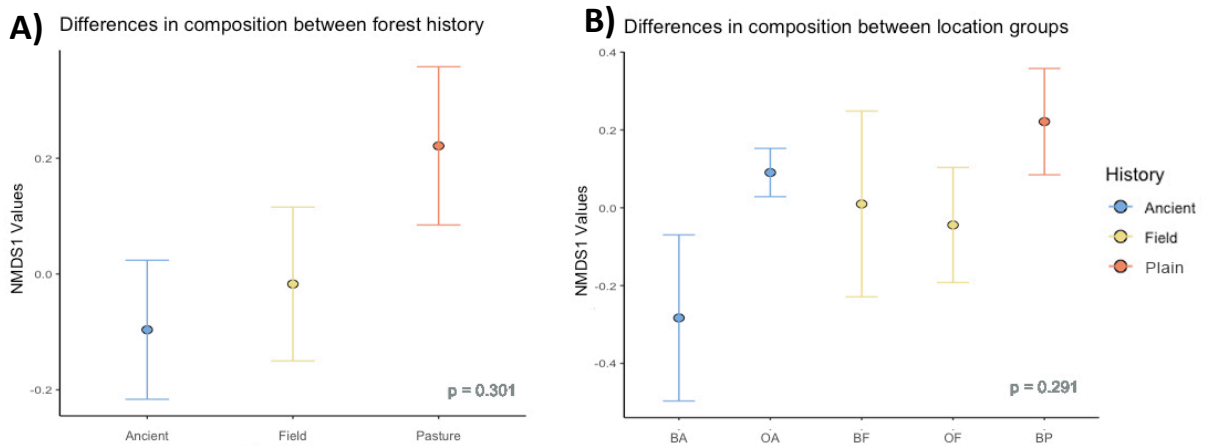


Figure 9: A) Average value of NMDS1 based on forest history groups and **B)** plant composition within each forest group with associated error bars. Values of significance are derived from ANOVA of the forest stands categorized by former land-use and forest history groups, respectively. Neither show significant difference between categories.

Looking at the rate at which the composition of stands with different land-use histories changed relative to each other through time, no significant difference in change occurred ($p = 0.351$). This means that even though there was a significant change in composition between 1998 and 2022 (Figure 8B), the change is evenly distributed through the different types of forest stands which were investigated in this thesis. Figure 10 shows the difference in change between 1998 and 2022, grouped by land-use history.

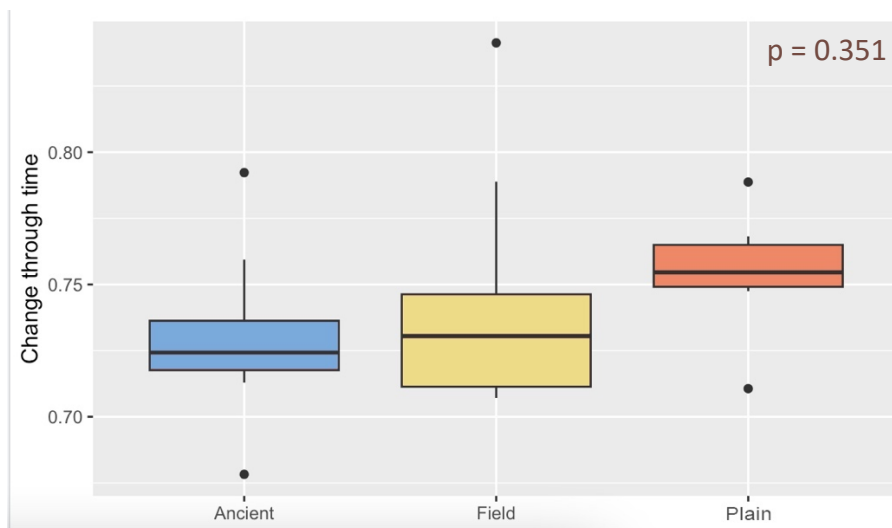


Figure 10: Changes in composition between 1998 and 2022 grouped by land-use history. The p-value is derived from an ANOVA and show no significant difference between the land-use history groups.

