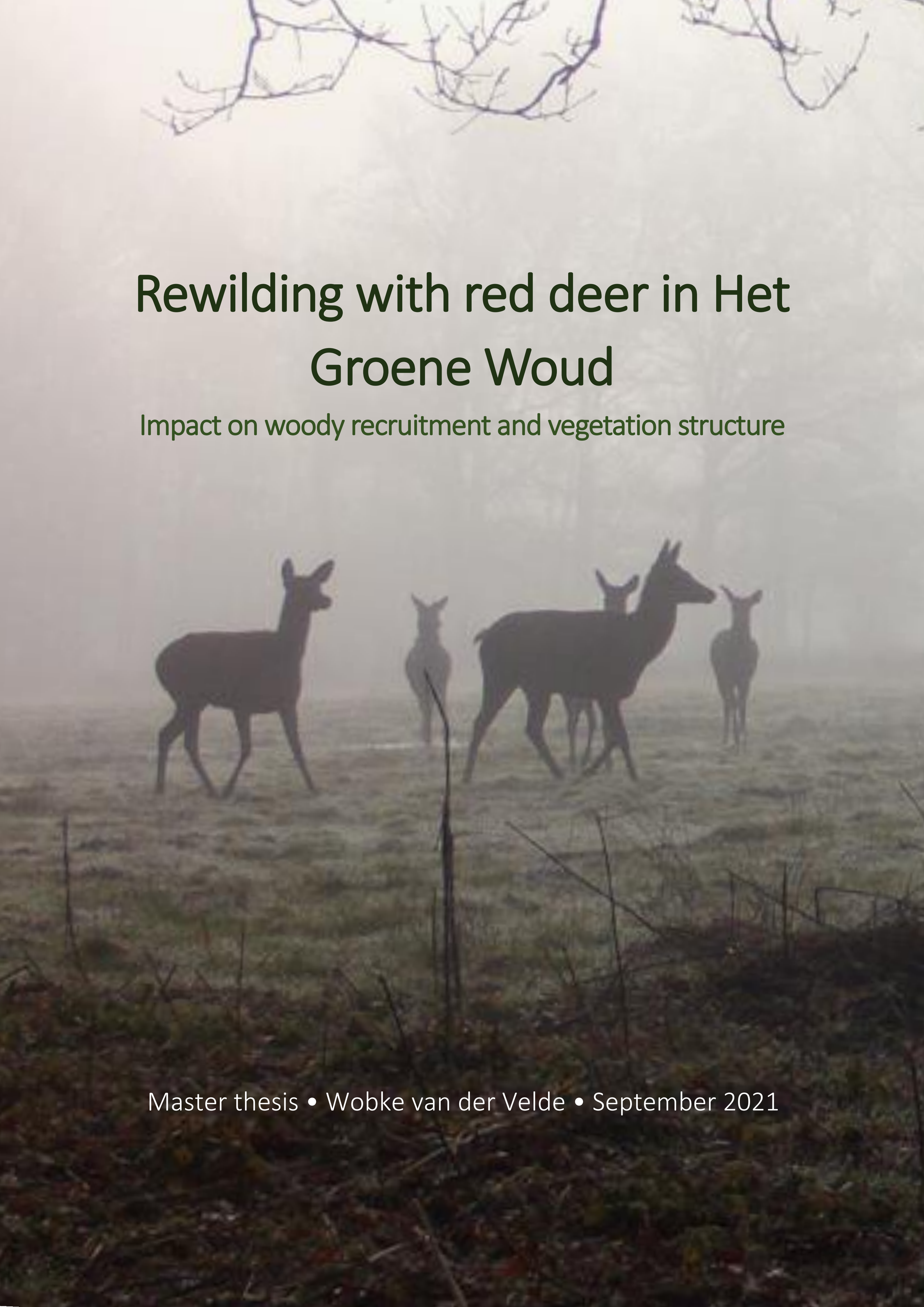

Rewilding with red deer in Het Groene Woud

Impact on woody recruitment and vegetation structure

Master thesis • Wobke van der Velde • September 2021

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Summary

In national landscape Het Groene Woud, located in the Dutch province of Noord-Brabant, nature managers reintroduced red deer to increase the ecological value of the area. As intermediate feeders, red deer forage on both woody and grassy vegetation, and can, through top-down interactions, broadly impact their environment. The idea is that red deer, in combination with other herbivores like cattle and roe deer, can increase the graduality of the transitions between grasslands and forests in Het Groene Woud, and can maintain a diverse, half-open landscape. To monitor if these goals are being obtained, the aim of this study was to measure woody recruitment and vegetation structure within the red deer enclosure, and to quantify how these can be linked to area use by red deer. I used camera traps to determine the area use by red deer in 2021, I used GPS data to determine historic area use, and I performed a field survey of eighty 20x20m plots to measure vegetation characteristics. I also used vegetation data from 2019, to measure vegetation change. In an elaborate statistical analysis, I then studied the interaction between red deer and the vegetation, and the influence of various covariates, like tree species, habitat type and coarse woody debris. I found that red deer preferred to stay in oak-hazel-alder forests and grasslands. I also found indications of red deer influencing the growth of saplings, possibly keeping them below a certain height. Interestingly, the results show that this effect differs per tree species. Furthermore, I found little indications of red deer influencing bramble growth, or increasing woody vegetation structure. In fact, grassland plots barely contained any woody structure. Restoring top-down trophic interactions, or trophic rewilding, has received increasing interest. The red deer enclosure of Het Groene Woud, together with this study, provide examples of the effect of rewilding with large herbivores, as well as on how to study these processes.

Acknowledgements

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Table of contents

1. Introduction

1.1 Loss and restoration of trophic functions

Humans have drastically altered the presence of large animals on Earth since the late Pleistocene. Fifty thousand years ago, at least 150 genera of mammalian megafauna (animals weighing more than 44 kg) populated our planet (Barnosky et al., 2004). Forty thousand years later, however, around two-third of those genera, together with several megafaunal reptile and bird species, had become extinct (Barnosky et al., 2004). While climatic effects might have played a role in these Late-Quaternary megafaunal extinctions, human arrival is thought to be the main driver of the disappearance of these large animals (Araujo et al., 2017; van der Kaars et al., 2017). Humans possibly impacted megafauna through hunting, habitat alterations, introduction of new species and spread of diseases (Koch & Barnosky, 2006). As this anthropogenic influence on the environment is still present in modern times, the threat to large-bodied wildlife continues (Smith et al., 2016).

This megafaunal extinction is not just a loss of species, it also leads to a loss of trophic functions (Cromsigt et al., 2018; Estes et al., 2011). In the present, it can be observed that large animals shape ecosystems, with their impact propagating through different trophic levels of their food webs (Estes et al., 2011). An example is the jaguar (*Panthera onca)*, whose loss in Venezuelan forests caused an eruption of herbivores, finally resulting in reduced plant recruitment and survival (Terborgh et al., 2001). Even though jaguars have no direct impact on vegetation, the absence of predators here determined the state of the forest. Another example is the reindeer (*Rangifer tarandus*), grazing of which reduces woody encroachment of tundra, which results in a higher surface albedo. By doing so, reindeer possibly limit local climate warming (Cohen et al., 2013; Te Beest et al., 2016). It is suggested that such trophic cascades occurred in the distant past as well (Cromsigt et al., 2018). There is evidence that the Late Quaternary megafaunal extinctions led to local climate warming (Doughty et al., 2010), biome shifts (J. L. Gill, 2014), changes in methane concentration (Smith et al., 2010), regionally reduced CO_2 sequestration (Doughty, Wolf, et al., 2016), and slowed-down nutrient cycles (Doughty, Roman, et al., 2016).

Over the last decades, conservation practices have begun to adopt the importance of trophic restoration. In 2006, “Pleistocene Rewilding” was suggested as a way to restore ecosystems through “reinstituting ecological and evolutionary processes that were transformed or eliminated by megafaunal extinctions” (Donlan et al., 2006). Later, this developed into the somewhat broader concept of trophic rewilding, where species are introduced to restore top-down trophic interactions and associated trophic cascades, aiming for self-regulating ecosystems (Svenning et al., 2016).

1.2 Red deer as ecosystem engineer

In the current European context, red deer (*Cervus elaphus*) is another animal that plays a potentially important role in shaping ecosystems, as it is one of the larger surviving, wild herbivores on this continent. The ungulate species often favours woodland habitats (Mitchell, 1977), but can also be found in shrublands (Alves et al., 2014) and sometimes even in treeless areas, such as the British moorlands (Whitehead, 1964). When red deer do live in forests, they usually prefer semi-open forest, making use of grassy clearings and woodland edges (Alves et al., 2014; Kuijper et al., 2009; Mitchell, 1977; Patthey, 2003). This is probably because these transition zones provide both qualitative food and shelter (Alves et al., 2014).
The ability to inhabit both forests and grasslands results from, among other things, the red deer’s feeding habit. Herbivores can be roughly divided into three different groups: browsers, grazers and

intermediate feeders (Figure 1, Hofmann, 1989). Browsers predominantly feed on material of dicotyledonous plants, like twigs and shrub leaves, while grazers consume graminoids like grass (Gordon, 2003). Intermediate feeders switch between the two consumption types, fluctuating with, for example, season and location (Gordon, 2003). Usually, however, they choose plant parts with low fibre content (Hofmann, 1989).

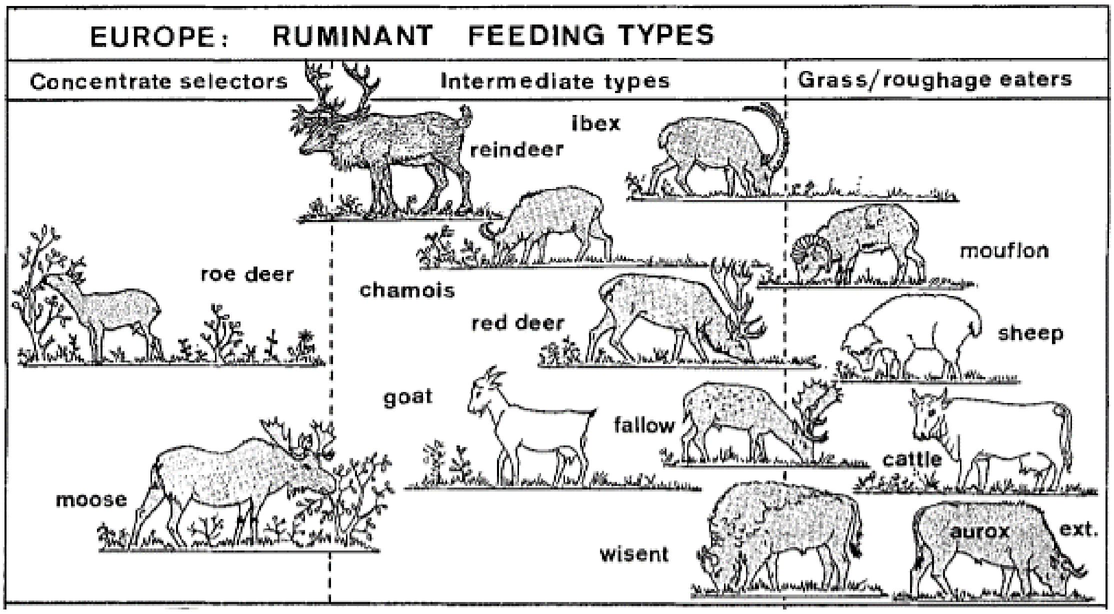


Figure 1 – European ruminants according to their feeding type. Species further to the right are more adapted to digest high fibre plants, like grasses. The red deer is here classified as an intermediate feeder. *From Hofmann (1989).*

Hofmann (1989) classified the red deer as a member of the latter group. This is confirmed by, for example, Dumont et al. (2005), who showed how hinds fed on grass during the winter, but predominantly consumed shrubs, seedlings and forbs during the other seasons. Other research also found the diet composition of red deer to consist of both concentrate plant material and graminoids (Cornelissen & Vulink, 1996; Krojerova-Prokesova et al., 2010; Storms et al., 2008). A brief overview of the diet of European red deer is given in table 1. Because of the red deer's ability to both browse and graze (Figure 3), the animal impacts vegetation in various ways.

Vegetation layer	Food type	Specific species
Tree layer	Deciduous tree leaves and twigs	Oak [2,5,6] Beech[2,5] Rowan[2,5,6] Birch[5] Alder buckthorn[4] Bird cherry[5,6]
	Tree bark	Scots pine[5] Douglas fir[5] Rowan[5] Elderberry[5]
Shrub layer	Leaves and twigs	Heather[1,5]
		Blueberry (also the roots)[1,4,5]
		Bramble[2,4,5]
Herb layer	Grasses	i.a. Wavy hair-grass[1,4,5]
	Herbs	i.a. Heath bedstraw[5]
	Fruits	Acorns[1,3,4]

Table 1 – Food source preferences of European red deer. *Adapted from Tielemans (2017).*

[1] (Bruinderink & Hazebroek, 1995)
[2] (Dumont et al., 2005)
[3] (Gebert & Verheyden-Tixier, 2001)
[4] (Krojerova-Prokesova et al., 2010)
[5] (Paulides, 2007)
[6] (Staines & Welch, 1981)

1.2.1 Impact on vegetation

Through their browsing, ungulates like red deer can decrease the number and height of tree saplings in forests (Churski et al., 2017; Kuiters & Slim, 2002). The preferred foraging height of red deer lies between 50 and 150 cm (Renaud et al., 2003). Because of this preference, browsing can limit a plant's potential to grow above a certain height. This has been referred to as the demographic bottleneck model (DBM), which states that "a consumer may limit a plant's recruitment from one demographic stage to another" (Churski et al., 2017). Churski et al. (2017) showed that ungulates like red deer drive demographic bottlenecks in temperate forests, as not a single tree was able to grow above 200 cm in their 5-year experiment. This idea is also supported by the findings of Kuijper, Cromsigt et al. (2010), who showed that ungulates did not significantly influence the presence of saplings below 50 cm, but did find a negative effect of these browsers on the density and abundancy of saplings above 50 cm. It should be noted that the studies of Kuijper, Cromsigt et al. (2010) and Churski et al (2017) were both located in the Polish Białowieża National Park, which is inhabited by multiple herbivores. Next to red deer, the area is roamed by, for example, bison, roe deer, wild boar, and rodents. The height of the demographic bottleneck might thus differ in areas with a different herbivore species composition.
In addition to their effect of trees, deer browsing can also result in decreased height of other woody species like bramble (Kuiters & Slim, 2002) and bilberry (Baines et al., 1994).

Figure 2 – As an intermediate feeder, red deer can both graze on grass (left), and browse on dicotyledonous plant parts like twigs (right).

Browsing by red deer can limit tree growth in heathlands and grasslands as well, thereby maintaining these open landscapes (Kuiters & Slim, 2002; Riesch et al., 2020). Herbivores that mainly graze, on the other hand, can have the opposite effect in grasslands. The consumption and trampling of grass, opens up the dense grass layer, allowing other plant species to germinate and grow (Kuiters & Slim, 2002). In certain pastures, this behaviour was found to stimulate the growth of non-grassy vegetation (Riesch et al., 2020; Schütz et al., 2003; Virtanen et al., 2002). The emergence of non-grassy vegetation in grasslands can promote tree establishment, even though browsers are present. This process is thoroughly described by Olff et al. (1999), and summarized in figure 3. The plants that emerge in grazed patches might be less palatable to herbivores than grass (Figure 3, B-C). For example, because they have spines or thorns, or because they are toxic. Patches with these plants are observed to function as refuges in which palatable plants, like broadleaved trees, can grow, resulting from so-called associational resistance (Figure 3, D; Olff et al., 1999; Smit et al., 2015; Uytvanck et al., 2008). When the tree grows, increased shadow results in the death of the non-palatable plants in the understory. This makes it difficult again for the tree to regenerate, thus in time the patch will often return to its grassy state (Figure 3,E-A). A certain amount of grazing pressure can therefore result in a dynamic mosaic landscape. Such associational resistance is most likely to take place in grassland with true grazers like cattle and horses (Olff et al., 1999), but the abundancy of nonpalatable plants has also been shown to increase under red deer foraging (Schütz et al., 2003).

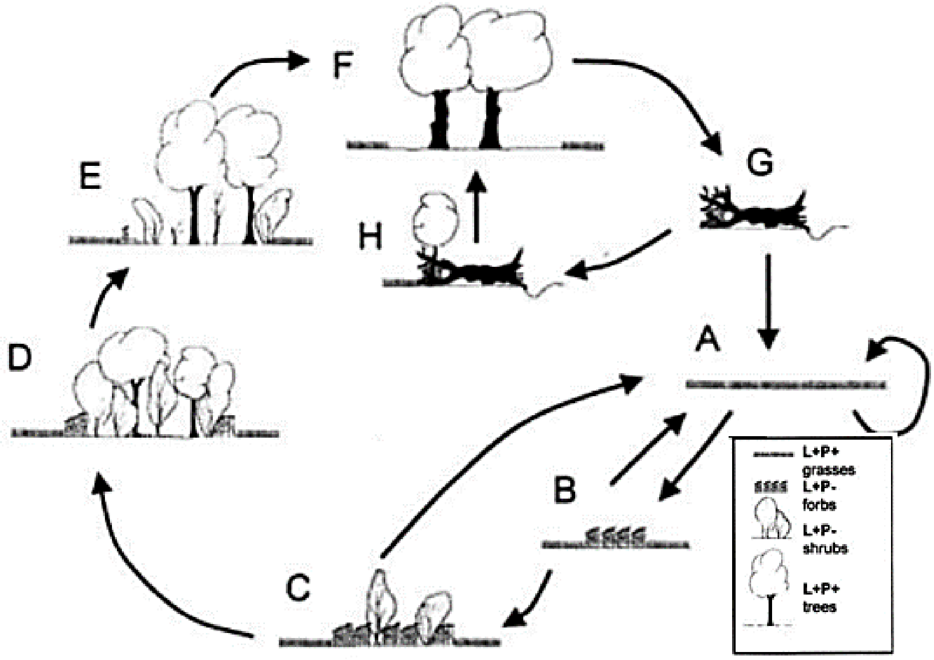


Figure 3 – Schematic drawing of the succession cycle when large herbivores are present, creating a dynamic mosaic landscape. By foraging on light demanding (L+), and highly palatable (P+) grass, herbivores make room for non-palatable (P-) plant species, which function as refuges in which trees can grow. Due to shade and grazing, there is little regeneration of the trees, making that eventually, the spot returns to a grassy state. *From Olff et al., (1999).*

1.2.2 Cascading effects

That red deer directly affect plants is a logical result of their herbivory, but like with other megafauna, the animal also indirectly influences flora and fauna. This can lead to a sustained, or even increased ecological value of their environment, for example in wood-pastures. A wood-pasture is a "vegetation structure of open woodland with scattered trees or forest patches in a matrix of grassland, tall grasses and shrubs" (Figure 4, Uytvanck et al., 2008). If such an environment is undisturbed, vegetation dynamics will often transform the open landscape into a dense forest (Bergmeier et al., 2010; Navarro et al., 2015).

The presence of red deer, however, can prevent this succession (Riesch et al., 2020; Smit et al., 2015). This effect is present in grasslands, but also where forest stands already occur, red deer browsing can result in canopy thinning (Schulze et al., 2018).

Figure 4 – Wood-pasture in North West England. *Photo by Brian Muelaner*

In such open forests, a greater amount of sunlight can reach the ground. Red deer could therefore increase the growing potential of understory vegetation. Indeed, when Ramirez et al. (2019) estimated understory vegetation cover as the cover percentage of heath, fern, shrub, moss and grass (all < 150 cm height), they found a higher understory vegetation cover in plots experiencing grazing by ungulates. Also Gill & Fuller (R. M. A. Gill & Fuller, 2007) observed a higher grass height in browsed forest plots. When browsing pressure is not too high, it is unlikely that red deer shortens all plant stems. The ungulate might therefore not only increase understory species diversity, but also the diversity in vegetation height. In this thesis, the diversity of plant species, plant abundancy, and vegetation layers, is referred to as 'vegetation structure'.
Red deer can thus aid in sustaining the vegetation structure and openness of wood-pastures. On the other hand, grazing herbivores, can promote tree recruitment in grasslands, as explained earlier. It is therefore believed that foraging by a combination of browsers, grazers and intermediate feeders, is a natural way to maintain the half-open character of wood-pastures, with a dynamic mosaic landscape of tree patches, shrubs and grassland (Schulze et al., 2018; Svenning et al., 2016; Vera, 2000).

Wood-pastures are known to be a highly diverse environment (Bergmeier et al., 2010; Navarro et al., 2015). Forests alternate with grasslands, with broad transition zones in between (figure 5; Bergmeier et al., 2010; Vera, 2000). Foraging by herbivores provides a certain amount of disturbance, which, according to the intermediate disturbance hypothesis (Connell, 1978; Grime, 1973), can increase species richness. The variability in vegetation structure, nutrient availability, light and shade conditions, and disturbance level results in many different micro-habitats. The landscape can therefore support many floral, faunal and fungal species (Bergmeier et al., 2010; Feber et al., 2001; Hartel et al., 2013; Riesch et al., 2020). In this way, large herbivores like red deer can be used in trophic rewilding.

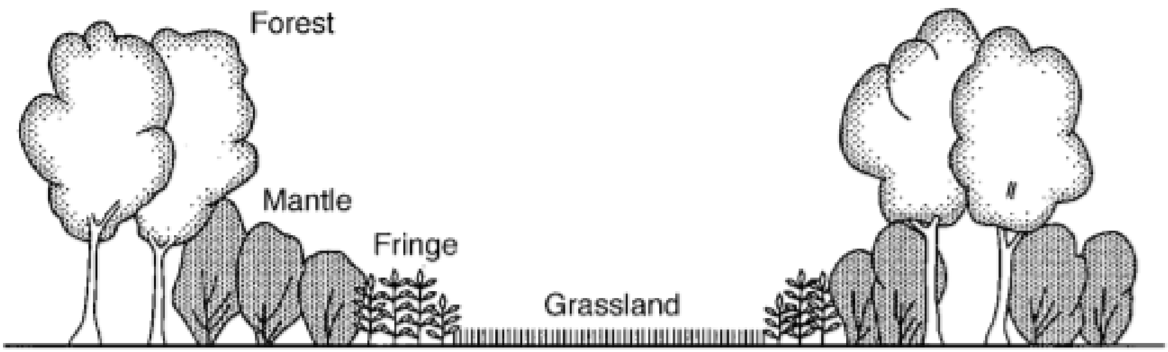


Figure 5 – Schematic drawing of a broad transition zone between forest and grassland. Compared to abrupt boundaries, these gradual boundaries offer include more plant species and structure and offer therefore more micro-habitats. These broad transition zones can therefore support a higher biodiversity. *From Vera (2000)*

1.3 Rewilding in Het Groene Woud

A nature area where such trophic rewilding with red deer is carried out is Het Groene Woud, which is located in the in the Dutch province of Noord-Brabant. This national landscape connects urban areas, cultural landscapes and nature reserves. In 2017, nature organization ARK Nature and nature area manager Het Brabants Landschap reintroduced the red deer in certain parts of Het Groene Woud. This animal was once a common appearance in the Netherlands (Worm, 2010), but its population size was strongly reduced between the 17th and 19th century and only a few dozen remained in the central Netherlands (de Groot et al., 2016; Worm, 2010). Later, the red deer was even included in the Dutch red list of endangered species (Hollander & van der Reest, 1994). With the reintroduction of red deer in Het Groene Woud, a native species was brought back that had been absent from Noord-Brabant for over 150 years (Simons & Houben, 2017). However, the intents of ARK Nature and Het Brabants Landschap reach further than this. The organizations reintroduced the ungulate to Het Groene Woud not just to help preserve the species, but also to restore its ecological function. Because of its historical agricultural function, Het Groene Woud contains both grasslands and forests, mostly with abrupt transitions between the two vegetation types (Figure 6). As described before, such abrupt transitions and structureless grasslands do not support the highest possible biodiversity. By reintroducing red deer, in combination with Aberdeen Angus cattle and the already present roe deer, ARK Nature and Het Brabants Landschap aim to increase the graduality and structure of these transitions, and maintain a diverse, half-open landscape, supporting a high biodiversity (ARK Natuurontwikkeling, n.d.).

