Effects of Canopy Cover and Soil Disturbance on the Herbaceous Layer in Dalby Söderskog National Park between 2010 and 2019

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Effekter av krontäckning och markstörning på fältskiktsvegetationen i Dalby Söderskogs nationalpark mellan 2010 och 2019

Salomé Castro Rojas

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Abstract

Temperate deciduous forests are dynamic ecosystems where changes in light and soil conditions may affect the diversity and abundance of species on the herbaceous vegetation layer. In the national park Dalby Söderskog, located in southern Sweden, the tree canopies have opened due to tree diseases such as ash dieback and Dutch elm disease. At the same time, the arrival of wild boars has influenced soil conditions.

This study investigates the impact of changes in canopy cover and soil disturbance on the diversity and abundance of the forest herbaceous layer in Dalby Söderskog National Park between 2010 and 2019. It was hypothesized that (1) more open tree canopies are expected to increase both abundance and species diversity of the ground vegetation, and that (2) increased wild boar rooting leads to decreased cover and species diversity.

Based on vegetation surveys in 74 permanent sample plots, species richness and percentage ground cover of spring ephemerals, summer herbs, and woody species in the ground vegetation layer were related to wild boar rooting intensity, soil pH, soil moisture, and canopy cover using simple and multiple linear regression analyses.

The results revealed that reducing canopy cover and increasing soil pH were associated with higher herbaceous cover and species richness in the summer herb ground layer group. The wild boar rooting activity had a negative impact on spring ephemerals, while the woody species showed weak or no significant responses in relation to the environmental variables tested.

These results indicate that soil disturbance was the primary factor influencing the spring ephemeral vegetation, while changes in summer herbs were strongly correlated with changes in light availability. In combination, these factors have caused considerable shifts in the diversity and abundance of the ground vegetation in Dalby Söderskog between 2010 and 2019. These outcomes help understand the responses of the forest floor vegetation to disturbances and may inform biodiversity conservation strategies in temperate broadleaved forests.

Keywords: herbaceous layer, ground vegetation, permanent plots, temperate deciduous forest, tree canopy cover, wild boar rooting

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Forewords

"Forests are indispensable — they are homes for life in all its forms, regulators of climate, providers of resources, and sources of beauty and inspiration. But above all, they are reminders of our responsibility. To protect. To restore. To care."

- My father[1], a forester and a lifelong advocate for nature conservation.

From an early age, I have heard my father talk about forests as ecosystems and living, breathing communities—complex, interconnected, and vital. His words echo a truth that transcends science alone: forests are not just spaces of green. They are reservoirs of life, balance, and meaning. This understanding forms the heart of my work and inspires the focus of this study.

[1] Mauricio Castro Schmitz, Regenerative Agriculture Director Latin America, The Nature Conservancy, personal communication 2025-04-26.

1. Introduction

The herbaceous layer, also known as the “regeneration layer”, is defined according to Gilliam (2007) as “the forest stratum composed of all vascular plant species that are 1 meter (m) or less in height”. The ecological importance of the herbaceous layer in a forest ecosystem is usually concerned with three aspects of its influence on the forest: (1) the importance of the herbaceous layer for overall species diversity, (2) the importance of the herbaceous layer key role as the site of early competitive interactions for the regeneration of dominant canopy species, and (3) the contribution of the herbaceous layer to the forest ecosystem function (Rawlik and Jagodziński, 2019; Gilliam, 2007). In summary, the forest herbaceous layer is a critical component and an early indicator of forest health and ecosystem dynamics (LaPaix, Freedman, and Patriquin, 2009; National Park Service, 2025; Durak, Bugno-Pogoda, and Durak, 2022).

Microclimate conditions beneath the tree’s canopies further shape the dynamics of the herbaceous layer. Under a closed, undisturbed tree canopy, organisms are exposed to a microclimate characterized by having less direct sunlight and wind, resulting in more stable and suitable temperature and moisture conditions compared to open areas (Hill et al., 2023; Lenk et al., 2024). However, different disturbance factors can cause a reduction in canopy cover by creating gaps, altering the microclimate, and impacting the understory vegetation. Such factors include tree mortality caused by pests and pathogens or by climate extremes such as severe drought (Lenk et al., 2024).

While canopy cover and microclimate are two critical factors that influence the herbaceous layer, the foundation of the forest ecosystem lies in the soil itself. Soil properties such as soil pH, water availability, and nutrient availability directly affect plant growth, species composition, and regeneration success (Food and Agriculture Organization of the United Nations, 2015). Given the key roles of canopy cover and soil condition in molding the forest herbaceous layer and overall forest health, it is essential to study these interactions within specific contexts. Thus, Dalby Söderskog National Park, located in southern Sweden, provides an ideal setting for such studies due to the availability of long-term vegetation data from permanent sample plots.

Dalby Söderskog National Park is a protected broadleaved deciduous forest of 37 ha in size surrounded by agricultural land (Dalby Söderskog National Park, 2025; von Oheimb and Brunet, 2007). Established in 1918 and largely unmanaged since then, it was left to evolve naturally through succession (Dalby Söderskog National Park, 2025). However, in recent decades, the emergence of Dutch Elm Disease (DED) and ash dieback in the area has led to significant mortality among key species such as Wych elm (*Ulmus glabra*) and European ash (*Fraxinus excelsior*), contributing to a marked decline in canopy cover (Brunet et al., 2014;

Ruks, 2020; Peterken and Mountford, 1998). This caused a decline in canopy cover, creating gaps in the canopy and gradually altering the microclimate. Ultimately, increasing the amount of light reaching the forest floor vegetation over time.

Additionally, the area has experienced physical disturbance from wild boar rooting since 2011, which has been reported to significantly influence the cover of spring vegetation and the composition of the ground layer (Brunet and Amelung, 2020; Brunet et al., 2016). Wild boar (*Sus scrofa*)—now one of the most widespread mammals in the world (Castagnino, 2021)—feed on plant parts, fungi, seeds, larvae, and pupae found within the forest soil and vegetation (Biały, 1996; Barrios-Garcia and Ballari, 2012). In doing so, they break down plant residues and disturb large areas of ground vegetation through their rooting behavior (Biały, 1996). Referred to as "the forest tillers" by Faliński (1985), wild boars play a major role in defining the structure and characteristics of the forest floor's surface layer (Barrios-Garcia and Ballari, 2012).

These factors – canopy loss, soil disturbance by wild boar rooting, and soil condition – will likely affect the forest floor herbaceous layer. Although previous studies in Dalby Söderskog have suggested that these disturbances have influenced the forest floor structure (Brunet et al., 2014; von Oheimb and Brunet, 2007), the specific effects following 2013 have not yet been analyzed. Comprehending these processes is essential to proceed with biodiversity conservation and forest ecosystem management, especially in protected areas where natural disturbances can unfold without human intervention.

1.1 Aim of the study

This study examines the impact of environmental changes on the abundance and diversity of ground herbaceous vegetation in Dalby Söderskog National Park between 2010 and 2019. It is hypothesized that (1) more open tree canopies are expected to increase both abundance and species diversity and that (2) increased wild boar rooting leads to decreased cover and species diversity.

2. Material and methods

2.1 Study area

Dalby Söderskog is the smallest national park in Europe (Länsstyrelsen Skåne, 2025), covering only 37 hectares. It is a forested area found within the county of Skåne, the southernmost province in Sweden, approximately 10 km from Lund, and it is embraced by fertile arable fields and pasture land (Figure 1, Brunet, 2015). This forested area is situated on Baltic moraine clay, a calcareous and nutrient-rich substrate derived from the Weichsel glacial period. Its humus layer is classified as mull, and its soil is composed of a moist and wet Eutric Cambisol (von Oheimb and Brunet, 2007). The area has a suboceanic temperate climate, with a mean annual temperature of 7.5°C and an average precipitation of approximately 800 mm per year (von Oheimb and Brunet, 2007). The tree layer is mainly composed of Pendunculate oak (*Quercus robur*), European ash (*Fraxinus excelsior*), European beech (*Fagus sylvatica*), and wych Elm (*Ulmus glabra*) (von Oheimb and Brunet 2007).

2.2 Historical aspects

During the Middle Ages, the area was owned by the Augustinian monastery in Dalby, which came to be known as *Hästhagen* (meaning "horse pasture") (Dalby Söderskog National Park, 2025). During that period, the area was used to graze horses belonging to the monastery and the Danish royal court (Länsstyrelsen Skåne, 2025). Nowadays, one can still see the mysterious earthen rampart (Hästhagevallen) at the site, with a leftover fence that once separated the pasture between Söder and Norreskogen (Johansson, 2007). Over the past centuries, the forest has experienced variable grazing with varying intensities and intense periods of logging (Länsstyrelsen Skåne, 2025). It was not until the early 19th century, when the Royal Stud farm was relocated to Flyinge, that there was a reduction of grazing pressure in the area (Länsstyrelsen Skåne, 2025), forging the path to a forest succession of oak, beech, elm, and ash (von Oheimb and Brunet, 2007).

The area was declared a national park in 1918, which resulted in halting both grazing and logging. This allowed the area to develop freely into a mixed deciduous forest, marking the dawn of its extended use in scientific studies (Dalby Söderskog National Park, 2025). It is common for woody plants to grow after wooden meadows and pasture lands are left "abandoned." As a result, shade-tolerant species, such as beech and elm, began to dominate, replacing the areas previously occupied by light-demanding species that had been nourished through grazing and coppicing practices, like oak (Peterken and Mountford, 1998). The invasion of DED was first detected in the area at the end of the 1980s, ten years after the disease was identified in the surroundings of the Skåne region, and ash dieback was first spotted in southern Sweden in 2002 (Ruks, 2020). The disease resulted in massive canopy loss and high mortality among these main dominant and essential tree species (von Oheimb and Brunet, 2007; Ruks, 2020). In 2011, wild boar rooting disturbance was observed in the area, resulting in a significant initial reduction of spring ephemeral cover by up to 50% (Brunet et al., 2016).

