



# The effects of land use history on ground vegetation in sycamore (*Acer pseudoplatanus*) stands in southern Sweden

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Swedish University of Agricultural Sciences, SLU  
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# The effects of land use history on ground vegetation in sycamore (*Acer pseudoplatanus*) stands in southern Sweden

*Effekter av markanvändningshistorik på markvegetationen i bestånd av sykomorlönn (Acer pseudoplatanus) i södra Sverige*

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## Abstract

This study analyzes the influence of historical land use, environmental conditions, and stand characteristics on ground vegetation in sycamore (*Acer pseudoplatanus*) plantations in southern Sweden. By examining 30 sample plots with different land-use histories (post-pasture, post-agricultural, and ancient forest), 99 vascular plant species were recorded and categorized into forest specialists, generalists, woody, and open land species. A varied range of ground vegetation diversity among sites was found, although without any significant differences in the mean species richness across land-use histories. However, post-pasture plantations exhibited a significantly higher mean number of woody species (8.5) compared to other categories, which ranged from 4.3 to 5.0 species. Analysis of vegetation layers showed similar mean cover percentages for tree and herb layers across land-use categories, and shrub and moss layers displayed low variability. The cover of the herb layer and the number of generalist species decreased significantly with increased cover of the tree and shrub layers. This implies that denser canopy cover could inhibit the diversity and abundance of herbaceous vegetation. The results of non-metric multidimensional scaling (NMDS) analysis showed that historical land use, alongside soil pH and nitrogen levels, significantly influenced species composition. A strong positive correlation was observed between soil pH and species composition along NMDS Axis 1, as well as between nitrogen levels and Axis 1, indicating that soil fertility is a major driver of species distribution. Light availability and moisture were correlated with species composition along Axis 2, representing a gradient from darker, moister to lighter, drier conditions. Isolated post-agricultural sycamore plantations were found to be colonized by several forest specialist species within 60 years. However, some species, such as *Anemone nemorosa*, remained more abundant in areas with continuous forest cover. Although a direct comparison was not possible due to differences in sample plot size, an analogous study on ground vegetation in oak stands suggests similar trends, indicating that the plant diversity and colonization dynamics of sycamore and oak plantations might be comparable. However, further studies are necessary to confirm this pattern. These findings demonstrate the adaptability of sycamore plantations to different land-use histories and environmental conditions, highlighting their potential as valuable habitats for forest plant species.

*Keywords:* *Acer pseudoplatanus*, forest floor, forest herbs, recent woodland, post-agricultural forest, species richness, herbaceous understorey, plant colonization

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## Abbreviations

|      |                                     |
|------|-------------------------------------|
| D    | Simpson's Diversity Index           |
| NMDS | Non-metric Multidimensional Scaling |

# 1. Introduction

*Acer pseudoplatanus* (sycamore), a broadleaved tree belonging to the *Sapindaceae* family, is the largest native species of the *Acer* genus in Europe (Rusanen & Myking 2003; Weidema & Buchwald 2010). Originating from mountainous regions of Europe, this species thrives best in the temperate climate zone. Its natural range spans northern Asia Minor, central and eastern Europe, and mountain ranges in southern Europe, as well as the Caucasus and the eastern edge of the Caspian Sea (Rusanen & Myking 2003; Jaworski 2011; Krabel & Wolf 2013; Pasta et al. 2016) (Figure 1).



Figure 1. Map of the distribution range of the sycamore in Europe, including marked locations of introduction and naturalization (▲), as well as isolated populations (X), and marked study area (modified after Caudullo et al. 2017).

Since the 17th century, it has been introduced and has established self-sustaining populations north of its original range, notably in countries such as Denmark (1765) and Norway (1771). Remarkably, it even flourishes in the Arctic region of Norway, near Tromsø, where it grows vigorously and propagates (Larsen et al. 2005; Weidema & Buchwald 2010; Møller 2016). In southern Sweden, the first reports of

sycamore date back to the 1800s. Presently, sycamore trees are widely spread throughout southern Sweden, exhibiting a tendency for rapid colonization. The Swedish Forest Agency designates sycamore as an introduced species within the country (Berg & Nilsson 1997; Ringagård 2009; Sjöstedt 2012; Felton et al. 2013).

## 1.1 Ecology of sycamore

Sycamore trees are prevalent in various types of forests, particularly those dominated by ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*). In these forests, sycamores often form a significant part of the main canopy alongside beech (Larsen et al. 2005). In mixed deciduous forests, sycamore trees coexist with other species such as oak (*Quercus* spp.), hornbeam (*Carpinus betulus*), and lime (*Tilia* spp.) (Szymanski 1985; Hein et al. 2009; Jaworski 2011; Iliev et al. 2022). While it is rarely found in pure stands, sycamore does cover small areas on steep limestone slopes where it forms its communities within the *Acerion pseudoplatani* alliance (Bodziarczyk & Świerkosz 2000; Straigyte & Baliuckas 2015).

Adapted to subatlantic and submediterranean climates, the sycamore thrives in temperate regions (Zareba 1964; Tillisch 2001; Jaworski 2011). Notably resilient to climate fluctuations, it can withstand considerable temperature variations, although spring frosts may occasionally affect young trees. However, due to its rapid growth, such instances typically pose minimal problems (Larsen et al. 2005). Typically found on slopes with ample sunlight exposure, sycamore thrives in areas with high air humidity. It grows in places with average annual temperatures ranging from approximately 5°C to 15°C but struggles in arid and excessively hot environments (Zareba 1964; Bingelli 1994; Joyce et al. 1998; Jaworski 2011; Pasta et al. 2016). The microclimates within maple forests vary significantly, with some stands exhibiting warmer climates compared to others characterized by cooler and moister conditions (Bodziarczyk & Świerkosz 2000).

Sycamore is a shade-tolerant species that thrives in areas with disturbances, particularly along woodland edges with fertile soil conditions. It shows a tendency to become the dominant tree species following various disturbances such as clear cuttings, landslides, wind-throws, or fires (Evans 1984; Boyd 1992; Collet et al. 2008; Felton et al. 2013; Møller 2016).

Sycamore thrives in various soil types but shows a preference for moist, but well-drained soils. It can tolerate sandy or clayey soils, although it flourishes best in soils with a clay content that aids in water and nutrient retention. Additionally, it prefers slightly acidic to neutral soils, with pH levels ranging from 5.5 to 7.5, and shows a particular affinity for soils rich in calcium carbonate (Evans 1984; Suszka et al.

1996; Tillisch 2001; O'reilly 2002; Larsen et al. 2005; Jensen et al. 2008; Seneta & Dolatowski 2008). While it can tolerate occasional waterlogging, prolonged saturation is detrimental to its growth, particularly when water stagnates within 40cm of the soil surface (Jensen et al. 2008). Sycamore positively responds to increased soil nitrogen. Elevated nitrogen levels promote sycamore growth, whereas high organic carbon content hinders its development (Larsen et al. 2005; Jensen et al. 2008; Jerczynski et al. 2018).

Sycamore reaches maturity at a relatively young age. Free-range sycamore trees typically become fertile between the ages of 25 and 30, with seed production intensifying as the tree grows larger (Pigott & Warr 1989; Suszka et al. 1996; Joyce et al. 1998; Shouman et al. 2017; Iliev et al. 2022). Sycamore seeds demonstrate robust adaptation to shaded or partially lit environments and have the ability to spread over relatively long distances (Boyd 1992; Rusanen & Myking 2003; Collet et al. 2008; Barthélémy et al. 2009; Weidema & Buchwald 2010; Felton et al. 2013). Despite their early high tolerance for shade, sycamore trees progressively require more light as they mature (Tillisch 2001; Delagrangé et al. 2006; Collet et al. 2008; Weidema & Buchwald 2010; Felton et al. 2013).

## 1.2 Land-use history

Anthropogenic land use changes have significantly impacted biodiversity in temperate ecosystems, primarily due to habitat loss and fragmentation. This impact is caused by the historical clearing of forests for agriculture, followed by tree planting or spontaneous regeneration of abandoned agricultural land. These processes have created a mosaic of agricultural fields, post-agricultural forest patches, and parts of ancient forests in the present landscape (Peterken & Game 1984; Flinn & Vellend 2005; Hermy & Verheyen 2007; Jamoneau et al. 2012; Brunet et al. 2021). These landscapes prompt fundamental ecological questions about the factors influencing species abundance and distribution (Flinn & Vellend 2005; Hermy & Verheyen 2007).

The legacies of past agricultural practices continue to shape forests and their plant communities across Europe. The vegetation and soil composition of forests that have regrown on former agricultural land differs significantly from those that were never cleared or from those that existed before agricultural disturbances (Koerner et al. 1997; Flinn & Vellend 2005; Hermy & Verheyen 2007). Agriculture can influence vegetation directly by eliminating local forest species and their propagules, and indirectly by modifying environmental conditions (Flinn & Vellend 2005).

Forest plants, in particular, possess life-history traits that make them vulnerable to habitat loss and fragmentation, such as restricted seed dispersal, brief seed dormancy, poor seedling recruitment, and protracted pre-reproductive periods (Whigham 2004; Flinn & Vellend 2005; Brunet et al. 2021). The current vegetation in these forests often reflects the specific type of former agricultural use, whether pasture, croplands, or hay meadow, with species responding differently to each form of agriculture (Koerner et al. 1997; Wulf 2004; Flinn & Vellend 2005). For instance, herbaceous species that favor open environments are the first to colonize old fields, but the species richness and composition of old pastures are often more similar to that of ancient forests. This similarity is partly due to the absence of plowing, which allowed remnants of forest plant populations to survive (Glitzenstein et al. 1990; Koerner et al. 1997; Wulf 2004; Flinn & Vellend 2005).

### 1.3 Objectives of the thesis

Forests are encountering intricate challenges, posing risks to their biodiversity and long-term stability. With diseases and aggressive pests on the rise, coupled with complex climate changes, forest ecosystems are confronted with numerous hurdles (Broadmeadow et al. 2005; Sturrock et al. 2011). To address these challenges and bolster stand resilience, maintaining species diversity is crucial (Thompson et al. 2009).

Sycamore emerges as a potential solution to impending issues. Its ecological advantages, such as enhancing soil fertility with valuable mineral compounds, along with its beneficial economic value as a premium timber species, are gaining recognition across Europe (Szymanski 1985; Rusanen & Myking 2003; Hein et al. 2009; Zastocki et al. 2012). Sycamore, with its capacity to adjust to changing climates, could fill the ecological gap left by declining ash or elm (*Ulmus* spp.) populations due to devastating diseases (Felton et al. 2013; Santini & Faccoli 2015).

Given the potential significance of sycamore for future forest ecosystems, it becomes important to understand its impact on ground vegetation diversity, as this layer contains a large part of the vascular plant diversity in temperate forests (Gilliam 2016). However, knowledge regarding the species composition and diversity of ground vegetation in sycamore stands planted outside its natural range is limited. Therefore, this study aims to fill this knowledge gap for southernmost Sweden.

In southern Sweden, sycamore stands have been planted for timber production since the 1940s, on sites with varying land-use histories (Brunet et al. 2012). Many forest herbs have a relatively low dispersal capacity and the composition and diversity of

the ground vegetation are, therefore, strongly influenced by land-use history (Flinn & Vellend 2005). To unravel the relative effect of former land use, this study compares sycamore stands with different land-use histories.

Based on the study by Brunet (2007) and utilizing data on forest history, stands were selected from the following categories:

1. plantations on ancient woodland sites without previous Norway spruce (*Picea abies*) plantation;
2. plantations on ancient woodland sites with previous Norway spruce plantation;
3. plantations on formerly open pastures contiguous with ancient woodland;
4. plantations on former arable land contiguous with ancient woodland;
5. plantations on former arable land isolated from ancient woodlands by open land.

The following hypotheses were tested, based on the general assumption that plant species richness is higher in stands with less historical disturbance:

1. a) Plantations on ancient woodland sites exhibit the highest number of plant species, and  
b) contain more forest specialist species compared to other stands.
2. Plantations on ancient woodland sites without previous Norway spruce contain more species than plantations with previous Norway spruce.
3. Plantations on post-pastures contain more species than plantations on arable land.
4. a) Plantations on arable land contiguous with ancient woodland contain more species compared to isolated plantations on arable land, and  
b) contain more forest specialist species than isolated plantations on arable land.
5. The species composition of sycamore plantations differs depending on land-use history.

## 2. Materials and methods

### 2.1 Study area

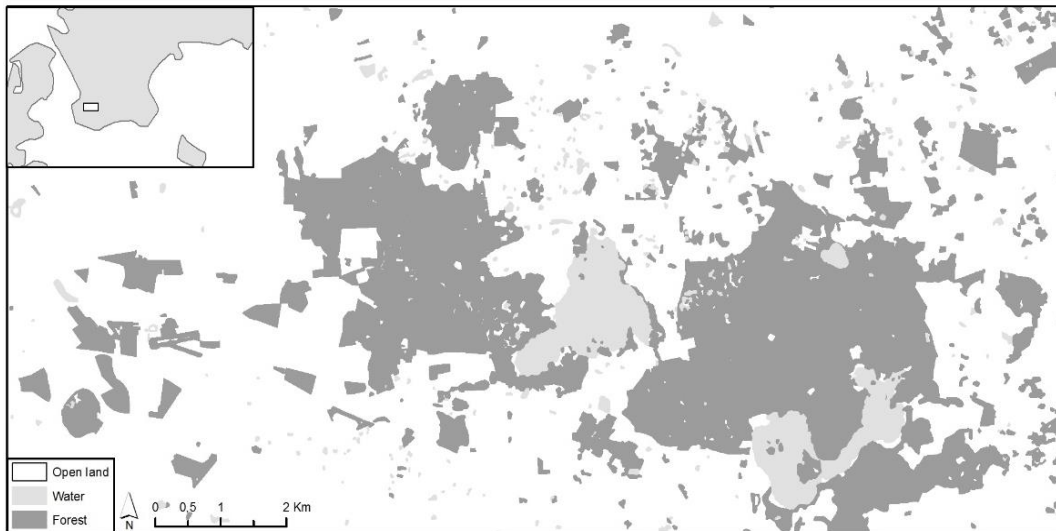
The study was carried out in sycamore plantations within the forests of Torup and Skabersjö (55°32'N, 13°11'E), located in the nemoral vegetation zone, Skåne region of southernmost Sweden (Figure 2), where the mean annual temperature in the study area is around 9°C, and the mean annual precipitation varies from approximately 650 to 700 mm. In the study area, the typical duration of the vegetation period spans approximately 230 days (data from smhi.se, mean values 1991-2020, retrieved 3 August 2024).