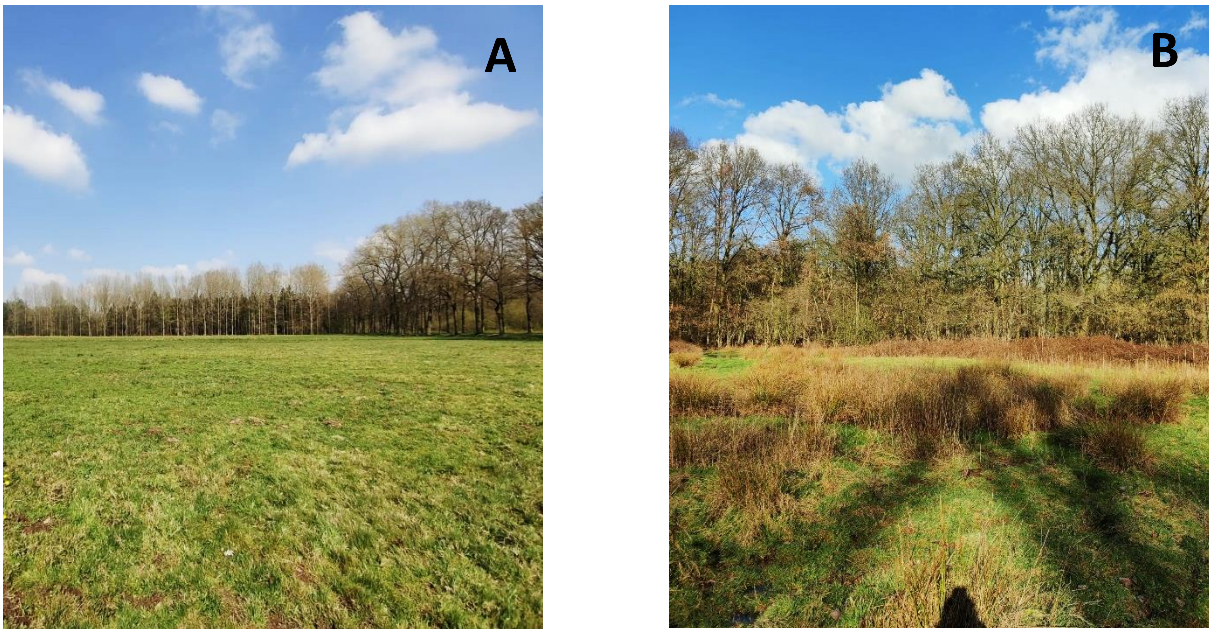


Figure 6 – Two different locations in Het Groene Woud deer reserve, where grassland and forest meet. One with a very open grassland and an abrupt transition to forest **(A),** and one with a slightly more structural grassland, and a more gradual transition to forest, yet still less than desired **(B)**.

1.4 Research problem

As described in paragraph 1.2, there are various indications that red deer can help increase the ecological value of a wood-pasture system like Het Groene Woud. This does depend, however, on numerous factors, like the presence of other animals, climate and soil properties, plant abundancy, and plant species composition. For example, a factor influencing ungulate-vegetation interactions is lying deadwood. Browsing by ungulates is found to be lower at sites with lying deadwood larger than 50x50x100 cm, as these logs can form escape impediments in case of predation (Kuijper et al., 2013, 2015). An ecosystem response to browsing also highly depends on ungulate density. While the beneficial effects of ungulate browsing on flora and fauna have been observed (Feber et al., 2001; Riesch et al., 2020; Schulze et al., 2018), high browsing pressure can also have a deleterious effect on habitats and animals (Dolman et al., 2010; Feber et al., 2001; R. M. A. Gill & Fuller, 2007; Kirby, 2001; Morecroft et al., 2001).
The interaction between red deer and their environment is thus a very complex system. Yet our understanding of the impact of red deer on their ecosystem is mostly based on research that is conducted at a relatively small ecological scale (Riesch et al., 2020). For example, by looking at how red deer influence specific plant communities (Weisberg & Bugmann, 2003). Also, these studies are often conducted over a relatively short time span. Research on how red deer impact their ecosystem

over many years is therefore lacking (Weisberg & Bugmann, 2003). Even when research is conducted at a larger ecological scale and over a larger time span, the findings are often so location-specific, that it is difficult to assess if those results will also apply to other nature areas.
It is thus important to monitor if the introduction of red deer in Het Groene Woud gives the desired results. This has been done in the past by linking vegetation structure and openness to the red deer's area usage (Allen, 2019; Tielemans, 2017). Repeating these studies is valuable, as results of the interaction between red deer and their environment might only be observable after a certain amount of time. In addition, a new area was added to the red deer enclosure in 2020, in which the interaction has not yet been studied yet.

To obtain a quantitative status of the red deer and the vegetation in Het Groene Woud, I looked at, among other things, how woody recruitment is affected by the presence of red deer. In this research, woody recruitment is represented by the number of tree individuals below 150 cm. Furthermore, I looked at how vegetation structure is influenced by red deer. As described before, in thesis vegetation structure is described as the diversity of plant species, plant abundancy, and vegetation layers. However, as this study was performed during the winter, I only looked at woody vegetation structure properties. In this research, vegetation structure is therefore determined by aerial cover, height and variation in height of bramble bushes, and height and variation in height of tree saplings. To summarize, this study is based on the following research question and subquestions:

How are woody recruitment and vegetation structure linked to area use by red deer, in the Groene Woud deer enclosure?

1. *How does the area use by red deer vary across the study area, and how has this changed since 2019?*
2. *How is woody recruitment linked to the area use by the red deer?*
3. *How is vegetation structure linked to the area use by red deer?*

To provide answers to these questions, I conducted a field survey in eighty plots across the reserve. I then used GPS data to determine the plot use by red deer between 2017 and 2019, and camera trap data to determine the plot use by red deer in 2021. Hereafter, I combined these data and performed a statistical analysis to measure the impact of red deer on the vegetation.

1.5 Hypotheses

Based on the literature as summarized in paragraph 1.2, I have formulated the following hypotheses:

Area use (SQ1): I expect the plot use by red deer of 2017-2019 and 2021 to correlate with each other, as I expect that the spatial use of red deer has not changed significantly in two years. However, I do not expect a 'perfect' correlation (r=1), as the data was recorded through different methods, in different seasons and because the deer enclosure was expanded.
I also expect to find the highest presence of red deer in grasslands and in forests with tree and shrub species that are preferred by red deer.

Woody recruitment (SQ2): In terms of woody recruitment, I expect to find one of two different outcomes. The first possibility is that, as the preferred foraging height of red deer lies between 50 and 150 cm, the red deer are attracted to plots with more saplings within this height class. In this case, I also expect those saplings to remain in this height class, as a result of red deer's browsing. If this is the case, plot use by red deer will be positively correlated to number of saplings of 50-150 cm.

Furthermore, I expect the plots in the old area to have more saplings of 50-150 cm than the plots in the new area, as saplings within in the new area have had a longer time to grow above 150 cm without browsing by red deer.
In addition, when comparing the 2021 data to the 2019 data, I expect to find a larger increase in tree saplings of heights between 50 and 150 cm in plots with a high red deer density, than in plots with a low red deer density.
Lastly, if these differences are the result of red deer browsing, I expect to see the greatest effect on tree species preferred by red deer, and in plots with little deadwood.

However, one can also formulate a different hypothesis, based on the research of Kuijper, Cromsigt et al. (2010), who found that browsing resulted in a decline in saplings above 50 cm. If the same applies in Het Groene Woud, one would expect to find less saplings of 50-150 cm in plots that have been visited more frequently by red deer. In this case, the old area would have less saplings of 50-150 cm. In addition, the number of saplings of 50-150 cm in plots with a high red deer density will have decreased more strongly since 2019, than plots with a low red deer density. Again, I expect to see the greatest effect on tree species preferred by red deer, and in plots with little deadwood.

Vegetation structure (SQ3): I expect that intermediate levels of browsing and grazing by red deer will create a more heterogeneous environment, with more variation in disturbance, and light and nutrient availability. Because of this, some stems will stay short, while other stems can grow tall. I therefore expect to find the highest variation in bramble and tree sapling height and in bramble aerial cover, at intermediate levels of RPU.
I also expect to find a higher variation in bramble and tree sapling height in the old area, compared to the new area.

2. Methods

For this thesis, I conducted a field study to assess the impact of red deer on the vegetation in Het Groene Woud. I repeated parts of earlier research done by Tielemans (2017) and Allen (2019), while also collecting additional data. I then processed these data and used them in a statistical analysis.

2.1 Research area

This research was based in the red deer enclosure located in The Mortelen & Scheeken nature reserve, which lies in the heart of Het Groene Woud (Het Brabants Landschap, 2019). Het Groene Woud can be translated as 'The Green Forest' in English. However, contrary to what the name suggests, the 35,000 ha area of Het Groene Woud is not only made up of forest. The area is a cultural landscape that consists of, mainly because of its agricultural history, a great variety of habitats including pasture, woodland, marsh, heath, fens, and also urban areas (Het Brabants Landschap, 2019). In the Mortelen & Scheeken, this landscape diversity is also driven by soil composition. Wet, loamy soils are covered with deciduous forest and rich meadows while coniferous forests and fields cover the sandier soils. Historically, all the landowners required a piece of each habitat type, which has resulted in a landscape with many small parcels of land (Het Brabants Landschap, n.d.). This mosaic landscape attracts a great diversity of flora and fauna, and Brabants Landschap has been transforming the Mortelen and Scheeken into a nature reserve since the second half of the 20th century. However, the division of the landscape into lots of small parcels also resulted in abrupt boundaries between habitat types. As described in the introduction of this thesis, this was one of the reasons for Brabants Landschap and ARK Nature to reintroduce red deer in this area, as these animals are believed to be able to increase vegetation structure, and the graduality of the transitions between grassland and forest (ARK Natuurontwikkeling, n.d.).

In March 2017, thirteen red deer were released in the reserve. At the time, the reserve consisted of a fenced area of about 300 ha, split by the A2 motorway. Areas on both sides of the highway are connected through a fifty meter wide ecoduct (Dekker & Houben, 2018). In 2020, a new ecoduct over the railway on the west side of the reserve was opened, expanding the red deer enclosure by about 100 ha (figure 7; figure 8; ARK Natuurontwikkeling, 2020). Currently, a total of 46 red deer (17 stags, 17 hinds and 12 calves) live in the area together with roe deer, Aberdeen Angus cattle and numerous smaller animals (personal communication, Brabants Landschap, 2021).

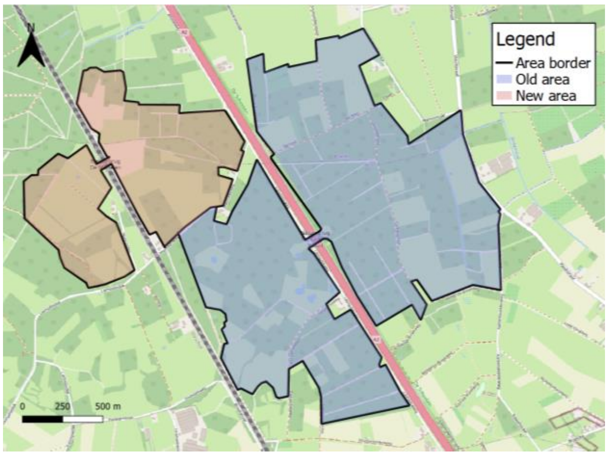


Figure 7 – Outline of the red deer reserve in Het Groene Woud. Highlighted are the old area (blue), and the new area (pink).

Figure 8 – Ecoduct over the railway in the red deer reserve in Het Groene Woud

2.2 Plot selection

Tielemans (2017) distinguished six habitat types in the red deer enclosure*: bramble-alder, grassland, oak-hazel-alder, oak-poplar-hazel, poplar-hazel-alder, and spruce. Within* each habitat type, Tielemans randomly distributed ten research plots of 20x20 m, resulting in a total of sixty plots. The southwest corners of these plots were marked by wooden poles and their GPS coordinates were saved. These plots were remeasured by Allen (2019). As only a few of the wooden poles remained, I only used their GPS coordinates to locate these plots.

In addition to the original plots, I laid out new plots in in the expansion area of the reserve. For this, I first mapped the different habitat types within this area, based on the same habitat types used by Tielemans (2017). The new area provided mainly the same habitat types as the old area. However, *spruce forest* was not assigned to the new area, and one new forest type was added: *birch-pine forest*. As the size of the new area is roughly one-third of the old area, twenty plots were distributed over the new area. The new identified habitat type birch-pine forest received five plots, while the other five habitat types received three plots. This resulted in a total of eighty plots throughout the entire reserve (Table 1; Figure 9, Figure 10A-G). QGIS was used to randomly distribute the new plots over the habitat types. The coordinates of each plot are listed in appendix A. However, as GPS-devices have an accuracy of about 5 meters (van Diggelen & Enge, 2015), most plots were also marked by carving an arrow in the tree closest to the southwest corner of the plot (Figure 10H). This was done to guide future researchers to the right location.

Table 1. Habitat types present in the red deer enclosure. #Plots depicts how many research plots were placed inside each habitat

Habitat	Location	#Plots
Birch - Scots pine	New	5
Bramble - Alder	Old & New	13
Grassland	Old & New	13
Norway spruce	Old	10
Oak – Hazel – Alder	Old & New	13
Oak – Poplar - Hazel	Old & New	13
Poplar – Hazel - Alder	Old & New	13

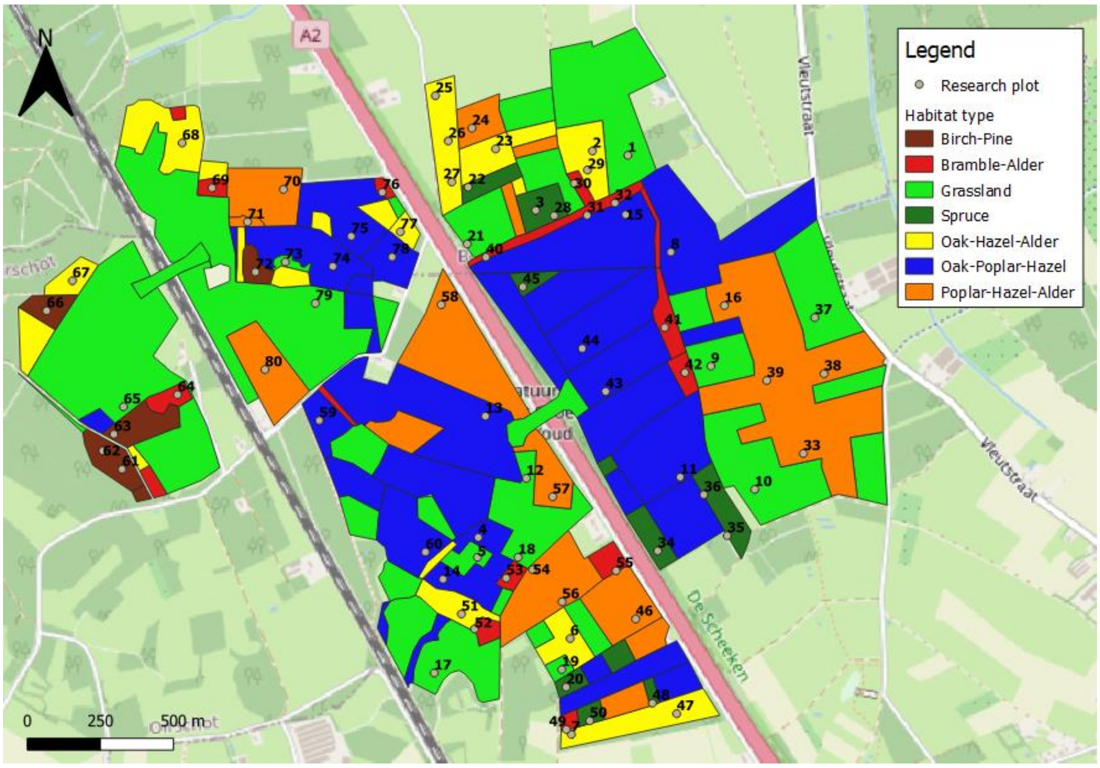


Figure 9 – Map of the red deer reserve, with the location of the research plots. Colours depict the different habitat types.

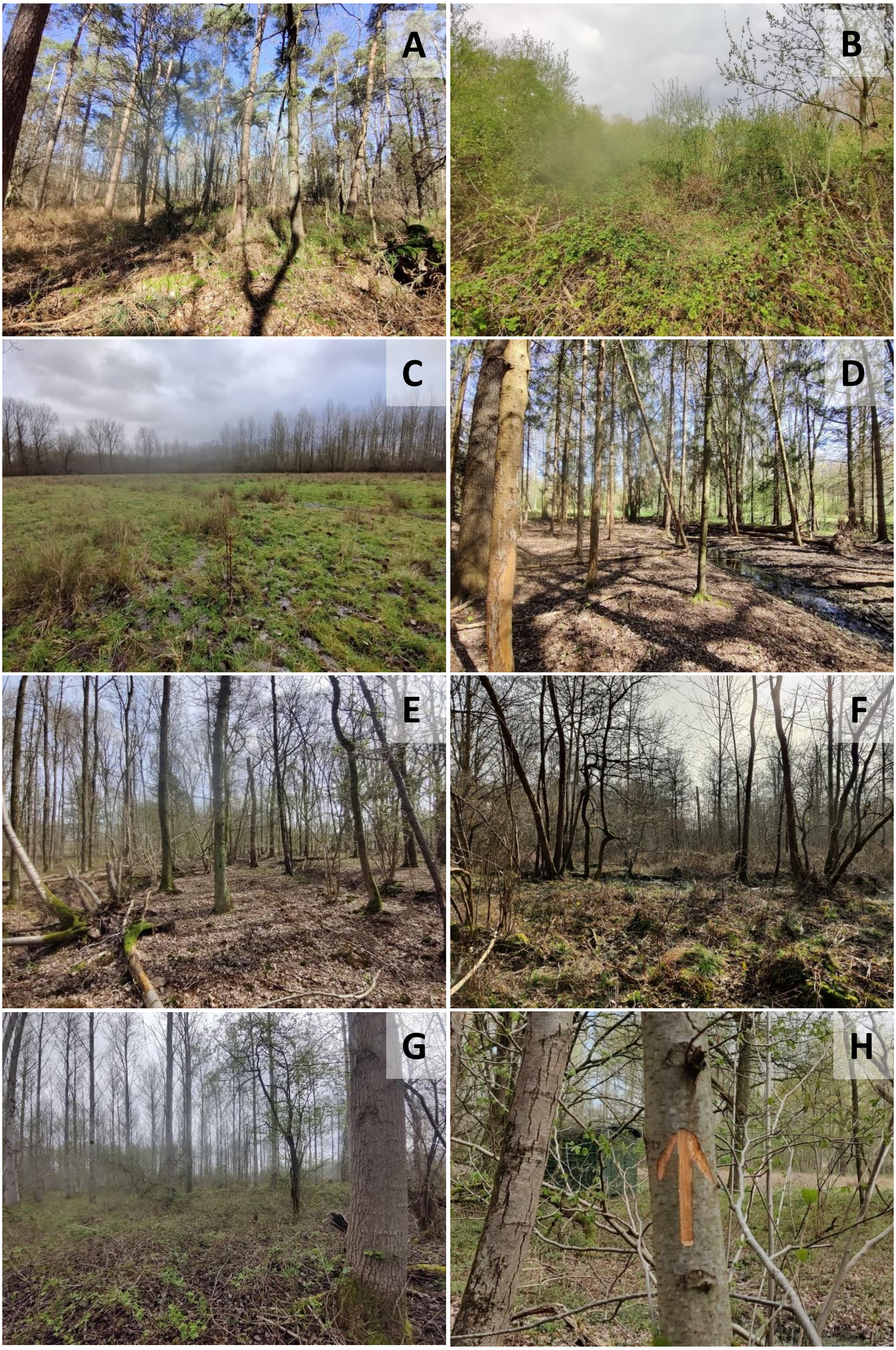


Figure 10 – Pictures of the seven habitat types and the carved arrow used to mark the southwest corner of each plot. Birch-Pine, plot 62 **(A)**, Bramble-Alder, plot 52 **(B)**, Grassland, plot 9 **(C)**, Spruce, plot 28 **(D)**, Oak-Hazel-Alder, plot 23 **(E)**, Oak-Poplar-Hazel, plot 60 **(F)**, Poplar-Hazel-Alder, plot46 **(G)**, Carved arrow to mark the southwest corner of a plot **(H).**

2.3 Data collection

2.3.1 Field survey

Woody recruitment and vegetation structure was measured through a field survey of each plot. This field study was carried out between February 25th and April 30th, 2021 (appendix B). I repeated all measurements done by Allen (2019), to provide Brabants Landschap and ARK Nature with continuous vegetation data through time. However, not all data was used in this research. This paragraph therefore only discusses the measurements of data used in this thesis. An overview of all measured variables and the field survey form is given in appendix C.

Using the GPS coordinates provided by Tielemans (2017), I located the south-west corner of each plot, after which I used a compass, rope and sticks to mark the plot's boundaries. Within each 20x20 m plot, I identified and counted all woody vegetation individuals taller than 150 cm. I also noted the number of lying deadwood individuals with dimensions of at least 50x50x100 cm.
After this, I laid out five circles with a 2m radius, each subdivided into four quadrants (figure 11). Within these circles, I recorded the height and species of every woody plant individual under 150 cm and wrote down if they showed signs of browsing. Besides the tree measurements, I also determined aerial cover, height and browsing of bramble for each quadrant within the circles. For the determination of aerial cover, I followed the same method as Allen (2019) to ensure continuity of the data. In this method, it is assumed that bramble, other shrubs, common rush, other graminoids, nettle, other forbs, ferns, mosses and bare soil together always make up 100% of a quadrant, and that they do not overlap. Bramble height was measured using the drop-disc method (Stewart et al., 2001). At the centre of each quadrant, I dropped a cardboard disc of a diameter of 30 cm onto the bramble layer and noted the height at which the disc came to rest as the height of the layer (figure 12). Evidence of browsing of bramble was recorded by writing down per quadrant if browsing occurred. See table 2 for a summary of these variables.