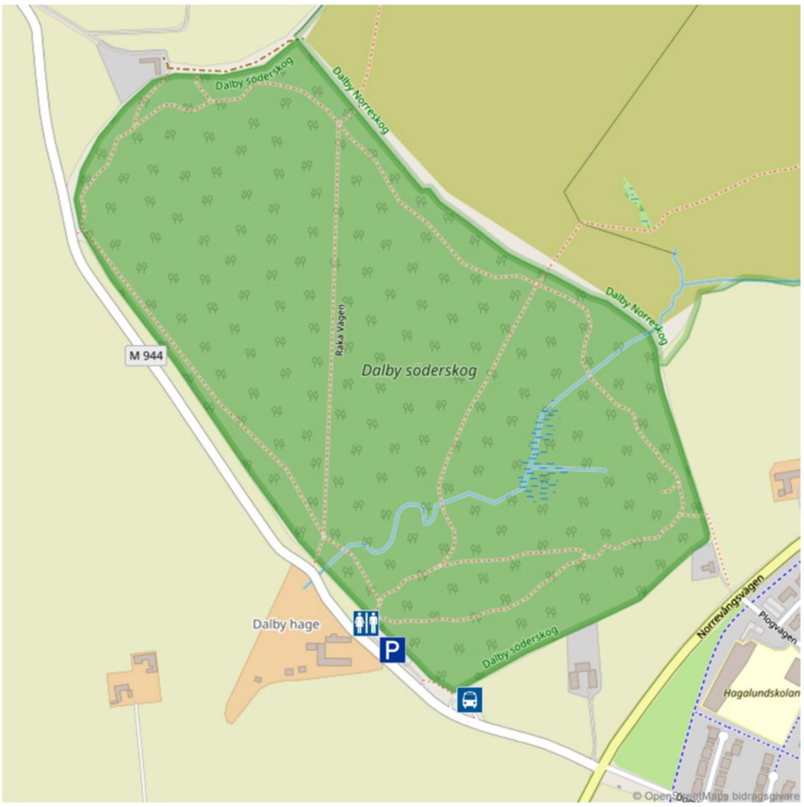

Figure 1: Map of the study area Dalby Söderskog National Park in Skåne, southern Sweden (Turist information Lund, 2025)

2.3 Sampling design

In 1935, the ecologist Bertil Lindquist established sample plots along a system of transect lines to study the forest structure and its vegetation (Brunet et al., 2014). A straight path intersecting the forest was used as a baseline, and different sample plots were arranged along transects perpendicular to the path. Seventy-four plots were created as part of a plan of long-term research to cover the Dalby Söderskog National Park area, as seen in Figure 2. The distance between the transected lines was 50 m, and the distance between the plots on the transect was 100 m, although due to the stand margins, some distances were 50 or 75 m.

In early spring of 2010, these plots were re-established. This was done using an aerial photograph of the forest, Lindquist's map as an overlap in ArcPad, and the corresponding GPS coordinates (Brunet et al., 2016).

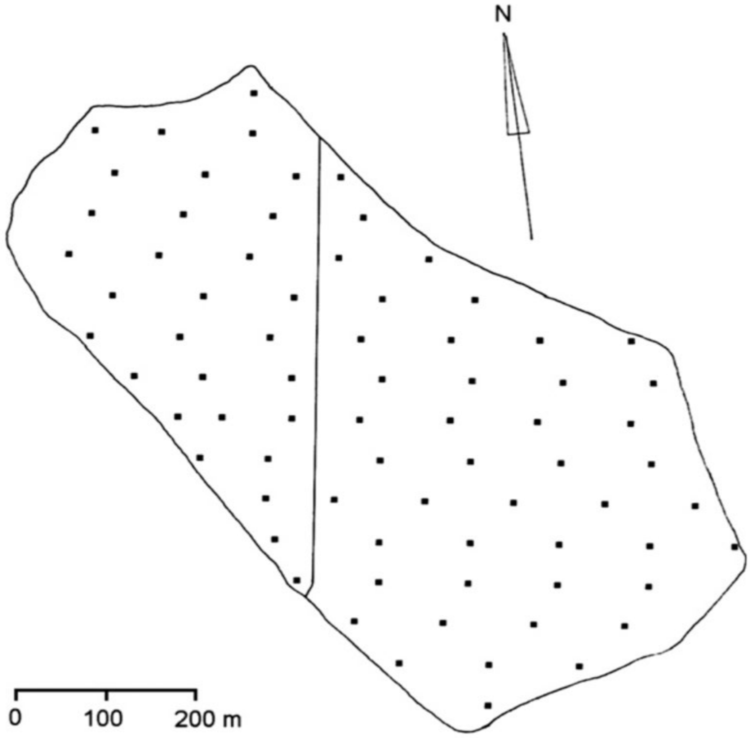

Figure 2: The approximate location of the 74 sample plots in Dalby Söderskog

2.4 Data collection

This study utilizes the grid sample reconstructed and established in 2010. The data was collected in 2010 and again in 2019 by Jörg Brunet. This thesis aims to compare and identify the changes in the forest floor vegetation over these nine years. Soil sample collection and chemical analysis were done by Kea Amelung in 2019 (Amelung, 2019).

2.4.1 Survey of vegetation layer

In order to evaluate the prevalence and quantity of vegetation in the area, the appearance of all vascular plants and their percentage cover were recorded, which was visually estimated in the 74 plots in both survey years. The ground vegetation layer (height 0-0.8 m height, including saplings of woody species) was cataloged in 1 x 1 m sample plots. The woody canopy layers were surveyed in 4 x 4 m sample plots, with the same center point as the 1 x 1 m plots, following Lindqust's original method (von Oheimb and Brunet, 2007). The cover of canopy species was estimated separately in four height classes: T1: (> 15 m), T2: (8-15 m), S1: (2-8 m), and S2: (0.8-2 m). Total canopy cover was calculated as the sum of all four height classes. Therefore, total canopy cover may exceed 100% cover. The species were grouped into different functional categories in the ground layer: spring ephemeral herbs, summer herbs, and woody species in the ground layer. Based on previous studies in the area (Brunet et al., 2016), the most common spring ephemerals incorporated *Anemone nemorosa, Anemone ranunculoides, Ranunculus ficaria,* and *Corydalis cava.* The most common species in the summer herbs group included *Aegopodium podagraria, Circaea lutetiana, Geum urbanum,* and *Poa trivialis.* Lastly, among the woody species found in the herbaceous layer are, e.g., *Fagus sylvatica, Fraxinus excelsior,* and *Quercus robur* (Brunet et al., 2016).

The percentage of species cover in the ground vegetation was estimated for individual species in the following steps: 0.5; 1, 2, 3, 4, 5, 6, 8, 10, 12, 15, 20, 25 and in further 5% steps up to 100% (Brunet et al., 2016). Due to overlapping foliage of different species, the total cover may exceed 100%. Changes in the cover of the ground layer species between 2010 and 2019 were calculated by subtracting 2019 cover values from 2010 value for each functional group. The data recording occurred during the spring and summer, at peak seasonal vegetation abundance.

2.4.2 Canopy cover

The crown cover of tree and shrub species in the four canopy layers was estimated visually in each plot using the same % steps as for the ground layer. While it is not an exact way of measuring direct light, this method has been shown to reliably reflect the understory vegetation composition in structurally complex temperate forests when carried out by trained observers (Depauw et al., 2020).

2.4.3 Evaluation of wild boar rooting

Wild boar rooting was quantified as a cumulative sum from annual surveys (2010 - 2019), where 0 meant no rooting, 0.5 meant light rooting, and 1 meant moderate/heavy rooting per year (Brunet et al., 2016).

2.4.4 Soil analysis

Soil samples were analyzed for pH using $CaCl_2$, water content (%), and moisture class. After removing the leaf litter layer, two soil samples were taken from each sample plot's topsoil (0-5 cm). According to Amelung (2019), the soil pH was measured as follows: 10 grams of dry soil was weighed into a 100 ml PE bottle. The soil sample was then filled with 50 ml of a 0.01 M $CaCl_2$ solution and shaken for about an hour and a half using an orbital shaker. Then, the pH was measured electrometrically. The moisture class of the soil surface was estimated during the sampling; it was classified into three different classes on a scale of 1 to 3. 1 was for fresh soil, 2 was for moist soil, and 3 was for wet soil. Lastly, gravimetric water content (%) was measured from fresh soil samples (Amelung, 2019).

2.5 Data analysis

The total percentage cover of the woody and herbaceous layer of each of the 74 plots was determined through the use of the percentage cover data collected in 2010 and 2019. The total cover of each plot's four woody canopy layers and of the ground layer was calculated by summing the cover percentage of all species and separately for spring ephemerals, summer herbs, and woody species in the ground layer. In addition, species richness of the ground layer was calculated for spring ephemeral herbs, summer herbs, and woody species. Differences in mean cover values between 2010 and 2019 were anlyzed with paired t-tests in Minitab (version 24.1.3).

Changes in the ground vegetation layer were studied in relation to the tree and shrub canopy cover, as the tree canopy is anticipated to have a dominant role in shaping light availability, moisture, and microclimate conditions near the forest ground. Apart from the canopy cover, three additional environmental factors were included in the analysis as they might come to influence the ground vegetation as well:

- Soil moisture content
- Soil pH **(**$CaCl_2$**)**
- Wild boar rooting intensity

Multiple linear regression analysis was implemented to statistically test the relationship between the cover and species richness of the ground vegetation layer and the explanatory environmental factors (canopy cover, rooting sums, and soil conditions). Linear regression and associated fitted line plots were calculated to visualize the effects of the statistically significant factors revealed by the multiple regression. The importance of these responses and relationships was evaluated using the r-square values and p-values to determine which factors statistically impact the three different species groups of the ground vegetation layer.

Regression analyses and visualization were completed using RStudio (version 2024.12.0+402) with R (version 4.3.2). Key packages included tidyverse, janitor, and ggplot2 (RStudio Team, 2024; RStudio Team, 2024; Wickham, H., 2016; Wickham et al., 2019; Firke, S., 2023.).