The study site lies within a terrain shaped by glacial moraines overlaying early Tertiary limestone and altitudes fluctuate between 25 meters and 75 meters above sea level. The varied topography and historical land usage have resulted in a diverse array of forest soils, comprising eutric and dystric cambisols, as well as podsols found in sufficiently drained locations. Primarily, these wooded areas are characterized by the dominance of pedunculate oak (*Quercus robur*) and European beech (*F. sylvatica*) (Brunet 2007; Brunet et al. 2011). Furthermore, deciduous hardwood forests (identified as *Quercus-Fagetum*) are commonly found in well-drained areas with dystric and eutric cambisols, as mentioned by Brunet (2004).

In the past, particularly during the mid-Holocene period, the landscape of this Swedish region was predominantly characterized by mixed oak forests, as emphasized by Berglund (1992) and Brunet (2007). The recent historical context had a relevant influence on the present structure of this area. The conversion of arable land, pastures, and ancient forests into plantations by the estate foresters since approximately 1920 has significantly expanded the overall forest area, primarily comprising plantations of Norway spruce (*P. abies*), oak, and beech, but also including sycamore plantations (Brunet 2004; Brunet 2007; Brunet et al. 2011).

Specific areas within this forest were identified based on research of historical sources such as maps and forest management plans (Brunet 2004, 2007; Brunet et al. 2011, 2021). The study area's central and eastern regions are dominated by two

large, contiguous forests, with plantations adjacent to ancient woodland sites or connected by newer forests, while the western part is surrounded by arable land and features an agricultural landscape with a few isolated forest patches (Figure 2) (Brunet 2004; Brunet 2007; Brunet et al. 2011; Brunet et al. 2021).



*Figure 2. Map of the forests of Torup and Skabersjö estates. Most of the studied sycamore stands are located in the western of the two large forest areas on the map, while the isolated post-arable stands are located in some of the smaller westernmost forest patches. The insert map shows the location of the study area in southernmost Sweden (map courtesy of Emma Holmström).*

The term “ancient forest” refers to areas that have been continuously wooded since the earliest survey maps. They currently include large areas of naturally regenerated managed beech forest, managed plantations of both coniferous and broadleaved trees, and semi-natural mixed broadleaved stands. Sycamore plantations were either directly established on formerly arable land and open pastures or succeeded after one generation of Norway spruce (Brunet 2004; Flinn & Vellend 2005; Brunet 2007; Brunet et al. 2011).

The plantations of sycamore in the study area are unique within Sweden due to their high number of stands, wide range of stand ages, and varying degrees of spatial isolation from colonization sources, providing an opportunity to study the long-term colonization processes of forest plant species within relatively uniform environmental conditions (Brunet 2004; Brunet 2007; Brunet et al. 2011).



## 2.2 Site selection

Using information on land-use history in a series of historical maps and forest management plans, 30 stands were selected for research (see Appendix 1). The selected stands included six plots each in the following land-use categories:

1. Plantations on ancient woodland sites without prior Norway spruce plantations;
2. Plantations on ancient woodland sites with prior Norway spruce plantations;
3. Plantations on formerly open pastures contiguous with ancient woodland;
4. Plantations on former arable land contiguous with ancient woodland;
5. Plantations on former arable land isolated from ancient woodland by open land.

These woodlands managed for wood production, are regularly thinned and feature canopies primarily dominated by planted sycamore, with occasional oak, beech, birch (*Betula pendula*), ash, and larch (*Larix decidua*). The stands vary in age between 40 and 85 years, with a mean age of approximately 60 years (Appendix 1).

Plots selected for this study have not been recently thinned, as thinning temporarily disturbs soil and light conditions resulting in short-term changes in ground vegetation abundance and composition.

## 2.3 Field survey

The floristic survey was conducted during 2023 and 2024 in 30 stands with sycamore as a main canopy species. Summer species were surveyed between 14 September and 20 September 2023, and vernal species were studied between 18 April and 21 April 2024.

In each of the 30 stands, a sample plot area of 10 x 10 m was selected within the interior part of stands dominated by sycamore in the canopy layer. Within each 100 m<sup>2</sup> plot, all species of herbaceous vascular plants, shrubs, and trees shorter than 1 m were documented as herb layer vegetation (ground cover, layer C). The percentage of ground cover for each species was visually estimated using the Braun-Blanquet cover classes (Braun-Blanquet 1932), ranging from 0.5% to 100%: where 5 indicates the species covers 75 to 100% of the sample plot area, 4 indicates 50 to 75%, 3 indicates 25 to 50%, 2 indicates 5 to 25%, 1 indicates 1 to 5%, and + indicates less than 1%. Additionally, all tree species exceeding 8 meters in height (trees, layer A) and woody species ranging from 1 to 8 meters in height (woody understory, layer B) were separately recorded within each plot. The total cover

percentage for each of the three layers was also estimated. Furthermore, the cover classes for species in layers A and B were documented, and the total cover of epigeic bryophytes (layer D) was estimated in all plots.

## 2.4 Data analysis

All herbaceous species were classified into three primary habitat preference groups (Heinken et al. 2022). The first group, forest specialist species (categories 1.1 and 1.2 in Heinken et al. 2022), occurs exclusively in forests, including closed-canopy areas and forest edges. Forest generalist species (category 2.1) are found in both forests and open areas. The third group, open land species (categories 2.2 and O), includes all other species that do not fit the criteria for forest specialists or generalists. Additionally, woody species in the herbaceous layer (<1m) were treated as a separate group (Appendix 2).

Differences in mean species richness and the number of forest and woody species across land-use categories were compared using interval plots with means and 95% confidence intervals. Statistical significance was tested with ANOVA and Tukey-test or with the Kruskal-Wallis test, followed by pairwise Mann-Whitney U- tests for non-normally distributed data, specifically the species richness of habitat preference groups, the cover of vegetation layers, and the abundance of individual forest specialist species with occurrence in at least nine sample plots (30% frequency). In addition, also abundance of *Anemone nemorosa*, the dominating vernal species, was tested. These statistical analyses were performed in Minitab 21.4.3 (Minitab Inc., 2024).

Non-metric Multidimensional Scaling (NMDS) analysis was conducted using the software program PAST4 (Hammer & Harper 2024). The NMDS was performed using the abundance class values (Braun-Blanquet ranges) and the Bray-Curtis similarity index, with 9999 permutations, was selected due to its ability to effectively quantify similarity or dissimilarity in species abundance across land-use categories (Ho 2008). Additionally, a PERMANOVA test with 9999 permutations was applied in PAST4 to evaluate whether there were significant differences in composition between land-use categories.

The following environmental variables were included as supplementary variables in the NMDS ordination to explain their influence on species composition. Based on Tyler et al. (2021), unweighted mean indicator values for light, moisture, pH, and nitrogen were calculated for the herb layer (C) and analyzed to explain variation along the ordination axes in NMDS. These variables were also used to analyze differences between the five land-use groups. Indicator values had a normal

distribution, allowing the application of ANOVA and the Tukey test. Furthermore, linear regression analyses were performed to explore the relationship between light levels and tree canopy cover, as well as the relationship between access to light and species richness in sycamore plantations. These statistical analyses were performed in Minitab 21.4.3 (Minitab Inc., 2024).

Simpson's Diversity Index was calculated for all plots. Simpson's Diversity Index (D) quantifies the association between species richness (the variety of different species present) and species evenness (the distribution of individuals among those species) within an ecosystem (Mendes et al. 2008), where:

$$D = \frac{N(N - 1)}{\sum n(n - 1)}$$

N = total number of organisms of all species, n = total number of organisms of a given species.

Based on Tomascik and Sander (1987), the diversity index was computed for all identified species using Braun-Blanquet cover classes, where:

$$D = \frac{C(C - 1)}{\sum c(c - 1)}$$

C= total coverage of all species, c= total coverage of an individual species.

To simplify the calculations, Braun-Blanquet cover classes were converted to their corresponding percentage ranges by selecting the mean value within each range: Class 5 to 88%, Class 4 to 63%, Class 3 to 38%, Class 2 to 15%, Class 1 to 3%, and Class + to 1%. Variations in the diversity index values between different stand groups were compared using ANOVA, following a normality test.

## 3. Results

### 3.1 Species richness

A total of 99 vascular plant species were identified across all plantation categories, with species numbers varying among the different categories (Table 1). Furthermore, within the identified species, 27 were classified as forest specialists, 34 as forest generalists, and 8 as open land species. Additionally, 30 woody species were recorded in the herbaceous layer (Appendix 2). Among the forest specialists, three species (*Adoxa moschatellina*, *Anemone ranunculoides*, and *Gagea spathacea*) were classified as vernal species. Similarly, among the generalist species, three were characterized as vernal species (*A. nemorosa*, *Gagea lutea*, *Ranunculus ficaria*).

Table 1. Number of vascular plant species found in sample plots in sycamore plantations with different land-use histories. Species classification of herbaceous species into forest specialists, generalists, and open land species according to Heinken et al. (2022).

| Stand type      | Total | Specialists | Generalists | Open land | Woody |
|-----------------|-------|-------------|-------------|-----------|-------|
| All plots       | 99    | 27          | 34          | 8         | 30    |
| Ancient         | 46    | 17          | 17          | 3         | 9     |
| Ancient-spruce  | 50    | 18          | 19          | 0         | 13    |
| Pasture         | 61    | 19          | 19          | 1         | 22    |
| Arable adjacent | 54    | 20          | 19          | 2         | 13    |
| Arable isolated | 47    | 12          | 16          | 3         | 15    |

In the ancient woodland sites with prior Norway spruce category, 50 species were recorded. Both the ancient woodland sites without prior Norway spruce (46) and former arable land isolated from ancient forest categories exhibited similar species counts, each comprising 47 species. The open pasture contiguous with the ancient forest category displayed the highest species count, with 61 species, followed closely by the post-arable category, which recorded 54 species. The total number of forest specialist species varied from 17 to 20 in all categories, except for the isolated arable plots where only 12 species were recorded (Table 1).

Mean total species richness in the herb layer varied from 19.0 to 23.5 species, without any significant differences ( $p > 0.05$ ) between the different stand categories (Fig. 3). Hypotheses 1a, 2, 3, and 4a were therefore rejected.

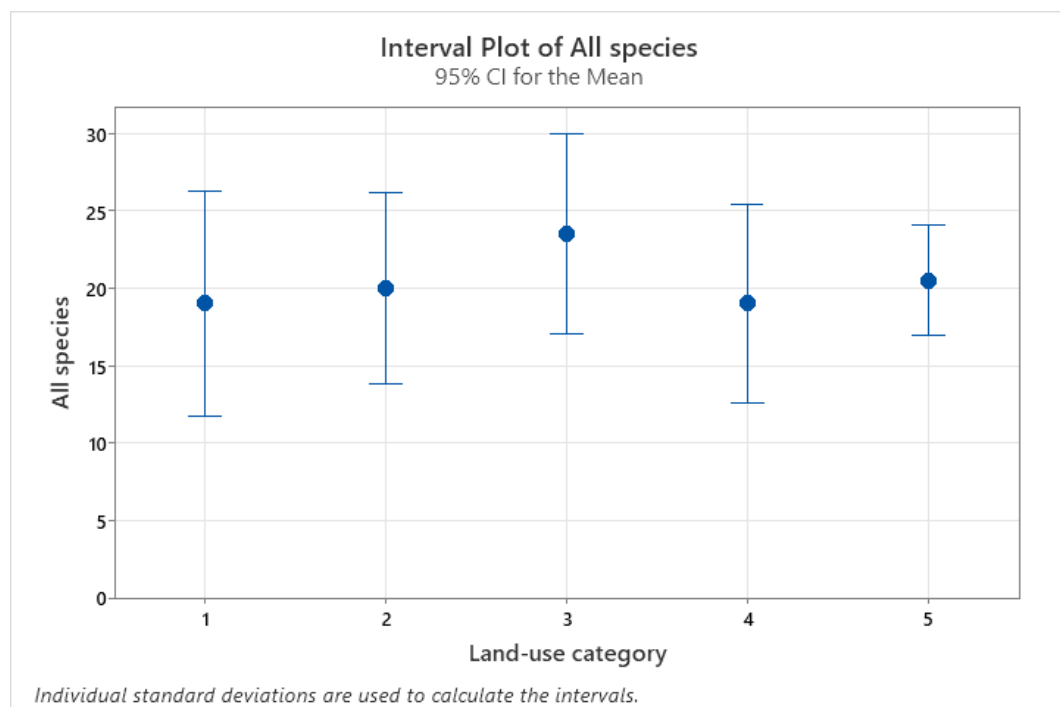


Figure 3. Interval plot of the total number of vascular plant species in the herb layer of sample plots in sycamore plantations of different land-use categories. Given are mean values and 95% confidence intervals. Land-use categories are 1-ancient, 2-ancient-Picea, 3-pasture, 4-arable-adjacent, and 5-arable-isolated. Differences between pairs of plot groups are all non-significant ( $p > 0.05$ ) according to ANOVA and Tukey-test.

Mean number of forest specialist species varied from 5.7 to 8.7 in the different land-use categories. There was a slight trend of decreasing species richness with increasing historical disturbance intensity, but variation between plots of the same category was large and no significant differences ( $p > 0.05$ ) were observed (Fig. 4). Hypotheses 1b and 4b were therefore rejected.