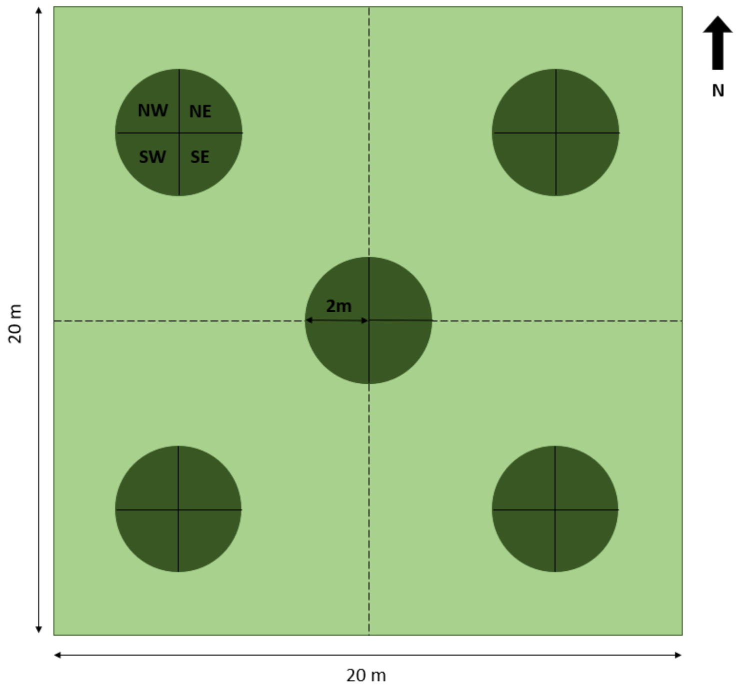


Figure 11 – Layout of the 20x20m research plot, and the five subplots with a radius of 2m. Each subplot is divided into four quadrants (oriented to northwest, northeast, southeast, and southwest).

Figure 12 – Drop-disc method. To measure bramble height, a cardboard disc was dropped onto the vegetation layer. On the measuring tape in the centre of the disc, I could then read at which height the disc came to rest. I then noted this value as bramble height in that quadrant.

Table 2 - Variables measured during the field survey and used in this thesis. A complete list of vegetation characteristics collected during the field survey, including variables not used in this research, is provided in appendix C.

Scale	Variable	Unit	Method
20x20 plot	# Tree species individuals > 150 cm	-	Count
	# Lying deadwood	-	Count
Circle (r=2) within plot	# Tree species individuals < 150 cm	-	Count
	Height of tree individuals < 150 cm		Measuring tape
	Signs of browsing tree individuals < 150 cm	-	Visual assessment
Quadrant within circle	Height bramble	cm	Drop-disc method
	Aerial cover bramble	%	Visual estimation
	Browsing occurrence bramble	-	Visual assessment

2.3.2 Red deer area use

In previous studies on red deer dispersal in Het Groene Woud, GPS collar data were used (Allen, 2019; Dekker & Houben, 2018). However, the collars that provided that information are no longer used since 2019. Consequently, there is no GPS data available on the space use of red deer in the new area, or their space use in the old area during 2020 and 2021. In this study, I therefore used the GPS data, but also placed camera traps to collect new data on the area use of red deer. In this way, the GPS data functions as historic account of red deer area use, while the camera trap data offer a current image.

GPS data

When the red deer were released in the Groene Woud deer enclosure, two hinds and two stags were put on a GPS collar (Dekker & Houben, 2018). Between September 2018 and March 2019, batteries started to fail, and the collars came off. The dataset used in this research contains a total of 59,464 data points (table 3).

Camera traps

Camera traps were used to record red deer presence in each plot. The 29 available trail cameras (table 4; figure 13) were randomly assigned to the first 29 plots, where they recorded animal presence for three weeks. After three weeks, I moved the cameras to the next randomly selected 29 plots, and after again three weeks, the cameras were moved to the remaining plots. In three session, I thus recorded all plots for three weeks (appendix B).

The cameras were set to take three 8MP photos when triggered. In the first session, the cameras had a trigger interval of 0.6 seconds, in the second and third session, I changed this to 3 seconds. Each camera was also scheduled to take 'time-lapse photos' during two hours of twilight in the morning and two hours of twilight in the evening, with an interval of fifteen minutes. This was done to increase the chance of capturing red deer, which are especially active during those hours. The exact times of these time-lapse photos differed per session, matching changing sunrise and sunset.

All cameras were hung at knee height, approximately 70 cm from the ground. I placed the cameras in the spot with the best view of the plot, usually in the south-west corner, with a diagonal view of the north-east corner. The cameras never faced southward, to avoid overexposure by sunlight.

Finally, before removing each camera, I performed a so-called 'walk-test': I walked away in front of the camera, while stopping every two meters to let the camera take a photo of me. I did this until I reached a distance of twenty meters. These walk-test photos were later used as an indication of the detection distance of the camera. In this way, I could correct for the difference between camera models and the variance in vegetation openness between plots.

In total, 107,751 photos were taken by the cameras between January and May 2021. This was around the same time I conducted the field surveys. The photos therefore represent recent area use by red deer.

Table 3 – Number of GPS data points per individual, of the red four deer tracked after reintroduction in Het Groene Woud.

Collar ID	Sex	First month in dataset	Last month in dataset	Data points
22295	Hind	March 2017	March 2019	20950
22296	Hind	March 2017	February 2019	19796
22297	Stag	March 2017	September 2018	16493
22298	Stag	June 2018	October 2019	2225

Table 4 – Number of cameras per model, used to track red deer in Het Groene Woud between January and May 2021

Model	# cameras
Bushnell core DS low glow	19
Browning Dark Ops HD Pro X Mode	4
Bushnell trophy camera	6
Bushnell	2

Figure 13 – Trail camera attached to a tree.

2.4 Data processing

2.4.1 Vegetation data

After I collected the data, I entered all field survey data in an Excel spreadsheet. From the raw data, I then calculated the following variables at plot scale (see also table 5):

a. Average height [cm], aerial cover [%] and browsing [%] of bramble
b. Total number of adult trees (> 150 cm)
c. Total number of saplings (< 150 cm)
d. Number of saplings per height class (<50 cm, 51-100 cm, 101-150 cm)
e. Number of alder, birch, bird cherry, hazel, oak, poplar and rowan saplings per height class (<50 cm, 51-100 cm, 101-150 cm)
f. The change in variables a-e, compared to 2019. This was calculated by subtracting the 2019 value from the 2021 value.
g. Standard deviation sapling height [cm]
h. Standard deviation of bramble height [cm]
i. Amount of lying deadwood per plot, averaged for 2019 & 2021

In addition, I used Jacob's Selection Index, or JSI, (Jacobs, 1974) to determine if the red deer showed a preference for certain tree species. I did this for each tree species of which a sapling was found in the research plots. JSI of species *i* was obtained according to the following formula:

$$JSI_i = \frac{r_i - p_i}{r_i + p_i - 2r_ip_i}$$

Where p = proportion of habitat available, and r = proportion of habitat used. For example, p_{Alder} = Number of alder saplings / total number of saplings, and r_{Alder} = Number of browsed alder saplings / total number of browsed saplings.

Finally, a variable showing the plot use by red deer was computed, as described in the next paragraph.

2.4.2 Relative Plot Use by red deer

To study the relation between red deer and vegetation, I computed a variable called Relative Plot Use by red deer (RPU) as an indicator of the presence of red deer in the research plots. I calculated two different RPU values per plot, one based on the GPS data and one based on the camera trap data. I then combined both to obtain an average RPU per plot.

GPS data

To calculate the red deer's plot use from the GPS data, I mapped the datapoints in QGIS, together with the research plots. I then created a circular buffer around the plots with a diameter of 50 m and let QGIS count all the GPS data points within that buffer. I used a diameter of 50 meters, as Allen (2019) used a similar method and found that a 20 m diameter under-represented the presence of red deer, while 50 m provided a more accurate representation. The number of data points within the buffers were then used as the plot use by red deer of the accompanying plot for the time period of 2017-2019. In this chapter I will refer to this variable as PU19.

Camera trap data

To calculate the red deer's plot use from the camera trap data, I first annotated the photos in the open-source online photo-processing tool 'TRAPPER' (Bubnicki et al., 2016). Here, I classified all red deer photos and noted the number of individuals per frame. When less than five minutes passed between triggers, the photos were seen as the same red deer observation. In such a case, the frames were grouped into one sequence. For each sequence, I noted the maximum number of red deer individuals observed at the same time in that sequence, which I then used as the number of red deer present in the plot area during the entire sequence.

With these data, I calculated the plot use (PU) by red deer for plot *i* as follows:

$$PU21_i = \frac{Red\ deer_i\ /\ Time_i}{Visibility_i}$$

Where Red deer is the total number of red deer observed in the plot (the number of frames on which red deer were observed times the maximum number of individuals visible in those frames), Time is the number of days during which the plot was studied and Visibility is the detection distance of the camera in meters, as described in paragraph 3.3.1. In this chapter I will refer to this variable as PU19.

Combining GPS and camera trap data

As PU19 and PU21 were calculated in different ways and are based on different data, the two variables cannot be combined or compared directly. I therefore normalized PU19 and PU21 separately, so that both variables were ranged between zero and one, thereby calculating the Relative Plot Use (RPU) by red deer. This was done according to the following formulas:

$$RPU19_i = \frac{PU19_i - \min(PU19)}{\max(PU19) - \min(PU19)} \qquad RPU.N21_i = \frac{PU21_i - \min(PU21)}{\max(PU21) - \min(PU21)}$$

Where min(PU19) is the smallest plot use value found within the 2019 GPS data, and max(PU19) the largest value. With this normalization formula, the plot with the smallest value receives a zero, the plot with the highest value receives a one, and all the other plots are scaled in between, relative to the other plots in that period. Each plot thus received two separate Relative Plot Use values, one for 2019 (RPU19) and one for 2021 (RPU21).

With these normalized, relative variables, I then calculated the average RPU over the two periods per plot, as:

$$RPU_i = \frac{RPU19_i + RPU21_i}{2}$$

In this thesis, I will refer to this average variable simply as RPU.

Finally, RPU was also turned into a categorical variable: RPU.Cat. This was done as some statistical models were easier to interpret with a categorical RPU instead of a continuous RPU. RPU.Cat contains three categories: Low RPU, Medium RPU, and High RPU. The boundaries of these categories were based on the tertiles of the RPU data, so that each category contains about one-third of the plots.

Table 5 offers an overview of all variables used in this research.

Table 5 – Variables used in the statistical analysis of this research, divided per subquestion.

Subquestion	Variable	Explanation
1. Area use	RPU21	Relative Plot Use by red deer, scaled from 0-1. Based on photo data from 2021
	RPU19	Relative Plot Use by red deer, scaled from 0-1. Based on GPS data from 2017-2019
	Habitat	Indicates in which habitat type the plot lies

2. Woody recruitment – Old vs new area	Saplings	Number of trees < 150 cm in 2021, per plot
	Location	Indicates if the plot lies in the new or the old area
	Height class (HC)	Indicates, per plot, how many saplings belong in HC1 (0-50 cm), HC2 (51-100 cm), or HC3 (101-150 cm)
	Species	Indicates, per plot, how many saplings belong one of the following species: alder, birch, bird cherry, hazel, oak, poplar, rowan
	Deadwood	Average number of lying deadwood (>50x50x100 cm) in 2019 and 2021, per plot
2. Woody recruitment – 2019 vs 2021	Individuals	Total number of trees in a plot, both < 150 cm and > 150 cm
	Stage	Indicates if the tree individual is an adult tree (> 150 cm) or sapling (< 150 cm)
	RPU	Relative Plot Use by red deer per plot, averaged for 2019 and 2021
	ΔTrees	Change in number of trees (adult & sapling) between 2019 and 2021
	ΔSaplings	Change in number of saplings between 2019 and 2021
3. Vegetation structure	Bramble height	Average bramble height in 2021, per plot
	Bramble cover	Average aerial bramble cover in 2021, per plot
	Δ Bramble height	Change in average bramble height between 2019 and 2021, per plot
	Δ Bramble cover	Change in average bramble aerial cover between 2019 and 2021, per plot
	Bramble browsing	Average bramble browsing in 2021, per plot
	SD bramble height	Standard deviation bramble height in 2021, per plot
	Sapling height	Average sapling height in 2021, per plot
	SD sapling height	Standard deviation sapling height in 2021, per plot

2.5 Statistical analysis

To interpret the data, I performed a statistical analysis. If this research would have been based on a controlled design, where two areas shared the exact same conditions, except for red deer presence in one area and red deer absence in the other, it would be possible to directly measure the effect of red deer plot use. However, such a design was not possible within the timeframe of this research. I therefore used various statistical models in which I alternated explanatory variables and I used the combined results to deduce the red deer's effect on the vegetation. This analysis was performed in RStudio (version 1.2.5019). If a significant interaction was identified, the model was analysed using a type III sum of squares, while type II sum of squares was used when no interaction was found. If I found a significant effect of one of the explanatory variables, pairwise comparison of the means were conducted using Tukey's method with the *emmeans* package, version 1.6.1 (Lenth et al., 2020). All variables named in the next paragraphs are explained in table 5.

2.5.1 Area use

To research how the spatial use by red deer varies across the study area and how this has changed since 2019, I used the following ANOVA model:

$$RDP19\&21 \sim Habitat * Year$$

Following this, I performed a Spearman's correlation test between RPU19 and RPU21, to directly observe how the two variables relate to each other.

2.5.2 Woody recruitment

To research how woody recruitment is linked to the area use by red deer, I used two methods. First, I compared woody recruitment in the new area with the old area. In a way, this mimics a controlled design, where the new area functions as a control group, as red deer have been present in the old area for a longer time than in the new area. Second, I compared the data I collected in 2021, with the data Allen (2019) collected two years earlier and related the change in woody recruitment between these two years in each plot to the average RPU value of each plot.

Comparison of old versus new area

For the comparison of woody recruitment between the old and the new area, I first tested if the total number of saplings differed between the two areas, as observed in 2021. Since this is count data, I used a Poisson regression model:

$$Saplings \sim Location$$

As discussed before, there is no real control group, so it is not possible to directly measure the impact of red deer on the vegetation. I therefore expanded the model with various explanatory variables that can indicate the red deer's involvement. The following combinations of explanatory variables were used:

a. Location * Height class
b. Location * Height class * RPU21
c. Location * Height class * Habitat
d. Location * Height class * Deadwood
e. Location * Height class * Species

The relationship between these explanatory variables and the dependent variable *Saplings* was tested using either a Poisson regression, or a quasi-Poisson regression, depending on for which model the statistical assumptions were met.

Comparison of years

For the comparison of woody recruitment between 2019 and 2021, I first tested if the total amount of saplings differed between the two years. In the same model, I tested if the total amount of adult trees differed between the two years. This was done to check if the two datasets are comparable. If a significant change in adult trees was observed, it would be a sign of inconsistency between Allen's (2019) data and the recent data, as it is not expected that the number of adult trees changes a lot in just two years. This led to the following linear model:

$$Trees \sim Year * Stage$$

Where stage is either adult (> 150 cm), or sapling (< 150 cm). I then tested how the change in tree individuals between years was influenced by RPU with the following linear model:

$$\Delta Trees \sim Stage * RPU$$

As woody recruitment is the main interest of this subquestion, I then continued the research with only change in saplings (< 150 cm) as dependent variable, excluding adult tree individuals. Just as with the comparison of areas, as described before, I used a simple linear model:

$$\Delta Saplings \sim Height\ class$$

Which I then expanded with the following combinations of explanatory variables:

a. Height class * RPU
b. Height class * Habitat
c. Height class * RPU.Cat * Deadwood

Finally, the change in saplings was specified for each of the seven dominant tree species: Alder, Birch, Bird cherry, Hazel, Oak, Poplar, and Rowan. I then used a linear model to test how this change is influenced by both Height class and RPU:

$$\Delta Species_i \sim Height\ class * RPU$$

2.5.3 Vegetation structure

To test how vegetation structure in the area was influenced by red deer, I used three approaches.

First, to get an overall view changes in bramble abundancy, I used and ANOVA model to compare the height and aerial cover of bramble of 2017 (Tielemans, 2017), 2019 (Allen, 2019) and 2021. This was not done for sapling height, as the historical data on this variable was not readily available.

Second, I performed linear regression tests with RPU as explanatory variable and the following dependent variables:

a. Bramble height
b. Bramble cover
c. ΔBramble height
d. ΔBramble cover
e. Bramble browsing
f. SD Bramble height
g. Sapling height
h. SD sapling height

Third, I compared the vegetation structure in the old area with the new area. For this, ANOVA models were used, with Location as explanatory variable and the following dependent variables:

a. Bramble height
b. Bramble cover
c. SD Bramble height
d. Sapling height
e. SD Sapling height

3. Results

This chapter summarizes the main results of this study. Full results of the statistical tests are presented in appendix D.

3.1 Area use

The Relative Plot Use by red deer (RPU) of each plot is shown in figure 14. During the collection period of the GPS and camera trap data, red deer made use of various parts of the reserve. The camera trap data shows that the animals have also been using the new area extensively. Whether RPU can be linked to habitat type and how RPU19 and RPU21 are related, is discussed in the next paragraphs.

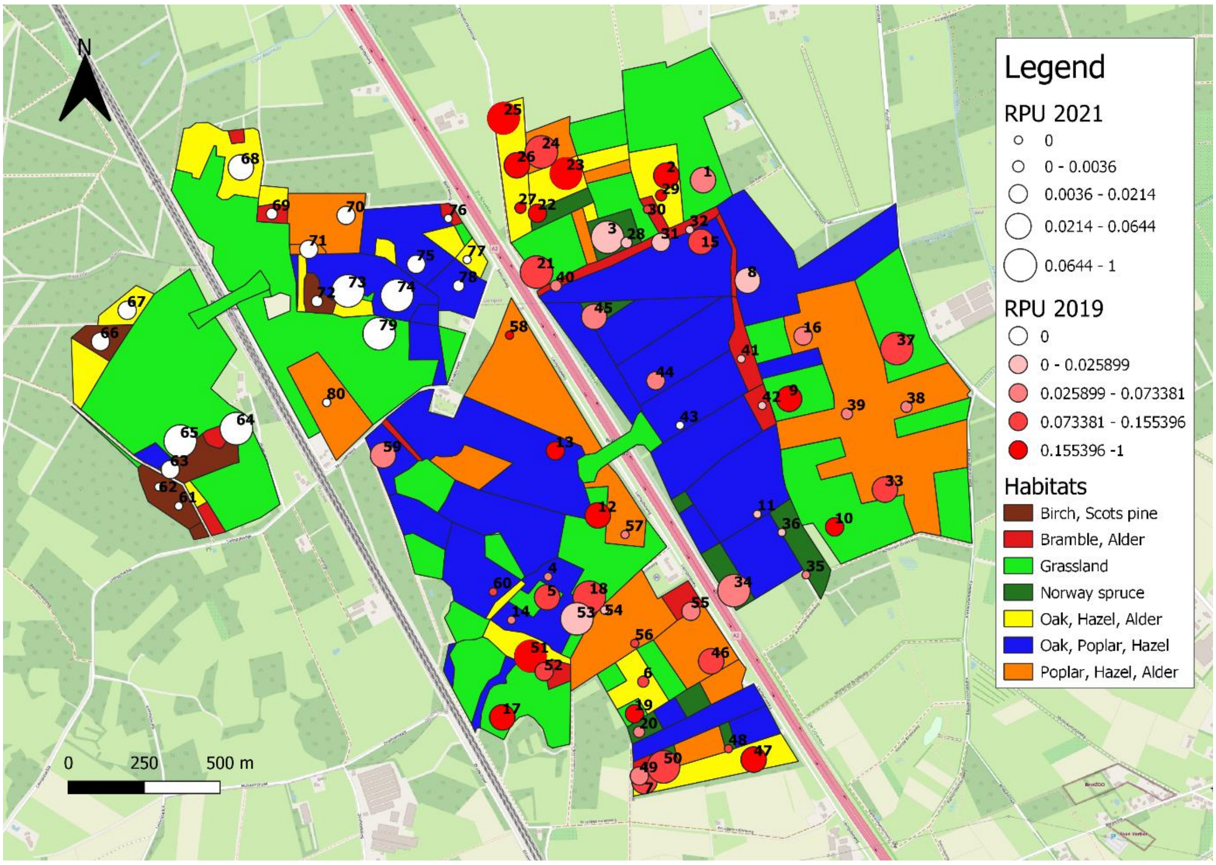


Figure 14 – Relative Plot Use (RPU) in 2021 and 2019, per research plot in the red deer reserve in Het Groene Woud. The size of a circle depicts the RPU21 of that plot, where a bigger size means a higher plot use in 2021. The colour of a circle depicts the RPU19 of that plot, where a darker red means a higher plot use in 2019. To generate this picture, both RPU21 and RPU19 were divided into five equal parts, or quintiles. The boundaries of each quintile are shown in the legend, note that these differ between RPU21 and RPU19. The coloured surfaces depict the different habitat types.

3.1.1 Relationship RPU and Habitat type

ANOVA results indicate that RPU significantly differed between habitats ($F(5,104) = 3.57$ $p<0.01$), and between years ($F(1,104) = 12.66$, $p<0.01$). There was no significant interaction between Habitat and Year ($F(5,104) = x$, $p=0.45$). This shows that, while the median RPU was higher in 2019 than in 2021 (figure x), the distribution of RPU over the different habitats was similar for the two years. There is, however, an observed difference in RPU between the two years. Mean RPU21 per plot is 0.07, while mean RPU19 is 0.17, almost 2.5 times higher.

Pairwise comparison of the means for RPU19 and RPU21 together showed that mean RPU in the Oak-hazel-alder habitat was significantly higher than in the Bramble-alder habitat (p=0.02) and Oak-poplar-hazel habitat (p=0.02; figure 15). One difference between the Oak-hazel-alder habitat and the other two forest types is that the research plots in Oak-hazel-alder forests contained a relatively high amount of adult rowan, oak and birch trees (figure 16A), and a relatively high amount of rowan saplings (Fig.16B). Although no significant difference between *grassland* and other habitats was found, the data do indicate that in both years red deer did not only prefer Oak-hazel-alder, but also *Grassland* habitats. In 2021, red deer were also more often found in spruce habitats than in other forests (figure 15).

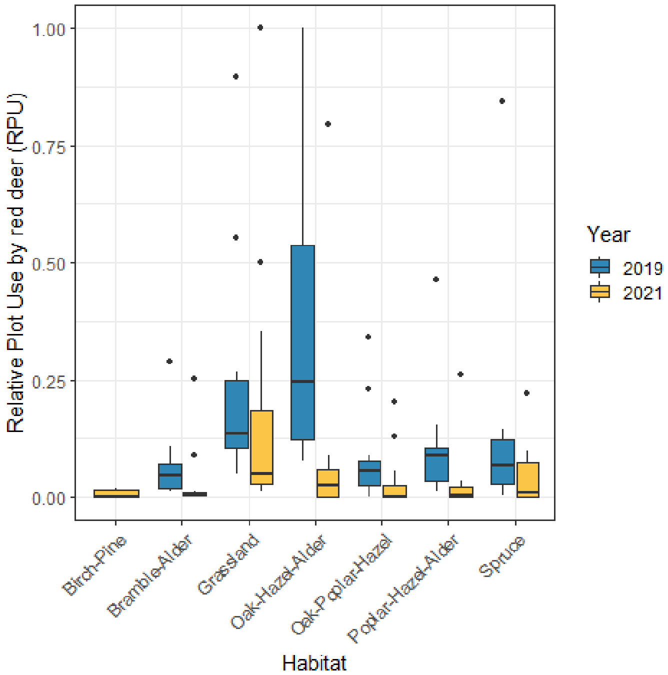


Figure 15 – Relative Plot Use (RPU) by red deer per habitat type, as found in period 2019 and period 2021. Period 2019 (blue) is measured with GPS data on four red deer, between march 2017 and October 2019. Period 2021 (yellow) is measured with camera-trap data, measured between January and May 2021. The figure shows that, in both periods, the highest RPU was found in grasslands and Oak-Hazel-Alder forests.