4 DISCUSSION

4.1 Change in composition

When comparing how the forest stands change through time, the average arrow in Figure 8A is a close match to the direction of the vectors of pH and moisture (Figure 7). The negative correlation between NMDS2 and moisture suggests that the forests have become moister over time. Conversely, the positive correlation between NMDS2 and pH indicates a decrease in pH values, showing that the stands have turned more acidic. Moisture and soil acidity are closely related, with higher moisture levels leading to more acidic soils (Keddy, 2017).

Anthropogenic disturbance often includes drainage of the natural hydrology when establishing a forest as it increases the survival rate of trees used in plantations (Brookhuis and Hein, 2016). Modern management try to mimic the processes of natural habitats, including filling in ditches for water to naturally moisten the soil to encourage the growth of rarer species associated with wetter habitats (Brunet et al., 2010). This is done in the Bidstrup forest stands, increasing the moisture over time. Soil acidity can be highly influenced by moisture content of the stand, as well as the quality and amount of leaf litter being put into the system, and a decrease in pH is a natural part of aging deciduous forest where beech leaves fall to the ground every autumn (Persson et al., 1987).

4.2 Forest stands characteristics

Certain forest stands exhibited atypical structural characteristics, deviating from typical forest composition by lacking close-growing trees and a closed canopy cover. Such stands, identified as outliers in the dataset, may not be recognized as forests by casual observers. BA5 is one such outlier and is the stand with the highest species richness, containing a total of 61 species. This stand has been subjected to heavy management and clearing of trees, leading to an increase in light, and subsequent large proportion of species with high light requirements (Su et al., 2019). Species include *Trifolium repens* and *Prunella vulgaris*, which have a high tolerance for both light and disturbance (Tyler et al., 2021). The stand contains a cleared area that spans plots 2, 3 and 4, including a footpath with which plot 4 was partially situated on top of, explaining the high species richness as the soil seed bank can quickly germinate after increased exposure to light (Eriksson, 1996; Hill, 1979; Mercier et al., 2019). The end of the transect was characterized by a higher density of beech trees, as well as typical forest conditions and a prevalence of common forest species, as management was

less prominent here. The high species richness and variation in species within the same transect shows the influence active management can have (Morton and Hill, 2014).

Some stands were ambiguous in which species of tree was dominant, particularly among oak stands. Due to oak trees' high light requirements, especially during their juvenile phase, they are less competitive than other common tree species (Castaño-Santamaria et al., 2021). When located in close proximity to stands dominated by other tree species like beech or hornbeam (*Carpinus betulus*), oak stands are easily overtaken by the more competitive trees (Kunstler et al., 2005; Le Due and Havill, 1998). Hornbeam was observed in three different oak stands, with an abundance of 31 in OF1, three times as high as oak. Having a higher tolerance for shade and a lower compensation point of light will give beech and hornbeam a competitive advantage, and oak-dominated stands may eventually become overrun in the absence of active management intervention (Le Due and Havill, 1998; Tyler et al., 2021).

4.3 Differences in species occurrence and observer bias

In the examined forest stands, there were several new species observed in the 2022 dataset that were not present in 1998 (Table 3). As they were observed in three or more stands, they are seen as established inhabitants of the Bidstrup forest area, having migrated in from surrounding stands or sprouted from the seed bank (Brunet and von Oheimb, 1998; Eriksson, 1996). None of the disappearing or appearing species are found on the Danish red list of threatened species (Moeslund et al., 2019), though this is to be expected as threatened species are low in numbers and hard to detect with our method of vegetation analysis in such a limited area. *Dryopteris expansa* is a new appearance in the Bidstrup forest, and is an uncommon fern on Zealand (Mossberg and Stenberg, 2014).