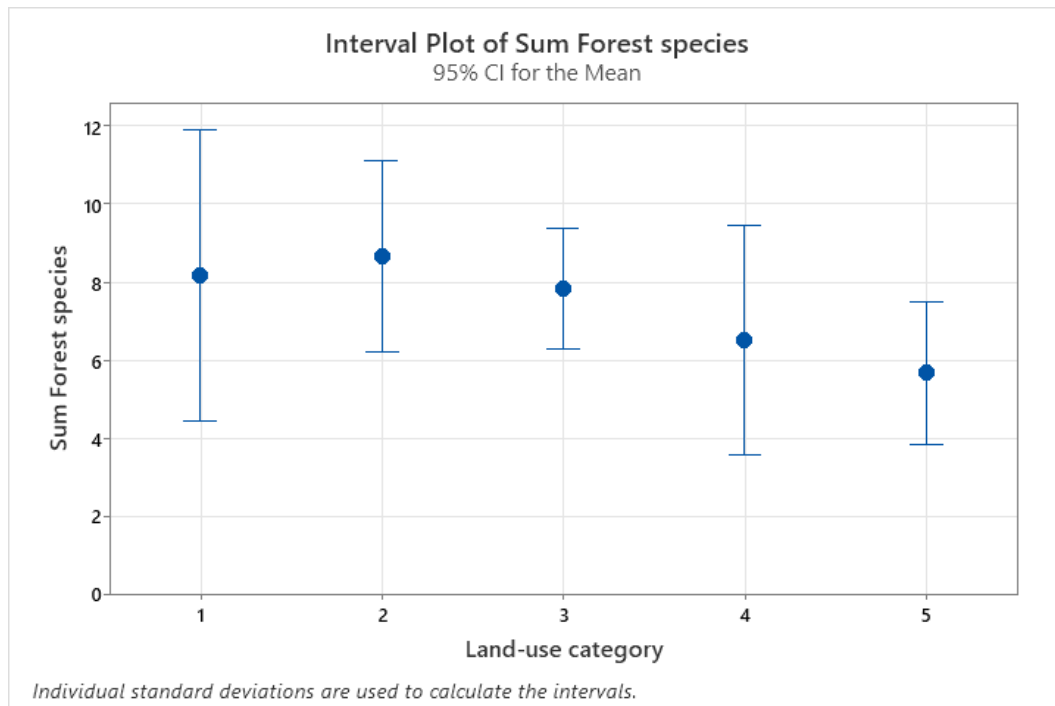


Figure 4. Interval plot of the number of forest specialist plant species in the herb layer of sample plots in sycamore plantations of different land-use categories. Given are mean values and 95% confidence intervals. Land-use categories are: 1-ancient, 2-ancient-Picea, 3-pasture, 4-arable-adjacent, and 5-arable-isolated. Differences between pairs of plot groups are all non-significant ( $p > 0.05$ ) according to ANOVA and Tukey-test.

Mean number of generalist species varied from 6.0 to 9.2 in the different land-use categories (Appendix 3a). There was a slight trend of increasing species richness with increasing historical disturbance intensity, but variation between plots of the same category was large and no significant differences ( $p > 0.05$ ) were observed (Appendix 3a). Similarly, there were no significant differences ( $p > 0.05$ ) in the richness of open land species among these stand types, which generally were very low (Appendix 3b).

The mean number of woody species was relatively consistent and low in ancient woodlands with and without previous Norway spruce, post-arable plantations adjacent to ancient woodlands, and former arable land isolated from ancient forests, all ranging from 4.3 to 5.0 species. However, post-pasture plantations had a notably higher mean number of 8.5 woody species (Figure 5). There were no significant differences ( $p > 0.05$ ) across all categories, except for ancient forest and post-pasture, where a significant difference was observed ( $p = 0.033$ ).

Statistical analysis revealed no significant differences ( $p > 0.05$ ) in Simpson's Diversity Index across the various stand types for all identified species.

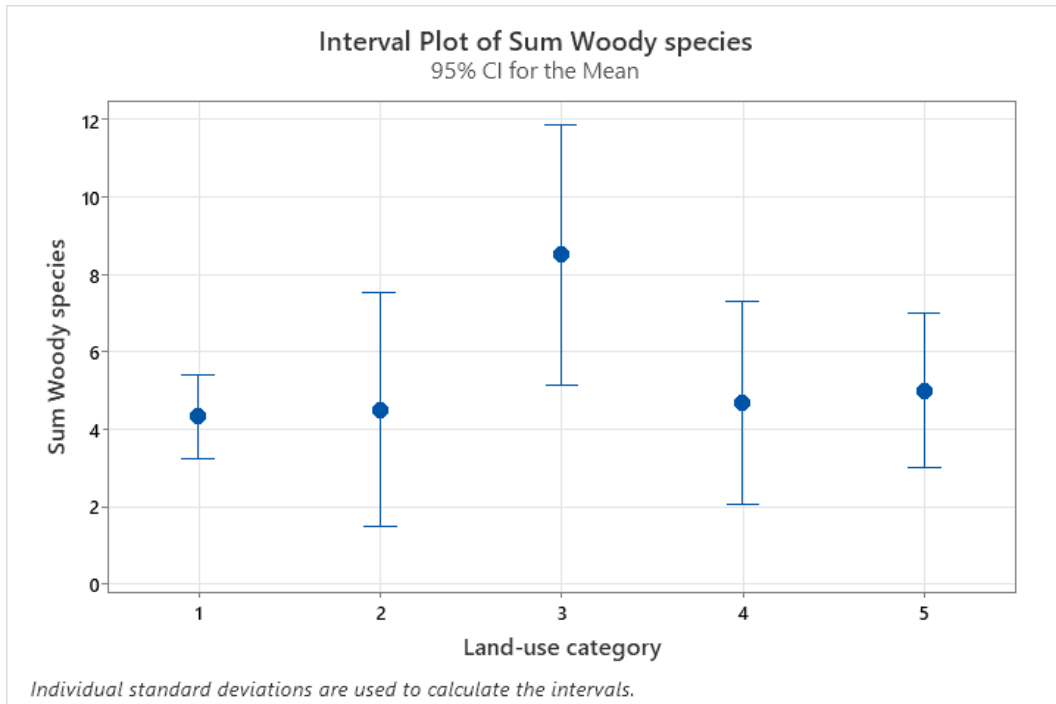


Figure 5. Interval plot of the number of woody plant species in the herb layer of sample plots in sycamore plantations of different land-use categories. Given are mean values and 95% confidence intervals. Land-use categories are: 1-ancient, 2-ancient-Picea, 3-pasture, 4-arable-adjacent, and 5-arable-isolated. Differences between pairs of plot groups are all non-significant ( $p > 0.05$ ) according to ANOVA and Tukey-test, except for the pair between category 3 and category 1 (ANOVA:  $p=0.033$ ;  $F=3.11$ ,  $R\text{-sq: } 33.2\%$ ).

### 3.2 Species distribution

There was a large variability concerning distribution patterns among forest specialist species (Table 2). Among the 13 species with an overall frequency of at least 30%, Kruskal-Wallis tests revealed significant differences in cover between plot groups for six species. *Lamiastrum galeobdolon* and *Melica uniflora* were ranked highest in ancient plots, *Dryopteris carthusiana* and *Oxalis acetosella* ranked highest in post-pasture plots, *Mercurialis perennis* ranked highest in post-arable plantations, and *Schedonorus giganteus* was ranked highest in isolated post-arable plantations. No significant differences in mean ranks of abundance classes were found for the remaining seven species (Table 2, Appendix 4). In addition, *A. nemorosa* was ranked highest in ancient plots (Table 2). While this species was present in several post-agricultural sample plots, it still had a much lower abundance there compared to plots in ancient forest (Figure 6).

Table 2. Frequency of forest specialist species and *Anemone nemorosa* in sample plots in sycamore plantations with different land-use histories (n=6 per category). P-values according to Kruskal-Wallis tests of the cover class estimates.

| Species/plot group               | Ancient | Ancient<br>( <i>Picea</i> ) | Post-<br>pasture | Post-<br>arable | Isolated<br>P-a | P-<br>value  |
|----------------------------------|---------|-----------------------------|------------------|-----------------|-----------------|--------------|
| <i>Anemone nemorosa</i>          | 100     | 100                         | 50               | 50              | 50              | <b>0.001</b> |
| <i>Athyrium filix-femina</i>     | 67      | 50                          | 17               | 17              | -               | 0.054        |
| <i>Circaea lutetiana</i>         | 50      | 17                          | 17               | 50              | 33              | 0.327        |
| <i>Dryopteris carthusiana</i>    | 33      | 67                          | 100              | 17              | 67              | <b>0.024</b> |
| <i>Lamium galeobdolon</i>        | 67      | 67                          | 17               | -               | 17              | <b>0.019</b> |
| <i>Melica uniflora</i>           | 67      | 83                          | 33               | -               | -               | <b>0.008</b> |
| <i>Mercurialis perennis</i>      | 50      | 33                          | -                | 100             | -               | <b>0.001</b> |
| <i>Milium effusum</i>            | 67      | 100                         | 67               | 83              | 83              | 0.129        |
| <i>Oxalis acetosella</i>         | 50      | 50                          | 83               | 17              | -               | <b>0.040</b> |
| <i>Poa nemoralis</i>             | 83      | 50                          | 83               | 33              | 83              | 0.227        |
| <i>Schedonorus giganteus</i>     | -       | 33                          | 17               | 33              | 83              | <b>0.022</b> |
| <i>Stellaria holostea</i>        | 67      | 100                         | 100              | 33              | 67              | 0.322        |
| <i>Stellaria nemorum</i>         | 50      | 67                          | 17               | 17              | 50              | 0.180        |
| <i>Viola reichenb./riviniana</i> | 67      | 50                          | 83               | 17              | 17              | 0.252        |

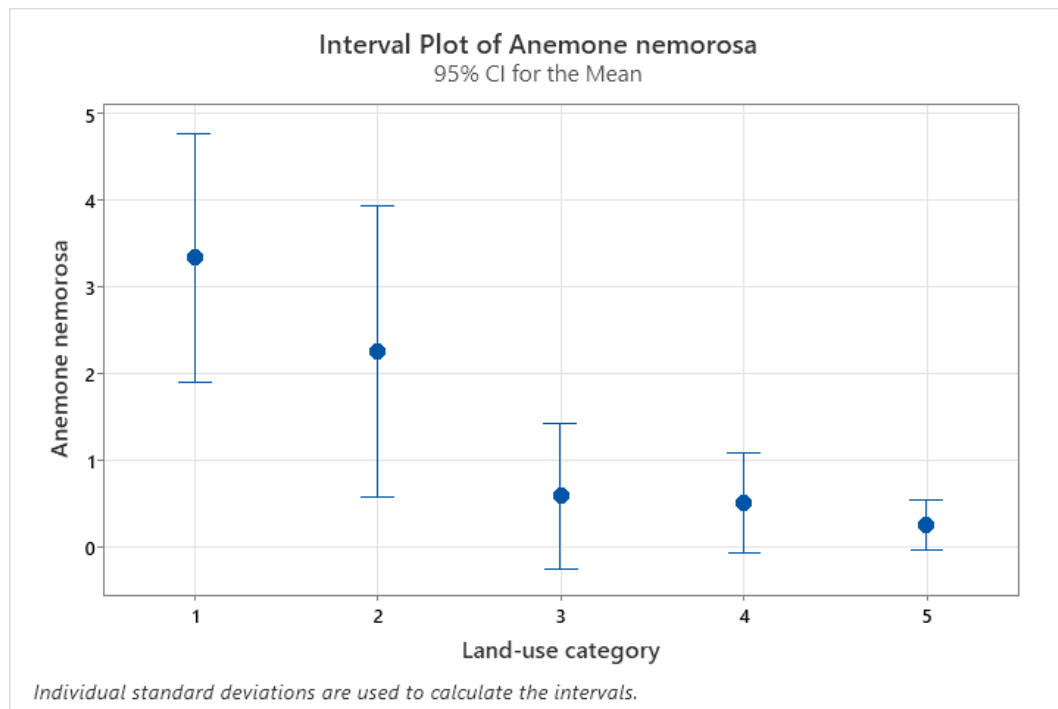


Figure 6. Interval plot of abundance class of *Anemone nemorosa* in sample plots in sycamore plantations of different land-use categories. Given are mean values and 95% confidence intervals. Land-use categories are: 1-ancient, 2-ancient-*Picea*, 3-pasture, 4-arable-adjacent, and 5-arable-isolated. Differences between pairs of plot groups are significant ( $p < 0.05$ ) according to pairwise Mann-Whitney U-tests for pairs between categories 1 and 3 ( $p=0.022$ ), 4 ( $p=0.041$ ), and 5 ( $p=0.035$ ) and between categories 2 and 5 ( $p=0.037$ ).



### 3.3 Vegetation layer abundance

The mean cover (%) of the tree layer was relatively similar across land-use categories and ranged from 69 to 82%, while the mean cover of the shrub layer varied from 10 to 22%. The mean herb layer cover varied from 53 to 71%. The mean cover of the moss layer was generally low and varied from 3 to 9% (Appendix 5a-d). There were no statistically significant differences among pairs of land-use categories for the four different vegetation layers. The cover of the herb layer and the number of generalist species both decreased significantly with increasing cover of the tree and shrub layer (Figures 7 and 8).

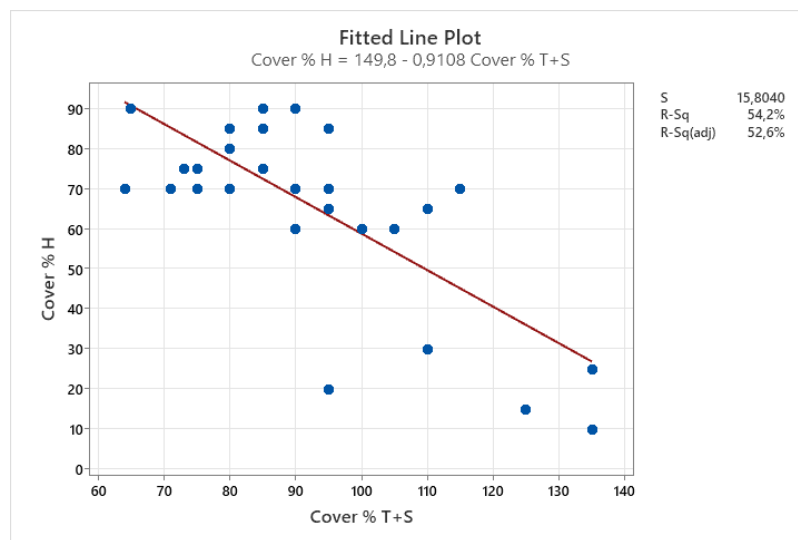


Figure 7. Total cover of the herb layer in relation to the cover sum of the tree and shrub layers. *F*-value 33.1 and *P*-value < 0.001 according to linear regression.