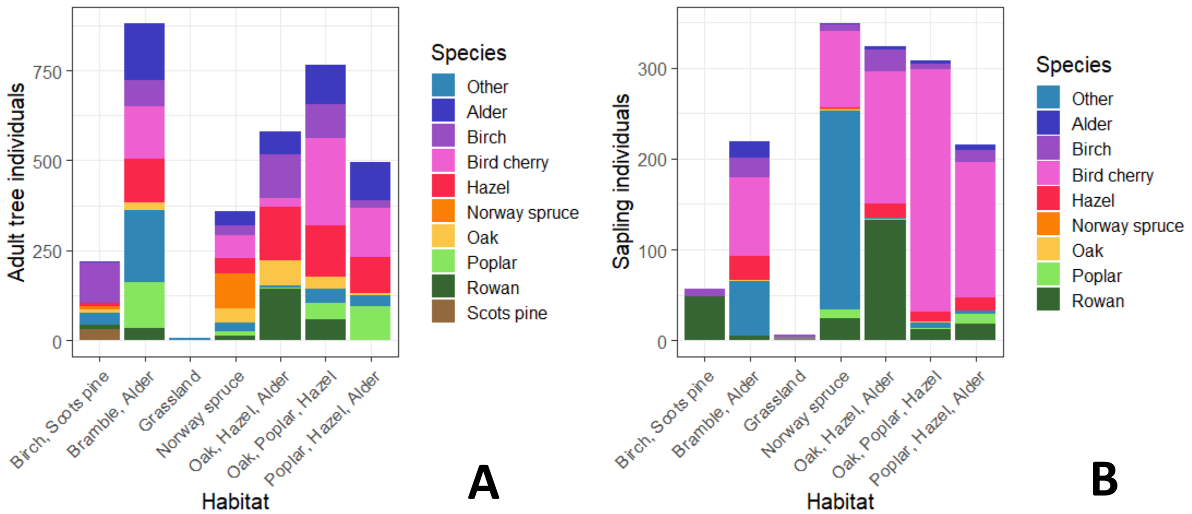


Figure 16 – Distribution of tree species over the habitat types, as found in the field survey of 2021. For adult trees (> 150 cm) **(A)**, and saplings (< 150 cm) **(B)**. Different colours depict different tree species.

3.1.2 Relationship RPU19 and RPU21

Figure 17 shows that plots with a high RPU19, are different plots than the ones with a high RPU21. Still, results of Spearman's correlation show a positive association between the RPU19 and RPU21 ($r_s(56) = 0.3$, $p=0.01$).

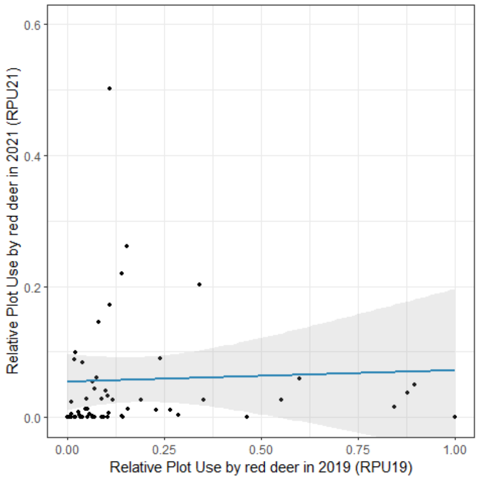


Figure 17 – Correlation between Relative Plot Use by red deer in 2019 (RPU19), and in 2021 (RPU21). The 95% confidence interval is depicted in grey. Note that this figure only shows RPU values of plots in the old area, as red deer were not yet present in the new area when RPU19 measurements took place.

3.2 Woody recruitment

The number of saplings found during this study and that of Allen (2019) is shown in figure 18. In both 2019 and 2021, an important part of the woody recruitment was located in the northeast corner of the area. In 2021, the new area also accounted for a large share of the saplings. Saplings were found in all habitat types, but only one *grassland* plot contained saplings: in the quadrants in plot 73, four willow and two birch saplings were found. All species of which saplings were found are shown in table 6, together with JSI, a measure of preference by the ungulates in the area. How woody recruitment differed between the old and the new area, and how it differed between 2019 and 2021, is discussed in de next paragraphs.

Table 6 – Sapling (trees < 150 cm) species most selected for by herbivores in the Groene Woud deer enclosure, as determined through the Jacob's Selection Index. Where the total number of sapling individuals recorded (N) is 1472. The Jacob's Selection Index was calculated as: D = (r/N – p/N) / (r/N + p/N – 2 x r/N * p/N).

Species	Total number recorded in 2021 (p)	Total number individuals browsed in 2021 ®	Jacob's Selection Index (D)
Hornbeam	1	1	0.63
Poplar	23	20	0.60
Alder	32	22	0.51
Elderberry	3	2	0.49
Hazel	67	38	0.45
Alder buckthorn	2	1	0.37
Birch	83	32	0.27
Rowan	240	70	0.14
Bird cherry	732	150	-0.11
Unknown	6	1	-0.16
Hawthorn	59	1	-0.87
Sycamore maple	219	1	-0.97
Ash	1	0	-1.00
Norway spruce	1	0	-1.00
Oak	3	0	-1.00

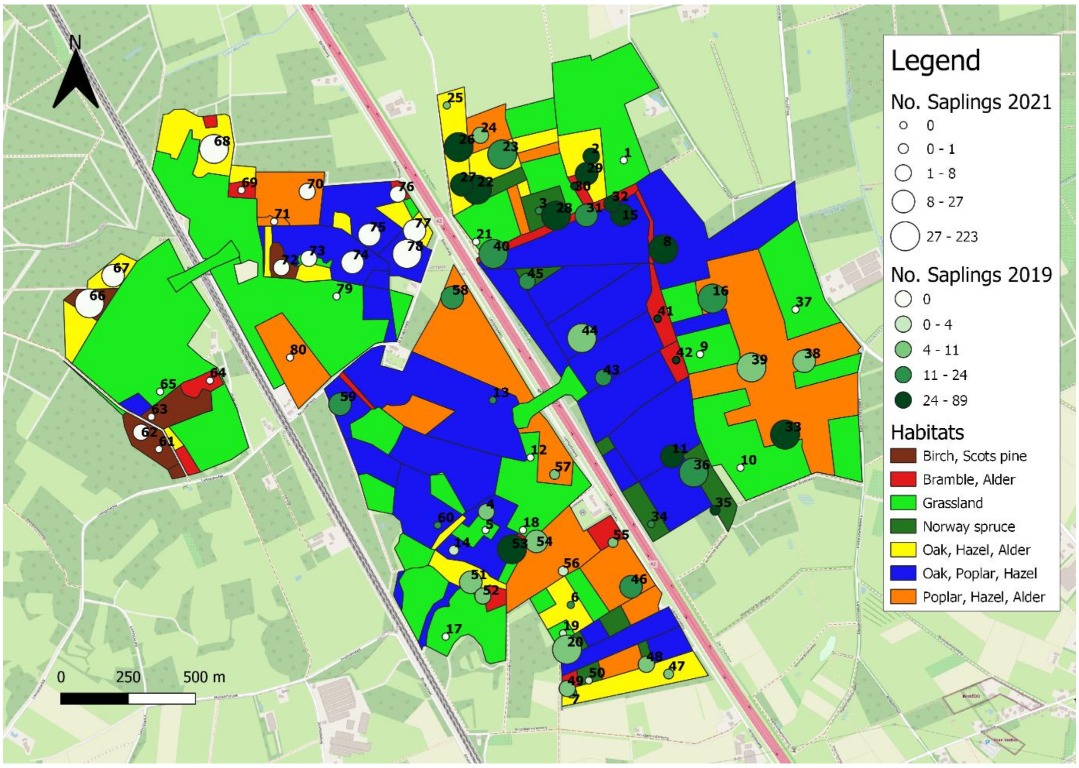


Figure 18 - Distribution of saplings (< 150 cm) in 2011 and 2019, per research plot in the red deer reserve in Het Groene Woud. The size of a circle depicts the number of saplings in 2021 within that plot, where a bigger size means a higher number. The colour of a circle depicts the number of saplings in 2019 within that plot, where a darker green means a higher number. To generate this picture, the number of saplings per plot in 2021 and 2019 were both divided in to five equal parts, or quintiles. The boundaries of each quintile are shown in the legend, note that these differ between 2021 and 2019. The coloured surfaces depict the different habitat types.

3.2.1 Difference in woody recruitment between the old and the new area

The difference in woody recruitment between the old and the new area was tested through a generalized Poisson model. The results show that, in 2021, the mean number of saplings per plot in the old area does not significantly differ from the mean number of saplings per plot in the new area ($p = 1.00$; table 7; figure 19).

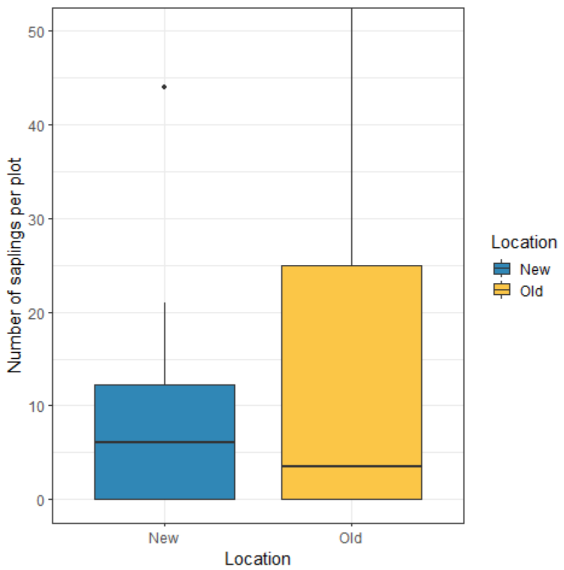


Figure 19 – Number of saplings per plot in the new and the old area, as found in the research plots during the field survey in 2021. Here, saplings are all trees below 150 cm. The new area is depicted in blue, and the old area in yellow.

Table 7 – Statistical results from the generalized linear models used to compare woody recruitment in the old and new area. Only significant relations ($p \leq 0.05$) are shown. In the case of a significant interaction between predictors, significant main effects of individual predictors are not shown. See appendix D for an overview of all results and see table 5 for the definitions of all variables.

Model	Model type	Predictor(s)	*p*-value	X^2-value
Saplings ~ Location	Quasi-Poisson	No significant effect		
Saplings ~ Location * HC	Poisson, with outliers	Location:HC	< 0.001	35.63
	Poisson, without outliers	Location:HC	< 0.001	15.93
Saplings ~ Location * HC * Habitat	Quasi-Poisson	Location:Habitat	< 0.001	21.60
Saplings ~ Location * HC * RPU	Quasi-Poisson	HC	< 0.001	26.94
Saplings ~ Location * HC * Deadwood	Quasi-Poisson	HC	< 0.001	32.02
		Deadwood	0.02	5.52
Saplings ~ Location * HC * Species	Quasi-Poisson	Species	< 0.001	287.26
		HC	< 0.001	71.78

Influence of Height class and Location

Height class (HC) and Location significantly interact ($p<0.001$; Table 7), thus the number of saplings differs per height class and that this distribution over height classes differs between the areas. How exactly this differs depends, however, on the inclusion or exclusion of outliers. Based on Cook's distance, plot 28, 68 and 78 were identified as outliers.

In the model with outliers, the mean number of saplings significantly differs per height class, in the new area as well as the old area (figure 20A). Pairwise comparison of the means showed that in both areas, the mean number of saplings in HC1 is higher than in HC2 ($p<0.001$), while the mean number of saplings in HC2 is higher than in HC3 ($p<0.01$). Furthermore, the mean number of saplings in HC1 is higher in the old area than in the new area ($p<0.01$), while the mean number of saplings in HC2 and HC3 is higher in the new area ($p=0.02$ & $p<0.01$, respectively).

In the model without outliers, a similar trend is visible where the mean number of saplings decreases as the height class increases (figure 20B). However, pairwise comparison of the means showed that this is only significant in the old area ($p<0.001$), while in the new area, the mean number of saplings per height class does not significantly differ ($p = 0.32$). In addition, the mean number of saplings in HC1 is higher in the old area than in the new area ($p<0.001$), but the mean number of saplings in HC2 and HC3 is not significantly different between the two areas ($p = 1.00$).

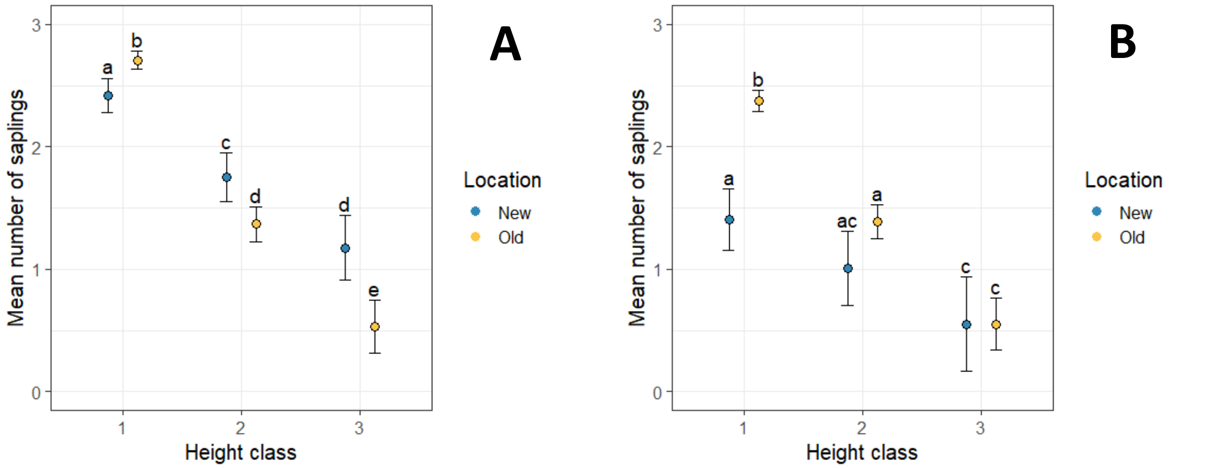


Figure 20 – Relation between height class and the number of saplings, in the new and the old area, as measured in the field survey in 2021. In case of the model with outliers **(A)**, and without outliers (plots 28,68,78) **(B)**. In both figures, the new area is depicted in blue, and the old area in yellow, whiskers show the 95% confidence interval. Height class 1 includes saplings <50 cm, height class 2 includes saplings of 51-100 cm, and height class 3 includes saplings of 101-150 cm. Different letters distinguish groups with significantly different means (p ≤ 0.05) according to Tukey's method.

Influence of Height class, Location and RPU21

No significant interaction is found between RPU21 and Height class (p=0.90) or RPU and location (p = 0.96; Table 7). The results also show that there is no significant main effect of Location (p = 0.80) or RPU (p=0.26). Only height class significantly affects the mean number of saplings in this model (p<0.001). Even though there is no significant effect of RPU21 on the number of saplings, figure 21 does indicate a negative trend between the number of saplings and RPU21.

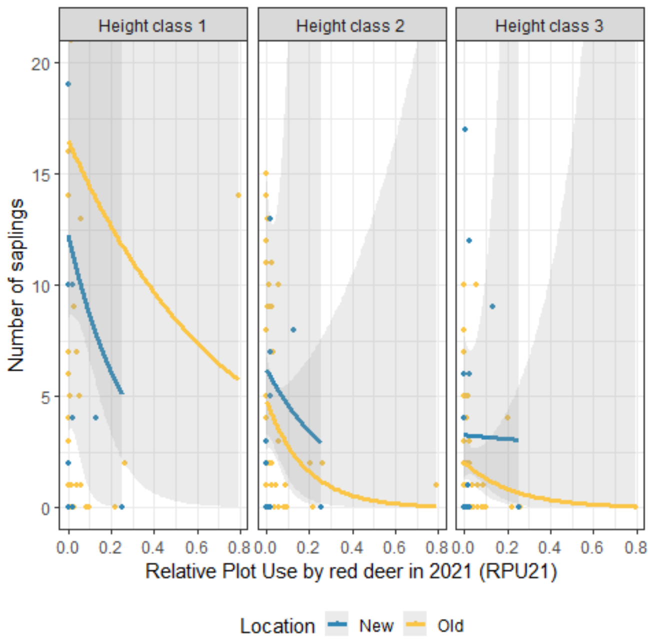


Figure 21 – Relation between Relative Plot Use in 2021 (RPU21) and number of saplings per plot, in the new and the old area, for each height class, as measured in the field survey in 2021. In the figure, the new area is depicted in blue, and the old area in yellow, and the 95% confidence interval is depicted in grey. Height class 1 includes saplings <50 cm, height class 2 includes saplings of 51-100 cm, and height class 3 includes saplings of 101-150 cm.

Influence of Height class, Location and Habitat

Habitat and Location significantly interact (p<0.001; Table 7), thus the number of saplings differs per habitat type and that this distribution over habitat types differs between areas. There is no significant effect of Height class (p=0.77). Plots within Birch-pine or Spruce habitats were not included in this model, as these habitat types only occur in either the old or the new area. The raw data show that de median number of saplings in the Oak-hazel-alder and Oak-Poplar-Alder habitats is higher in the new area, while the median number of saplings in the Bramble-alder and Poplar-hazel-alder habitats is higher in the old area (figure 22A). The statistical analysis shows, however, no significant difference in mean number of saplings per height class between the different habitat types (Table 7, figure 22B). Pairwise comparison of de means shows that the only difference exists in HC1 saplings between the new and old area, in the Oak-hazel-alder habitat.

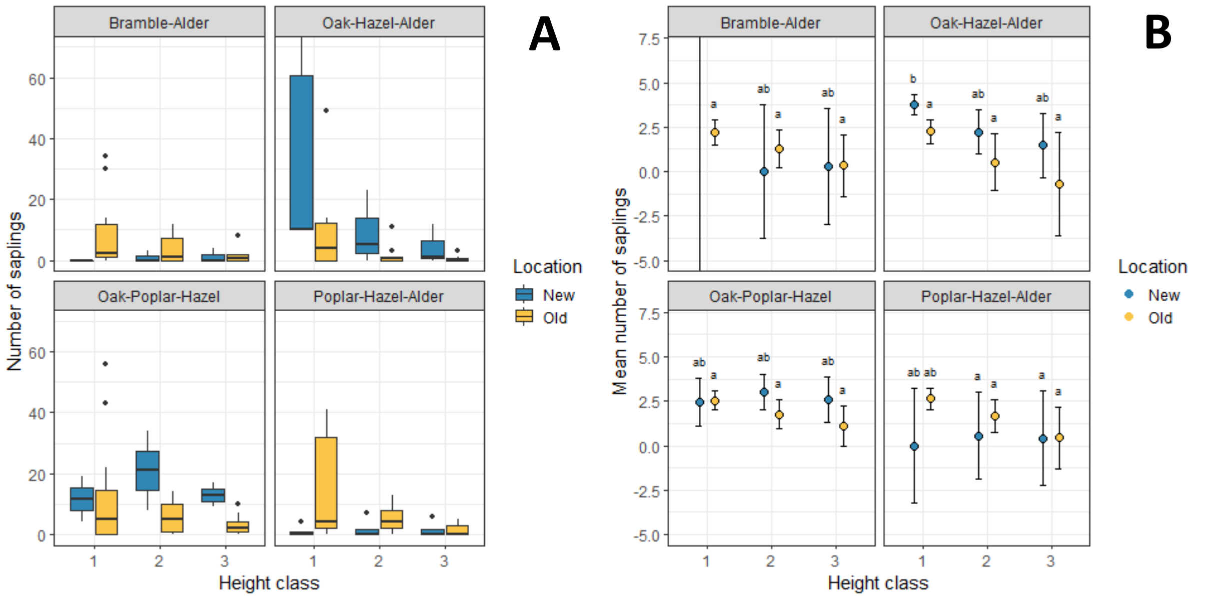


Figure 22 – Relation between height class and number of saplings per plot in the new and the old area, for each habitat type, as measured in the field survey in 2021. Shown are the raw data **(A)**, and the results from the Poisson regression **(B)**. In both figures, the new area is depicted in blue, and the old area in yellow, whiskers show the 95% confidence interval. Height class 1 includes saplings <50 cm, height class 2 includes saplings of 51-100 cm, and height class 3 includes saplings of 101-150 cm. The habitat types Spruce and Birch-Pine were not included in this figure, as these are not present in both areas. In figure B, different letters distinguish groups with significantly different means (p ≤ 0.05) according to Tukey's method. Also in figure B, a vertical line without mean point depicts zero individuals found of that species within that height class.

Influence of Height class, Location and Deadwood

No significant interaction is found between the average amount of lying deadwood and Location (p = 0.77), or between Deadwood and Height class (p = 0.81; Table 7). The results also indicate no significant main effect of location (p = 0.44). There is, however, a significant main effect of Deadwood (p=0.02), and Height class (p<0.001), as the mean number of saplings in HC1 significantly increases as the amount of lying deadwood increases (figure 23). Deadwood does not significantly affect saplings in HC2 and HC3.

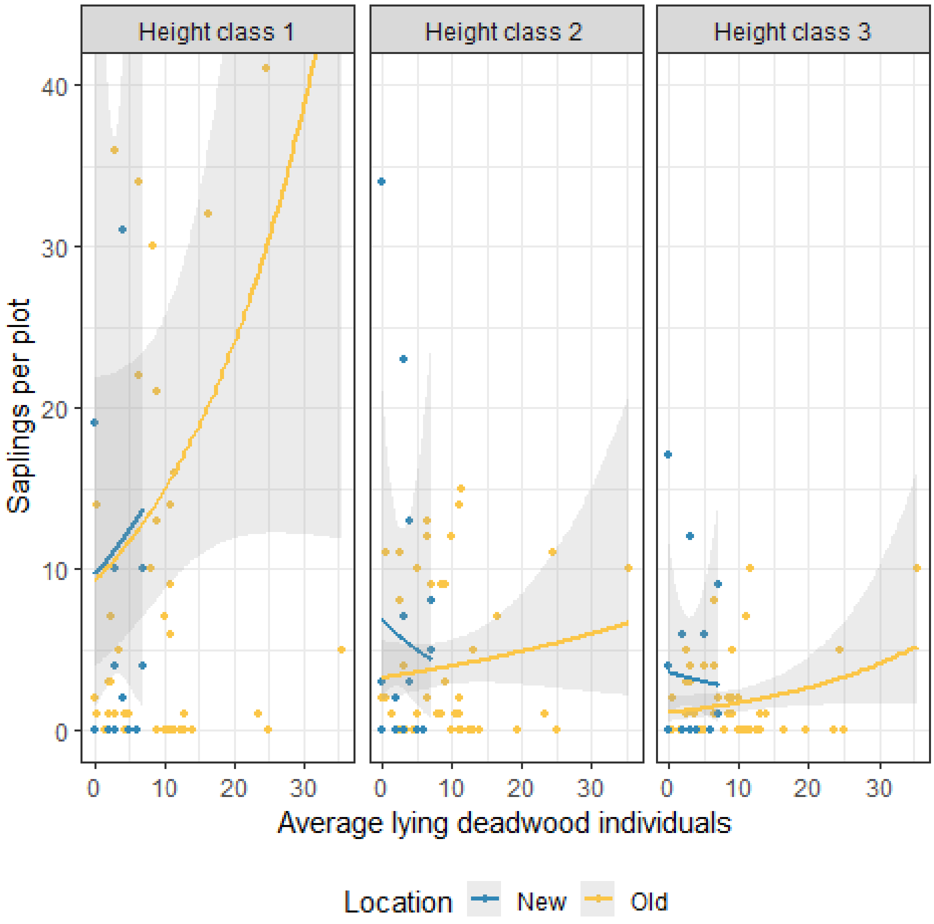


Figure 23 – Relation between the average amount of lying deadwood per plot, and the number of saplings per plot, in the new and the old area, for each height class, as measured in the field survey in 2021. In the figure, the new area is depicted in blue, and the old area in yellow, and the 95% confidence interval is depicted in grey. Height class 1 includes saplings < 50 cm, height class 2 includes saplings of 51-100 cm, and height class 3 includes saplings of 101-150 cm. Lying deadwood per plot was averaged for 2019 and 2021.