3. Results

3.1 Regression analysis

Multiple linear regression analysis models were calculated to study the effects of soil pH ($CaCl_2$), soil moisture (water content in %), wild boar rooting intensity, and the total canopy cover in 2019 on abundance and species richness of spring ephemerals, summer herbs, and woody vegetation cover in 2019. The results are presented in the following sections and an overview of the changes in cover and species richness of the three functional groups in the ground layer is provided in Table 1.

Table 1: Cover and species richness (standard error) of three functional groups in the ground layer of Dalby Söderskog in 2010 and 2019. P-values according to paired t-tests (n = 74).

Variable	Mean (SE) 2010	Mean (SE) 2019	P-value
Spring ephemeral cover	62.8 (3.1)	45.3 (2.9)	<0.001
Summer herb cover	30.9 (4.5)	26.2 (3.5)	0.264
Woody species cover	18.2 (2.6)	13.1 (2.3)	0.038
Spring ephemeral species richness	2.7 (0.1)	2.6 (0.1)	0.184
Summer herb species richness	1.7 (0.2)	3.1 (0.3)	<0.001
Woody species richness	1.8 (0.1)	1.6 (0.1)	0.200

3.1.1 Spring ephemeral cover

The mean cover of spring ephemerals decreased significantly from 63 to 45 % between 2010 and 2019 (Table 1). The multiple regression for the spring vegetation indicated that approximately 20.1% of the variability in spring ephemeral abundance in 2019 could be explained by the model predictors (R^2 = 20.1%, adjusted R^2 = 15.5%, p = 0.003).

Among the tested predictors, wild boar rooting intensity was the only factor that demonstrated a statistically significant impact (p = 0.001), displaying a negative relationship with the abundance of spring vegetation (coefficient = -4.27), suggesting that heavier rooting intensity by wild boar was associated with a lower abundance of this vegetation group.

Soil pH had a nearly significant adverse effect (p = 0.058), while the water content (p = 0.517) and canopy cover (p = 0.729) did not significantly affect the spring vegetation.

3.1.2 Summer herb cover

The mean cover of summer herbs did not change significantly between 2010 and 2019 (Table 1). The multiple regression for the summer vegetation showed that the model could explain 47.6% of the variability in summer herb abundance (R^2 = 47.6%, adjusted R^2 = 44.5%, $p < 0.001$).

Among the examined predictors, canopy cover demonstrated a highly significant negative correlation with this vegetation group ($p < 0.001$, coefficient = -0.334), suggesting that denser tree canopy cover reduced the abundance of summer herbs. Furthermore, soil pH ($CaCl_2$) had a statistically significant positive effect ($p = 0.004$, coefficient = 14.98), stating that a higher pH level is associated with a greater abundance of summer herbs. However, soil moisture (water in %) showed a positive correlation but was only marginally statistically significant ($p = 0.054$), while wild boar rooting had no significant impact on the summer vegetation abundance ($p = 0.803$).

3.1.3 Woody species cover

The mean cover of woody species in the ground layer decreased significantly from 18 to 13 % between 2010 and 2019 (Table 1). The multiple regression for woody species indicated that the model explained 13.9% of the variability in woody vegetation abundance in 2019 (R^2 = 13.9%, adjusted R^2 = 8.9%).

Although the general explanatory power of the model is relatively low, the regression was still statistically significant ($p = 0.034$). Among the predictors, soil pH ($CaCl_2$) negatively affected the abundance of woody vegetation ($p = 0.037$, coefficient = -9.02), suggesting that higher pH is associated with fewer woody species. Furthermore, wild boar rooting intensity also had a significant adverse effect ($p = 0.004$, coefficient = -2.92), stating that an increased rooting activity by wild boar reduced the woody species' abundance. However, neither soil moisture ($p = 0.812$) nor canopy cover ($p = 0.212$) significantly impacted this vegetation group.

3.1.4 Spring ephemeral species richness

Species richness of spring ephemerals did not change significantly between 2010 and 2019 (Table 1). The multiple regression model explained 14.7% of the variability in the number of spring species richness in 2019 by soil pH and moisture (R^2 = 14.7%, adjusted R^2 = 9.8%). The regression model was statistically significant overall ($p = 0.025$), although its explanatory power remained relatively low.

Among the tested predictors, soil pH significantly positively affected species richness ($p = 0.018$, coefficient = 0.584), suggesting that higher pH levels correlated with a greater number of spring species. In contrast, the soil moisture revealed a significant adverse effect ($p = 0.020$, coefficient = -0.0837), implying that higher soil moisture reduces species richness in the spring vegetation. Neither canopy cover ($p = 0.422$) nor wild boar rooting intensity ($p = 0.742$) significantly impacted the species richness of this model.

3.1.5 Summer herb species richness

Species richness of summer herbs increased significantly from 1.7 to 3.1 between 2010 and 2019 (Table 1). The multiple regression model explained a substantial portion of the variation, with a value of 53.5% (adjusted $R^2 = 50.8\%$), and was statistically highly significant ($p < 0.001$), suggesting a relatively good fit for explaining species richness in the summer vegetation in 2019.

Among the predictors, soil pH and canopy cover were the significant drivers of species richness. Soil pH showed a significant positive correlation ($p < 0.001$, coefficient = 1.79), suggesting that higher pH levels were associated with greater species richness during summer. On the other hand, canopy cover had a strong significant adverse effect ($p < 0.001$, coefficient = -0.0341), stating that denser canopy cover reduces summer herbs species richness. Neither soil moisture ($p = 0.122$) nor wild boar rooting intensity ($p = 0.286$) significantly impacted the species richness.

3.1.6 Woody species richness

Species richness of woody species did not change significantly between 2010 and 2019 (Table 1). The multiple regression model revealed a very low explanatory power, with only 4.2% (adjusted = 0%). The overall model was not statistically significant ($p = 0.554$).

3.2 Effects of canopy cover changes on ground cover changes

A comparison of the tree and shrub canopy cover between the years 2010 and 2019 (Figure 3) reveals a major overall decrease (Paired t-test, $p < 0.001$). In 2010, the canopy cover was relatively high, with a median of 142%. In 2019, the median canopy dropped close to 111%, suggesting a decrease in shrub and tree canopy cover. This loss in canopy cover reflects a substantial canopy opening, likely resulting from the ongoing dieback processes in the park's dominant tree species, including elm and ash.

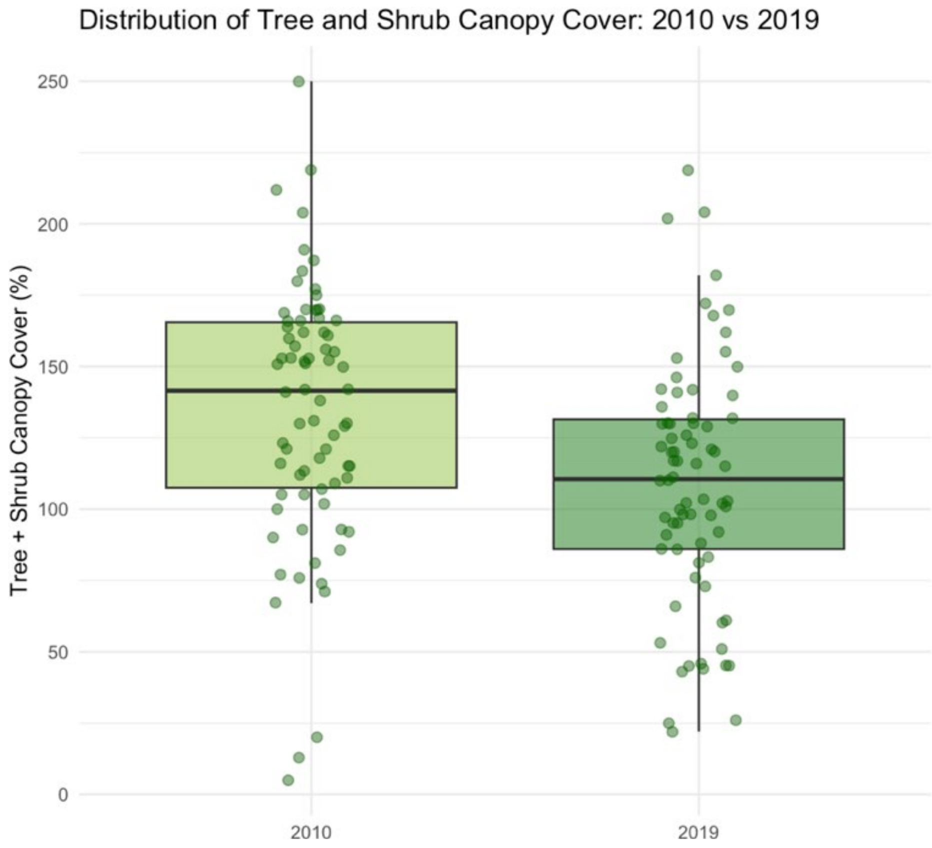

Figure 3: Tree and shrub canopy cover in 2010 and 2019. The boxplot represents the data distribution and its central tendency. Each box portrays the range of values in which the middle 50% of the data lies. (from the 25th to the 75th percentile). The horizontal line dividing each box indicates the median canopy cover. The vertical lines extending from the boxes – referred to as "whiskers"- reach out to the smallest and largest values that fall within 1.5 times the data range of values from the bottom and top quartiles, respectively. Any data points that fall outside this range are considered outliers and are displayed as individual dots.