Pteridium aquilinum was the only species which showed a preference for ancient forest stands in this thesis, while no other species displayed notable differences in occurrence between ancient and recent stands. *P. aquilinum* is a common fern found throughout Denmark (Mossberg and Stenberg, 2014), and have been shown to have an affinity for ancient forests in areas around England and northern Europe (Hermy et al., 1999). However, this affinity isn't prevalent everywhere, as the fern is indifferent to forest origin in regions where light or sandy soils are present (Peterken and Game, 1984). The substrate of Bidstrup

consists mostly of heavy clayey moraine, which can explain the lack of *P. aquilinum* in recent stands (Gravesen, 2021). Additionally, ferns often require open soils and high humidity to germinate their spores, which may be more readily available in ancient rather than recent forests (Hermy et al., 1999). Other fern species like *Dryopteris carthusiana* and *Gymnocarpium dryopteris* have also been shown to have an affinity for ancient forests, and could be expected to appear with *P. aquilinum* (Hermy et al., 1999; Hermy and Verheyen, 2007). However, these species had no preference in the stands measured for this thesis.

Performing vegetation analysis is highly dependent on the flora knowledge of the people in the field team, and differences in species identification expertise can lead to observation biases which are hard to control for (Milberg et al., 2008). For instance, *Stellaria neglecta* and *Stellaria media* have similar features and may have been subjected to misidentification (Mossberg and Stenberg, 2014). In the same location, *S. neglecta* was only found in 2022 and *S. media* only in 1998, likely because of observer bias rather than the whole populations of *S. media* being outcompeted by a *S. neglecta* population of similar size. *Holcus mollis* and *Holcus lanatus* is another example of possible misidentification observed bias (Milberg et al., 2008). Both species were found in 2022, but only *H. mollis* were reported in 1998. Migration can, however, be the reason for the higher frequency of *H. lanatus*, as this species does have a lower EIV for light (Tyler et al., 2021). All four species can have been present in both years but misidentified or overlooked. A bias of overreporting is likely with other species in the dataset, for example *Dryopteris expansa* (Milberg et al., 2008). This fern was not observed in 1998, but occurred in 6 different stands in 2022, despite its limited distribution and abundance in Denmark (Mossberg and Stenberg, 2014).

4.4 Measuring light and its influence

The NMDS analysis with 2022 species frequency data (Figure 6) revealed that light was the most influential environmental factor in explaining the composition of understory plant community in the forest stands of Bidstrup, mirroring the findings of other literature (e.g., Depauw et al., 2020; Govaert et al., 2021; Hubbell et al., 1999). When considering how the stands have changed between 1998 and 2022, a significant shift in composition was observed along all NMDS axes (Figure NMDS change). The shift occurred in the opposite direction of the explanatory variable of light, suggesting that the stands of 2022 are

comprised of a higher number of shade-tolerant species. This is consistent with the expectation that homogenous forests grow darker with age (Plue et al., 2013).

This thesis used a densiometer and CWM of EIV as measurements of light, with the two values displaying different degrees of light-related influence on stand composition (Figure 6). Our canopies were likely too dense to get good results with a densiometer, with an average canopy density of 12% compared to the recommended 20% or higher (Russavage et al., 2021). Because it did not show a significant correlation with any NMDS axis, the densiometer measurements are deemed suboptimal indicators of light in the investigated stands in Bidstrup. Light is generally a difficult variable to measure as most measurement tools only do point measurements in time, providing values which are highly dependent on weather and current cloud coverage (Francone et al., 2014). Using a densiometer or EIV instead of direct measurements represents efforts to avoid being affected by such variables.

User error could be a possible explanation for the poor performance of the densiometer as a proxy for canopy openness, as three different operators were responsible for recording the measurements, each of whom may have interpreted what constitutes an open quadrant differently based on the guidelines in the instruction manual (Forestry Suppliers inc, 2008). The direction of measurement can also influence the consistency of the results (Russavage et al., 2021). There are several ways to mitigate such user errors: having two people take measurements and averaging their values, having a single person do all canopy measurements, or increased training and consistency checks (Englund et al., 2000). The average of all plots was used as the forest stand value in the analysis of this thesis to minimize the influence of user error, but this approach is not without limitations.

EIV is an established and frequently used indicator of light conditions, as they are not affected by forest stand density and fluctuations in weather (Cornwell and Grubb, 2003; Diekmann, 2003; Perring et al., 2018). However, it does not accurately reflect the light conditions of environments in transition, as changes in species composition require time to adapt to new light environments, for example after the felling of a large tree increase available light (Gálhidy et al., 2006). This is particularly apparent in stands surrounded by other dark stands, where light-demanding species need to migrate large distances or have

long-lived seed banks already present in the soil (Bernhardt-Römermann et al., 2015; Bradshaw, 2004; Eriksson, 1996). Consequently, changes in the composition of species lag behind sudden changes in light conditions, which could influence the light values it provides. It is therefore difficult to assess the degree to which these values accurately describe the light conditions in the investigated forest, but it is nevertheless an established method and generally a good approximation of average light conditions (Diekmann, 2003).