Influence of Height class, Location and Species

No significant interaction is found between Species and Location (p = 0.46), or between Species and Height class (p = 0.32; Table 7). The results also indicate no significant main effect of Location (p=0.23). There is, however, a significant main effect of both Height class (p<0.001) and Species (p<0.001; Fig. x). Pairwise comparison of the means show that the mean number of Bird cherry saplings is higher than that of Birch, Hazel and Rowan (p<0.001, p<0.001, p<0.01, respectively). In addition, the mean number of Bird cherry saplings in HC1 is higher than in HC2 and HC3 (p=0.05).

Finally, comparison of the means show that the mean number of oak saplings is lower than that of all other species (figure 24). However, these differences are not significant due to large confidence intervals.

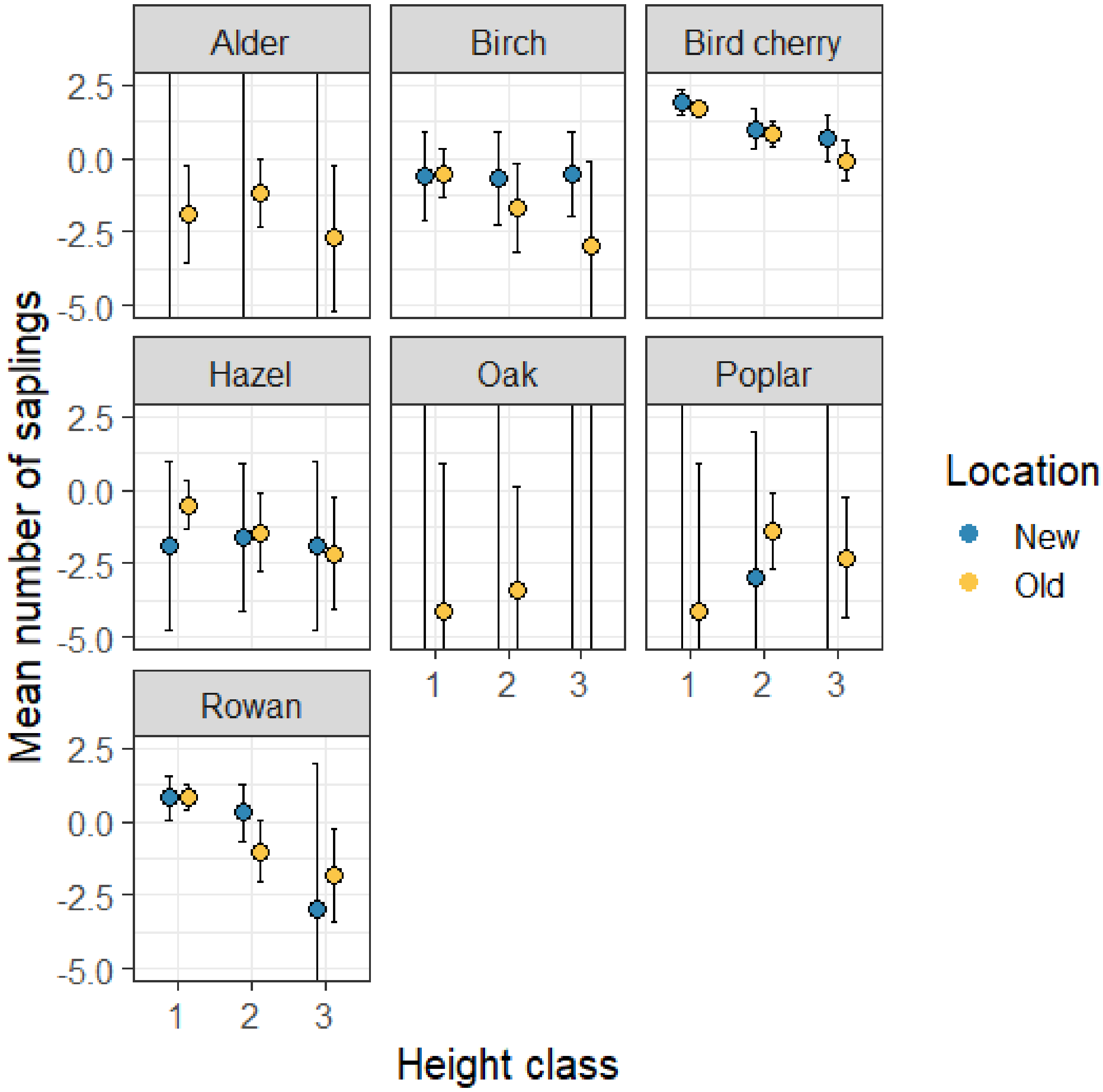


Figure 24– Relation between height class and number of saplings per plot in the new and the old area, for different tree species, as measured in the field survey in 2021. The new area is depicted in blue, and the old area in yellow, whiskers show the 95% confidence interval. Height class 1 includes saplings <50 cm, height class 2 includes saplings of 51-100 cm, and height class 3 includes saplings of 101-150 cm. Different letters distinguish groups with significantly different means ($p \leq 0.05$) according to Tukey's method. Furthermore, a vertical line without mean point depicts zero individuals found of that species within that height class.

3.2.2 Difference in woody recruitment between 2019 and 2021

The difference in woody recruitment between 2019 and 2021 was tested through a general linear model. Between 2019 and 2021, the median number of adult trees (> 150 cm) increased, while the median number of saplings (< 150 cm) decreased (figure 25). However, these changes were not significant (p = 0.97; Table 8).

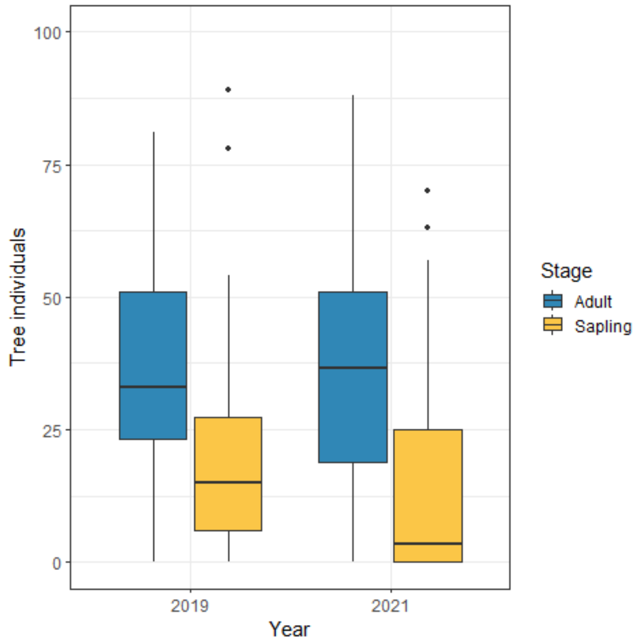


Figure 25 – Mean number of saplings and adult trees per plot, as measured in 2019 and 2021. Here, adult trees are > 150 cm (blue), and saplings are < 150 cm (yellow)

Table 8 – Statistical results from the general linear models used to compare woody recruitment in 2019 and 2021. Only significant relations (p ≤ 0.05) are shown. In the case of a significant interaction between predictors, significant main effects of individual predictors are not shown. See appendix D for an overview of all results and see table 5 for the definitions of all variables.

Model	Model type	Predictor(s)	*p*-value	F –value
Individuals ~ Year * Stage	Linear	Year	< 0.001	26.72
ChangeTrees ~ RPU * Stage	Linear	RPU	< 0.01	8.37
ChangeSaplings ~ HC * RPU	Linear	HC * RPU	0.02	3.97
ChangeSaplings ~ HC * Habitat	Linear	Habitat	< 0.001	7.80
ChangeSaplings ~ HC * RPU.Cat * Deadwood	Linear	HC * RPU.Cat	0.02	3.03
ChangeAlder ~ HC * RPU	Linear	No significant results		
ChangeBirch ~ HC * RPU	Linear	No significant results		
ChangeBirdCh ~ HC * RPU	Linear	HC	< 0.01	4.79
		RPU	0.01	6.70
ChangeHazel ~ HC * RPU	Linear	HC	< 0.01	5.18
ChangeOak ~ HC * RPU	Linear	HC * RPU	< 0.001	44.6
ChangePoplar ~ HC * RPU	Linear	RPU	0.04	4.27
ChangeRowan ~ HC * RPU	Linear	No significant results		

Influence of Stage and RPU

There is no significant interaction between Stage and RPU that influences the change in trees (p=0.31; table 8). The results also show no main effect of Stage on the change in trees (p=0.61), thus the change in adult trees (> 150 cm) and in saplings (< 150 cm) do not significantly differ. There is, however, a significant main effect of RPU (p<0.01), where the difference in trees becomes more negative as RPU increases (Fig. 15). RPU has a stronger effect on saplings than on adult trees, even though no significant difference is found between the two categories (figure 26).

Influence of Height class and RPU

The test from the previous paragraph was repeated, but now with only saplings, which are divided into three height classes. This test shows that there is a significant interaction between RPU and Height class (0.02; table 8). Figure 27 shows that the difference in saplings becomes more negative as RPU increases, mainly with saplings in HC1. Pairwise comparison of the means shows that the trend is significant for HC1, but not for HC2 and HC3 (table 8).

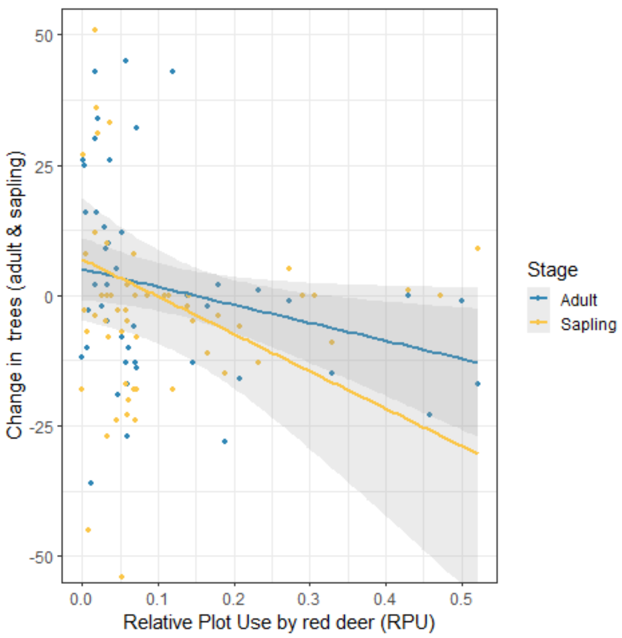


Figure 26 – Relation between Relative Plot Use by red deer (RPU) and change in adult trees and saplings per plot, between 2019 and 2021. Adult trees are > 150 cm (blue), and saplings are < 150 cm (yellow). The 95% confidence interval is depicted in grey. Change in trees was calculated by subtracting the 2019 value from the 2021 value.

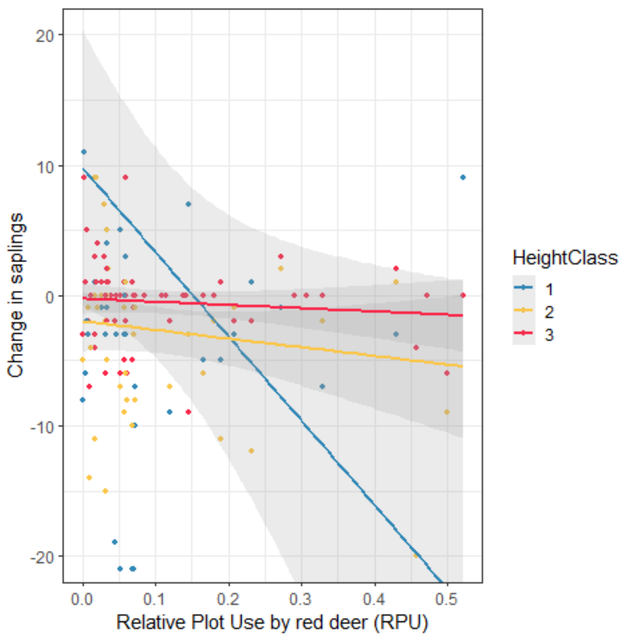


Figure 27 – Relation between Relative Plot Use by red deer (RPU) and change in saplings per plot between 2019 and 2021, for each height class. Height class 1 includes saplings <50 cm (blue), height class 2 includes saplings of 51-100 cm (yellow), and height class 3 includes saplings of 101-150 cm (red). The 95% confidence interval is depicted in grey. Change in saplings was calculated by subtracting the 2019 value from the 2021 value.

Influence of Height class and Habitat

There is no significant interaction between Height class and Habitat (p=0.20), or a significant main effect of Height class (=p=0.09; Table 8). There is, however, a significant main effect of habitat (p<0.001), thus the mean difference in saplings between 2019 and 2021 varies between habitats. Pairwise comparison of the means shows that the change in saplings in Oak-hazel-alder habitats is more negative than in Spruce habitats (p=0.02), but that other habitats do not significantly differ from each other. However, figure 28 shows that median sapling differences lie lower in the Oak-hazel-alder habitats than in most other habitats. Plots in Birch-pine habitats were not included in this model, as there were no Birch-pine habitats in the 2019 data.

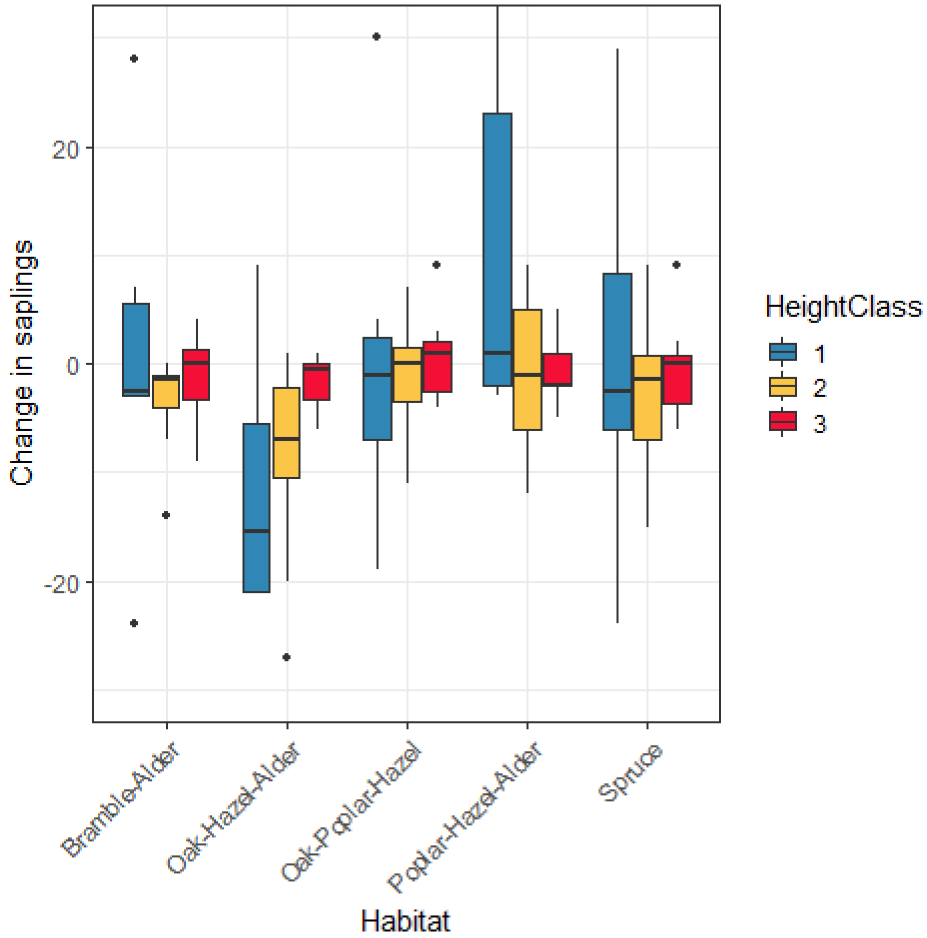


Figure 28 - Relation between habitat and change in saplings per plot between 2019 and 2021, for each height class. Height class 1 includes saplings < 50 cm (blue), height class 2 includes saplings of 51-100 cm (yellow), and height class 3 includes saplings of 101-150 cm (red). The habitat type Birch-Pine is not included in this figure, as this habitat type was not present in the vegetation survey of 2019. Change in saplings was calculated by subtracting the 2019 value from the 2021 value.

Influence of Height class, RPU and Deadwood

In the model with Height class, RPU and Deadwood as predictors, there is a significant interaction between Height class and RPU (figure 29; Table 8). There is, however, no significant effect of Deadwood.

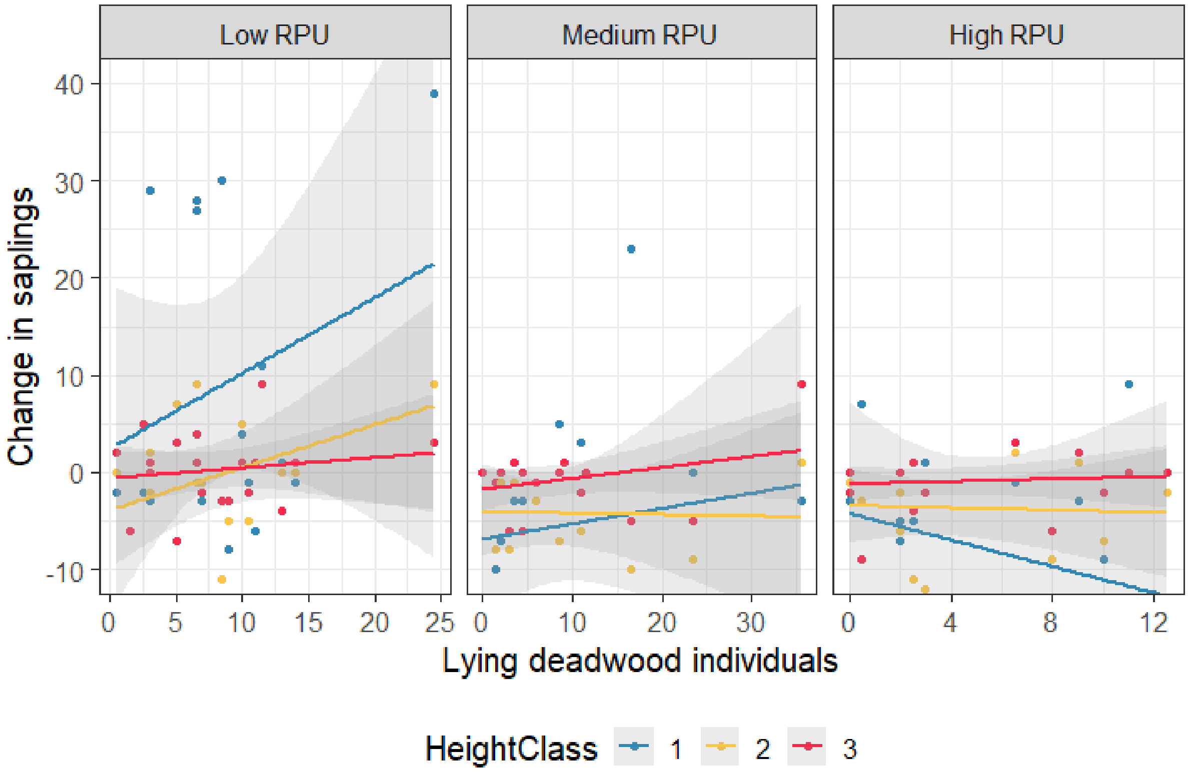


Figure 29 – Relation between the average amount of lying deadwood per plot, and the change in saplings per plot between 2019 and 2021, for three levels of RPU. Height class 1 includes saplings <50 cm (blue), height class 2 includes saplings of 51-100 cm (yellow), and height class 3 includes saplings of 101-150 cm (red). The 95% confidence interval is depicted in grey. Lying deadwood per plot was averaged for 2019 and 2021. Change in saplings was calculated by subtracting the 2019 value from the 2021 value. Low RPU lies below 0.038, Medium RPU lies between 0.038-0.11, High RPU lies between 0.11-0.52.

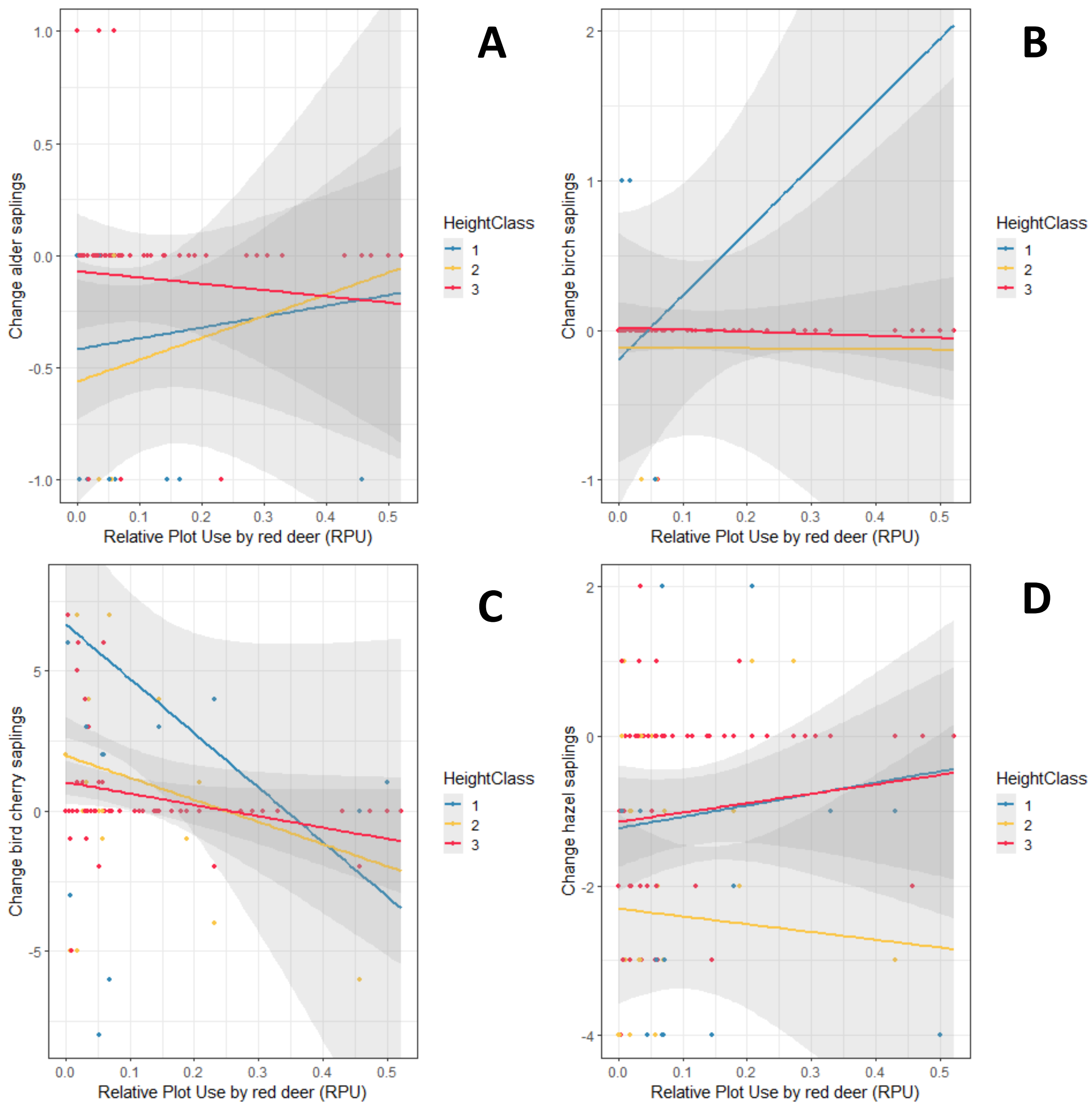
Influence of Height class and Species

Table 9 shows how the number of saplings of the most dominant tree species in the old area changed between summer 2019 and spring 2021. The total amount of saplings declined, resulting from a decline in alder, hazel and oak individuals. On the other hand, there was an increase in saplings of birch, bird cherry, poplar and rowan.