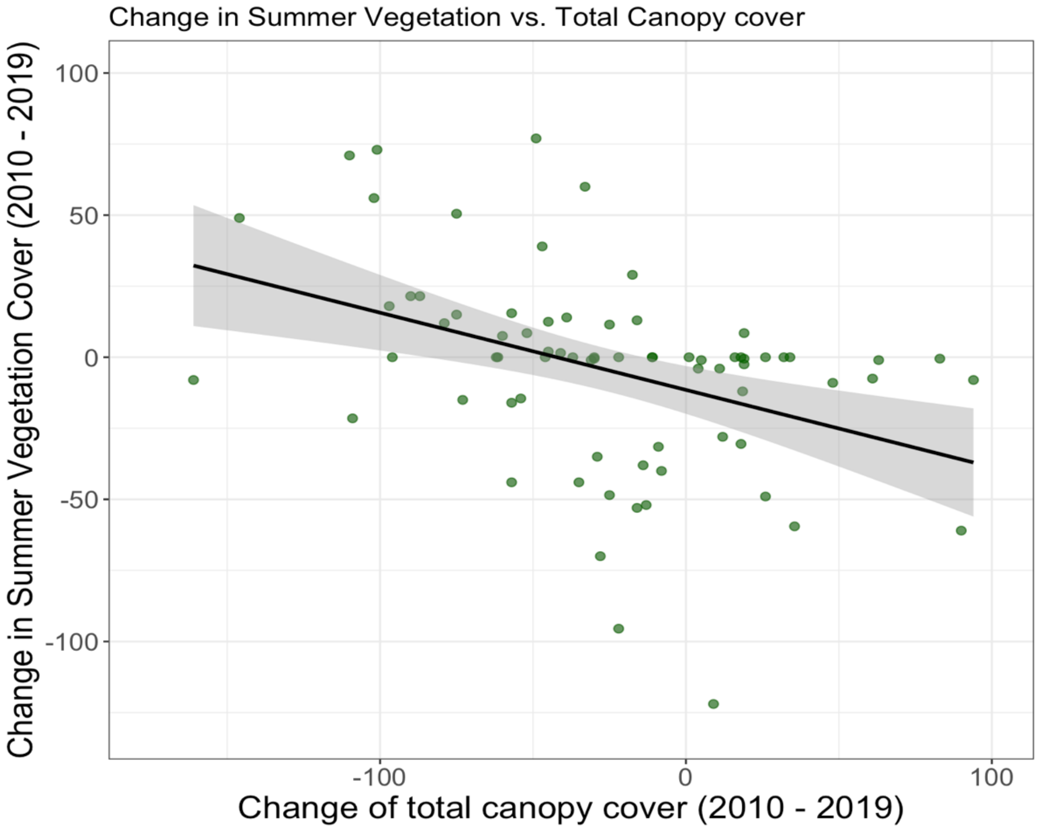

Figure 4: The change in summer herb vegetation cover in relation to the change in total canopy cover from 2010-2019 according to linear regression (n = 74). The black line represents the regression line, and the shaded area corresponds to the 95% confidence interval (Beers, 2025).

The difference between the sum of the two years' canopy cover layers (e.g., 2019 minus 2010) represents the net change in canopy cover over the study periods.

The following scatter plot with a fitted regression line (Figure 4) evaluates the influence of the change in the canopy over time on the change in summer herb vegetation cover. The linear regression analysis reveals a statistically significant negative relationship between these two variables (p-value = 0.0004). The slope estimates (-0.59) state that, for every 1% canopy cover increase, summer herbs cover decreases by about 0.59%. The model explains approximately 16% of the variation in summer herb cover change ($R^2 = 0.16$). However, when testing the change in spring ephmeral vegetation according to the change in the canopy layers (Appendix A.1), the result showed a positive but non-significant correlation (slope estimate: 0.073, p-value = 0.2982). A similar result was received for the woody ground vegetation (Appendix A.2). Although there was a slight negative trend, it was statistically non-significant (slope estimate:-0.05, p-values = 0.2828).

3.3 Effects of the tree and shrub canopy cover on the ground vegetation

A linear regression was conducted for each group to examine how total canopy cover of 2019 impacted the cover of the three functional groups of the ground vegetation. The regression analysis between the canopy cover and the spring ephemeral ground vegetation cover in 2019 revealed a positive but non-significant relationship (slope estimate = 0.09, p-value = 0.099, R^2 = 0.037). Although it has no statistical significance, the trend indicates that a high canopy cover may be weakly associated with increased spring ephemeral cover. However, only about 3.7% of the variation of the spring vegetaton cover was explained by the canopy cover of 2019 (Appendix B.1).

A similar result was extracted for the woody species although this association revealed a weak and non-significant negative association (Appendix B.2) (slope estimate = -0.21, p-value = 0.400). The model explained less than 1% of the variation in woody species cover (R^2 = 0.01), indicating that the total canopy cover has no influence in this case. In contrast, a statistically significant negative correlation was observed between the total canopy cover of 2019 and the summer herb cover (Figure 5) (Estimate = -0.79, p-vaue < 0.001, R^2 = 0.308). The model explains about 31% of the variation, implying that summer herb cover is suppressed under denser canopy conditions.

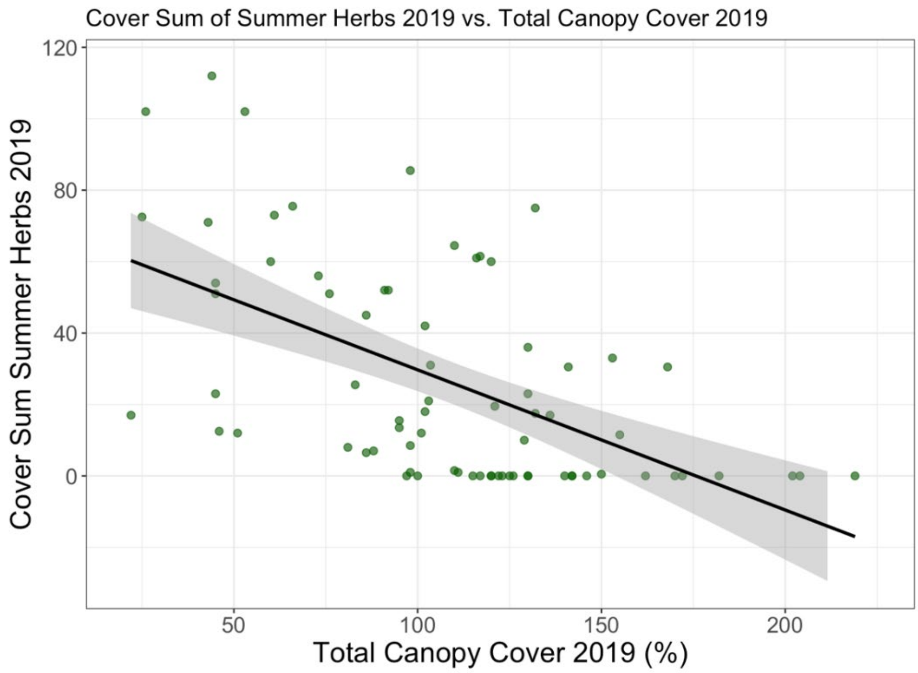

Figure 5: Summer herb cover 2019 in relation to canopy cover 2019 (%). Each point represents each individual permanent sample plot. The black line represents the regression line, and the shaded area corresponds to the 95% confidence interval.

3.4 Changes in species richness

The change in the total canopy cover between 2010 and 2019 influenced the species richness of the ground vegetation differently depending on the species group. The relationship between the spring ephemeral species richness and the canopy cover was positive but not statistically significant (Estimate = 7.58, P-value = 0.388, R^2 = 0.01). The model explained just 1% of the variation in canopy change (Appendix C.1), stating that the canopy dynamics do not drive changes in the spring species richness.

Conversely, a statistically significant negative relationship was noted between the change in summer green herbs species richness and canopy cover change (Estimate = –8.92, $p < 0.001$, $R^2 = 0.22$). This indicates that areas where the canopy cover decreased the most, tended to exhibit the largest increase in summer herbs. The model explained about 22% of the variation, supporting the idea that at decrease in canopy cover made it possible for more summer herbs to establish and grow (Figure 6).

The relationship between the woody vegetation species richness and canopy cover was very weak and non-significant (Estimate = 1.68, $p = 0.729$, R^2 = 0.002). This result demonstrated that the richness of woody ground vegetation species was largely unaffected by the change in canopy cover (Appendix C.2).

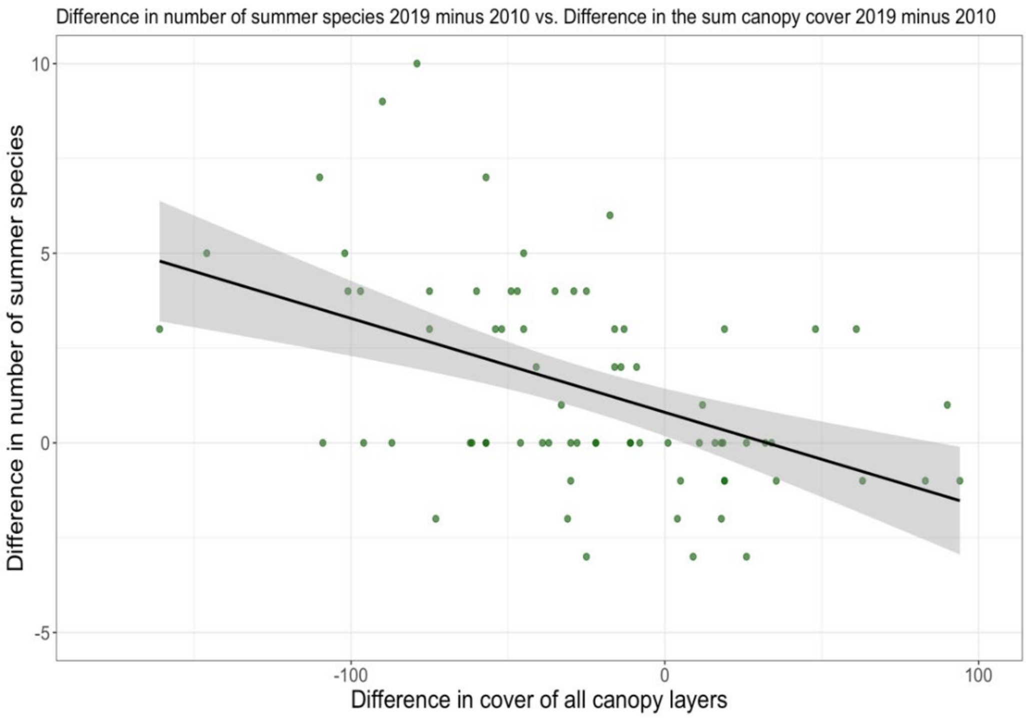

Figure 6: The change of summer herb species richness in relation to the change of tree and shrub canopy cover layer (%) from 2010-2019. Each point represents a permanent sample plot. The black line represents the regression line, and the shaded area corresponds to the 95% confidence interval.