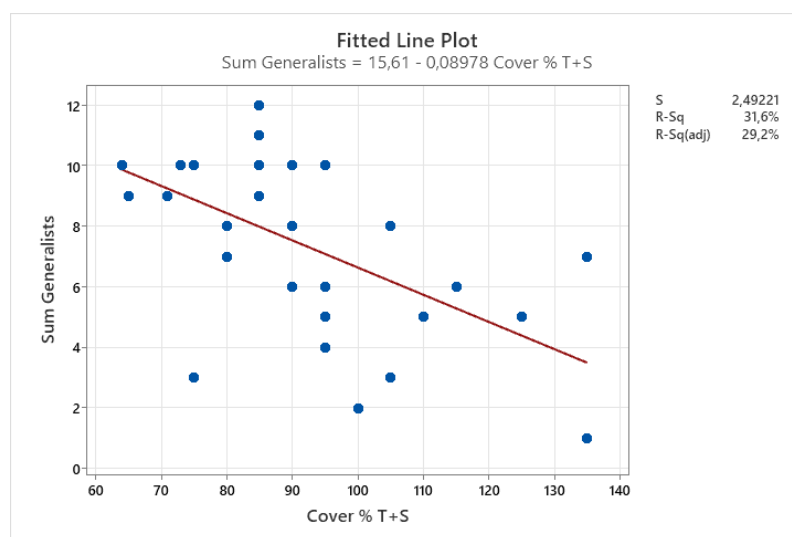


Figure 8. Number of generalist species in relation to cover the sum of the tree and shrub layers. *F*-value 12.9 and *P*-value = 0.001 according to linear regression.

### 3.4 Species composition

The non-metric multidimensional scaling in two dimensions analysis reveals relatively distinct groupings of land-use categories with environmental factors (light, moisture, pH, and nitrogen) represented by lines, indicating their influence on species composition (Figure 9). The first ordination axis mainly separates previously ploughed sample plots (post-arable) from non-ploughed plots (ancient and post-pasture), with nitrogen availability and pH being higher in post-arable plots. The second ordination axis separates ancient woodland plots from many, but not all, non-ancient ones. The results indicate that light availability is higher and soil moisture lower in post-pasture plantations and certain post-arable plots (Figure 9). These results support hypothesis 5. Ancient stands without previous Norway spruce and ancient plantations with Norway spruce before are relatively close, suggesting some overlap in species composition. The post-pasture category forms a separate cluster, indicating that species composition in post-pasture areas is distinct from other plantations. The post-arable category is somewhat dispersed, which suggests a higher variability in species composition in post-arable areas (Figure 9).

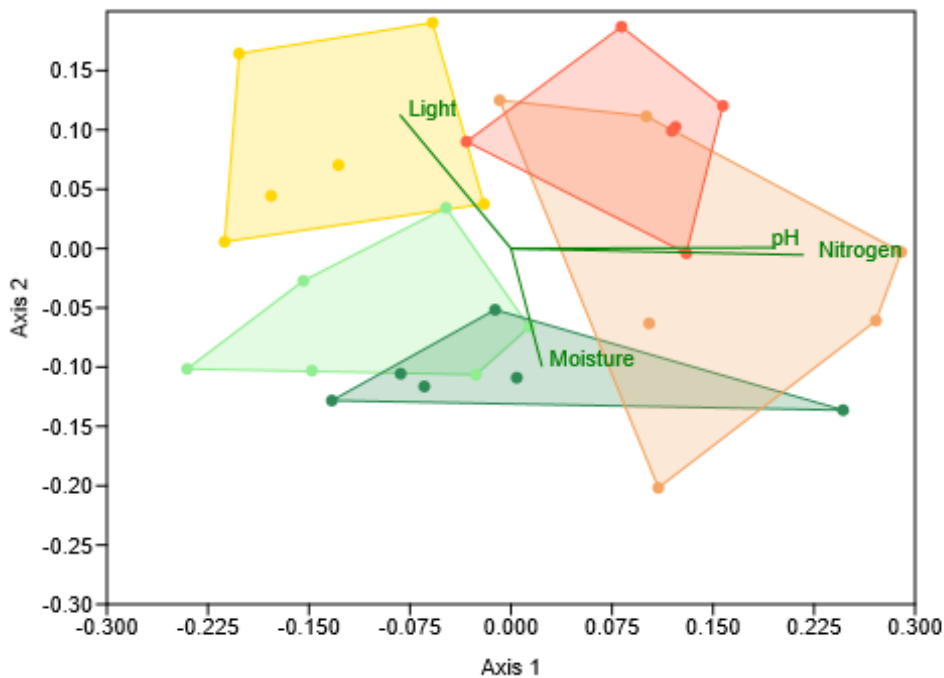


Figure 9. Non-metric multidimensional scaling of species abundance across different land-use categories with environmental variables influencing species composition: dark green- ancient woodland without Norway spruce, light green- ancient woodland with Norway spruce before, yellow- post-pasture, orange- post-arable, red- isolated post-arable. Lines indicate the impact of environmental factors, including mean indicator values for light, moisture, soil pH, and nitrogen, on species composition.

### 3.5 Environmental variables

The PERMANOVA test revealed significant differences in species composition between land-use categories (F-value = 2.911; p-value = 0.0001). Comparisons of the environmental variables indicate which factors may explain the compositional differences between land-use categories. Post-pasture and isolated post-arable stands have higher light indicator values compared to ancient and post-arable plantations (Figure 10).

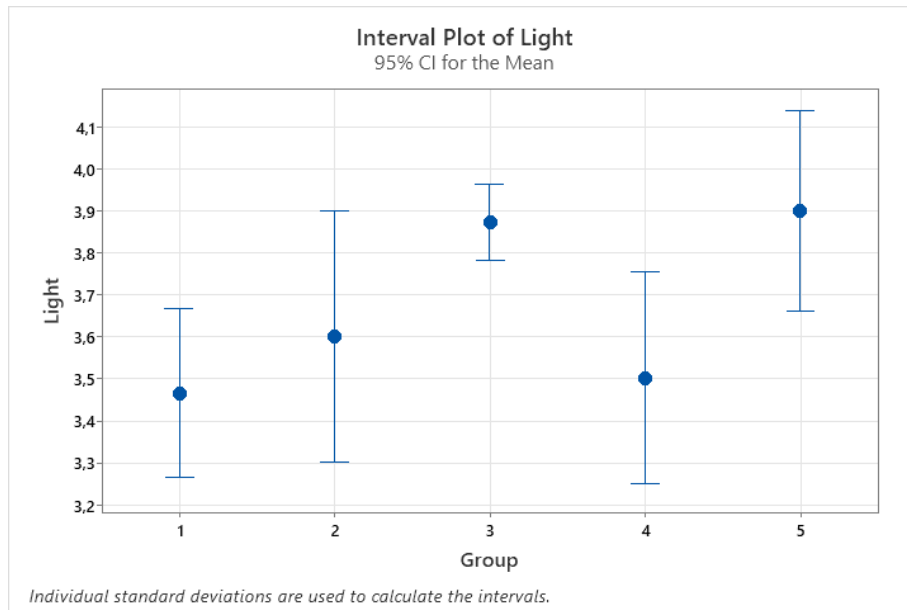


Figure 10. Interval plot of light indicator values of different land-use categories. Given are mean values and 95% confidence intervals. Land-use categories are: 1-ancient, 2-ancient-Picea, 3-pasture, 4-arable-adjacent, and 5-arable-isolated. The means of plot groups 1 and 4 are significantly lower than the means of groups 3 ( $p=0.025$ ;  $p=0.048$ ) and 5 ( $p=0.015$ ;  $p=0.030$ ).

Post-arable stands show higher soil reaction (pH) levels than post-pasture plots (Figure 11). Additionally, post-arable stands are richer in available nitrogen compared to post-pasture and ancient stands (Figure 12).

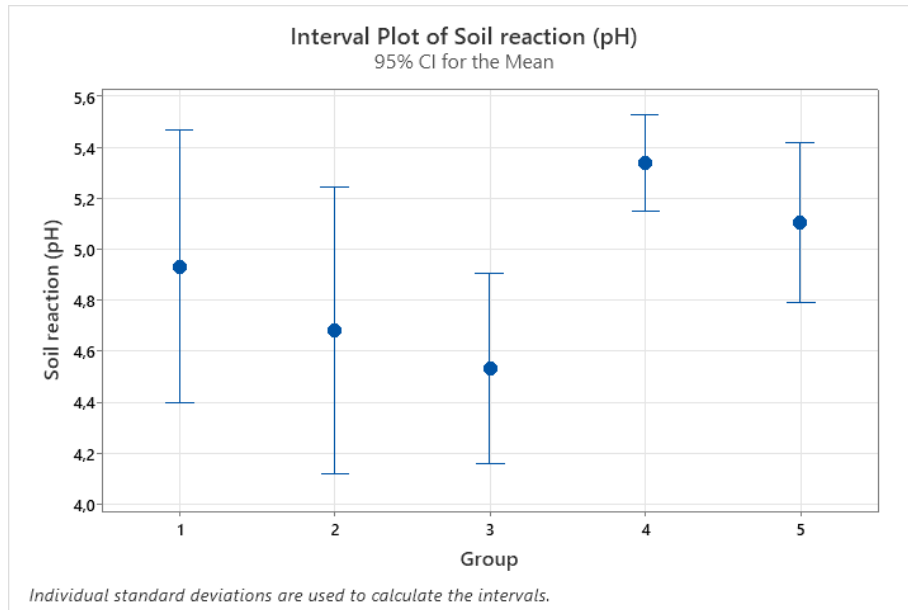


Figure 11. Interval plot of soil reaction (pH) indicator values of different land-use categories. Given are mean values and 95% confidence intervals. Land-use categories are: 1-ancient, 2-ancient-Picea, 3-pasture, 4-arable-adjacent, and 5-arable-isolated. The means of plot group 4 are higher than those of group 3 ( $p > 0.05$ ).

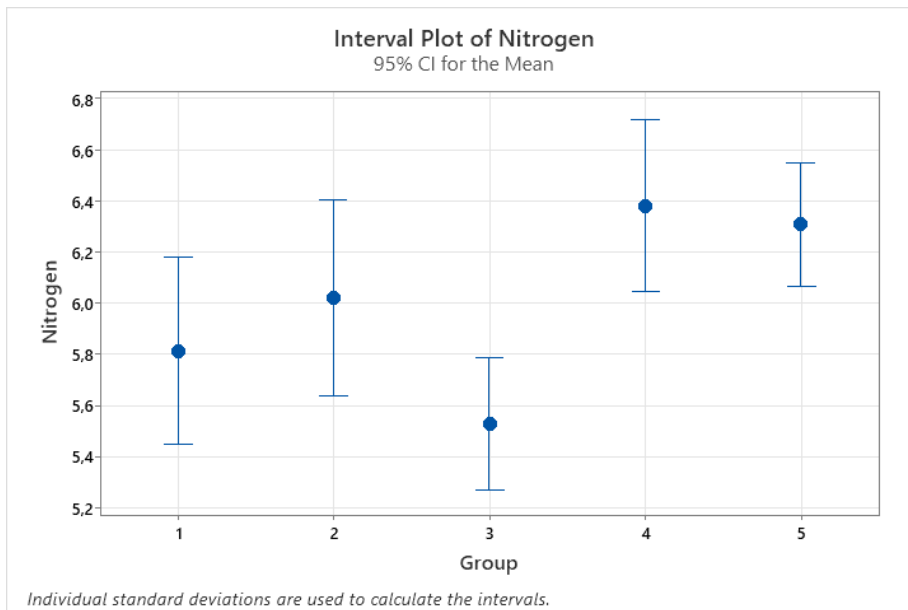


Figure 12. Interval plot of nitrogen indicator values of different land-use categories. Land-use categories are: 1-ancient, 2-ancient-Picea, 3-pasture, 4-arable-adjacent, and 5-arable-isolated. The means of plot groups 4 and 5 are higher than of group 3 (both  $p=0.001$ ), and the mean of group 4 is also higher than those of group 1 ( $p=0.027$ ).

Linear regression demonstrates that higher canopy cover is associated with lower mean light indicator values (Figure 13).

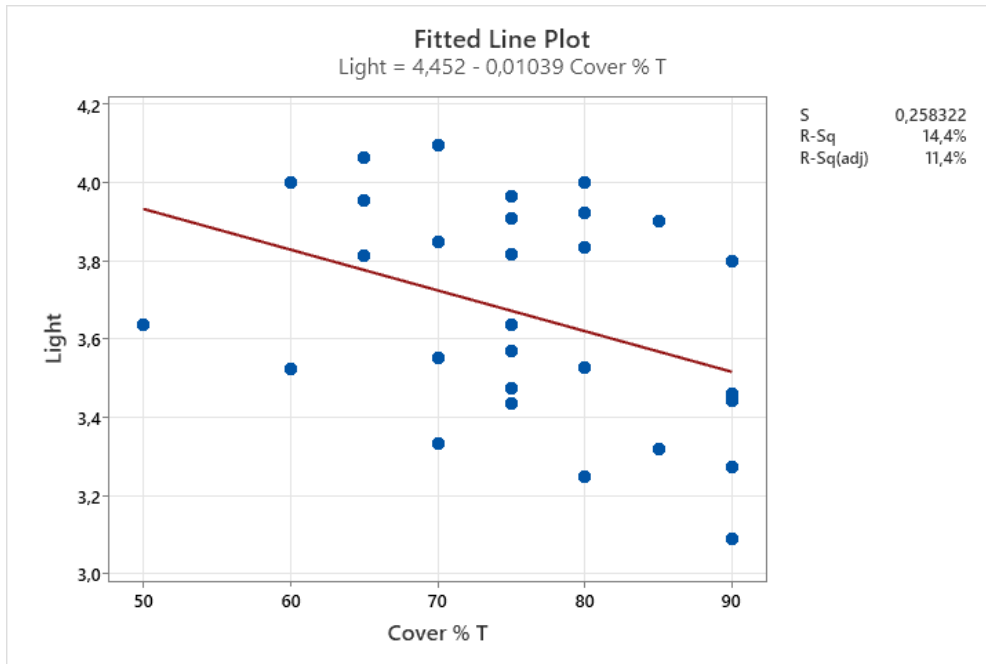


Figure 13. Linear regression between mean light indicator values and the cover sum of tree layer. F-value 4.72 and P-value = 0.038 according to linear regression.

Linear regression analysis was done across all species to assess the relationship between access to light and species richness (Figure 14). The results indicate that increased light availability has a positive effect on total species richness within the herb layer.