Table 9 – Change in number of saplings of the most dominant tree species between 2019 and 2021. Total change is given, as well as change per height class (HC). Height class 1 includes saplings <50 cm, height class 2 includes saplings of 51-100 cm, and height class 3 includes saplings of 101-150 cm. Decreases in numbers are marked red, increases in numbers are marked green, and unchanged numbers are marked blue.

Species	No. 2019	No. 2021	Change total	Change HC1	Change HC2	Change HC3
Alder	67	14	-53	-21	-26	-6
Birch	39	50	11	18	-7	0
Bird cherry	140	487	347	254	61	32
Hazel	312	52	-260	-61	-141	-58
Oak	308	2	-306	-289	-13	-4
Poplar	19	22	3	-6	3	6
Rowan	150	167	17	46	-28	-1
Total	**1035**	**794**	**-241**	**-59**	**-151**	**-31**

The relation between RPU and change in saplings differs per species (figure 30). In the case of alder, birch and rowan, there is no significant effect of RPU or Height class (figure 30A,B,G).
The change in bird cherry saplings significantly relates to both Height class and RPU. Here, the change in saplings becomes more negative as RPU increases, with the strongest effect in HC1 (figure 30C).
With hazel saplings, there is a significant difference effect of Height class, but no relation with RPU (Fig. figure 30D). In the case of oak saplings, there is a significant interaction between RPU and Height class (figure 30E). Saplings in HC1 strongly decline as RPU increases, while the difference in saplings of HC2 and HC3 remains relatively stable.
Lastly, there is a significant effect of RPU on the change in poplar saplings, where for all height classes, the change becomes more positive as RPU increases (figure 30F).



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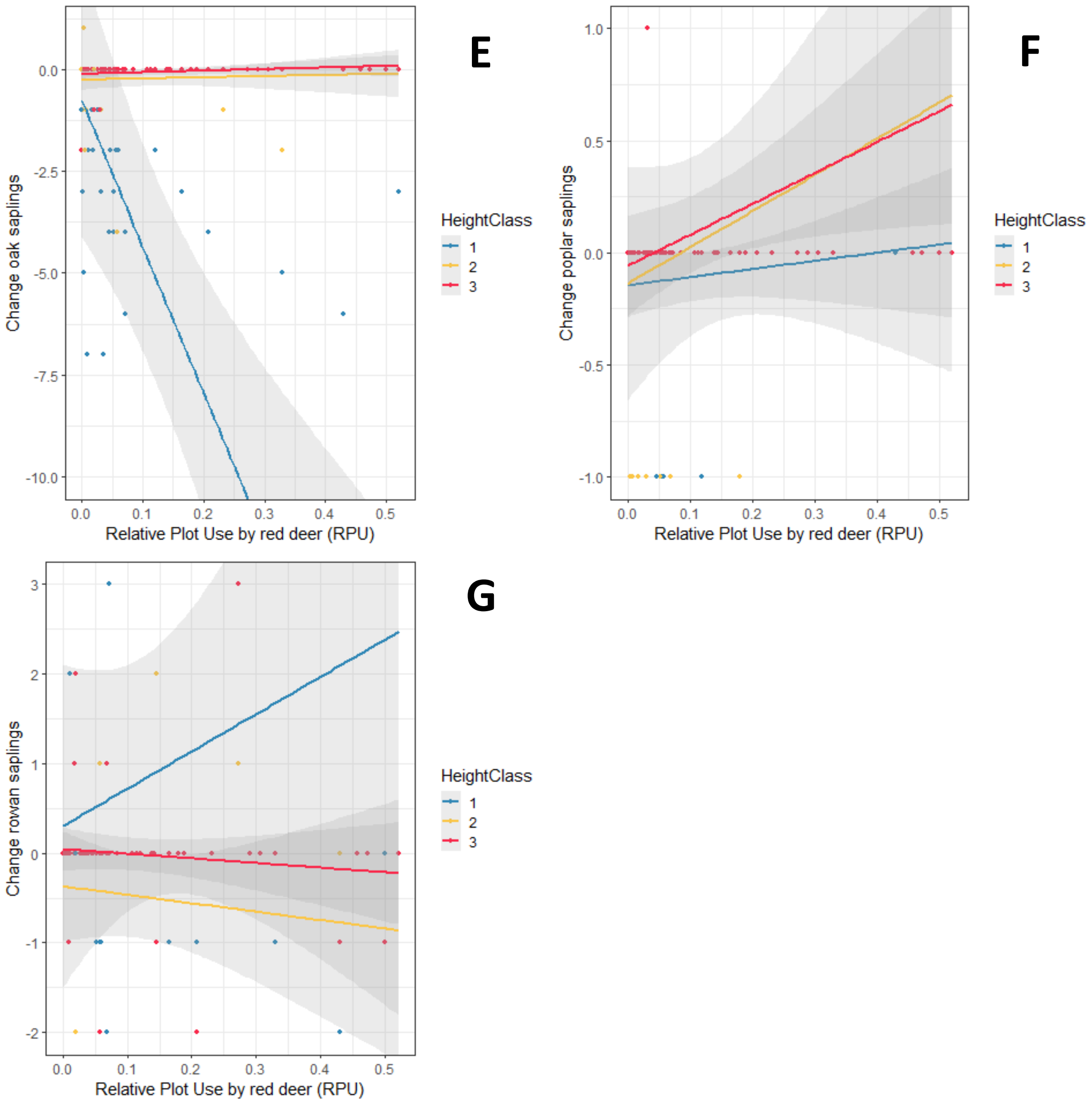

Figure 30 – Relation between Relative Plot Use by red deer (RPU) and change in saplings per plot between 2019 and 2021, per height class, for tree species separately. Changes are shown for alder **(A)**, birch **(B)**, bird cherry **(C)**, hazel **(D)**, oak **(E)**, poplar **(F)**, and rowan **(G)**. In all subfigures, height class 1 includes saplings <50 cm (blue), height class 2 includes saplings of 51-100 cm (yellow), and height class 3 includes saplings of 101-150 cm (red). The 95% confidence interval is depicted in grey. Change in saplings was calculated by subtracting the 2019 value from the 2021 value.

3.3 Vegetation structure

Two ANOVA models were used to provide a general view of changes in bramble height and cover between 2017, 2019 and 2021 (table 10). Bramble height significantly differed between years (figure 31A), while no significant difference was found for bramble cover (figure 31B). Pairwise comparison of the means showed that mean bramble height in 2017 was significantly higher than in 2019 (p=0.04), but that mean bramble height in 2021 did not significantly differ from that in 2017 (p=0.07), or 2019 (p=0.97). How RPU is related to vegetation structure, and how vegetation structure differs between the old and the new area, is discussed in the following paragraphs.

Table 10 – Statistical results from the ANOVA models used to analyse how bramble height can aerial cover changed between 2019 and 2021. Significant results are marked green (p ≤ 0.05), insignificant results are marked red (p > 0.05). See appendix D for an overview of all results, and table 5 for the definitions of all variables.

Response	Predictor	Model type	Slope	*p*-value	F-value
Bramble Height	Year	Linear	- 6.77	0.02	3.75
Bramble Cover	Year	Linear	- 4.92	0.71	0.35

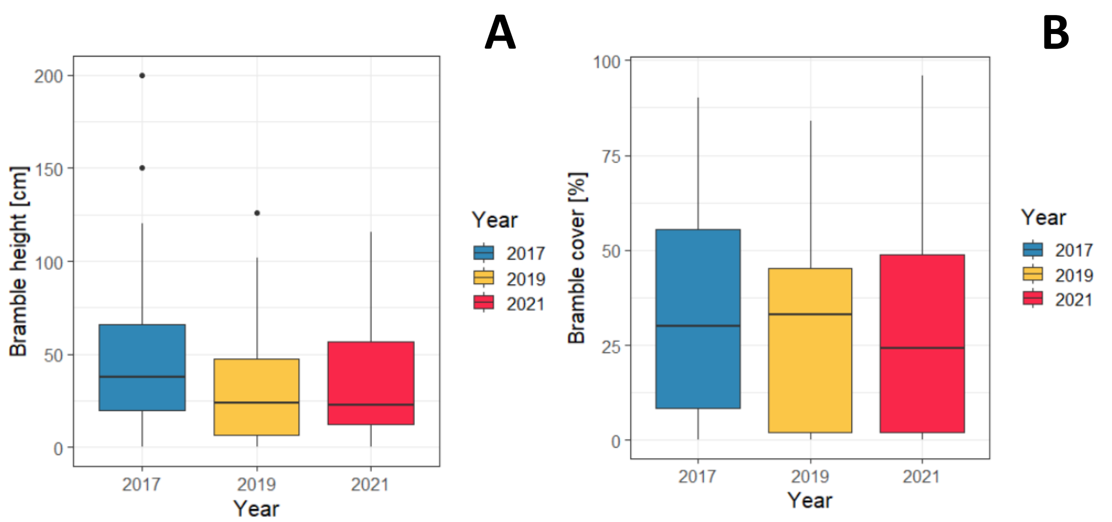

Figure 31 – Bramble height (A) and aerial cover (B) found in the vegetation surveys in 2017, 2019 and 2021. 2017 data are depicted in blue, 2019 data are depicted in yellow, and 2021 data are depicted in red. Values are only for the old area, as the new area was not measured in 2017 and 2019.

3.3.1 Influence of RPU on vegetation structure

The results of the linear models testing for the relation between RPU and the vegetation structure variables, are summarized in table 11. A higher RPU significantly correlates with lower bramble height, bramble cover and sapling height (figure 32A,B&D). The variation (SD) in bramble height declines as RPU increases, but this trend is not significant (figure 32C).

Table 11 – Statistical results from the linear models used to analyse the relationship between Relative Plot Use by red deer (RPU) and vegetation structure variables. Significant results are marked green (p ≤ 0.05), results close to the significant threshold are marked orange (p=0.06), and insignificant results are marked red (p ≥ 0.07). See appendix D for an overview of all results, and table 5 for the definitions of all variables.

Response	Predictor	Model type	Slope	*p*-value	F-value
Bramble Height	RPU	Linear, sqrt transformed	- 6.77	< 0.001	12.90
Bramble Cover	RPU	Linear, sqrt transformed	- 4.92	0.02	6.05
Change Bramble Height	RPU	Linear	- 19.53	0.32	1.01
Change Bramble Cover	RPU	Linear	- 25.54	0.12	2.51
Bramble Browsing	RPU	Linear	1.51	0.96	0.00
SD Bramble Height	RPU	Linear	- 2.88	0.06	3.76
Sapling Height	RPU	Linear	- 66.39	0.03	5.18
SD Sapling Height	RPU	Linear	7.06	0.53	0.40

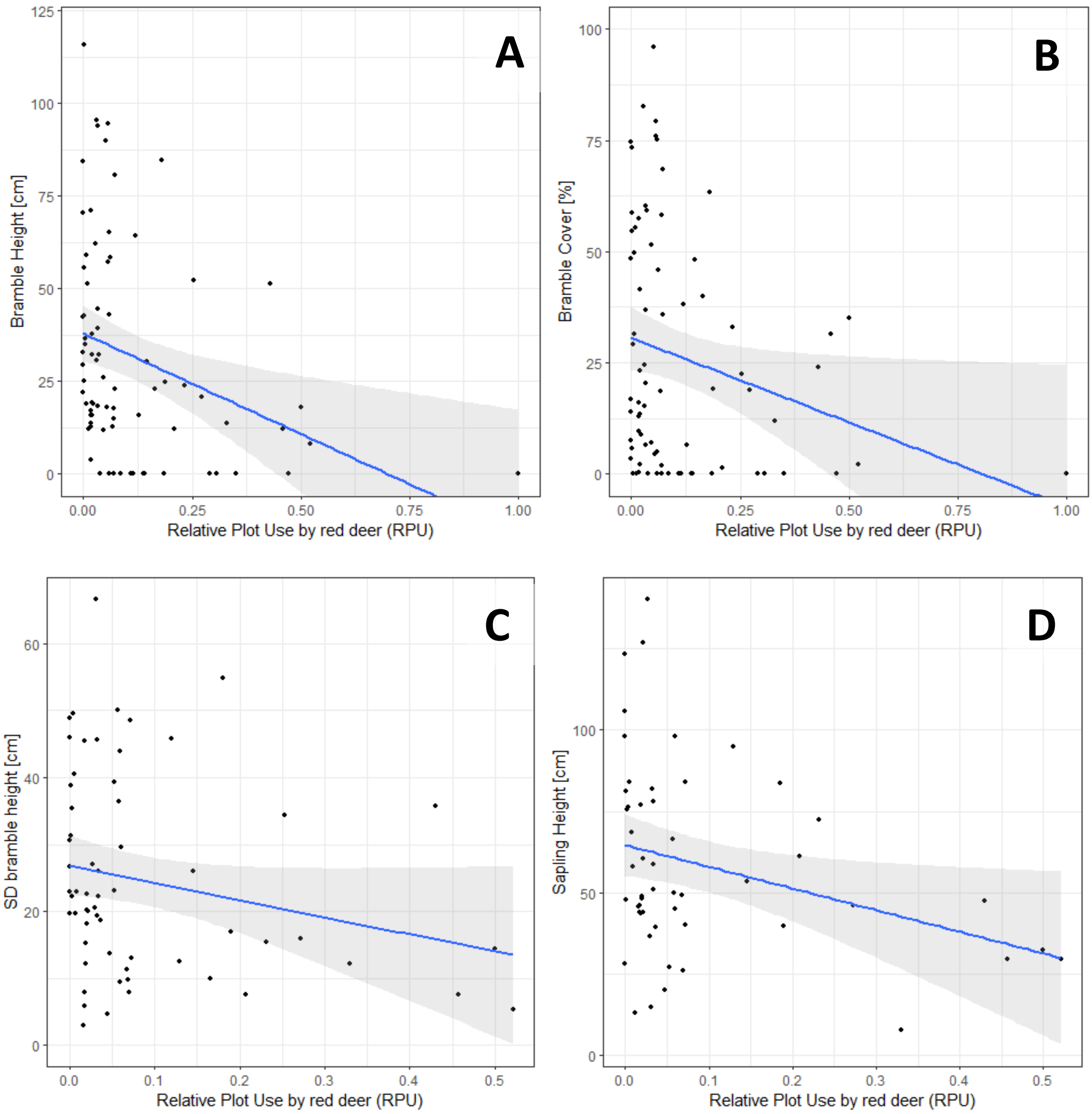

Figure 32 – Relation between Relative Plot Use by red deer (RPU) and various woody vegetation structure variables. Bramble height **(A)**, bramble cover **(B)**, standard variation in bramble height **(C)**, and sapling height **(D)**. Here, saplings are all tree individuals ≤ 150 cm. The 95% confidence interval is depicted in grey. Vegetation data is collected in the vegetation survey in 2021, RPU is the average value of relative plot use by red deer in 2019 and 2021.

3.3.2 Difference between the old and the new area

The results of the linear models testing for the relation between location and the vegetation structure variables, are summarized in table 12. Bramble cover and sapling height both significantly differ between the old and the new area. Mean bramble cover is 13.2 percent point higher in the old area than in the new area (figure 33). Mean sapling height, on the other hand, is higher in the new area (figure 34). Mean sapling height in the new area is namely 74 cm, while it is 54 in the old area.

Table 12 – Statistical results from the linear models used to analyse the relationship between location (old/new area) and vegetation structure variables. Significant results are marked green ($p \leq 0.05$), results close to the significant threshold are marked orange (p=0.06), and insignificant results are marked red ($p \geq 0.07$). See appendix D for an overview of all results, and table 5 for the definitions of all variables.

Response	Predictor	Model type	*p*-value	F-value
Bramble Height	Location	Linear	0.40	0.71
Bramble Cover	Location	Linear	0.05	3.99
SD Bramble	Location	Linear	0.58	0.31
Sapling Height	Location	Linear	0.03	4.91
SD Saplings Height	Location	Linear	0.30	1.11

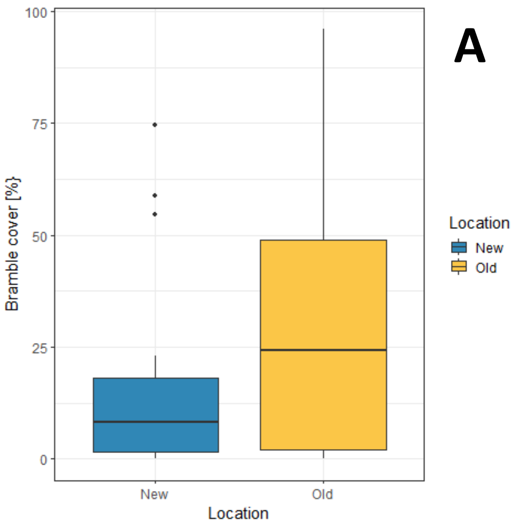

Figure 33 – Relation between location and bramble cover. Measured in the vegetation survey in 2021, in the new area (blue), and the old area (yellow).

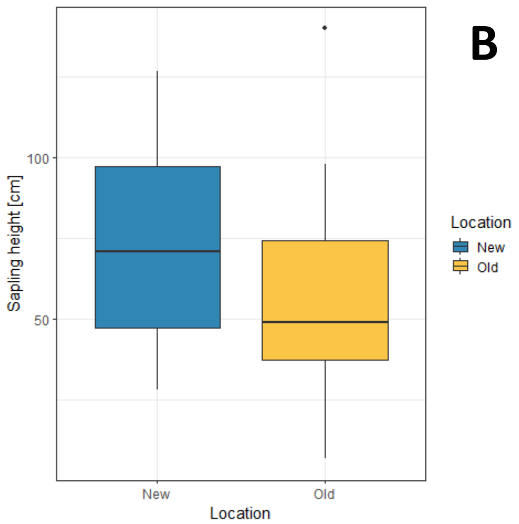

Figure 34 – Relation between location and sapling height. Here, saplings are all tree individuals ≤ 150 cm. Measured in the vegetation survey in 2021, in the new area (blue), and the old area (yellow).

4. Discussion

In this thesis, I studied how woody recruitment and vegetation structure are linked to area use by red deer, in the Groene Woud deer enclosure. While the research design of this study was not suitable to demonstrate any causal relationships between red deer and vegetation properties, the broad set-up did provide various insights in the natural processes that take place in Het Groene Woud. The results can thus be used as a starting point for further research, as well as to point out some aspects to consider when managing Het Groene Woud.

The camera traps and GPS collars recorded red deer throughout the reserve, but the red deer showed a preference for grasslands and oak-hazel-alder forests. This coincides with the deer's dietary preferences, as grass, oaks, and rowans were commonly present in these habitat types.
The statistical analysis provided several indications of red deer influencing woody recruitment. In the old area, more saplings below 50 cm were present than in the new area, while both areas contained about the same number of saplings with heights of 51-100 cm, and 101-150 cm. This suggests that in the old area, a smaller proportion of the saplings below 50 cm have grown to higher height classes. This is an indication of a demographic bottleneck, meaning that red deer might have caused the saplings to stay below 50 cm in the old area. While this pattern is generally present in the old area, the deer's impact on saplings differs between tree species. In the case of oak saplings, the number of saplings below 50 cm has strongly decreased, especially in plots where Relative Plot Use by red deer was high. There are several explanations for the different tree species responses. For example, regeneration of oak saplings might be low due to the foraging of red deer on acorns.
The results showed no significant interacting effect of red deer and lying deadwood on the change in saplings. As no natural predator of the red deer is currently present in het Groene Woud, it could be that red deer do not avoid escape impediments, and thus still browse on saplings near dead tree trunks.
Bramble height has been stable between 2019 and 2021, but I found no clear substantiation for the involvement of red deer in this process. Neither did I find an effect of red deer on bramble or sapling structure.
The researched grassland plots contained hardly any woody recruitment or woody vegetation structure, which might result from the red deer's browsing, possibly in combination with other pressures, like mowing practices.

4.1 Area use

Even though Relative Plot Use of 2019 and 2021 differed on plot-level, both variables provided the same overall view, as the dispersion of red deer over different habitat types did not significantly differ between years. In both years, red deer made use of the entire reserve, but preferred oak-hazel-alder forests and grasslands (figure 15). Compared to the other broad-leaved forests, the oak-hazel-alder forests contained in 2021 a lot of adult rowan, oak and birch trees, as well as rowan saplings (figure 16A&B). Based on the calculated Jacob's Selection Index (table 6), it is surprising that red deer preferred oak-hazel-alder forests, as the low scores of rowan, oak and birch trees suggest that red deer did not prefer to feed on these species. However, these results might be influenced by the relatively small number of saplings that was found. Especially in the case of oak saplings, of which I observed only three individuals during the field survey, the low Jacob's Selection Index value might not represent actual avoidance by red deer. In fact, earlier studies do indicate a dietary preference for rowan, oak and birch trees (table 1). In addition, personal observations of Allen (2019) and mine showed that Rowan was the most commonly debarked tree species (figure 35). This explains why, even during the winter months, red deer often visited oak-hazel-alder forests. That the deer showed a preference for

grasslands as well, is also in line with expectations, as grass is an important food source of red deer, especially during winter (Cornelissen & Vulink, 1996; Dumont et al., 2005; Krojerova-Prokesova et al., 2010; Storms et al., 2008).
To answer subquestion 1, this study showed that, since their reintroduction in 2017, red deer have made use of the entire reserve, but showed a preference for grasslands and oak-hazel-alder forests. This preference did not significantly change between 2019 and 2021.

Figure 35 – Forest stand in Het Groene Woud, where all rowan trees are debarked.

4.2 Woody recruitment

4.2.1 Saplings and height classes

In 2021, there was no significant difference in the total amount of saplings between the old and new area, but the number of saplings per height class did vary between the two locations. The difference between figures 20A and 20B shows that including or excluding the outliers (plots 28, 68 and 78) heavily influences the results. I will therefore draw conclusions from the most cautious model, the model without outliers. That model shows that in both the new and the old area, height class 1 (1-50 cm) contained the highest number of saplings. The mean number of saplings below 50 cm was also significantly higher in the old area, compared to the new area. Furthermore, the number of saplings decreased as the height class increased. While this seems to have occurred in both areas, this difference was only significant in the old area. These data thus indicate that something in the old area caused a relative increase of saplings of lower than 50 cm, while this pattern was less apparent in the new area.

Red deer browsing can be the driver of this difference. In the study of Renaud et al. (2003), the preferred foraging height of red deer was between 50-150 cm, matching height class 2 and 3 of my research. Kuijper, Cromsigt et al., (2010) also found that the amount of saplings taller than 50 cm decreased when red deer were present, while the amount of saplings below 50 cm remained equal, or increased. Possibly, red deer in Het Groene Woud also select the taller saplings, shortening them by browsing. This then results in more saplings lower than 50 cm, and less saplings higher than 50 cm. That this pattern was more apparent in the old area, where red deer have been browsing for a longer period of time, indicates that red deer browsing can indeed be the cause of the unequal distribution between height classes.