To further explore the factors highlighting the observed change in summer green herbs between the two years, the relationship between the total sum of 2019 canopy cover and the number of summer species was examined (Figure 7). There was a similar evident negative relation (Estimate = –0.785, $p < 0.001$), stating that a high sum of canopy cover in 2019 was related to fewer summer herb species.

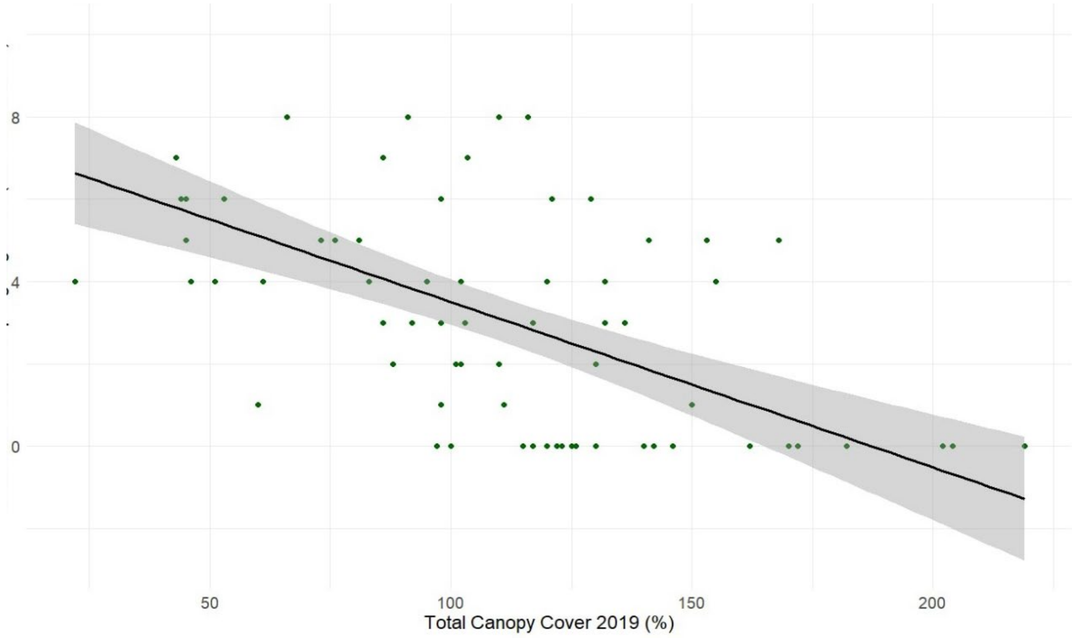

Figure 7: Number of summer herbs 2019 in relation to 2019 total canopy cover (%). Each point represents a permanent sample plot. The black line represents the regression line , and the shaded area corresponds to the 95% confidence interval.

3.5 Effects of wild boar rooting (2011 – 2019)

Rooting by wild boar was not recorded in 2010, but started to occur in 2011. The median rooting sum 2011-2019 was 3.5, ranging from 0 (no rooting, eight plots) to 9.5 (1 plot), and a first quartile of 1.875 and a third quartile of 5.0. Wild boar rooting recorded in 2011 and 2019 demonstrated significant correlations with two of the three functional groups of ground vegetation in 2019. The spring vegetation cover in 2019 (p-value = 0.0021*,* Figure 8) revealed a significant negative relationship: a higher total rooting over the period is associated with reduced spring vegetation cover. The model explained about 12.4% of the variation in spring ephemeral vegetation cover ($R^2 = 0.1235$).

Furthermore, an additional analysis revealed a significant negative correlation when testing the relationship between the total sum of wild boar rooting activity and the difference in cover of spring ephemeral species between 2019 and 2010 ($p < 0.001$; Figure 9). The regression model explained 31.8% of the variation in the change in spring ephemeral cover, suggesting that a higher level of accumulated wild boar rooting activity was associated with a more substantial decline in spring vegetation cover.

However, the 2019 summer herb vegetation cover was not significantly affected by the rooting of the wild boars ($p = 0.307$, *Appendix D.1*); the model indicated that only about 1.5% of the variation was explained by the rooting ($R^2 = 0.015$).

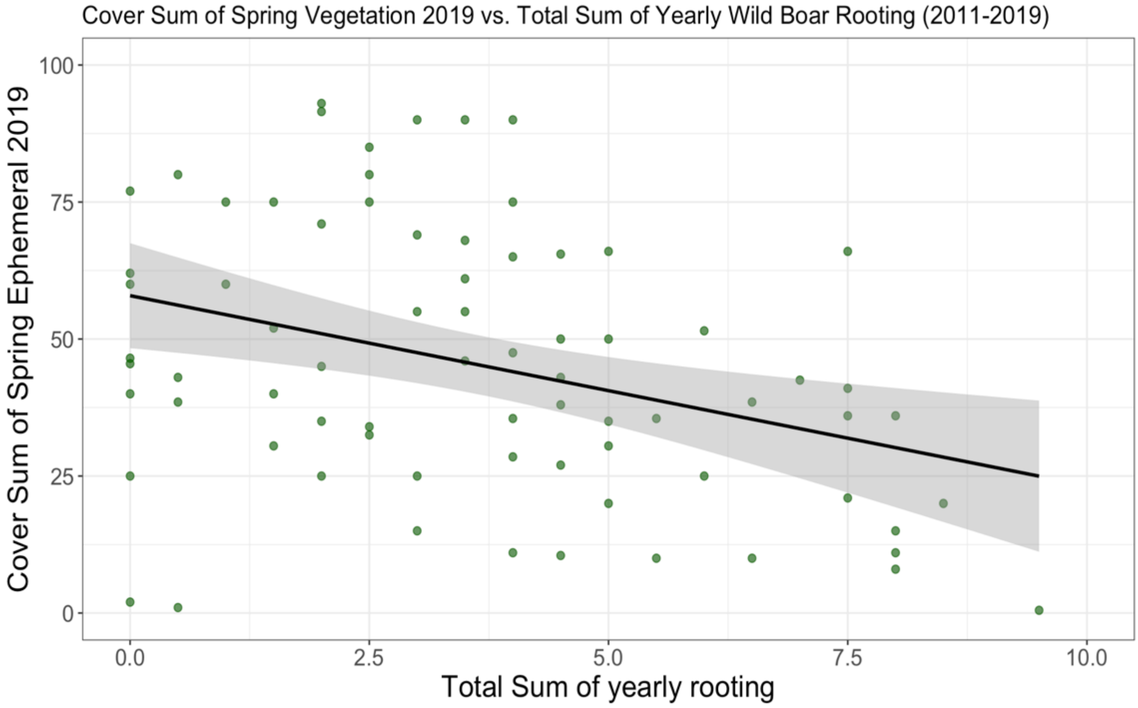

Figure 8: Spring ephemeral cover 2019 in relation to wild boar rooting (2011-2019). Each point represents a permanent sample plot. The black line represents the regression line, and the shaded area corresponds to the 95% confidence interval.

A weak, but significant negative relationship was observed between the woody vegetation cover and wild boar rooting (p-value = 0.025, Appendix D.2). Nevertheless, the wild boar rooting did not impact the species richness of the ground vegetation groups. However, with further testing, it was observed that there was a significant positive relationship that emerged between the cover change of summer herbs and wild boar rooting ($p = 0.0085$, $R^2 = 0.092$). It interestingly suggested that the increase in wild boar rooting activity was associated with increased summer herbs cover from 2010-2019 (Figure 10).

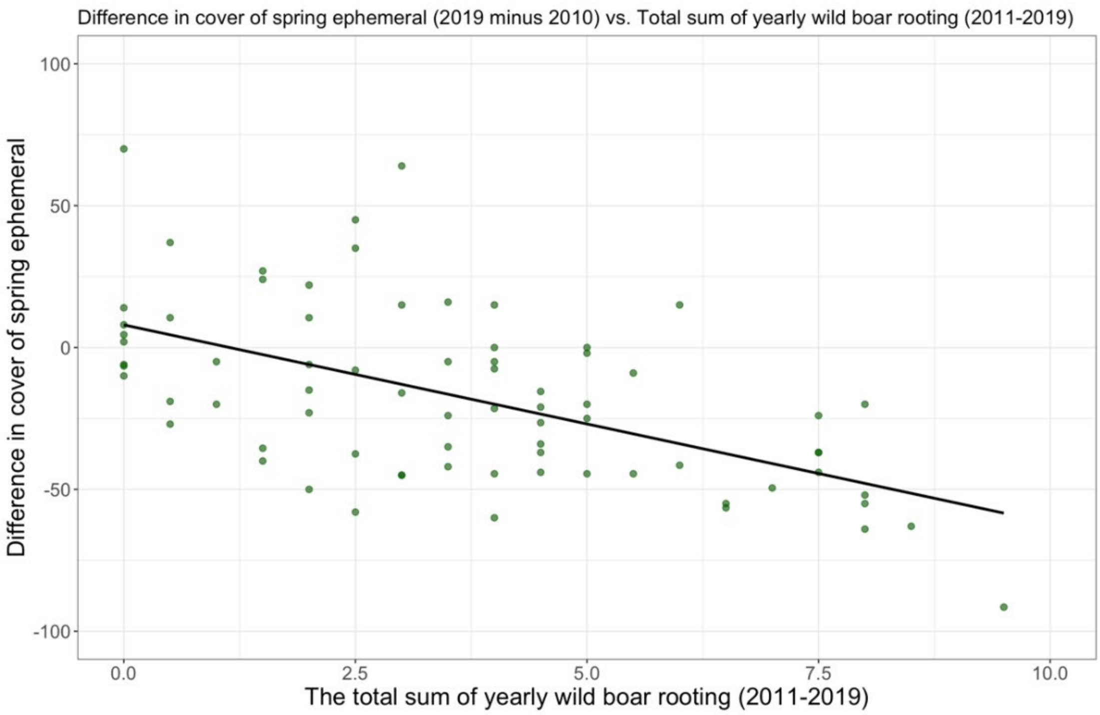

Figure 9: Difference in cover of spring ephemerals (2019 minus 2010) in relation to the total sum of wild boar rooting (2011-2019). Each point represents a permanent sample plot. The black line represents the regression line..