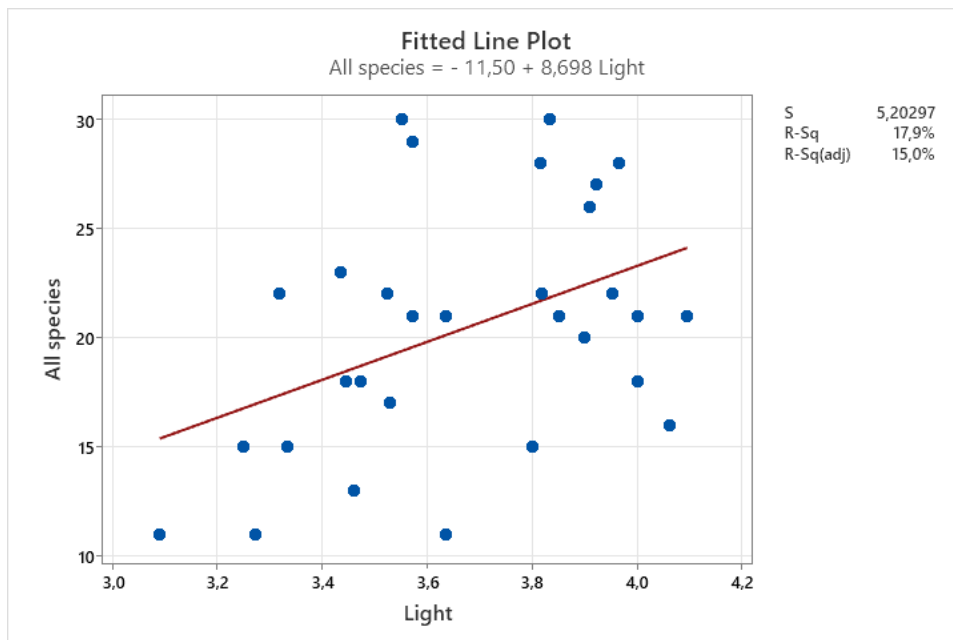


Figure 14. Linear regression between mean light indicator values and the sum of all species. F-value 6.10 and P-value = 0.020 according to linear regression.

## 4. Discussion

### 4.1 Species richness

Temperate forests often contain high plant diversity with numerous species. (Berg et al. 1994; Brunet 2007; Brunet et al. 2011). Recently established woods are often poorer in species compared to ancient ones (Peterken & Game 1984; Flinn & Vellend 2005). However, mean plot species richness did not differ between land-use categories in sycamore plantations of the present study, neither for total species richness nor for forest specialist species. Consequently, all hypotheses regarding species richness (1a, 2, 3, and 4a) must be rejected. Differences in the total species pools were also small between plot groups, except for a smaller pool of forest specialist plants in isolated post-arable plantations and a larger pool of woody species in post-pasture plantations. The results therefore suggest that 60 years after sycamore planting, the species richness of forest specialists and generalists in post-agricultural sycamore plantations is approaching the levels found in ancient forest sites. There were, however, species-specific differences among forest specialists which will be discussed below.

The relatively high number of generalist species may be attributed to their rapid colonization abilities, as noted by Brunet et al. (2011). Many generalist species are prevalent in agricultural and open land areas, as well as in tall herb communities along roads, ditches, and forest edges (Brunet et al. 2011). In their study, Brunet et al. (2011) observed that the high species richness of generalists remained consistent in both contiguous and isolated oak plantations, a pattern that aligns with our observations in sycamore stands. Another contributing factor to the high number of generalist species may be their prevalence in various habitats. Wulf (2004) suggested that intensive forestry practices, such as drainage, in ancient woodlands have led to an invasion of generalist species. These species grow more vigorously and thus become severe competitors for forest species.

A notably high number of woody species was noted in sycamore plantations, particularly in post-pasture plantations, which had an average of 8.5 woody species and a total of 22 species. This abundance can be attributed to their effective

dispersal abilities (Wulf & Heinken 2008; Sciama et al. 2009; Brunet et al. 2011). The proximity to ancient woodlands also facilitates colonization, as noted by Müller et al. (2007), likely contributing to the high number of woody species. Another contributing factor could be human selection over centuries, leading to a large prevalence of trees in wood pastures. Garbarino & Bergmeier (2014) mentioned that in silvopastoral habitats, acorn-producing trees were highly valued for animal feed. Other researchers have noted that trees in wood pasture persist due to their small size and high light requirements, often thriving at woodland margins or being preserved as relics on land that has been converted to forest (Van Uytvanck et al. 2008; Garbarino & Bergmeier 2014; Plieninger et al. 2015).

## 4.2 Species distribution

The findings of this study indicate a relatively rapid recolonization of forest species in sycamore plantations on post-pasture and post-arable lands, even in areas isolated from seed sources. Dzwonko & Loster (1989) noted that differences in vegetation between land-use types can be explained by two primary factors: soil fertility and colonization ability. Firstly, variations in soil fertility influence plant recolonization after cultivation abandonment. Secondly, plant species exhibit different colonization abilities, with those having a high dispersal rate more likely to be found in previously cultivated areas compared to adjacent old forests (Dzwonko & Loster 1989; Dzwonko 2001). The rapid recolonization of forest species observed in this study is an unexpected contrast with the general expectations described in the literature. According to Brunet (2007), isolated plantations usually accumulate forest plants more slowly than those contiguous with ancient forests. Other authors pointed out that it might have taken 50-100 years for forest specialists to colonize new stands next to old woodland, and even longer when recent woodlands are isolated (Brunet & Von Oheimb 1998; Wulf 2004).

The colonization rates of forest species in nearby stands are influenced by several factors, including the size and distance of source populations, seed production, seed size and morphology, and dispersal mechanisms (Kolb & Diekmann 2005; Brunet et al. 2011). Wulf (2004) noted that most forest species found in recent woodlands possess the ability to disperse long-distance, facilitating their rapid establishment in new areas. In total, we recorded 27 forest specialists in our study, showing significant variation in their distribution patterns across stand categories.

The ability of forest species to colonize new areas varies widely (Valtinat et al. 2008). In our study, *Anemone nemorosa*, a geophyte known for forming extensive vernal carpets in European ancient forests (Brunet 2007; Brunet et al. 2011), was found in plots of all land-use categories but only slowly developed larger local

populations in post-agricultural plots. This species was still much more abundant in ancient stands, suggesting a preference for older, undisturbed forest conditions over more recently established plantations. Valtinat et al. (2008) noted that *A. nemorosa* thrives in base-rich, nutrient-rich soils typical of broadleaved woodlands. Another contributing factor could be the relatively low colonization rate of *A. nemorosa*. Brunet et al. (2011) observed that *A. nemorosa* required 60-80 years to colonize nearby plantations, highlighting its slow establishment in new habitats. Among forest specialists, *L. galeobdolon* and *M. uniflora* were poor colonizers of post-agricultural plantations. Both species are adapted to short-distance dispersal by ants and are generally considered ancient woodland indicator species (Brunet 2007).

Wulf (2004) suggested that the relatively large number of forest species in post-pasture plantations could be attributed to the ability of forest specialists to survive in small populations within pastures. This may be one reason why we observed a similar number of forest species in post-pasture stands compared to plantations in ancient forests. Additionally, other authors have noted that some herbaceous woodland species can find niches outside traditional woodlands and tolerate pasture environments (Inghe & Tamm 1988). Brunet (1994) identified species such as *Luzula pilosa*, *Maianthemum bifolium*, *O. acetosella*, *Poa nemoralis*, and *Viola reichenbachiana* that can thrive in these conditions, and which all were common in post-pasture sycamore plantations. Thus, the relatively high number of forest species in post-pasture areas could be a combined result of recent colonizations and remnant populations from the pasture period.

Several forest specialists had frequently colonized post-arable plantations. For example, the herbs *Circaea lutetiana*, *M. perennis*, and the grasses *Milium effusum* and *S. giganteus* were notably abundant in post-arable plantations, a trend also documented by Brunet (2007). These acid-sensitive and nutrient demanding species find suitable habitats in the fertile post-arable soils. Valtinat et al. (2008) also noted that *S. giganteus* and *C. lutetiana* were more abundant in forest stands on former fields compared to ancient woodland stands. Furthermore, they identified higher occurrences of species such as *A. moschatellina* and *P. nemoralis* in these habitats. Our study supports these findings, as these species were also most abundant in post-arable plantations for sycamore stands. Additionally, Brunet (2004) noted that fast colonizers like *C. lutetiana*, *M. effusum*, and *S. giganteus* have demonstrated significant seed dispersal capabilities. These seeds can adhere to various surfaces and be dispersed effectively through multiple methods. For instance, studies have shown that seeds can be spread by walking dogs through forests or the fur of wild boar and roe deer (Heinken 2000; Heinken & Raudnitschka 2002; Brunet 2004). Moreover, Brunet (2004) also observed that ferns such as *Dryopteris* spp. and *Athyrium filix-femina* are efficient colonizers. Their spores can be effectively



dispersed by the wind and can also be carried in the fur of larger mammals, facilitating their spread in new environments.

Furthermore, to fully understand the process of forest species recolonization in sycamore plantations, further research is crucial. Current studies suggest that typical forest species may establish themselves in new stands adjacent to ancient forests within 50 to 100 years (Brunet & Von Oheimb 1998; Wulf 2004). Given that our sycamore plantations are around 60 years old, additional time is needed to thoroughly observe and understand this process.

### 4.3 Vegetation cover

Herb layer cover in sycamore stands was rather similar across different land-use categories. However, herb layer cover decreased with increasing cover of the woody layers, independently of land-use history. Such a relation was expected as the productivity of the herb layer in forests is strongly limited by light availability (Ellenberg & Leuschner 2017). Furthermore, we observed a significant decrease in the number of generalist species as the cover of the tree and shrub layers increased. This indicates that the relatively high shade levels in sycamore stands may affect more light-demanding species and reduce species richness and cover (Bingelli 1994; Flinn & Vellend 2005; Felton et al. 2013).

### 4.4 Species composition

Various factors, including soil diversity, topography, microclimate, and land-use history influence the vegetation diversity (Dzwonko & Loster 1989; Flinn & Vellend 2005). In our study, we conducted a non-metric multidimensional scaling analysis to assess the impact of environmental variables such as soil pH, nitrogen levels, moisture, and light availability on plant species diversity. The NMDS effectively highlighted the variation among the five plot groups and identified the most critical environmental drivers.

#### 4.4.1 Soil reaction (pH) and nitrogen

Our findings indicate that soil reaction (pH) and nitrogen (N) levels significantly influence herb layer composition and diversity in sycamore plantations. Post-arable stands exhibit higher soil pH levels than post-pasture areas, which was also observed by Falkengren-Grerup et al. (2006) and Brunet (2007). Other authors observed that soils recovering from agricultural use typically exhibit higher pH and nutrient concentrations and lower organic matter content than soils under

continuous forest cover (Koerner et al. 1997; Flinn & Vellend 2005). The elevated pH levels in post-arable areas can likely be attributed to agricultural fertilization practices such as liming (Falkengren-Grerup et al. 2006; Brunet 2007; Valtinat et al. 2008). Consequently, these post-arable stands have higher nitrogen availability than post-pasture and ancient stands. The increased nitrogen levels may result from rapid nitrification processes, as suggested by Valtinat et al. (2008)

The number of herb layer species increases significantly with higher soil pH (Tyler 1989). In sycamore plantations, basiphilous and nitrophilous forest species were notably abundant in post-arable stands. Similarly, Koerner et al. (1997) observed a rise in nitrogen-demanding species and a decline in slow-dispersing species, such as *Anemone nemorosa*, in previously cultivated forests compared to ancient stands. Our study found a frequent occurrence of nitrophilous species in post-agricultural plantations, a pattern also noted by Valtinat et al. (2008). Species such as *Galeopsis tetrahit*, *Geum urbanum*, *Impatiens parviflora*, *Lactuca muralis*, *Rubus idaeus*, *Silene dioica*, and *Urtica dioica*, all known as nitrophilous species (Koerner et al. 1997), were more abundant in these areas. Notably, *U. dioica* was observed across all plantation categories but was most frequent in post-arable stands.

#### 4.4.2 Light

Ecological factors that frequently restrict plant colonization and diversity are light availability and density of the overstory vegetation layers (Tyler 1989; De Keersmaeker et al. 2004; Felton et al. 2010; Hedwall et al. 2013; Márialigeti et al. 2016). Several authors have noted that canopy openness, which determines light conditions on the forest floor, plays a significant role in shaping ground vegetation (Neufeld & Young 2003; Márialigeti et al. 2016). Our study confirms the influence of light availability on species richness and composition in sycamore plantations.

Light availability at ground level in sycamore plantations is probably somewhat lower than in oak plantations (Brunet 2007), but higher than in beech stands (Janík et al. 2016). In this study, the mean cover (%) of the tree layer ranged from 69 to 82%, while the mean cover of the shrub layer varied from 10 to 22%. While the results show that there are no significant differences in the estimated canopy cover of tree and shrub layers between different land-use categories, the ordination analyses indicate some effects of light availability on the herb layer vegetation.

Linear regression analysis demonstrated that the vegetation gradient along Axis 2 is closely related to mean light indicator values. Furthermore, ANOVA showed that post-pasture stands and isolated post-arable stands had the highest mean light values. There may be two alternative reasons for the lack of direct effects of canopy cover on the light indicator values. First, visual estimation of canopy cover may not

be a reliable method to assess light availability. However, the significant negative effect of canopy cover on herb layer cover (Figure 6) indicates that the method may be relatively reliable. Second, the higher light indicator values in the two groups could be related to delayed colonization by shade-tolerant species due to dispersal limitation.

Forest species, including both vernal and summer species, have varying light requirements. *O. acetosella* is strongly associated with dense tree canopies due to their high shade tolerance (Tyler 1989). Brunet (2007) found that shade-tolerant forest plants can easily colonize post-agricultural plantations, provided that relatively closed canopy conditions are maintained.

The tree canopy plays a crucial role in shaping the abundance and composition of forest floor vegetation (Barbier et al. 2008; Hart & Chen 2008; Hedwall et al. 2013). While some species, like grasses, are more adaptable to higher light availability, others depend on shaded conditions to thrive (Meier et al. 1995). Meier et al. (1995) noted that less common species with specific environmental requirements may struggle to adapt to changes in canopy cover caused by logging or other disturbances. Species with small and fragmented populations such as *Oxalis acetosella* are at a higher risk of extinction and more vulnerable to environmental disruptions. Forest species associated with ancient forests may persist in reduced numbers, largely due to their ability to adapt to gap-phase succession (Meier et al. 1995). However, further research is needed to fully understand how these dynamics play out in sycamore plantations specifically.