4.5 Ancient forests and forest stand proximity

Though the peninsula of Røsnæs, with close proximity to Bidstrup, has been shown to have compositional differences between ancient woodland, planted woodland and scrub (Petersen, 1994), no significant differences in vegetation composition were found between forest stands of different forest histories, neither from visual inspections of the NMDS analysis (Figure 6), nor from the ANOVA results (Figure 9). This is in line with the findings of Graae et al. (2003) which showed no difference between soil or vegetation composition in the same forest stands in Bidstrup. This can nonetheless change as environmental variables evolve. Ancient and recent forests have been shown to respond differently to simulated global warming, suggesting that local regulators of canopy closure drive changes through time (Depauw et al., 2020). Only 24 years passed between the two samplings of the Bidstrup stands, making it possible that the stands will diverge more as time passes and the composition responds to higher median temperatures (Castaño-Santamaria et al., 2021).

Forest stand proximity to other stands of different previous usage could have been a problem when looking for big differences. Species' ability to migrate is highly dependent on their dispersal ability and closeness to other suitable habitats (Bernhardt-Römermann et al., 2015; Brunet and von Oheimb, 1998; Hermy et al., 1999). The assumption of forest stands situated on old fields or plains having a lower number of ancient forest species as these have a hard time reestablishing in recent forests (Hermy et al., 1999), were not met in this thesis. As seen in Figure 1, ancient stands, stands on old fields and stands on old plains are situated with close proximity all over Bidstrup, providing favorable conditions for migration, and leaving the stands with a mix of shared ruderal and forest species. Recent forests with high connectivity to ancient forests have greater diversity when compared to isolated recent

forests, suggesting that the stands of Bidstrup have an overall higher diversity than they would without the presence of ancient forest stands (Peterken and Game, 1984).

5 CONCLUSION

For this thesis, 28 forest stands of three different previous land-use history were investigated in Bidstrup, Denmark. The aim was to look for differences in understorey vegetation composition between 1998 and 2022, and whether availability of light and different land-use history influenced the composition. Light is shown to be the most important environmental variable for stand composition, and a significant change in overall forest stand composition was found between 1998 and 2022, in which the forest stands have become darker. This is in line with expectations for aging forest stands as older forests are shown to be darker.

Ellenberg Indicator Values for light showed significant correlations with the analysis, while field measurements using a densiometer did not corroborate the EIV in such dense forest stands. Only one species, *Pteridium aquilinum*, showed affinity to ancient forest, but no significant differences in vegetation composition could be seen in stands of different land-use histories.

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APPENDIX A – OVERVIEW OF FOREST HISTORY

Table A1 provides an overview of the age and planting time of the different forest stands in Bidstrup. The information was obtained from various sources, including topographical maps from 1820s, management plans for the Bidstrup area from 1842, and correspondence with Bo Fritzboøger and forest manager Hans Jessen. All stands are older than 90 years old.

Ancient stands were established forests when the laws “Landboreformerne” and “Fredskovsforordningen” were set in action in 1805 and have been continuously forested areas since before 18th century. Field stands are placed on former agricultural lands which were plowed and fertilized. Plain stands are placed on areas which were formerly used for husbandry and grazing.

Table A1: Forest location, which land-use history group it belongs to, time of which the forest stand was planted and its age. General notes about the forest stands along with notes about management practices provide information about how heavily it has been managed since the previous measurements in 1998.