Other tests, however, seem to contradict this conclusion. If red deer cause an increase of saplings lower than 50 cm, one would expect to find that their favoured habitat, oak-hazel-alder forests, contained more saplings below this height in the old area, compared to the new area. However, in these forests the opposite was found to be true (figure 22B). The comparison of woody recruitment in 2019 and 2021 also provided results opposing this pattern. Here, an increase in relative plot correlated with a decrease in saplings smaller than 50 cm (figure 27). This decrease occurred in oak-hazel-alder forests, again the habitat type where red deer were most commonly present (figure 28). These results can thus be a signal that the unequal distribution of saplings between height classes in the old area is not caused by red deer browsing. However, there is also another explanation.
When looking at the relation between Relative Plot Use by red deer, and the change in saplings lower than 50 cm for each species individually, it becomes clear that mainly oak saplings in this height class decreased since 2019 as Relative Plot Use increased (figure 30). Saplings below 50 cm of other species often stayed quite stable, or even increased as the Relative Plot Use by red deer increased. It might thus be that the observed pattern, where red deer cause an increase in saplings lower than 50 cm, generally occurs in Het Groene Woud, but does not apply to oak saplings. This is in line with the findings of Kuijper, Cromsigt et al., (2010). As discussed, their research showed little effect of herbivore exclosures on the abundancy of saplings below 50 cm. However, the number of oak saplings below 50 cm did increase in the absence of herbivores.
There are various possible explanations for the decrease in oak saplings lower than 50 cm. Firstly, while literature shows that the preferred foraging height of red deer generally lies between 50 and 150 cm, it is possible that the deer also select smaller saplings of specific tree species, like oak. Secondly, it might be possible that browsed oak saplings have a higher mortality than those of other species. When the oak saplings die instead of 'returning' to the smallest height class, this results in fewer oak saplings below 50 cm, compared to other species. Thirdly, the decrease in oak saplings might result from the fact the red deer eating acorns (Bruinderink & Hazebroek, 1995; Gebert & Verheyden-Tixier, 2001; Paulides, 2007). During autumn in oak mast years, this can even account for 50.1 percent of their diet (Picard et al., 1991). This elimination of oak seeds prevents oak regeneration and might therefore also have result in a lower number of oak saplings below 50 cm. Finally, it is possible that red deer are not the cause of the decrease in HC1 oak saplings. Numerous other herbivores, like roe deer and rodents, were present in Het Groene Woud during this study. This will be further discussed with the limitations stated in paragraph 4.4.

4.2.2 Grasslands

Another result from the field survey was that the grassland plots contained remarkably little saplings. Only plot 73 contained a couple willow and birch saplings (figure 36A). Plots 73 and 19 were located in areas with high, grassy vegetation, but, in general, the researched grassland plots were very open (figure 36B). I performed most vegetation measurements during winter and early spring, which partly influenced this image. Still, the grasslands do not yet show the mosaic structure that is aimed for. Currently, mowing occurs in all grasslands in the reserve, in order to prevent pit rush from dominating the area. However, only 30-40% of the grassy areas is mowed, to maintain variability and provide opportunities for woody encroachment (personal communication, Brabants Landschap, 2021). Yet there is little woody recruitment in the grasslands, so it might be possible that red deer remove most saplings that germinate here.

Figure 36 – Different grasslands in Het Groene Woud. Plot 73 with willow saplings **(A)**, and plot 18, with little vegetation structure **B)**

4.2.3 Deadwood

Lying deadwood was present in many plots (figure 37). In both the old and the new area, the number of saplings below 50 cm significantly increased as the abundancy of deadwood increased (figure 23). This supports earlier findings on how coarse woody debris can increase sapling survival (Kuijper et al., 2013, 2015; Smit et al., 2012; van Ginkel et al., 2021). Yet, no effect of deadwood on the number of saplings larger than 50 cm was found. Also, red deer and deadwood did not have a significantly interacting effect on sapling change since 2019 (figure 29). Kuijper et al., (2015) showed that red deer avoided coarse woody debris more often when in close proximity of a wolf habitat, or a wolf core area. Another study showed that browsing of saplings was lower at high levels of deadwood, but only inside a wolf core area (Kuijper et al., 2013). Also the studies of Smit et al., (2012) and van Ginkel et al., (2021) found place in forests where wolves were present. While red deer in Het Groene Woud might experience some predation stress from humans, dogs and vehicles, no natural predator of red deer is present in the deer enclosure. Therefore, there might be no need for the red deer to be vigilant and avoid large deadwood stems. Currently, wolves are recolonizing various parts of the Netherlands, and one individual has even settled in the east of Noord-Brabant (Bij12, 2021). Wolves might thus also come to Het Groene Woud. Also, culling of red deer might be carried out in the future. Both factors can increase the perceived unsafety of red deer, and the interacting effect of deadwood and red deer on sapling survival might thus emerge in time.

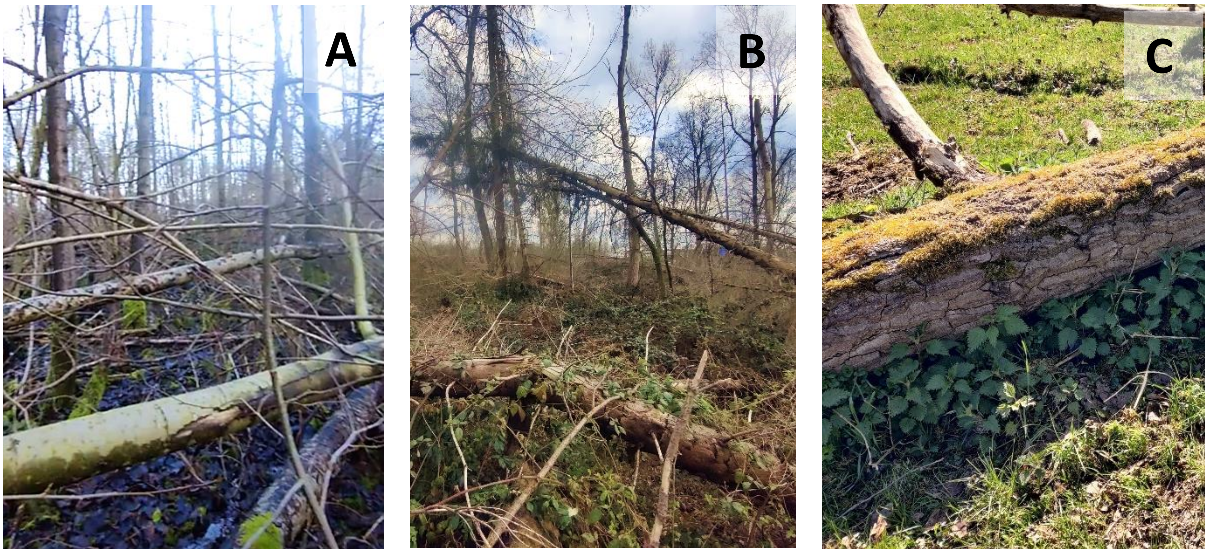

Figure 37 – Lying deadwood in Het Groene Woud. In plot 39 **(A), plot** 34 **(B)**, plot 37 **(C)**

To answer subquestion 2, I found some indications that red deer in Het Groene Woud affect woody recruitment. For example, the number of saplings below 50 cm was significantly higher in the old area. However, this effect was not equal for all tree species and sapling height classes. The results indicate that red deer especially influence the number of oak saplings below 50 cm, as in the research plots the number of HC1 oaks saplings decreased from 308 in 2019, to 2 in 2021. In order to prevent a decline of the tree species diversity currently present in Het Groene Woud, it is thus important to not only monitor overall changes in sapling abundancy, but to do this per specifically per species.

Furthermore, woody recruitment was barely present in the grasslands. This is a process that takes time, so findings might be different in the future. However, this study shows that it can be valuable to change mowing practices, or to manually create grazing refuges, for example by placing large woody debris on the grasslands, as is suggested by Smit et al. (2015).

Lastly, the number of saplings lower than 50 cm was higher in plots with a large amount of deadwood. However, the results show no significant interaction between red deer and deadwood. This might change if predation pressure increases in the future.

4.3 Vegetation structure

Regarding the vegetation structure, I hypothesised that standard deviation, as a measure of variation, of bramble and sapling height would be highest at intermediate levels of RPU. I also expected the variation in bramble and sapling height to be highest in the old area, as that area has experienced red deer pressure for a longer time.

This hypothesis could not be confirmed, as the standard deviation of sapling height showed no significant relationship with Relative Plot Use by red deer, and the standard deviation of bramble and sapling height did not significantly differ between the old and the new area (tables 11 & 12). The standard deviation of bramble height did also not significantly relate with the deer's plot use (table 11). However, as the p-value of the latter test was 0.06, and thus very close to the significance threshold of 0.05, it can still be valuable to interpret the results. Following the intermediate disturbance hypothesis, variation in bramble height would peak at intermediate levels of the deer's plot use, thus showing a non-linear relationship. The negative, linear relationship that is visible in figure 32A might thus indicate that the system was already past the intermediate levels of RPU, where browsing pressure is so high that most bramble stems are eaten, thereby shortening all of them (figure 38).

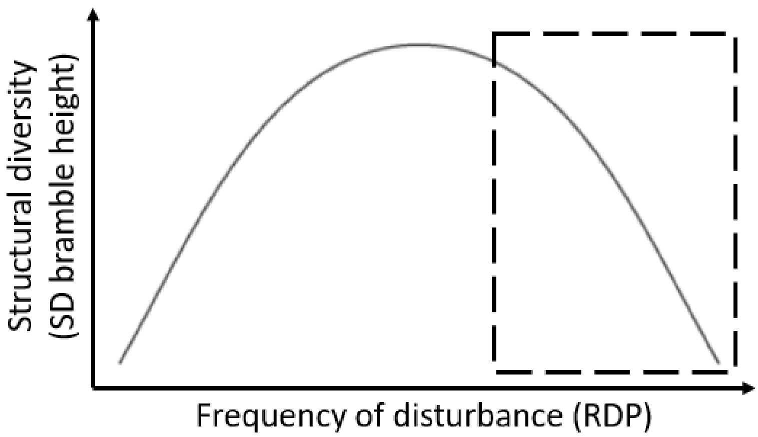

Figure 38 – Hypothesized relationship between the frequency of disturbance and structural diversity of bramble, where is assumed that the frequency of disturbances equals RPU. When a negative relationship between RPU and the SD of bramble height is found, this could mean that the system experiencing high levels of RPU, as indicated by the dashed square.

Yet, none of the other results of this thesis indicate that bramble bushes experience high browsing pressure by red deer. Relative Plot Use by red deer did not significantly relate to change in bramble cover and height, and the results showed no significant relationship between Relative Plot Use and bramble browsing (table 11). It seems therefore unlikely that red deer browsed the bramble bushes so extensively, that the standard deviation in bramble height decreased.
The results did show a negative relationship between Relative Plot Use and bramble height and cover (table 11, figures 32A & 33B). But based on the absent relation between Relative Plot Use and change in bramble height, it is doubtful that this results from red deer actively decreasing bramble height. Possibly, the height of bramble influenced the deer's plot use, instead of the other way around: red deer might have been attracted to plots with low bramble density. Indeed, both the GPS as the camera trap data indicated that, during the study periods, red deer avoided bramble-alder habitats (figure 15). Multiple research plots were covered with very dense bramble bushes (figure 39). As red deer avoid browsing in areas with large dead trees (Kuijper et al., 2013, 2015), it is possible that this high and tough vegetation forms escape impediments, like lying deadwood, and is therefore avoided by red deer.

That red deer had no significant negative impact on bramble height in Het Groene Woud, seemingly contradicts with other studies that showed how deer browsing can reduce bramble height (Joys et al., 2004; Kirby, 2001; Kuiters & Slim, 2002; Morecroft et al., 2001; Pellerin et al., 2010). However, the latter studies are all not red deer specific, and only measure the browsing effect of different ungulate species together, like roe, muntjac, fallow and/or red deer. Furthermore, the red deer's preference for bramble seems to differ per location. Bramble was found to be an important food source of red deer living in a reserve in Northeast France, an area with nutrient-poor, acidic soil (Storms et al., 2008). But rumen and pellet analysis showed the shrub was only occasionally eaten by red deer in the Polish Białowieża forest (Gebczynska, 1980), and a Czech floodplain forest (Krojerová-Prokešová, 2004), both nutrient-rich areas.

Figure 39 – Dense bramble layer, near plot 53.

That this research shows little impact of red deer on bramble growth can have multiple explanations. Firstly, bramble might not be an important food source for the deer. As the red deer reserve of Het Groene Woud is also located in a nutrient-rich area, the feeding habits of the red deer might show a strong resemblance with the feeding habits of the red deer in the Białowieża forests and the floodplain forest. Secondly, it is possible that the red deer do influence bramble, but that the change in bramble height cannot yet be observed between 2019 and 2021, a longer timeframe could give different results. Thirdly, the bramble bushes might have grown about the same amount as they have lost due to browsing. This would mean there is no net decrease in height, but that without browsing, mean bramble height would have been higher. Bramble height has been stabile since 2019 (figure 31). But, as bramble is a nitrophilous species (Van Den Berg et al., 2016), and the deer enclosure is located in a nutrient-rich area, it is unlikely that this stagnation exists without outside pressure. However, it is not possible to link this to red deer, as other herbivores like roe deer can also be the cause of the stable bramble height (see limitations under paragraph 4.4).

While the results show no clear effect of red deer on bramble height, they do provide indications of such an effect in the case of sapling height. Sapling height in the old and the new area significantly differed, as the mean height was 74 cm in the new area, but only 54 cm in the old area (figure 34). This difference may have emerged from the longer time at which red deer have been present in the old area, as the average sapling height in the old area coincides well with the browsing height preferences found by Renaud et al. (2003), and Kuijper, Cromsigt et al (2010).

To answer subquestion 3, bramble height and aerial cover have remained stable since 2019, and the results show no evidence to support the hypothesis that red deer have increased variability in bramble or sapling height in Het Groene Woud. As red deer seemed to have little effect on bramble growth, and avoid plots with dense bramble, it is unclear whether the current pressure of red deer will change bramble structure in the reserve. However, the stabile bramble height and cover do suggest that something is affecting the bramble's growth. Additional research covering a larger timespan and excluding the effects of other environmental factors is needed to further understand this process, as will be discussed in the next paragraph. The results did indicate an effect of red deer on sapling height. This shows that, when browsing pressure is not too high, red deer might increase height variance of saplings in the future. Lastly, as described in the previous paragraph, most grasslands were still very open and contained little woody vegetation structure.

4.4 Limitations and implications for future research

While the data have been collected and analyzed carefully, and various trends can be recognized from the results, there are some limitations of the study to keep in mind when interpreting the results and to consider for future research.

Causality: As discussed, this research was not based on a controlled design, meaning that it is not possible to prove a causal relationship between red deer presence and vegetation responses. Differences in plant properties might emerge from different red deer browsing intensity, but it might also result from various environmental factors like differences in seed dispersal opportunities, nearby vegetation, climatic conditions, but also the presence of other herbivores. Red deer are not the only herbivores present in the Groene Woud deer enclosure. The area is also roamed by cattle, roe deer, and rodents (figure 40). To further investigate the role of red deer in Het Groene Woud, additional research controlling for these factors is required. This can be especially interesting in the case of bramble, as bramble height remained stable since 2019, but the amount of browsing on bramble did not significantly relate to plot use by red deer, suggesting that it was not red deer that stunted bramble growth.

By dividing the data into different habitat types, I partly adjusted for differences in climatic factors. However, these differences are even better controlled for when installing herbivore exclosures and comparing data from within these exclosures to data collected just outside these exclosures. A follow-up research using this method can therefore distinguish herbivore effects from other environmental effects. In addition, to differentiate between red deer browsing and foraging by other herbivores, one can use camera traps to measure Relative Plot Use of not only red deer, but also roe deer, cattle and other herbivores, expanding the method of this thesis.

Vegetation structure: In this study, the assessment of vegetation structure was limited to sapling and bramble properties. The main reason for this was that data was collected during the winter, in which many other plant groups had not fully developed yet. However, other plant groups are also important contributors to vegetation structure. To fully assess vegetation structure, I therefore recommend conducting a study specifically focussing on this subject, in which other plant groups like herbs, grasses and other woody plants are included. Those data should be collected during the summer, when most plants are fully developed, and the data can be compared with the research of Allen (2019).

Sample size: An extensive field survey was conducted, collecting data on eighty plots throughout the reserve. Still, various tests remained inconclusive due to large variance in the results. This became especially a problem when dividing the data into categories, like habitat type, or tree species, as those categories were represented by a relatively small sample, so the replication per actual category was low. Increasing both temporal and spatial scale of the research will result in more data and thus more representative results. Increasing spatial scale can be highly intensive. In order to do this, I recommend using GPS collars instead of camera traps to monitor red deer presence, and to decrease the amount of vegetation measurements. Another option is to continue with only a few habitat types that are of interest, but to increase the plots within those habitats.

Vegetation cover and height: When measuring vegetation cover and height, I followed the same method as Allen (2019). If my research were to be repeated, use of this method ensures continuity of the data. However, if a new study is set up, I advise to revise the method. With the estimation of vegetation cover, it was assumed that the researched vegetation groups always made up 100% of a quadrant, without overlap. This was often unrepresentative, as vegetation layers often did overlap, and the cover of tree stems was not taken into account. Vegetation height was measured by dropping a cardboard disc onto the vegetation layer. However, the height at which the disc came to rest often depended more on the width of the plant, then on the height. I therefore recommend taking various samples of the absolute height of the plant and calculating an average.

Camera traps versus GPS collars: Both camera traps and GPS collars have been proven useful to assess red deer presence. However, the camera trap data showed a lot of variance. Reliability would increase if the cameras were rotated several times, assessing the same plot at different moments. Advantages of using camera traps over GPS collars, is that the photos can be used to observe multiple species, and that the deer do not have to wear a collar. A large disadvantage is, however, that placing camera traps and photo analysis are very time-consuming.

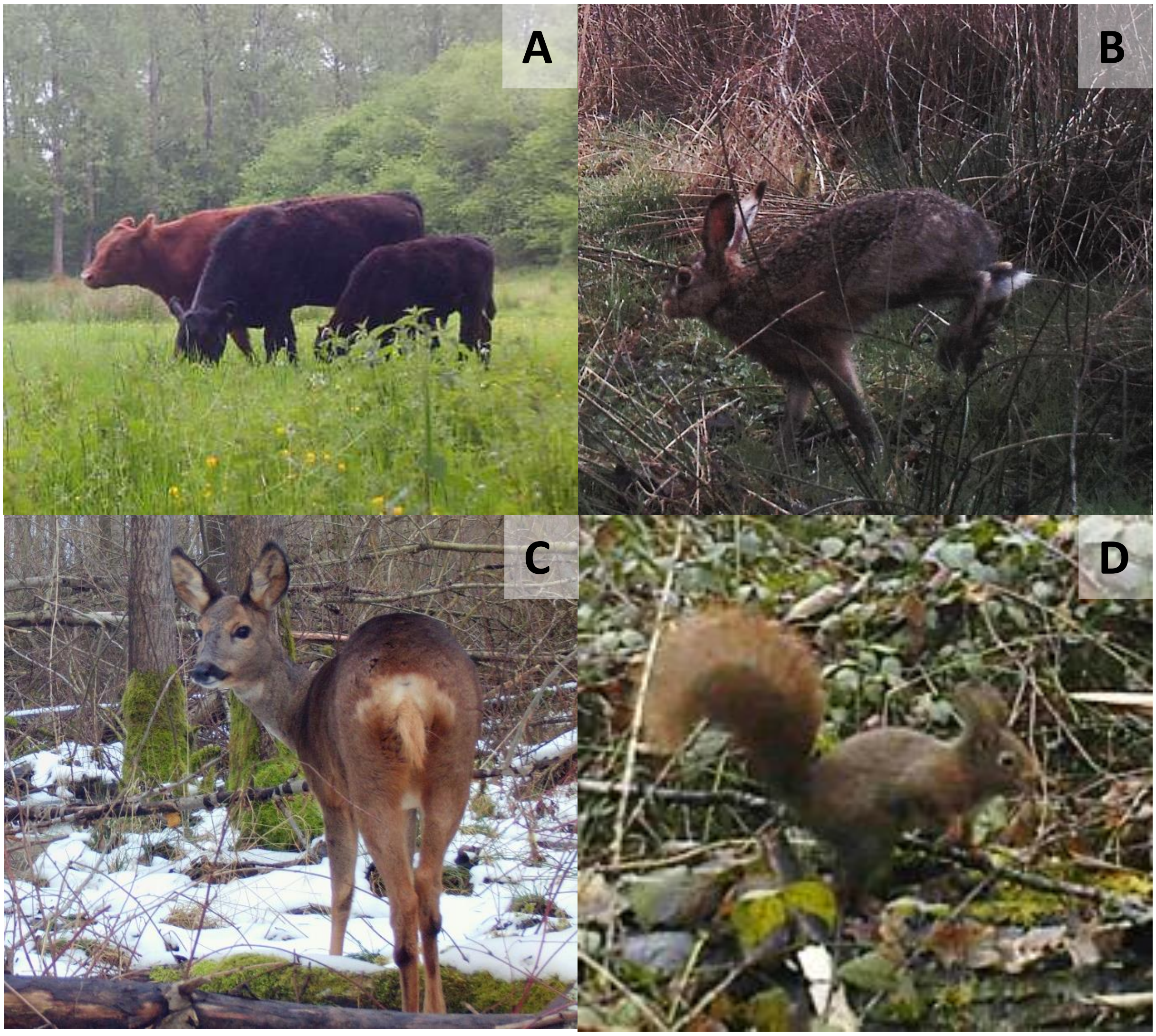

Figure 40 – Examples of other herbivores that are not included in this research but do affect the vegetation in Het Groene Woud. Black Aberdeen cattle **(A)**, Hare **(B)**, Roe deer **(C)**, Red squirrel **(D)**.

4.5 Implications for rewilding practices

Rewilding practices can take place in all kinds of environments, but a type of environment that has been getting more and more attention regarding this subject, is abandoned European farmland. Estimates show that between 2000 and 2030, 20 million ha of land may be disengaged from its agricultural use, and be left unattended (Pereira & Navarro, 2015). These areas are often wood-pastures, with high ecological value. However, without the disturbance of cattle or other large herbivores, succession turns these half-open landscapes into dense forests, losing the heterogeneity that is associated with a high species richness (Navarro et al., 2015). This land abandonment is thus often accompanied with various socioeconomic and ecological problems (Helmer et al., 2015). Rewilding Europe is an organisation that works to bring back megafauna to these areas, providing a habitat for these species and maintaining the ecological value of areas (Helmer et al., 2015). When implementing such new methods of nature conservation, it is important to keep monitoring whether the intended results are being achieved, and how nature, society and economy interact with each other (Jepson, 2016).

As a wood-pasture system in which rewilding with large herbivores takes place, the red deer reserve in Het Groene Woud can function as an example for these other rewilding practices. It can show, for example, how vegetation changes in a nutrient-rich area with herbivores, how different animal species interact with each other, and how rewilding projects are received when they take place in a highly populated area. Together with earlier studies in this area (e.g. Allen, 2019; Dekker & Houben, 2018; Tielemans, 2017), this thesis adds to the knowledge on rewilding with red deer and can function as an example on how to research herbivore-plant interactions on a large scale.

5. Conclusion

In the Dutch national landscape Het Groene Woud, rewilding is used to increase the ecological value of the area. By reintroducing red deer, together with roe deer and cattle, ARK Nature and Het Brabants Landschap aim to create more vegetation structure in the forests and grasslands, and to increase the graduality of the transition zones between the vegetation types. In this research, I studied how woody recruitment and vegetation structure in Het Groene Woud could be linked to area use by red deer. The results provide indications of an effect of red deer on woody recruitment, and show how the deer seem to affect different tree species in different ways. Little evidence was found to support the idea that red deer increase woody vegetation structure. Especially in grasslands, woody vegetation was barely present. However, as vegetation structure is not made up of mere woody vegetation, and as these processes might only be observable over a longer amount of time, additional research is needed in which other vegetation groups are included.