## 4.5 Comparison with oak plantations

The results of this study can be compared with published data on oak (*Quercus robur*) plantations of the same land-use categories and from the same study area (Brunet et al. 2011). However, the results are not directly comparable as the size of the oak plots was 500 m<sup>2</sup> and thus contained a greater number of species compared to the sycamore plantations. Both types of plantations exhibit similar general patterns in species richness, with ancient woodland plantations having the highest mean number of forest specialist species, followed by non-isolated post-arable stands and isolated post-arable stands having the lowest number of species. In both oak and sycamore stands the difference between ancient and non-isolated plantations was, however, not statistically different, indicating a high restoration potential in non-isolated stands. For isolated post-arable plantations, the oak stands had significantly less forest specialists, while this difference was not significant in the sycamore stands of this study. One possible reason could be that the number of replicate stands was lower in this study (6, 6, 6) compared to the oak study (12, 16,

9). The general patterns observed in these studies indicate that sycamore plantations, like oak plantations, can be colonized by a large number of forest specialist species within a time scale of decades.

## 5. Conclusions

In conclusion, this study emphasizes the important influences of historical land use, environmental characteristics, and canopy structure on ground vegetation in sycamore (*A. pseudoplatanus*) plantations in southern Sweden. While there was no significant variation in overall species richness between land-use histories, post-pasture sites showed a significantly higher abundance of woody species. Denser canopy cover has a negative impact on the diversity of herb layer species and the abundance of generalist species. The non-metric multidimensional scaling analysis identified soil pH and nitrogen levels as key determinants of species composition, with light and moisture additionally influencing species composition. Remarkably, isolated post-agricultural sycamore plantations were relatively quickly colonized by several forest specialists. However, certain species, such as *Anemone nemorosa*, continue to prefer older, less disturbed habitats, emphasizing the necessity of maintaining ancient forest conditions. In general, the findings indicate a relatively high potential of sycamore plantations for both maintenance and restoration of the herbaceous forest flora. Further research is necessary to fully understand how sycamore forests can contribute to biodiversity and their potential role in enhancing ecological resilience.

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# Popular science summary

## **Sycamore - threat or chance?**

In southern Sweden, the sycamore is a relatively new species, with the first reports emerging in the 1800s. Today, these trees are common and known for their rapid spread across the region. The Swedish Forest Agency classifies sycamore as an invasive species due to its tendency to rapidly colonize new areas. Despite this categorization, sycamore plantations present an opportunity to investigate how these trees interact with the environment and support biodiversity.

Our research investigated sycamore plantations with various land-use histories, including ancient forest, post-pasture, and post-arable sites. We discovered that plantations on former pastures supported a higher number of woody plants than those on post-agricultural sites, even though the total number of plant species remained constant across these sites. We also found that both post-pasture and post-arable plantations after ca 60 years supported a similar number of forest specialist species as plantations in ancient forest.

We also looked at the relationship between plant diversity and tree cover density. Our research revealed that generalist plants were less common in areas with denser canopies. This implies that the variety of vegetation at ground level may be restricted by greater tree cover. Plant communities were significantly shaped by soil properties, including soil acidity (pH) and nitrogen levels. We observed that different plant species thrived at different light and moisture levels, demonstrating the importance of these environmental factors in establishing plant distribution.

Surprisingly, forest plants recovered quickly on former agricultural land, indicating that sycamore trees play a positive role in rapidly establishing forest groundcover conditions. However, the preference of certain plants, such as *Anemone nemorosa*, is an example of the continued need to protect old forests and less altered habitats. The results of our study demonstrate that, despite being considered invasive, sycamore forests can maintain and improve plant diversity in historically altered landscapes. However, further research is required to completely understand their role in biodiversity and ecological resilience.

## Acknowledgements

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## Appendix 1

List of the studied forest stands in the Torup-Skabersjö area. Data are based on information on historical and current forest management plans and maps (Brunet, unpublished data).

| Stand ID | Stand area, ha | Canopy tree species        | Stand age 2023 | Land-use type  | <i>Picea</i> before | Location   |
|----------|----------------|----------------------------|----------------|----------------|---------------------|------------|
| 220      | 1              | <i>Quercus-Acer</i>        | 55             | ancient forest | no                  |            |
| 296      | 1,1            | <i>Betula-Acer-Fagus</i>   | 55             | ancient forest | no                  |            |
| 297      | 3,3            | <i>Quercus-Acer-Fagus</i>  | 75             | ancient forest | no                  |            |
| 135-138  | 4              | <i>Acer-Fraxinus-Fagus</i> | 85             | ancient forest | no                  |            |
| 165      | 0,7            | <i>Acer-Betula</i>         | 65             | ancient forest | no                  |            |
| 225      | 0,5            | <i>Acer-Betula</i>         | 75             | ancient forest | no                  |            |
|          |                |                            |                |                |                     |            |
| 37a      | 0,7            | <i>Acer</i>                | 65             | ancient forest | yes                 |            |
| 59n      | 1,67           | <i>Acer</i>                | 61             | ancient forest | yes                 |            |
| 250      | 0,8            | <i>Quercus-Acer</i>        | 75             | ancient forest | yes                 |            |
| 182      | 0,5            | <i>Acer</i>                | 75             | ancient forest | yes                 |            |
| 238      | 0,7            | <i>Acer-Betula</i>         | 45             | ancient forest | yes                 |            |
| 259      | 0,4            | <i>Acer-Betula</i>         | 40             | ancient forest | yes                 |            |
|          |                |                            |                |                |                     |            |
| 54d      | 1,11           | <i>Acer</i>                | 59             | post-pasture   | yes                 | contiguous |
| 55n      | 0,45           | <i>Acer-Larix</i>          | 61             | post-pasture   | yes                 | contiguous |
| 56a      | 0,74           | <i>Acer</i>                | 63             | post-pasture   | yes                 | contiguous |
| 64f      | 0,53           | <i>Acer</i>                | 59             | post-pasture   | yes                 | contiguous |
| 65f      | 1,53           | <i>Acer</i>                | 56             | post-pasture   | yes                 | contiguous |
| 65k      | 0,22           | <i>Acer</i>                | 60             | post-pasture   | yes                 | contiguous |
|          |                |                            |                |                |                     |            |
| 36f      | 0,89           | <i>Acer</i>                | 58             | post-arable    | yes                 | contiguous |
| 32d      | 0,3            | <i>Acer</i>                | 56             | post-arable    | no                  | contiguous |
| 67l      | 0,47           | <i>Acer</i>                | 59             | post-arable    | no                  | contiguous |
| 87e      | 0,4            | <i>Acer</i>                | 65             | post-arable    | no                  | contiguous |
| 87w      | 0,7            | <i>Acer</i>                | 65             | post-arable    | no                  | contiguous |
| 144      | 1,1            | <i>Acer</i>                | 55             | post-arable    | no                  | contiguous |
|          |                |                            |                |                |                     |            |
| 14 i     | 0,54           | <i>Acer</i>                | 43             | post-arable    | yes                 | isolated   |
| 4 f      | 0,47           | <i>Acer</i>                | 69             | post-arable    | yes                 | isolated   |
| 5e       | 2,1            | <i>Betula-Acer</i>         | 52             | post-arable    | yes                 | isolated   |
| 8 d      | 0,39           | <i>Fraxinus-Acer</i>       | 49             | post-arable    | yes                 | isolated   |
| 47 e     | 0,58           | <i>Acer</i>                | 68             | post-arable    | yes                 | isolated   |
| 7h       | 1,85           | <i>Larix-Acer</i>          | 62             | post-arable    | yes                 | isolated   |

## Appendix 2

List of vascular plant species found in the studied sample plots in sycamore plantations in the Torup-Skabersjö area. Given are also frequencies of occurrence (%) of the species in the five land-use categories (n=6) and overall frequency (n=30). Classification into habitat groups is according to Heinken et al. (2022).

| Species/plot group                  | Ancient | Ancient<br>( <i>Picea</i> ) | Post-<br>pasture | Post-<br>arable | Isolated<br>P-a | Overall<br>frequency | Habitat<br>group |
|-------------------------------------|---------|-----------------------------|------------------|-----------------|-----------------|----------------------|------------------|
| <i>Adoxa moschatellina</i>          | -       | -                           | 17               | 33              | 33              | 17                   | Forest           |
| <i>Anemone ranunculoides</i>        | 33      | -                           | -                | 17              | -               | 10                   | Forest           |
| <i>Athyrium filix-femina</i>        | 67      | 50                          | 17               | 17              | -               | 30                   | Forest           |
| <i>Brachypodium sylvaticum</i>      | -       | -                           | -                | 33              | -               | 7                    | Forest           |
| <i>Calamagrostis arundinacea</i>    | -       | -                           | 17               | -               | -               | 3                    | Forest           |
| <i>Carex sylvatica</i>              | -       | -                           | -                | 17              | -               | 3                    | Forest           |
| <i>Circaea lutetiana</i>            | 50      | 17                          | 17               | 50              | 33              | 33                   | Forest           |
| <i>Dryopteris carthusiana</i>       | 33      | 67                          | 100              | 17              | 67              | 57                   | Forest           |
| <i>Elymus caninus</i>               | -       | -                           | -                | 33              | -               | 7                    | Forest           |
| <i>Gagea spathacea</i>              | -       | 33                          | 17               | 17              | 17              | 17                   | Forest           |
| <i>Galium odoratum</i>              | -       | -                           | -                | 17              | -               | 3                    | Forest           |
| <i>Gymnocarpium dryopteris</i>      | -       | -                           | -                | 17              | -               | 3                    | Forest           |
| <i>Impatiens parviflora</i>         | 17      | 17                          | 17               | 50              | 17              | 23                   | Forest           |
| <i>Lamiastrum galeobdolon</i>       | 67      | 67                          | 17               | -               | 17              | 33                   | Forest           |
| <i>Luzula pilosa</i>                | -       | -                           | 33               | -               | -               | 7                    | Forest           |
| <i>Maianthemum bifolium</i>         | 17      | 17                          | 33               | -               | -               | 13                   | Forest           |
| <i>Melica uniflora</i>              | 67      | 83                          | 33               | -               | -               | 37                   | Forest           |
| <i>Mercurialis perennis</i>         | 50      | 33                          | -                | 100             | -               | 37                   | Forest           |
| <i>Milium effusum</i>               | 67      | 100                         | 67               | 83              | 83              | 80                   | Forest           |
| <i>Oxalis acetosella</i>            | 50      | 50                          | 83               | 17              | -               | 40                   | Forest           |
| <i>Poa nemoralis</i>                | 83      | 50                          | 83               | 33              | 83              | 67                   | Forest           |
| <i>Polygonatum multiflorum</i>      | 17      | 17                          | 17               | -               | -               | 10                   | Forest           |
| <i>Schedonorus giganteus</i>        | -       | 33                          | 17               | 33              | 83              | 33                   | Forest           |
| <i>Stachys sylvatica</i>            | 17      | 17                          | -                | -               | -               | 7                    | Forest           |
| <i>Stellaria holostea</i>           | 67      | 100                         | 100              | 33              | 67              | 73                   | Forest           |
| <i>Stellaria nemorum</i>            | 50      | 67                          | 17               | 17              | 50              | 40                   | Forest           |
| <i>Viola reichenbach./riviniana</i> | 67      | 50                          | 83               | 17              | 17              | 47                   | Forest           |
| <i>Aegopodium podagraria</i>        | 17      | -                           | -                | 50              | -               | 13                   | Generalist       |

|                                  |     |     |     |     |     |     |            |
|----------------------------------|-----|-----|-----|-----|-----|-----|------------|
| <i>Agrostis capillaris</i>       | 17  | 17  | 50  | 33  | 50  | 33  | Generalist |
| <i>Alliaria petiolata</i>        | -   | -   | -   | 17  | 33  | 10  | Generalist |
| <i>Anemone nemorosa</i>          | 100 | 100 | 50  | 50  | 50  | 70  | Generalist |
| <i>Angelica sylvestris</i>       | -   | -   | -   | 17  | -   | 3   | Generalist |
| <i>Calamagrostis epigejos</i>    | -   | -   | 17  | -   | -   | 3   | Generalist |
| <i>Carex pilulifera</i>          | -   | 33  | -   | -   | -   | 7   | Generalist |
| <i>Dactylis glomerata</i>        | 67  | 67  | 83  | 83  | 83  | 77  | Generalist |
| <i>Deschampsia cespitosa</i>     | 33  | 50  | 67  | 17  | -   | 33  | Generalist |
| <i>Deschampsia flexuosa</i>      | -   | 17  | -   | -   | -   | 3   | Generalist |
| <i>Dryopteris filix-mas</i>      | 67  | 83  | 50  | 33  | 67  | 60  | Generalist |
| <i>Epilobium montanum</i>        | -   | -   | -   | -   | 33  | 7   | Generalist |
| <i>Fragaria vesca</i>            | -   | -   | -   | 17  | -   | 3   | Generalist |
| <i>Gagea lutea</i>               | -   | 17  | -   | -   | -   | 3   | Generalist |
| <i>Galanthus nivalis</i>         | 17  | -   | -   | 17  | -   | 7   | Generalist |
| <i>Galeopsis tetrahit</i>        | 17  | 17  | -   | -   | -   | 7   | Generalist |
| <i>Galium aparine</i>            | -   | 17  | 33  | 33  | 50  | 27  | Generalist |
| <i>Geranium robertianum</i>      | -   | 17  | 17  | 33  | 33  | 20  | Generalist |
| <i>Geum urbanum</i>              | -   | 33  | 50  | 100 | 100 | 57  | Generalist |
| <i>Hypericum maculatum</i>       | 17  | -   | -   | -   | -   | 3   | Generalist |
| <i>Juncus effusus</i>            | 33  | -   | 50  | -   | -   | 17  | Generalist |
| <i>Lactuca muralis</i>           | -   | 17  | 17  | -   | -   | 7   | Generalist |
| <i>Lapsana communis</i>          | -   | -   | -   | 17  | 17  | 7   | Generalist |
| <i>Lathyrus linifolius</i>       | 17  | -   | 17  | -   | -   | 7   | Generalist |
| <i>Poa trivialis</i>             | 17  | 17  | -   | -   | -   | 7   | Generalist |
| <i>Pteridium aquilinum</i>       | -   | -   | 33  | -   | -   | 7   | Generalist |
| <i>Ranunculus ficaria</i>        | 50  | 50  | 50  | 84  | 100 | 67  | Generalist |
| <i>Scrophularia nodosa</i>       | 17  | 17  | -   | -   | -   | 7   | Generalist |
| <i>Silene dioica</i>             | -   | 33  | 17  | 17  | 17  | 17  | Generalist |
| <i>Solanum dulcamara</i>         | -   | -   | -   | -   | 17  | 3   | Generalist |
| <i>Taraxacum sect. Ruderalia</i> | 33  | -   | 17  | -   | 33  | 17  | Generalist |
| <i>Torilis japonica</i>          | -   | 33  | 17  | 17  | 50  | 23  | Generalist |
| <i>Urtica dioica</i>             | 67  | 50  | 33  | 83  | 100 | 67  | Generalist |
| <i>Veronica hederifolia</i>      | -   | -   | 33  | 33  | 83  | 30  | Generalist |
| <i>Vicia sepium</i>              | 17  | -   | -   | -   | -   | 3   | Generalist |
| <i>Arctium sp.</i>               | 17  | -   | -   | -   | 17  | 7   | Open       |
| <i>Carex spicata</i>             | 17  | -   | -   | -   | -   | 3   | Open       |
| <i>Cirsium vulgare</i>           | -   | -   | -   | 17  | -   | 3   | Open       |
| <i>Geranium macrorrhizum</i>     | -   | -   | -   | 17  | -   | 3   | Open       |
| <i>Lamium album</i>              | -   | -   | -   | -   | 17  | 3   | Open       |
| <i>Ornithogalum umbellatum</i>   | -   | -   | -   | -   | 17  | 3   | Open       |
| <i>Rumex sp.</i>                 | 17  | -   | -   | -   | -   | 3   | Open       |
| <i>Solidago canadensis</i>       | -   | -   | 17  | -   | -   | 3   | Open       |
| <i>Abies sp.</i>                 | -   | -   | 17  | -   | -   | 3   | Woody      |
| <i>Acer platanoides</i>          | -   | -   | 33  | 17  | -   | 10  | Woody      |
| <i>Acer pseudoplatanus</i>       | 100 | 100 | 100 | 100 | 100 | 100 | Woody      |