Forest	History	Planted	Age	Notes and management since 1998
BA1	Ancient	pre 1800	250+	Canopy thinning 2-3 times. Veteranisation of trees in 2022.
BA2	Ancient	pre 1800	250+	Windfall early 1999.
BA3	Ancient	pre 1800	250+	Not possible to examine for this thesis.
BA4	Ancient	pre 1800	250+	Windfall 1999, canopy thinning at least once, thinning in 2020.
BA5	Ancient	pre 1800	250+	Strong canopy thinning of the upper canopy and almost clearing the understory to create a grazed forest in 2012. Veteranisation of trees several times.
BA6	Ancient	pre 1800	250+	Strong canopy thinning of the upper canopy and almost clearing the understory to create a grazed forest in 2012. Veteranisation of trees several times.
BA7	Ancient	Pre 1800	250+	Canopy thinning 3 times.
BF1	Field	c. 1880	142	Canopy thinning and understory thinning one time. Upkeeping forest trails.
BF2	Field	c. 1890	132	Windfall 1999. Canopy thinning and understory thinning one time. Upkeeping forest trails.

BF3	Field	1893	212	The last 20 meters of transect was planted with conifers in 1924, changed for beech at some unknown time later. Canopy thinning and understorey thinning. Upkeeping forest trails.
BF4	Field	1818	204	Not examined for this thesis, turned into a dog park around 1999
BF5	Field	c. 1880	142	<i>No information</i>
BF6	Field	c. 1880	142	Canopy thinning.
BP1	Plain	c. 1920	102	Strong canopy thinning of the upper canopy and almost clearing the understorey to create a grazed forest in 2012. Veteranisation several times.
BP2	Plain	c. 1860	162	Thinning 2-3 times, veteransitation in 2020
BP3	Plain	c. 1860	162	Thinning 2-3 times, veteransitation in 2020
BP4	Plain	c. 1920	102	Thinning 2-3 times, veteransitation in 2020
BP5	Plain	c. 1895	127	<i>No information</i>
BP6	Plain	c. 1890	132	was mixed stand of plain and fields in 1807
OA1	Ancient	pre 1800	250+	Thinning 2-3 times
OA2	Ancient	pre 1800	250+	Thinning 2-3 times
OA3	Ancient	pre 1800	250+	Thinning 2-3 times
OA4	Ancient	pre 1800	250+	Thinning 2-3 times
OA5	Ancient	pre 1800	250+	Thinning 2-3 times
OA6	Ancient	pre 1800	250+	Thinning 2-3 times
OF1	Field	c. 1910	112	Thinning 2-3 times
OF2	Field	c. 1910	112	Thinning 2 times
OF3	Field	1892	130	Thinning 1 time
OF4	Field	c. 1920	102	Thinning 2 times, thinning of understorey in 2019
OF5	Field	c. 1900	122	Thinning 1 time

APPENDIX B – DATAPPOINTS REMOVED OR CHANGED

Table B1 shows an overview of all changes and exclusions which were done when digitalizing the data. Changes of names were mostly a result of a plant only being determined to genus during the spring field season, while being able to be fully determined when re-visiting the sites in summer. Exclusions from the dataset were mostly done when the plant was seen as a young plant in spring but not seen again in the summer and therefore assumed to have perished.

Table B1: The changes which were made to the dataset during digitalization.

Location	Removed/changed datapoints
BA1	<i>Quercus sp.</i> changed to <i>Quer rob</i>
BA2	<i>Carex sp.</i> changed to <i>Carex rem</i>
BA4	Ferns changed to <i>dryo car</i> , <i>athy fil</i> and <i>pter aqu</i> , <i>Carex sp.</i> to <i>Carex rem</i>
BA5	Fern changed to <i>pter aqu</i> and <i>dryo fel</i> , <i>Cirsium sp.</i> to <i>Cirs pal</i> , <i>Cerastium</i> to <i>Cera fon</i> , <i>Epilobium sp.</i> to <i>Epil mon</i> , <i>Rumex sp.</i> to <i>Rume san</i> , <i>Carex sp.</i> removed, <i>Gagea sp.</i> to <i>Gage spa</i>
BA6	“kimplante”, <i>Asteraceae sp.</i> and <i>Agrostis sp.</i> removed, all found in summer but not further investigated. <i>Cerastium sp.</i> to <i>Cera fon</i> , <i>Quercus sp.</i> to <i>Quer rob</i> . <i>Hiracium sp.</i> removed, only found in spring.
BA7	<i>Athyrium sp.</i> changed to <i>Athy fil</i> , <i>Crataegus sp.</i> to <i>Crat lae</i> , <i>Gagea sp.</i> to <i>Gage spa</i>
BF1	Fern changed to <i>pter aqu</i>
BF2	<i>Festuca sp.</i> changed to <i>Fest gig</i> , <i>Epilobium sp.</i> to <i>Epil mon</i> , <i>Rumex sp.</i> to <i>Rume san</i> , <i>Poa sp.</i> to <i>Poa annu</i>
BF3	<i>Betula sp.</i> removed
BF5	Fern changed to <i>Athy fil</i>
BP1	Fern changed to <i>Dryo dil</i> , grass changed to <i>mili effu</i> , <i>Agrostis sp.</i> to <i>Agro cap</i> , <i>Rubus sp.</i> to <i>Rubu ida</i>
BP2	Fern changed to <i>Athy fil</i>
BP3	Fern changed to <i>dryo exp</i> and <i>dryo car</i>