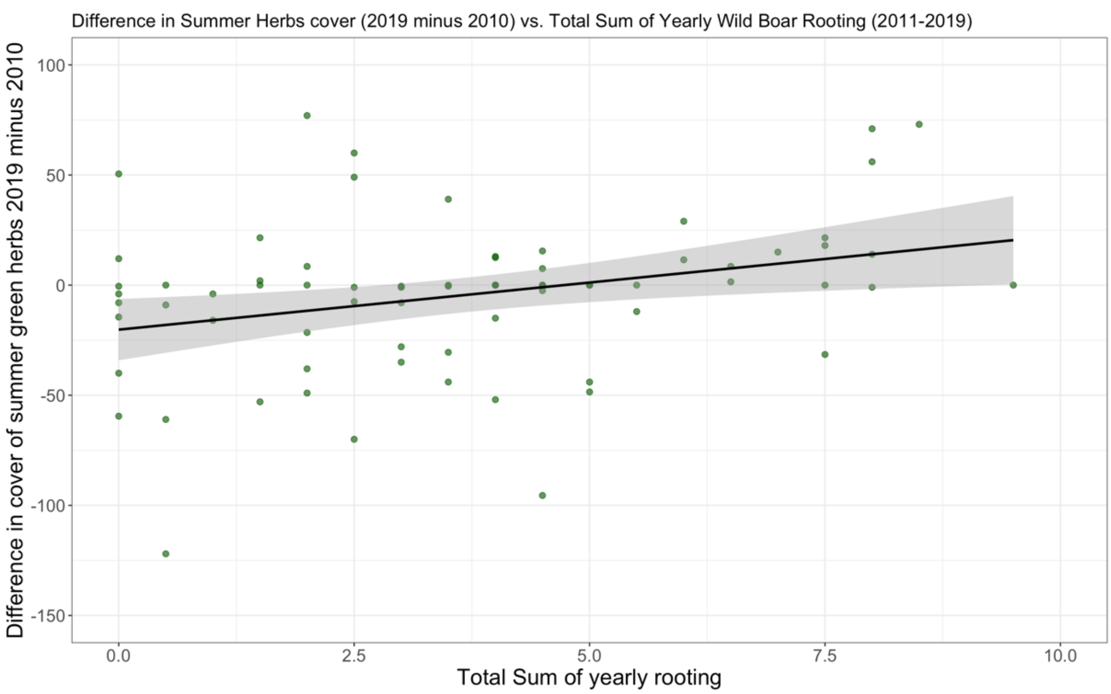

Figure 10: Relationship between the total sum of yearly wild boar rooting (2010–2019) and the change in cover of summer herbs between 2010 and 2019). Each point represents a permanent sample plot. The black line represents the regression line, and the shaded area corresponds to the 95% confidence interval.

3.6 Effects of soil pH on ground vegetation

It was observed that the cover of summer herbs in 2019 showed a significant positive relationship with soil pH ($CaCl_2$) ($p < 0.001$, $R^2 = 0.22$, Figure 11), suggesting that a higher pH level is connected to an increase in summer herbaceous cover. In contrast, spring ephemeral and woody vegetation cover showed no significant responses to soil pH ($p = 0.30$ and $p = 0.34$, respectively). Although the regression lines had a slight negative trend, the explained variance was very low ($R^2 \approx 0.01$), indicating that pH did not influence their vegetation cover in 2019.

Futhermore, an analysis between soil pH and the number of summer herbs species observed in 2019 (Figure 12) shows a statistically significant positive relationship ($p < 0.001$), indicating that higher soil pH is associated with an increase in summer herbs species richness. The model accounted for 23.9% of the variance in the number of summer herbs observed.

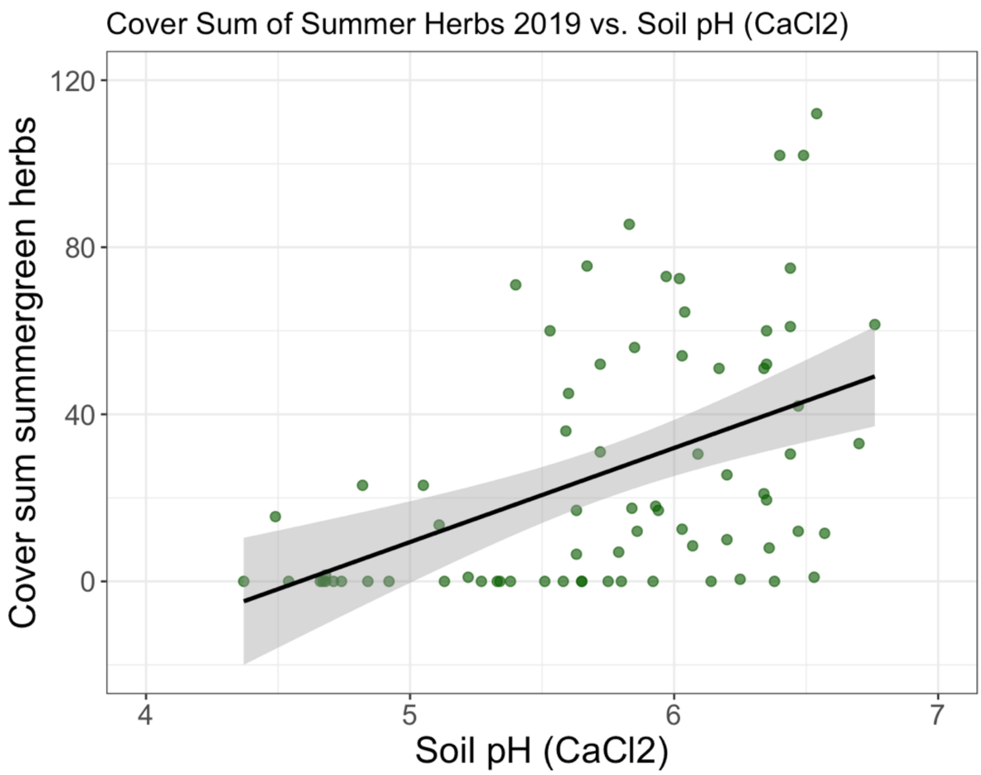

Figure 11: Relationship between soil pH ($CaCl_2$) and the cover sum of summer herbs in 2019. Each point represents a permanent sample plot. The black line represents the regression line, and the shaded area corresponds to the 95% confidence interval.

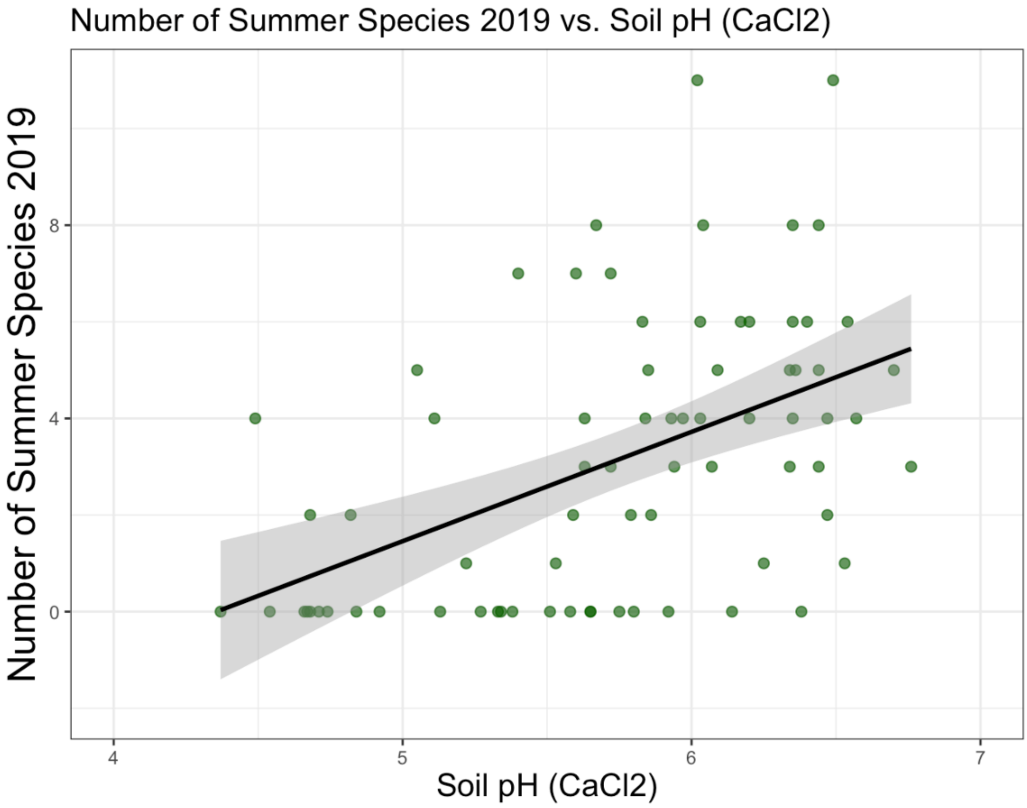

Figure 12: Relationship between soil pH (measured in $CaCl_2$) and the number of summer herb species in 2019. Each point represents a permanent sample plot.. The black line represents the regression line, and the shaded area corresponds to the 95% confidence interval.

4. Discussion

4.1 Key findings

This study has disclosed that changes in canopy cover and soil conditions substantially influenced the ground vegetation in Dalby Söderskog National Park between 2010 and 2019. Clear positive effects were observed in the summer herb vegetation cover as an effect of the reduction of canopy cover, supporting hypothesis 1. On the other hand, the spring ephemeral and woody species vegetation showed a weak or non-significant response to canopy cover changes.

Wild boar rooting intensity was another relevant factor, which significantly reduced the abundance of spring ephemeral cover, supporting hypothesis 2. However, in contrast to hypothesis 2, the rooting activity of the wild boar increased the abundance of summer herbs, suggesting an unexpected positive effect of soil rooting which mostly happened in winter on growth conditions of summer herbs. The positive relation between soil pH and summer herb species richness and cover in 2019 further reinforced the role of soil conditions in shaping forest ground vegetation.