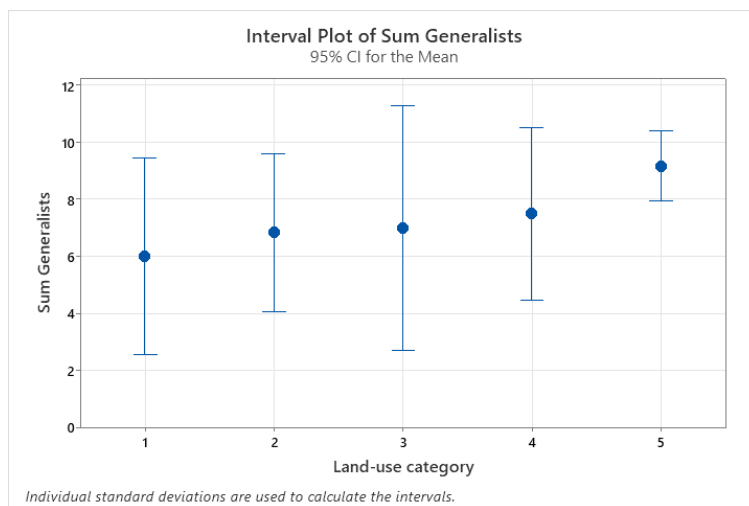


|                              |     |    |    |    |    |    |       |
|------------------------------|-----|----|----|----|----|----|-------|
| <i>Betula pendula</i>        | 17  | 17 | -  | -  | -  | 7  | Woody |
| <i>Corylus avellana</i>      | 33  | 33 | -  | 17 | -  | 17 | Woody |
| <i>Crataegus laevigata</i>   | -   | -  | 17 | 67 | 17 | 20 | Woody |
| <i>Crataegus monogyna</i>    | -   | -  | -  | -  | 50 | 10 | Woody |
| <i>Fagus sylvatica</i>       | 100 | 83 | 83 | 50 | 17 | 67 | Woody |
| <i>Frangula alnus</i>        | -   | 17 | 33 | -  | -  | 10 | Woody |
| <i>Fraxinus excelsior</i>    | 83  | 33 | 50 | 50 | 50 | 53 | Woody |
| <i>Lonicera periclymenum</i> | 17  | -  | 17 | -  | -  | 7  | Woody |
| <i>Picea abies</i>           | -   | -  | 67 | -  | -  | 13 | Woody |
| <i>Populus tremula</i>       | -   | -  | 17 | -  | -  | 3  | Woody |
| <i>Prunus avium</i>          | -   | 17 | 50 | 17 | -  | 17 | Woody |
| <i>Prunus serotina</i>       | -   | -  | 17 | 17 | -  | 7  | Woody |
| <i>Prunus spinosa</i>        | -   | -  | 17 | -  | -  | 3  | Woody |
| <i>Quercus robur</i>         | 17  | 33 | 67 | 33 | 17 | 33 | Woody |
| <i>Quercus rubra</i>         | -   | -  | 17 | -  | 17 | 7  | Woody |
| <i>Rhamnus cathartica</i>    | -   | -  | 17 | -  | -  | 3  | Woody |
| <i>Ribes alpinum</i>         | -   | -  | 17 | -  | -  | 3  | Woody |
| <i>Rubus caesius</i>         | -   | -  | -  | -  | 17 | 3  | Woody |
| <i>Rubus fruticosus</i>      | -   | 33 | 83 | 17 | -  | 27 | Woody |
| <i>Rubus idaeus</i>          | 33  | 17 | 33 | 17 | 83 | 37 | Woody |
| <i>Sambucus nigra</i>        | -   | -  | -  | 33 | 50 | 17 | Woody |
| <i>Sambucus racemosa</i>     | -   | 33 | -  | -  | 17 | 10 | Woody |
| <i>Sorbus aucuparia</i>      | -   | -  | 67 | -  | 17 | 17 | Woody |
| <i>Symphoricarpus albus</i>  | -   | -  | -  | -  | 17 | 3  | Woody |
| <i>Tilia cordata</i>         | -   | 17 | 17 | -  | -  | 7  | Woody |
| <i>Ulmus glabra</i>          | 33  | 17 | 17 | 33 | 50 | 30 | Woody |

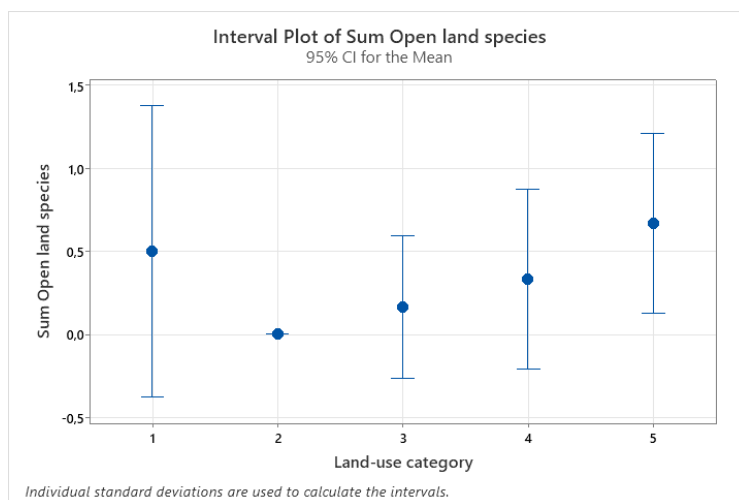
## Appendix 3

Interval plots of number of a) generalist and b) open land plant species in the herb layer of sample plots in sycamore plantations of different land-use categories. Given are mean values and 95% confidence intervals. Land-use categories are: 1- ancient, 2-ancient-Picea, 3-pasture, 4-arable-adjacent, 5-arable-isolated. Differences between pairs of plot groups are all non-significant ( $p > 0.05$ ) according to ANOVA and Tukey-test (generalists) and Kruskal-Wallis test and pairwise Mann-Whitney U-tests (open land species).

a)



b)



## Appendix 4

Statistics of Kruskal-Wallis tests for selected herb layer species.

### Kruskal-Wallis Test: *Anemone nemorosa* versus Land-use category

#### Descriptive Statistics

| Land-use category | N  | Median | Mean Rank | Z-Value |
|-------------------|----|--------|-----------|---------|
| 1                 | 6  | 3,00   | 25,7      | 3,16    |
| 2                 | 6  | 2,00   | 21,3      | 1,81    |
| 3                 | 6  | 0,25   | 11,0      | -1,40   |
| 4                 | 6  | 0,50   | 11,0      | -1,40   |
| 5                 | 6  | 0,25   | 8,5       | -2,18   |
| Overall           | 30 |        | 15,5      |         |

#### Test

| Null hypothesis        | Ho: All medians are equal            |         |         |
|------------------------|--------------------------------------|---------|---------|
| Alternative hypothesis | Hi: At least one median is different |         |         |
| Method                 | DF                                   | H-Value | P-Value |
| Not adjusted for ties  | 4                                    | 17,57   | 0,002   |
| Adjusted for ties      | 4                                    | 18,33   | 0,001   |

### Kruskal-Wallis Test: *Athyrium filix-femina* versus Land-use category

#### Descriptive Statistics

| Land-use category | N  | Median | Mean Rank | Z-Value |
|-------------------|----|--------|-----------|---------|
| 1                 | 6  | 0,75   | 21,7      | 1,92    |
| 2                 | 6  | 0,25   | 18,5      | 0,93    |
| 3                 | 6  | 0,00   | 13,2      | -0,73   |
| 4                 | 6  | 0,00   | 13,2      | -0,73   |
| 5                 | 6  | 0,00   | 11,0      | -1,40   |
| Overall           | 30 |        | 15,5      |         |

#### Test

| Null hypothesis        | Ho: All medians are equal            |         |         |
|------------------------|--------------------------------------|---------|---------|
| Alternative hypothesis | Hi: At least one median is different |         |         |
| Method                 | DF                                   | H-Value | P-Value |
| Not adjusted for ties  | 4                                    | 6,05    | 0,195   |
| Adjusted for ties      | 4                                    | 9,28    | 0,054   |

### Kruskal-Wallis Test: *Circaea lutetiana* versus Land-use category

#### Descriptive Statistics

| Land-use category | N  | Median | Mean Rank | Z-Value |
|-------------------|----|--------|-----------|---------|
| 1                 | 6  | 0,25   | 17,5      | 0,62    |
| 2                 | 6  | 0,00   | 12,2      | -1,04   |
| 3                 | 6  | 0,00   | 12,2      | -1,04   |
| 4                 | 6  | 0,50   | 19,7      | 1,30    |
| 5                 | 6  | 0,00   | 16,0      | 0,16    |
| Overall           | 30 |        | 15,5      |         |

## Test

|                        |   |                |                |
|------------------------|---|----------------|----------------|
| Null hypothesis        | Ho: All medians are equal                         |                |                |
| Alternative hypothesis | H <sub>1</sub> : At least one median is different |                |                |
| <b>Method</b>          | <b>DF</b>   | <b>H-Value</b> | <b>P-Value</b> |
| Not adjusted for ties  | 4   | 3,39           | 0,494          |
| Adjusted for ties      | 4   | 4,63           | 0,327          |

## Kruskal-Wallis Test: *Dryopteris carthusiana* versus Land-use category

### Descriptive Statistics

| Land-use category | N  | Median | Mean Rank | Z-Value |
|-------------------|----|--------|-----------|---------|
| 1                 | 6  | 0,00   | 11,0      | -1,40   |
| 2                 | 6  | 0,50   | 17,7      | 0,67    |
| 3                 | 6  | 0,75   | 23,0      | 2,33    |
| 4                 | 6  | 0,00   | 9,0       | -2,02   |
| 5                 | 6  | 0,50   | 16,8      | 0,41    |
| Overall           | 30 |        | 15,5      |         |

## Test

|                        |   |                |                |
|------------------------|---|----------------|----------------|
| Null hypothesis        | Ho: All medians are equal                         |                |                |
| Alternative hypothesis | H <sub>1</sub> : At least one median is different |                |                |
| <b>Method</b>          | <b>DF</b>   | <b>H-Value</b> | <b>P-Value</b> |
| Not adjusted for ties  | 4   | 9,69           | 0,046          |
| Adjusted for ties      | 4   | 11,20          | 0,024          |

## Kruskal-Wallis Test: *Lamiastrum galeobdolon* versus Land-use category

### Descriptive Statistics

| Land-use category | N  | Median | Mean Rank | Z-Value |
|-------------------|----|--------|-----------|---------|
| 1                 | 6  | 1,5    | 21,3      | 1,81    |
| 2                 | 6  | 1,5    | 20,8      | 1,66    |
| 3                 | 6  | 0,0    | 12,3      | -1,01   |
| 4                 | 6  | 0,0    | 10,5      | -1,56   |
| 5                 | 6  | 0,0    | 12,6      | -0,91   |
| Overall           | 30 |        | 15,5      |         |

## Test

|                        |   |                |                |
|------------------------|---|----------------|----------------|
| Null hypothesis        | Ho: All medians are equal                         |                |                |
| Alternative hypothesis | H <sub>1</sub> : At least one median is different |                |                |
| <b>Method</b>          | <b>DF</b>   | <b>H-Value</b> | <b>P-Value</b> |
| Not adjusted for ties  | 4   | 8,25           | 0,083          |
| Adjusted for ties      | 4   | 11,80          | 0,019          |

## Kruskal-Wallis Test: *Melica uniflora* versus Land-use category

### Descriptive Statistics

| Land-use category | N  | Median | Mean Rank | Z-Value |
|-------------------|----|--------|-----------|---------|
| 1                 | 6  | 0,5    | 19,7      | 1,30    |
| 2                 | 6  | 0,5    | 22,8      | 2,28    |
| 3                 | 6  | 0,0    | 15,0      | -0,16   |
| 4                 | 6  | 0,0    | 10,0      | -1,71   |
| 5                 | 6  | 0,0    | 10,0      | -1,71   |
| Overall           | 30 |        | 15,5      |         |