BP4	Fern changed to <i>Dryo exp</i> , <i>Juncus sp.</i> removed
BP5	Fern changed to <i>Dryo fil</i>
BP6	<i>Luzula sp.</i> to <i>Luzu mul.</i> <i>Betula sp.</i> removed
OA1	<i>Quercus sp.</i> to <i>Quer rob</i> , <i>Gagea sp.</i> to <i>Gage spa</i>
OA2	Fern changed to <i>Gymn dry</i> , <i>Picea sp.</i> to <i>Pice abi</i>
OA3	<i>Quercus sp.</i> to <i>Quer rob</i> , <i>Gagea sp.</i> to <i>Gage spa</i>
OA4	Fern changed to <i>pter aqu</i> and <i>athy fil</i> , <i>Poa sp.</i> to <i>Poa nem</i> , <i>Quercus sp.</i> to <i>Quer rob</i>
OA5	Fern changed to <i>pter aqu</i> , <i>Poaceae sp.</i> removed. <i>Luzula sp.</i> to <i>Luzu pil</i> , <i>Poa sp.</i> to <i>Poa nem</i> , <i>Quercus sp.</i> to <i>Quer rob</i>
OA6	Fern changed to <i>Pter aqu</i> , <i>Quercus sp.</i> to <i>Quer rob</i>
OF1	Fern changed to <i>Dryo car</i> , <i>Quercus sp.</i> to <i>Quer rob</i>
OF2	Fern changed to <i>Athy fil</i> , <i>Agrostis sp.</i> removed, <i>Quercus sp.</i> to <i>Quer rob</i>
OF3	Fern changed to <i>Dryo exp</i> and <i>Athy fil</i> , <i>Poaceae sp.</i> , <i>Crataegus sp.</i> to <i>Crat lae</i> , <i>Quercus sp.</i> to <i>Quer rob</i>
OF4	Fern changed to <i>Dryo dil</i> and <i>Dryo dil</i> , <i>Impatiens sp.</i> to <i>Impa par</i> , <i>Quercus sp.</i> to <i>Quer rob</i>
OF5	Fern removed.

APPENDIX C – AVERAGE ELLENBERG INDICATOR VALUES

When an observed plant could only be determined to genus, an average EIV was made for that observation based on the possible species it could have been. EIV values obtained from Tyler et al. (2021). Table C1 shows an overview over the genus which this was relevant for.

Table C1: The species of which an average EIV was made to provide EIV for the observed genus.

Species	Genus
<i>C. cava</i>	<i>Corydalis</i>
<i>C. intermedia</i>	
<i>M. sylvaticum</i>	<i>Melampyrum</i>
<i>M. pratense</i>	
<i>S. cinerea</i>	<i>Salix</i>
<i>S. aurita</i>	
<i>S. caprea</i>	
<i>S. repens repens</i>	
<i>S. hastata</i>	
<i>P. avium</i>	<i>Prunus</i>
<i>P. cerasus</i>	
<i>R. rubrum</i>	<i>Ribes</i>
<i>R. spicatum</i>	
<i>V. riviniana</i>	<i>Viola</i>
<i>V. reichenbachiana</i>	