4.2 Interpretation of results

The total canopy cover across the 74 permanent study plots in Dalby Söderskog National Park demonstrated an apparent decrease between 2010 and 2019. The boxplots further underline the outstanding decline in both upper range and overall variation across the plots, signifying that even the densest part of the forest had a considerable loss of canopy. Such structural change is a probable effect of extensive tree and canopy mortality caused by ash dieback and Dutch elm disease detected in the area (Brunet et al., 2014; Ruks, 2020).

The observed decline in total tree canopy cover would cause critical alteration of the microclimate below the canopy and on the forest floor (Lenk et al., 2024), as well as increasing the amount of light reaching the forest ground vegetation; explaining the increase in summer vegetation. This aligns with findings by Depauw et al. (2020), who proved that canopy cover is a strong predictor of understory light-demanding vegetation of the understory. The results of this study affirm this link, as summer herb species – commonly light-demanding – reacted positively at the decrease of canopy cover. Spring ephemerals, however, mainly benefit from the early season light and absence of leaves in deciduous tree canopies, explaining their weak connection with canopy cover.

The spring ephemeral vegetation negatively correlated with the wild boar rooting activity, pointing out that physical disturbance plays a much greater role in this vegetation group than canopy cover dynamics. The sharp decline of spring ephemeral vegetation by the wild boar rooting is likely due to their vulnerability during early-season foraging. According to Biały (1996), wild boars actively seek "underground storage organs such as rhizomes, spring bulbs, and roots" often aiming for geophyte-rich patches. A typical example is the wood anemone (*Anemone nemorosa*), an early spring flowering plant native to the temperate European forest. Its shallow rhizomes, which enable rapid spring growth, make this species particularly vulnerable to rooting caused by wild boars (Biały, 1996).

In contrast, an interesting positive effect of wild boar rooting was observed on the cover of summer herbs. This may be explained by the fact that this vegetation group can come to profit from the soil turnover or/and minimization of other plants' competition, including competition for light during the transition period in late spring between spring ephermerals and summer green herbs (Horčičková, Brůna, and Vojta, 2019). According to Biały (1996), "boar rooting contributes to the formation of the morphological structure and properties of forest soil surface layers because of a systematic searching for food…".

The positive interaction between the summer herb species richnes and the soil pH affirms previous studies, which state that species richness in general is higher on calcareous soils (e.g. Wilson et al., 2001, Cheng et al., 2020, Škornik, 2024). To conclude, biotic disturbances due to tree diseases and soil rooting have changed abiotic growing conditions in terms of light and exposed mineral soil which has caused considerable changes in the abundance and diversity of the ground vegetation in Dalby Söderskog.

4.3 Implication of the results

The following findings emphasize the importance of considering how canopy cover and soil conditions impact vegetation on the forest floor when either managing or conserving a deciduous forest ecosystem. Even in protected forest areas like Dalby Söderskog National Park, natural disturbances—such as pest outbreaks and diseases or climate extremes like severe drought—can significantly modify the forest floor vegetation composition.

The observed increase of summer herbs as the tree canopy cover decreases suggests that light-demanding species can take quick advantage of any changing condition, potentially shifting the balance within the ground flora. Soil conditions, especially soil pH, play a significant role in further shaping these patterns.

Furthermore, the observed result of the wild boar rooting highlights the important role of the fauna in shaping the ground vegetation community. While wild boar rooting can have a large effect on sensitive vegetation, particularly spring ephemerals, which rely on shallow rhizomes, it can also increase spatial habitat heterogeneity and promote overall plant diversity (Rekiel, Więcek, and Sońta, 2024). These findings reveal that a complicated disturbance, recovery, and adaptation interplay shapes the forest floor's herbaceous diversity.

Knowing this, future management and monitoring could consider measurements such as controlling the wild boar density or promoting the regeneration of the forest canopy. These actions are particularly applicable given that Dalby Söderskog is vulnerable to diseases and pathogens that lead to further canopy loss. Such measurements could help maintain a balance of light and soil conditions in an area, safeguard the vulnerable herbaceous forest vegetation layers, and uphold the long-term conservation of deciduous forest biodiversity in naturally evolving ecosystems.

4.4 Study limitations

While soil conditions and canopy cover explained a large part of the observed changes and patterns, additional factors might also be important. For example, annual weather variation could affect plant cover as well a disturbance by humans as the National park has many visitors (National Park Service, 2021).

Secondly, the lack of direct light measurements might set some limitations in this study. Furthermore, the soil measurements were taken just in 2019, which limited a more dynamic view of soil condition change over time. Lastly, cover values were used instead of biomass, which might not fully represent productivity or species dominance.

4.5 Future research

Future research and studies should explore having more frequent surveys to detect short-term fluctuations and better resolve temporal species dynamics. Incorporating light measurement is greatly recommended, and expanding the soil measurement over the years could offer a clearer picture of the environmental controls in vegetation change. Furthermore, tracking animal activity and herbivory pressure could help clarify the role of fauna in the understory community shift.

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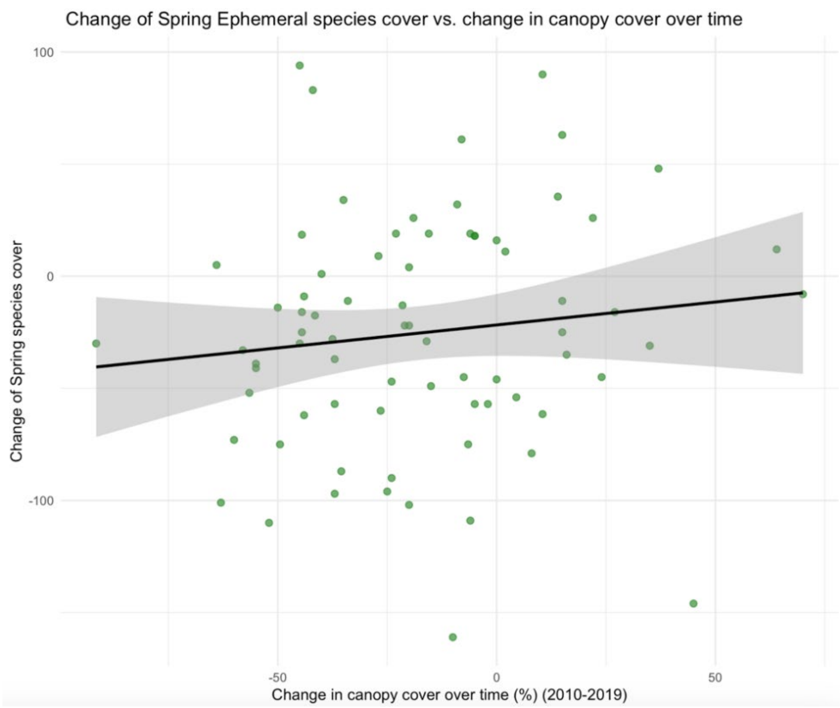
Appendix

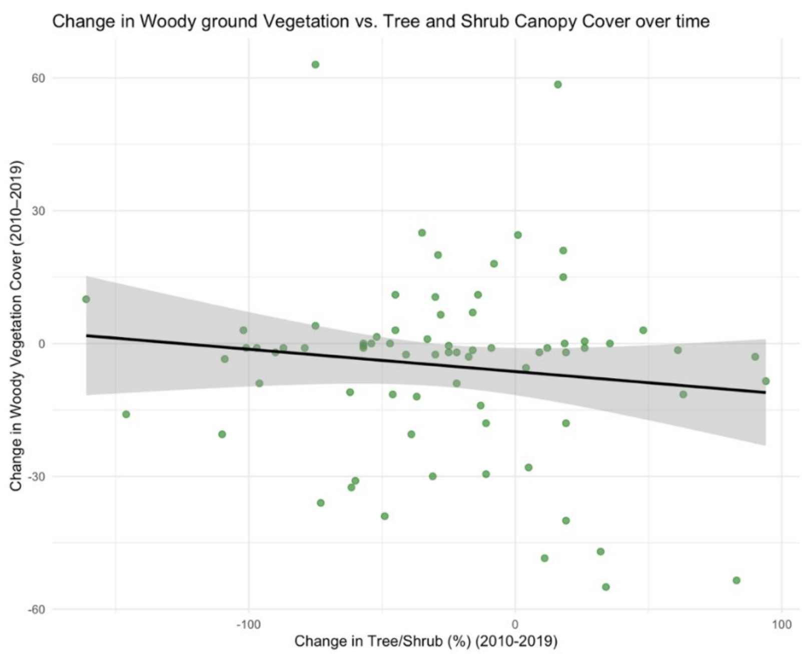
Appendix A.1

The change in spring ephemeral ground vegetation cover in relation to canopy cover change over time (2010-2019).



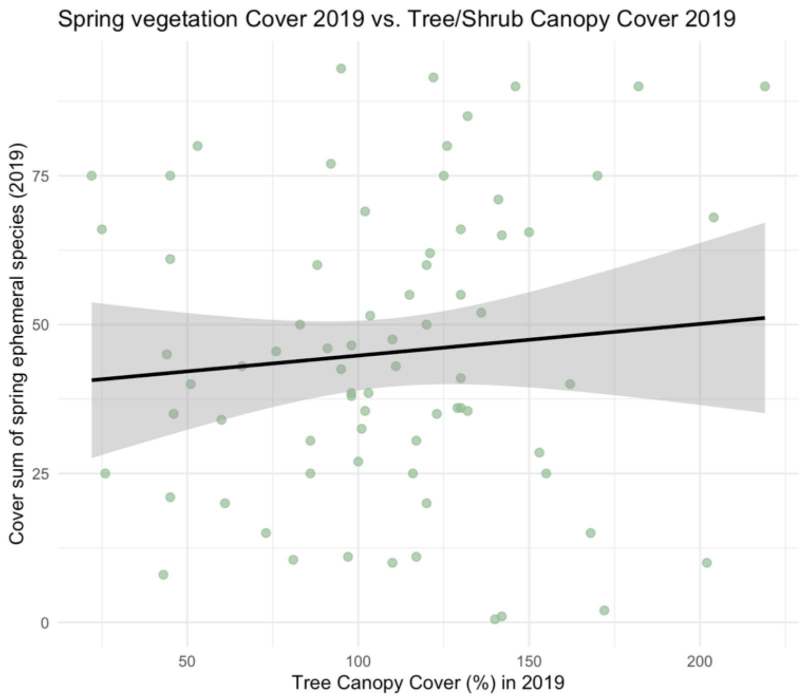
Appendix A.2

The change in woody ground vegetation species in relation to change in canopy cover over time (2010-2019).