## Test

|                        |   |                |                |
|------------------------|---|----------------|----------------|
| Null hypothesis        | Ho: All medians are equal                         |                |                |
| Alternative hypothesis | H <sub>1</sub> : At least one median is different |                |                |
| <b>Method</b>          | <b>DF</b>   | <b>H-Value</b> | <b>P-Value</b> |
| Not adjusted for ties  | 4   | 10,21          | 0,037          |
| Adjusted for ties      | 4   | 13,93          | 0,008          |

### Kruskal-Wallis Test: *Mercurialis perennis* versus Land-use category

#### Descriptive Statistics

| Land-use category | N  | Median | Mean Rank | Z-Value |
|-------------------|----|--------|-----------|---------|
| 1                 | 6  | 0,25   | 16,6      | 0,34    |
| 2                 | 6  | 0,00   | 15,0      | -0,16   |
| 3                 | 6  | 0,00   | 10,0      | -1,71   |
| 4                 | 6  | 1,50   | 25,9      | 3,24    |
| 5                 | 6  | 0,00   | 10,0      | -1,71   |
| Overall           | 30 |        | 15,5      |         |

#### Test

| Null hypothesis        | Ho: All medians are equal                         |         |         |
|------------------------|---|---------|---------|
| Alternative hypothesis | H <sub>1</sub> : At least one median is different |         |         |
| Method                 | DF  | H-Value | P-Value |
| Not adjusted for ties  | 4   | 13,19   | 0,010   |
| Adjusted for ties      | 4   | 17,81   | 0,001   |

### Kruskal-Wallis Test: *Milium effusum* versus Land-use category

#### Descriptive Statistics

| Land-use category | N  | Median | Mean Rank | Z-Value |
|-------------------|----|--------|-----------|---------|
| 1                 | 6  | 0,5    | 13,2      | -0,73   |
| 2                 | 6  | 0,5    | 19,0      | 1,09    |
| 3                 | 6  | 0,5    | 11,2      | -1,35   |
| 4                 | 6  | 0,5    | 13,1      | -0,75   |
| 5                 | 6  | 1,0    | 21,1      | 1,74    |
| Overall           | 30 |        | 15,5      |         |

#### Test

| Null hypothesis        | Ho: All medians are equal                         |         |         |
|------------------------|---|---------|---------|
| Alternative hypothesis | H <sub>1</sub> : At least one median is different |         |         |
| Method                 | DF  | H-Value | P-Value |
| Not adjusted for ties  | 4   | 5,69    | 0,224   |
| Adjusted for ties      | 4   | 7,13    | 0,129   |

### Kruskal-Wallis Test: *Poa nemoralis* versus Land-use category

#### Descriptive Statistics

| Land-use category | N  | Median | Mean Rank | Z-Value |
|-------------------|----|--------|-----------|---------|
| 1                 | 6  | 0,50   | 13,1      | -0,75   |
| 2                 | 6  | 0,25   | 12,9      | -0,80   |
| 3                 | 6  | 1,50   | 20,8      | 1,63    |
| 4                 | 6  | 0,00   | 11,6      | -1,22   |
| 5                 | 6  | 2,00   | 19,2      | 1,14    |
| Overall           | 30 |        | 15,5      |         |

#### Test

| Null hypothesis        | Ho: All medians are equal                         |         |         |
|------------------------|---|---------|---------|
| Alternative hypothesis | H <sub>1</sub> : At least one median is different |         |         |
| Method                 | DF  | H-Value | P-Value |
| Not adjusted for ties  | 4   | 5,33    | 0,255   |
| Adjusted for ties      | 4   | 5,65    | 0,227   |

### Kruskal-Wallis Test: *Oxalis acetosella* versus Land-use category

#### Descriptive Statistics

| Land-use category | N | Median | Mean Rank | Z-Value |
|-------------------|---|--------|-----------|---------|
| 1                 | 6 | 0,25   | 16,8      | 0,39    |
| 2                 | 6 | 0,25   | 17,8      | 0,70    |
| 3                 | 6 | 0,50   | 21,9      | 2,00    |

|         |    |      |      |       |
|---------|----|------|------|-------|
| 4       | 6  | 0,00 | 11,6 | -1,22 |
| 5       | 6  | 0,00 | 9,5  | -1,87 |
| Overall | 30 |      | 15,5 |       |

### Test

Null hypothesis Ho: All medians are equal  
 Alternative hypothesis H<sub>1</sub>: At least one median is different

| Method                | DF | H-Value | P-Value |
|-----------------------|----|---------|---------|
| Not adjusted for ties | 4  | 7,68    | 0,104   |
| Adjusted for ties     | 4  | 10,00   | 0,040   |

## Kruskal-Wallis Test: *Schedonorus giganteus* versus Land-use category

### Descriptive Statistics

| Land-use category | N  | Median | Mean Rank | Z-Value |
|-------------------|----|--------|-----------|---------|
| 1                 | 6  | 0,00   | 10,5      | -1,56   |
| 2                 | 6  | 0,00   | 14,8      | -0,21   |
| 3                 | 6  | 0,00   | 12,7      | -0,88   |
| 4                 | 6  | 0,00   | 15,7      | 0,05    |
| 5                 | 6  | 0,75   | 23,8      | 2,59    |
| Overall           | 30 |        | 15,5      |         |

### Test

Null hypothesis Ho: All medians are equal  
 Alternative hypothesis H<sub>1</sub>: At least one median is different

| Method                | DF | H-Value | P-Value |
|-----------------------|----|---------|---------|
| Not adjusted for ties | 4  | 7,97    | 0,093   |
| Adjusted for ties     | 4  | 11,48   | 0,022   |

## Kruskal-Wallis Test: *Stellaria holostea* versus Land-use category

### Descriptive Statistics

| Land-use category | N  | Median | Mean Rank | Z-Value |
|-------------------|----|--------|-----------|---------|
| 1                 | 6  | 0,5    | 13,0      | -0,78   |
| 2                 | 6  | 1,0    | 19,2      | 1,14    |
| 3                 | 6  | 1,0    | 19,2      | 1,14    |
| 4                 | 6  | 0,0    | 10,7      | -1,50   |
| 5                 | 6  | 1,0    | 15,5      | 0,00    |
| Overall           | 30 |        | 15,5      |         |

### Test

Null hypothesis Ho: All medians are equal  
 Alternative hypothesis H<sub>1</sub>: At least one median is different

| Method                | DF | H-Value | P-Value |
|-----------------------|----|---------|---------|
| Not adjusted for ties | 4  | 4,37    | 0,358   |
| Adjusted for ties     | 4  | 4,68    | 0,322   |

## Kruskal-Wallis Test: *Stellaria nemorum* versus Land-use category

### Descriptive Statistics

| Land-use category | N  | Median | Mean Rank | Z-Value |
|-------------------|----|--------|-----------|---------|
| 1                 | 6  | 0,25   | 16,2      | 0,21    |
| 2                 | 6  | 0,75   | 20,5      | 1,56    |
| 3                 | 6  | 0,00   | 11,5      | -1,24   |
| 4                 | 6  | 0,00   | 11,5      | -1,24   |
| 5                 | 6  | 0,25   | 17,8      | 0,73    |
| Overall           | 30 |        | 15,5      |         |

### Test

Null hypothesis Ho: All medians are equal  
 Alternative hypothesis H<sub>1</sub>: At least one median is different

| Method                | DF | H-Value | P-Value |
|-----------------------|----|---------|---------|
| Not adjusted for ties | 4  | 4,87    | 0,301   |
| Adjusted for ties     | 4  | 6,27    | 0,180   |

## Kruskal-Wallis Test: *Viola reichenb./riv.* versus Land-use category

### Descriptive Statistics

| Land-use category | N  | Median | Mean Rank | Z-Value |
|-------------------|----|--------|-----------|---------|
| 1                 | 6  | 0,50   | 17,7      | 0,67    |
| 2                 | 6  | 0,25   | 15,3      | -0,08   |
| 3                 | 6  | 0,50   | 20,1      | 1,43    |
| 4                 | 6  | 0,00   | 10,4      | -1,58   |
| 5                 | 6  | 0,00   | 14,1      | -0,44   |
| Overall           | 30 |        | 15,5      |         |

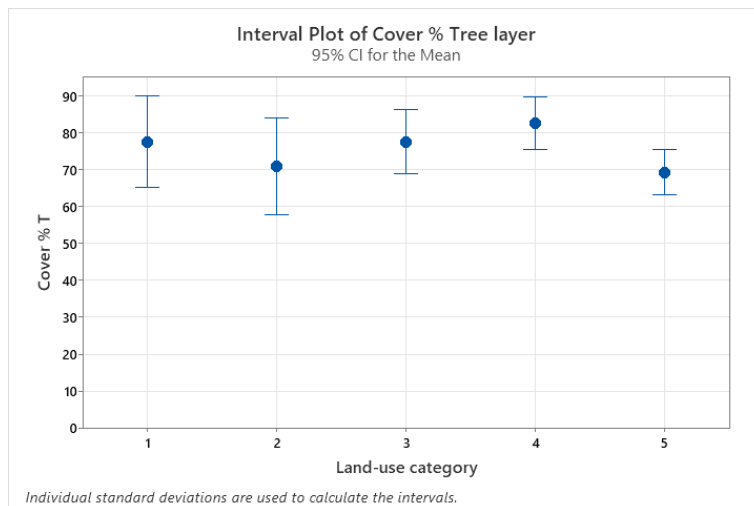
### Test

| Null hypothesis        | Ho: All medians are equal                         |         |         |
|------------------------|---|---------|---------|
| Alternative hypothesis | H <sub>1</sub> : At least one median is different |         |         |
| Method                 | DF  | H-Value | P-Value |
| Not adjusted for ties  | 4   | 4,15    | 0,386   |
| Adjusted for ties      | 4   | 5,36    | 0,252   |

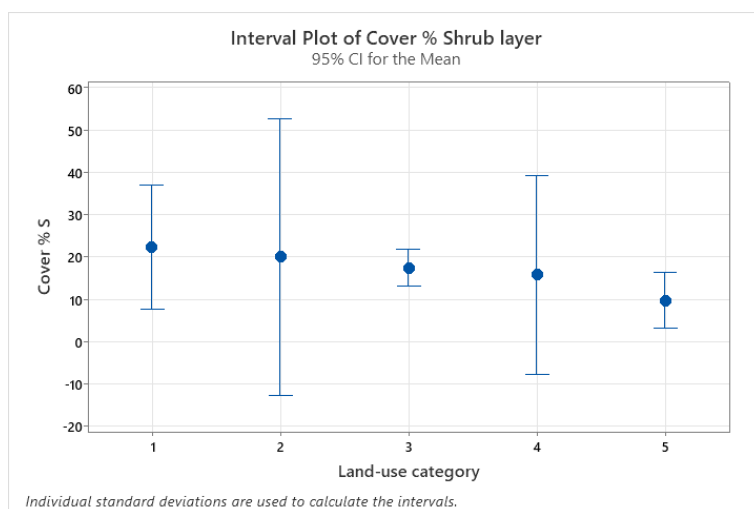
## Appendix 5

Interval plots of number of estimated cover % of the a) tree, b) shrub, c) herb and d) moss layers of sample plots in sycamore plantations of different land-use categories. Given are mean values and 95% confidence intervals. Land-use categories are: 1-ancient, 2-ancient-Picea, 3-pasture, 4-arable-adjacent, 5-arable-isolated. Differences between pairs of plot groups are all non-significant ( $p > 0.05$ ) according to pairwise Mann-Whitney U-tests.

a)

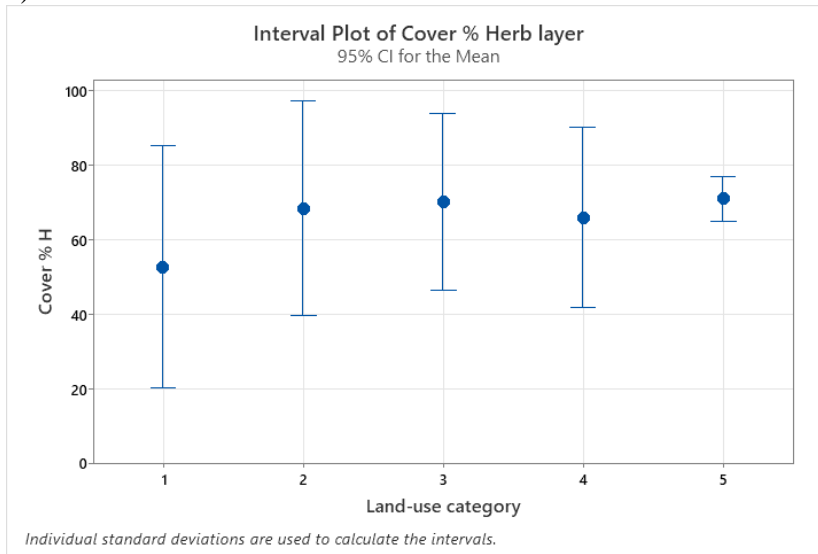


b)

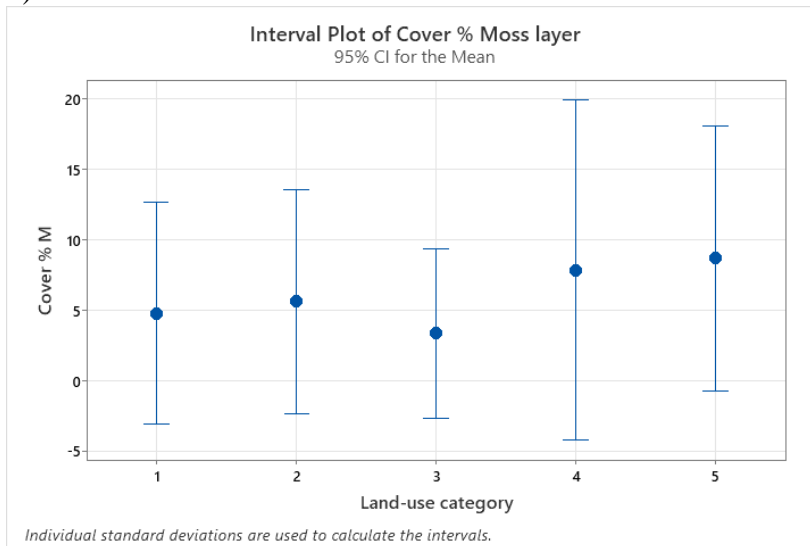




c)



d)



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