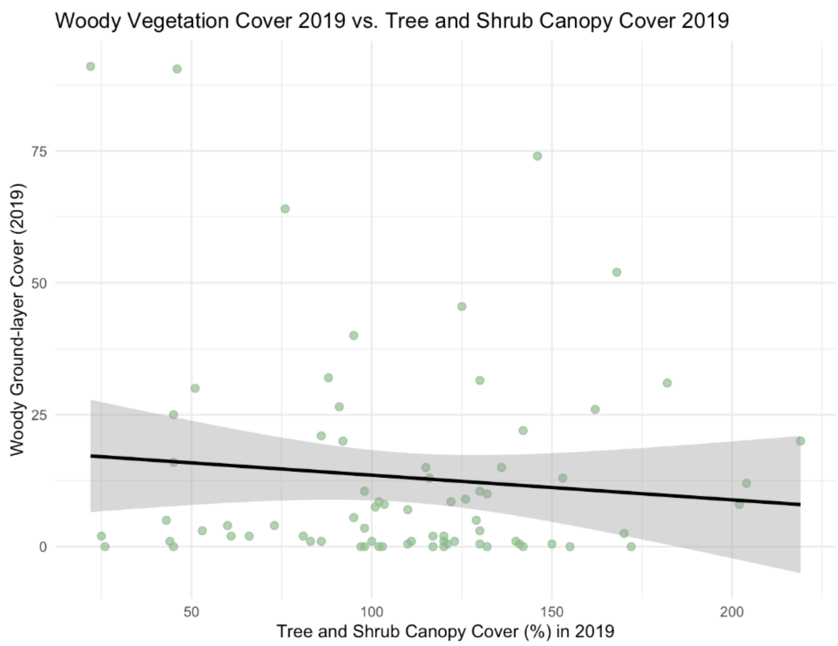
Appendix B.1

Spring herbaceous vegetation cover 2019 in relation to Tree/Shrub total canopy cover 2019.



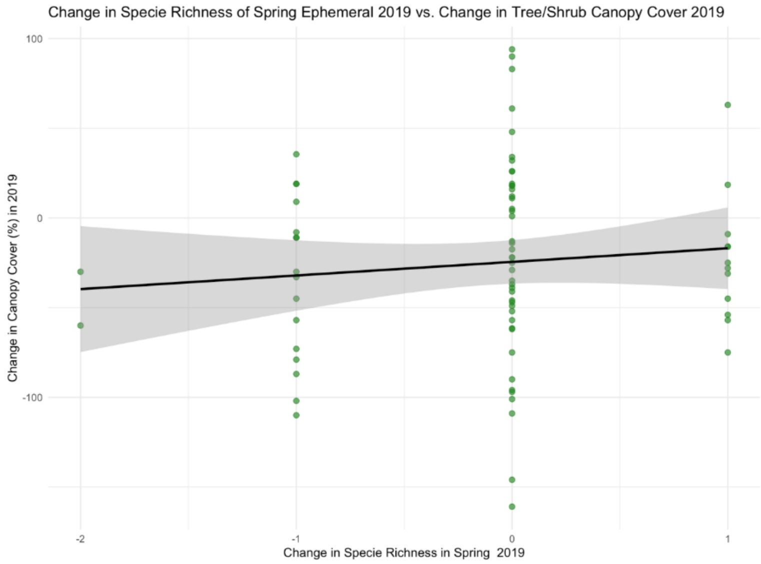
Appendix B.2

Woody ground vegetation cover 2019 in relation to Tree/Shrub total canopy cover 2019.



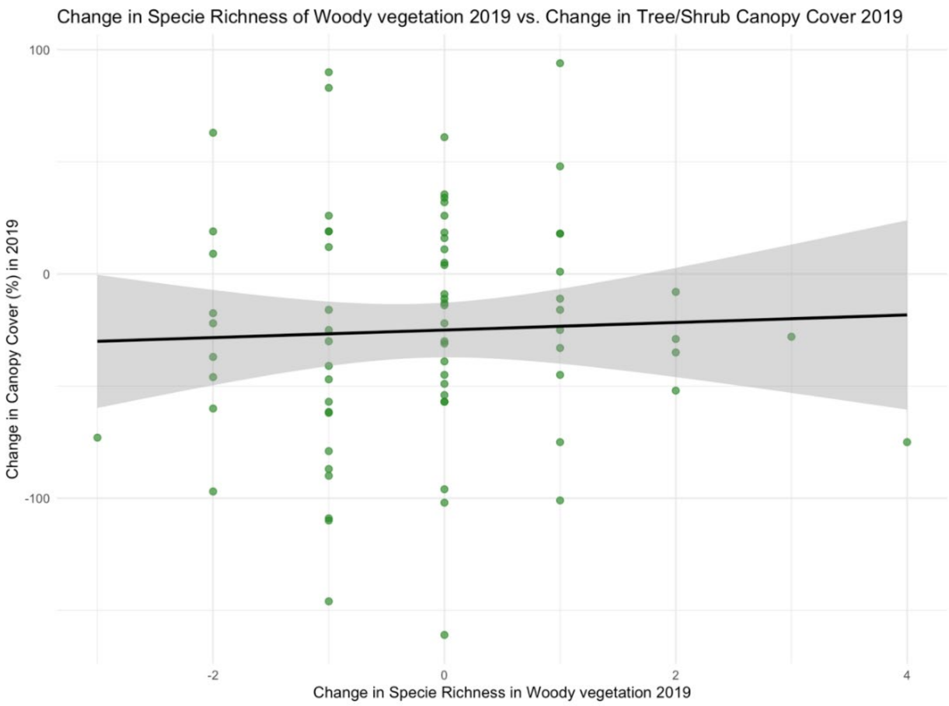
Appendix C.1

Change of spring ephemeral species richness 2019 in relation to change in canopy cover 2010-2019.



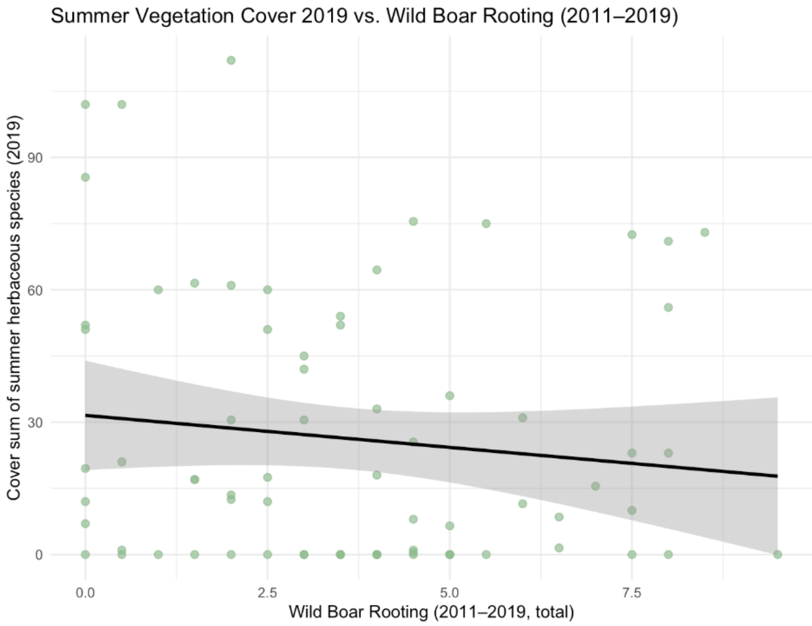
Appendix C.2

Change of woody species richness in relation to change in canopy cover 2010-2019.



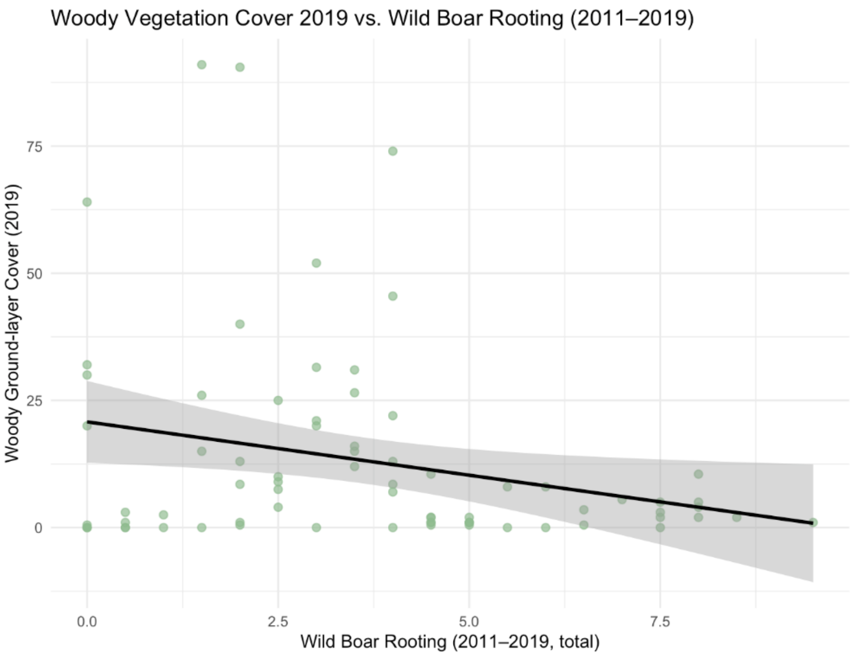
Appendix D.1

Wild boar rooting (2011-2019) in relation to summer herb cover 2019.



Appendix D.2

Wild boar rooting (2011-2019) in relation to woody species cover 2019.



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