Rewilding with large herbivores in wood-pastures is of increasing interest, but knowledge on the interaction between red deer and their environment is scarce, and often very location-specific. The findings of this study contribute to the literature on red deer in nutrient-rich, temperate areas. To further investigate the effect of red deer on woody recruitment and vegetation structure, a large-scaled study using grazing exclosures is recommended. However, this research can be used as an example on how to monitor and study red deer in a nature area, with minimal interference.

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Appendix A – Research plots and their locations

Table A1 – Overview of the research plots and their location. Coordinates are given in Dutch Grid (Rijksdriehoek coordinates), and mark the southwest corner of the plot. The location indicates whether the plot lies in the old or the new area. The habitat type in which the plot lies is given as well.

PlotNr	X (Easting)	Y (Northing)	Location	Birch - Scots pine	Bramble -Alder	Grassland	Norway spruce	Oak - Hazel - Alder	Oak - Poplar-Hazel	Poplar -Hazel - Alder
1	154568	395364	Old			x				
2	154447	395379	Old					x		
3	154253	395176	Old				x			
4	154057	394057	Old						x	
5	154054	393989	Old			x				
6	154371	393711	Old					x		
7	154375	393383	Old					x		
8	154715	395033	Old						x	
9	154852	394643	Old			x				
10	155002	394221	Old			x				
11	154747	394263	Old						x	
12	154221	394259	Old			x				
13	154081	394472	Old						x	
14	153936	393914	Old						x	
15	154561	395161	Old						x	
16	154898	394850	Old							x
17	153906	393593	Old			x				
18	154193	393989	Old			x				
19	154342	393605	Old			x				
20	154357	393545	Old				x			
21	154019	395061	Old			x				
22	154022	395255	Old				x			
23	154116	395386	Old					x		
24	154035	395457	Old							x
25	153910	395568	Old					x		
26	153954	395413	Old					x		
27	153966	395273	Old					x		
28	154316	395158	Old				x			
29	154430	395314	Old					x		
30	154385	395268	Old		x					
31	154429	395159	Old		x					
32	154524	395201	Old		x					
33	155168	394344	Old							x
34	154670	394011	Old				x			
35	154908	394063	Old				x			

36	154828	394203	Old				x			
37	155207	394809	Old			x				
38	155239	394617	Old							x
39	155043	394594	Old							x
40	154083	395016	Old		x					
41	154694	394775	Old		x					
42	154763	394621	Old		x					
43	154492	394556	Old						x	
44	154412	394703	Old						x	
45	154209	394914	Old				x			
46	154595	393778	Old							x
47	154735	393454	Old					x		
48	154652	393490	Old				x			
49	154358	393400	Old		x					
50	154438	393430	Old				x			
51	153999	393795	Old					x		
52	154044	393744	Old		x					
53	154152	393918	Old		x					
54	154243	393947	Old							x
55	154528	393943	Old		x					
56	154343	393837	Old							x
57	154311	394196	Old							x
58	153930	394853	Old							x
59	153513	394457	Old						x	
60	153876	394007	Old						x	
61	152839	394290	New	x						
62	152773	394353	New	x						
63	152922	394440	New	x						
64	153029	394545	New		x					
65	152844	394504	New			x				
66	152581	394832	New	x						
67	152669	394935	New					x		
68	153044	395406	New					x		
69	153146	395253	New		x					
70	153391	395248	New							x
71	153268	395136	New							x
72	153295	394965	New	x						
73	153397	394999	New			x				
74	153559	394984	New						x	
75	153622	395087	New						x	
76	153735	395247	New		x					
77	153802	395120	New					x		
78	153762	395016	New						x	
79	153500	394858	New			x				
80	153328	394636	New							x

Appendix B – Recording dates camera traps and vegetation survey

Table B1 – Dates at which the plot was recorded through a vegetation survey, and the start and end dates at which the plot was recorded with a camera trap. Plots 41 & 42 were not recorded with a camera trap, due to weather conditions.

Plot No.	Date vegetation survey	Start date camera trap	End date camera trap
1	2021-04-20	2021-02-19	2021-03-11
2	2021-04-01	2021-02-19	2021-03-11
3	2021-03-08	2021-03-11	2021-04-01
4	2021-04-07	2021-02-22	2021-03-15
5	2021-03-03	2021-02-02	2021-02-22
6	2021-04-22	2021-04-07	2021-04-28
7	2021-02-25	2021-02-01	2021-02-24
8	2021-04-09	2021-01-29	2021-02-19
9	2021-03-30	2021-01-29	2021-02-19
10	2021-03-18	2021-02-01	2021-02-20
11	2021-03-19	2021-02-20	2021-03-11
12	2021-04-07	2021-01-30	2021-02-22
13	2021-03-24	2021-03-15	2021-04-08
14	2021-04-13	2021-01-30	2021-02-22
15	2021-03-08	2021-01-28	2021-02-19
16	2021-03-30	2021-02-19	2021-03-15
17	2021-03-01	2021-02-02	2021-02-22
18	2021-04-22	2021-02-22	2021-03-16
19	2021-02-26	2021-03-16	2021-03-28
20	2021-04-22	2021-02-24	2021-03-16
21	2021-04-21	2021-04-01	2021-04-22
22	2021-04-21	2021-03-11	2021-04-01
23	2021-04-09	2021-03-11	2021-04-01
24	2021-03-19	2021-01-28	2021-02-19
25	2021-03-30	2021-01-28	2021-02-19
26	2021-04-21	2021-02-19	2021-03-11
27	2021-03-22	2021-01-28	2021-02-19
28	2021-04-26	2021-02-19	2021-03-11
29	2021-04-20	2021-01-28	2021-02-19
30	2021-04-01	2021-03-11	2021-04-01
31	2021-03-22	2021-02-19	2021-03-11
32	2021-03-08	2021-02-19	2021-03-11
33	2021-04-01	2021-03-15	2021-04-06
34	2021-04-09	2021-02-01	2021-02-20
35	2021-04-01	2021-04-06	2021-04-26
36	2021-04-20	2021-02-20	2021-03-15

37	2021-04-26	2021-02-20	2021-03-15
38	2021-03-18	2021-01-29	2021-02-20
39	2021-04-26	2021-01-29	2021-02-20
40	2021-04-21	2021-03-11	2021-04-01
41	2021-04-26		
42	2021-04-20		
43	2021-04-22	2021-03-15	2021-04-06
44	2021-04-21	2021-03-11	2021-04-06
45	2021-04-09	2021-03-11	2021-04-01
46	2021-04-19	2021-03-16	2021-04-06
47	2021-04-13	2021-03-16	2021-04-07
48	2021-04-30	2021-02-24	2021-03-16
49	2021-02-25	2021-02-24	2021-03-16
50	2021-02-26	2021-02-01	2021-02-24
51	2021-03-03	2021-03-16	2021-04-07
52	2021-04-30	2021-02-02	2021-02-22
53	2021-03-24	2021-02-02	2021-02-22
54	2021-04-07	2021-02-22	2021-03-16
55	2021-04-13	2021-03-16	2021-04-06
56	2021-03-01	2021-03-16	2021-04-07
57	2021-04-22	2021-01-30	2021-02-22
58	2021-03-25	2021-03-16	2021-04-08
59	2021-04-30	2021-02-22	2021-03-16
60	2021-03-04	2021-01-30	2021-02-22
61	2021-04-30	2021-02-16	2021-03-10
62	2021-03-05	2021-01-26	2021-02-16
63	2021-03-25	2021-01-26	2021-02-16
64	2021-04-08	2021-02-16	2021-03-10
65	2021-03-25	2021-03-10	2021-03-31
66	2021-04-19	2021-03-10	2021-03-31
67	2021-03-04	2021-03-10	2021-03-31
68	2021-03-31	2021-03-10	2021-03-31
69	2021-03-05	2021-01-27	2021-02-16
70	2021-04-08	2021-02-16	2021-03-10
71	2021-03-31	2021-03-10	2021-03-31
72	2021-04-08	2021-01-27	2021-02-10
73	2021-04-08	2021-03-10	2021-03-31
74	2021-03-31	2021-03-16	2021-04-08
75	2021-04-19	2021-02-16	2021-03-10
76	2021-04-19	2021-02-16	2021-03-10
77	2021-04-14	2021-01-27	2021-02-16
78	2021-03-05	2021-01-27	2021-02-16
79	2021-04-14	2021-02-22	2021-03-16
80	2021-04-14	2021-02-22	2021-03-16

Appendix C – Vegetation survey

Table C1 – Overview of all variables recorded in the field survey. Data on the following functional groups (f.g.) was collected: (1.Trees, 2. Bramble, 3. Other shrubs, 4. Common rush, 5. Other graminoids, 6. Nettle, 7. Other forbs, 8. Ferns, 9. Mosses, 10. Bare soil).

Scale	Variable	Unit	Method
20m x 20m plot	Aerial cover herb layer	%	Visual estimation
	Aerial cover shrub layer	%	Visual estimation
	Average height herb layer	cm	Measuring 6 samples
	Average height shrub layer	cm	Measuring 6 samples
	Aerial cover bramble, common rush & nettle (separately)	%	Visual estimation
	Average height bramble, common rush & nettle (separately)	cm	Measuring 6 samples
	Aerial cover dead wood	%	Visual estimation
	# Standing deadwood	-	Count
	# Lying deadwood	-	Count
	Tree species > 150 cm	-	Determination
	# Tree species individuals > 150 cm	-	Count
	Height trees > 150 cm	cm	Visual estimation (stick method)
	DBH trees > 150 cm	cm	Measuring tape
	Debarking/browsing trees > 150 cm	-	Visual assessment
Circle (r=2) within plot	# Tree species individuals	-	Count
	Height trees < 150 cm	cm	Measuring pole
	DBH trees > 150 cm	cm	Measuring tape
	Aerial cover f.g. 2-10	%	Visual estimation
	Height f.g. 2-9	cm	Drop-disc method 4 samples
	Coefficient of variation height f.g. 1-9	%	Calculate from measured height
Quadrant within circle	Browsing occurrence f.g. 2-9	-	Visual assessment

Fieldwork form

Date	Plot number	Plot description	Coordinates	Observer

	Plot Cover (%)	Sample height (cm)					
Herbaceous layer							
Forb/Herb							
Grass							
Shrub layer							
Bramble							
Common rush							

Deadwood		
Plot cover (%)	# standing	# lying (over 50x50x100 cm)

Trees above 1.50m in 20x20m plot			
Species	Height (m)	Diameter (cm, DBH)	Signs of debarking (yes/no)

5 circles, 2m radius within the 20x20m plot. 4 quadrants within each circle.

Circle 1

Functional group	Cover (%)				Drop-disc height (cm)				Browsing? (Y/N)			
	NE	SE	SW	NW	NE	SE	SW	NW	NE	SE	SW	NW
Bramble												
Other shrubs												
Common rush												
Other graminoids												
Nettle												
Other forbs												
Ferns												
Mosses												
Bare Soil												

Circle 2

Functional group	Cover (%)				Drop-disc height (cm)				Browsing? (Y/N)			
	NE	SE	SW	NW	NE	SE	SW	NW	NE	SE	SW	NW
Bramble												
Other shrubs												
Common rush												
Other graminoids												
Nettle												
Other forbs												
Ferns												
Mosses												
Bare Soil												

Circle 3

Functional group	Cover (%)				Drop-disc height (cm)				Browsing? (Y/N)			
	NE	SE	SW	NW	NE	SE	SW	NW	NE	SE	SW	NW
Bramble												
Other shrubs												
Common rush												
Other graminoids												
Nettle												
Other forbs												
Ferns												
Mosses												
Bare Soil												

Circle 4

Functional group	Cover (%)				Drop-disc height (cm)				Browsing? (Y/N)			
	NE	SE	SW	NW	NE	SE	SW	NW	NE	SE	SW	NW
Bramble												
Other shrubs												
Common rush												
Other graminoids												
Nettle												
Other forbs												
Ferns												
Mosses												
Bare Soil												

Circle 5

Functional group	Cover (%)				Drop-disc height (cm)				Browsing? (Y/N)			
	NE	SE	SW	NW	NE	SE	SW	NW	NE	SE	SW	NW
Bramble												
Other shrubs												
Common rush												
Other graminoids												
Nettle												
Other forbs												
Ferns												
Mosses												
Bare Soil												

Trees below 1.50 m within the 5 circles				
Circle No.	Species	Height (cm)	Browsing? (Y/N)	Debarking (Y/N)

Appendix D Statistical results

In this appendix, I present an overview of the results of the statistical test. In tables D1-3, I present the results of the linear models. In tables D4-D6, I present the post-hoc results that I refer to in chapter 3.

Table D1 – Statistical results from the generalized linear models used to compare woody recruitment in the old and new area. Significant relationships ($p \leq 0.05$) are marked green, insignificant relationship ($p > 0.05$) are marked red. In the case of a significant interaction between predictors, significant main effects of individual predictors are not shown. See table 5 for the definitions of all variables.

Model	Model type	Predictor(s)	*p*-value	X^2-value
Saplings ~ Location	Quasi-Poisson	Location	1.00	3.70*10 -06
Saplings ~ Location * HC	Poisson, with outliers	Location:HC	< 0.001	35.63
	Poisson, without outliers	Location:HC	< 0.001	15.93
Saplings ~ Location * HC * Habitat	Quasi-Poisson	Location:Habitat	< 0.001	21.60
		HC:Habitat	0.25	7.88
		Location:HC	0.48	1.46
		Location:HC:Habitat	0.95	1.69
Saplings ~ Location * HC * RPU	Quasi-Poisson	HC	< 0.001	26.94
		Location	0.80	0.06
		RPU	0.26	1.28
		Location:HC	0.55	1.21
		HC:RPU	0.90	0.21
		Location:RPU	0.96	0.00
		Location:HC:RPU	0.93	0.16
Saplings ~ Location * HC * Deadwood	Quasi-Poisson	HC	< 0.001	32.02
		Deadwood	0.02	5.52
		Location	0.44	0.59
		Location:HC	0.66	0.83
		Location:Deadwood	0.77	0.09
		HC:Deadwood	0.81	0.43
		Location:HC:Deadwood	0.93	0.14
Saplings ~ Location * HC * Species	Quasi-Poisson	HC	< 0.001	71.78
		Species	< 0.001	287.26
		Location	0.23	1.45
		Location:HC	0.31	2.37
		Location:Species	0.24	7.99
		HC:Species	0.32	13.67
		Location:HC:Species	0.97	4.64

Table D2 – Statistical results from the general linear models used to compare woody recruitment in 2019 and 2021. Significant relationships (p ≤ 0.05) are marked green, insignificant relationship (p > 0.05) are marked red. In the case of a significant interaction between predictors, significant main effects of individual predictors are not shown. See table 5 for the definitions of all variables.

Model	Model type	Predictor(s)	*p*-value	F –value
Individuals ~ Year * Stage	Linear	Year	< 0.001	26.72
		Stage	0.97	0.00
		Year * Stage	0.46	0.56
ChangeTrees ~ RPU * Stage	Linear	RPU	< 0.01	8.37
		Stage	0.61	0.25
		RPU * Stage	0.31	1.03
ChangeSaplings ~ HC * RPU	Linear	HC * RPU	0.02	3.97
ChangeSaplings ~ HC * Habitat	Linear	Habitat	< 0.001	7.80
		HC	0.90	0.11
		HC*Habitat	0.20	1.36
ChangeSaplings ~ HC * RPU.Cat * Deadwood	Linear	HC * RPU.Cat	0.02	3.03
		Deadwood	0.32	1.00
		HC * Deadwood	0.94	0.06
		RPU.Cat * Deadwood	0.26	1.35
		HC * RPU.Cat * Deadwood	0.70	0.55
ChangeAlder ~ HC * RPU	Linear	HC	0.23	1.47
		RPU	0.53	0.39
		HC*RPU	0.72	0.34
ChangeBirch ~ HC * RPU	Linear	HC	0.52	0.66
		RPU	0.24	1.40
		HC*RPU	0.21	1.58
ChangeBirdCh ~ HC * RPU	Linear	HC	< 0.01	4.79
		RPU	0.01	6.70
		HC*RPU	0.27	1.31
ChangeHazel ~ HC * RPU	Linear	HC	< 0.01	5.18
		RPU	0.70	0.15
		HC*RPU	0.75	0.29
ChangeOak ~ HC * RPU	Linear	HC * RPU	< 0.001	44.6
ChangePoplar ~ HC * RPU	Linear	RPU	0.04	4.27
		HC	0.49	0.71
		HC*RPU	0.61	0.50
ChangeRowan ~ HC * RPU	Linear	RPU	0.09	2.37
		HC	0.61	0.26
		HC*RPU	0.43	0.84

Table D3 – Pairwise comparison of the means subquestion 1. The comparisons were done using Tukey's method with the *emmeans* package, version 1.6.1 (Lenth et al., 2020). In the Comparison column, brackets clarify the names of the habitat types. The difference in mean is estimated by subtracting the second category from the first category, as stated in the Comparison column.

Figure in thesis	Model	Comparison	Estimated difference in mean	SE	t ratio	p value
Figure 15	Sapling ~ Location	(Bramble-Alder) - Grassland	-0.13218658	0.06095788	-2.1684905	0.261454
		(Bramble-Alder) - (Oak-Hazel-Alder)	-0.19808993	0.06095788	-3.2496199	0.01891122
		(Bramble-Alder) - (Oak-Poplar-Hazel)	-0.012336	0.05971371	-0.2065858	0.99994674
		(Bramble-Alder) - (Poplar-Hazel-Alder)	-0.03208341	0.06244487	-0.5137877	0.99553757
		(Bramble-Alder) - Spruce	-0.0497308	0.06095788	-0.8158223	0.96402324
		Grassland - (Oak-Hazel-Alder)	-0.06590335	0.05747164	-1.1467109	0.8605348
		Grassland - (Oak-Poplar-Hazel)	0.11985058	0.05615028	2.1344611	0.27802243
		Grassland - (Poplar-Hazel-Alder)	0.10010317	0.0590465	1.6953279	0.53798359
		Grassland - Spruce	0.08245578	0.05747164	1.4347213	0.70586759
		(Oak-Hazel-Alder) - (Oak-Poplar-Hazel)	0.18575393	0.05615028	3.3081571	0.0158709
		(Oak-Hazel-Alder) - (Poplar-Hazel-Alder)	0.16600653	0.0590465	2.8114543	0.06351683
		(Oak-Hazel-Alder) - Spruce	0.14835914	0.05747164	2.5814322	0.11111786
		(Oak-Poplar-Hazel) - (Poplar-Hazel-Alder)	-0.0197474	0.05776117	-0.3418803	0.99936668
		(Oak-Poplar-Hazel) - Spruce	-0.03739479	0.05615028	-0.665977	0.98524655
		(Poplar-Hazel-Alder) - Spruce	-0.01764739	0.0590465	-0.2988727	0.99967146

Table D4 – Pairwise comparison of the means subquestion 2, comparison old and new area. The comparisons were done using Tukey's method with the *emmeans* package, version 1.6.1 (Lenth et al., 2020). In the Comparison column, the numbers "1", "2", and "3" depict the different height classes of saplings: height class 1 includes saplings <50 cm, height class 2 includes saplings of 51-100 cm, and height class 3 includes saplings of 101-150 cm. Also in the Comparison column, brackets clarify the names of the habitat types. The difference in mean is estimated by subtracting the second category from the first category, as stated in the Comparison column.

Figure in thesis	Model	Comparison	Estimated difference in mean	SE	t ratio	P value
Figure 20A	Sapling ~HC * Location WITH OUTLIERS	1 New - 2 New	0.667306	0.12425387	5.370504	1.17E-06
		1 New - 3 New	1.2449403	0.15302531	8.135519	7.87E-14
		1 New - 1 Old	-0.2889901	0.08104488	-3.565803	4.88E-03
		1 New - 2 Old	1.0529684	0.10167101	10.356625	5.52E-14
		1 New - 3 Old	1.8884318	0.13038273	14.483757	0.00E+00
		2 New - 3 New	0.5776343	0.16848105	3.428482	7.99E-03
		2 New - 1 Old	-0.9562961	0.10741225	-8.903045	4.32E-14
		2 New - 2 Old	0.3856625	0.12371787	3.117274	2.25E-02
		2 New - 3 Old	1.2211259	0.14821867	8.238678	7.12E-14
		3 New - 1 Old	-1.5339304	0.1396965	-10.980449	4.93E-14
		3 New - 2 Old	-0.1919718	0.15259041	-1.258086	8.08E-01
		3 New - 3 Old	0.6434916	0.17305056	3.718518	2.75E-03

		1 Old - 2 Old	1.3419585	0.0802207	16.728332	0.00E+00
		1 Old - 3 Old	2.177422	0.1144466	19.025659	0.00E+00
		2 Old - 3 Old	0.8354634	0.12987203	6.432974	1.88E-09
Figure 20B	**Sapling ~HC * Location WITHOUT OUTLIERS**	1 New - 2 New	0.397301798	0.20194904	1.967336944	3.61E-01
		1 New - 3 New	0.852777326	0.23421056	3.64107121	3.69E-03
		1 New - 1 Old	-0.972556587	0.13524313	-7.191171643	9.68E-12
		1 New - 2 Old	0.016529302	0.14661246	0.112741456	1.00E+00
		1 New - 3 Old	0.851992705	0.16780309	5.077336263	5.69E-06
		2 New - 3 New	0.455475529	0.25070232	1.816798202	4.55E-01
		2 New - 1 Old	-1.369858385	0.16213505	-8.448872795	5.90E-14
		2 New - 2 Old	-0.380772496	0.17173317	-2.217233271	2.30E-01
		2 New - 3 Old	0.454690907	0.19014454	2.391290945	1.59E-01
		3 New - 1 Old	-1.825333914	0.20089536	-9.085993257	7.69E-14
		3 New - 2 Old	-0.836248024	0.2087186	-4.00658119	8.72E-04
		3 New - 3 Old	-0.000784622	0.22411184	-0.003501026	1.00E+00
		1 Old - 2 Old	0.989085889	0.08366345	11.82219756	0.00E+00
		1 Old - 3 Old	1.824549292	0.11688557	15.60970493	0.00E+00
		2 Old - 3 Old	0.835463403	0.12987203	6.432973947	1.88E-09
Figure 24	**Sapling * HC * Species * Location**	Alder - Birch	-8.4430024	568.5393174	-0.01485034	1.00E+00
		Alder - Bird cherry	-10.5953549	568.5392157	-0.018636102	1.00E+00
		Alder - Hazel	-8.024101	568.5393855	-0.014113536	1.00E+00
		Alder - Oak	3.1738419	826.0684215	0.003842105	1.00E+00
		Alder - Poplar	-2.0464508	733.981194	-0.002788152	1.00E+00
		Alder - Rowan	-8.9656671	568.5393939	-0.01576965	1.00E+00
		Birch - Bird cherry	-2.1523526	0.3803114	-5.659448551	3.18E-07
		Birch - Hazel	0.4189014	0.5811767	0.720781382	9.91E-01
		Birch - Oak	11.6168442	599.2932019	0.019384242	1.00E+00
		Birch - Poplar	6.3965516	464.2108335	0.01377941	1.00E+00
		Birch - Rowan	-0.5226647	0.58935	-0.886849471	9.75E-01
		Bird cherry - Hazel	2.5712539	0.471306	5.455593623	1.02E-06
		Bird cherry - Oak	13.7691968	599.2931054	0.02297573	1.00E+00
		Bird cherry - Poplar	8.5489041	464.210709	0.018415999	1.00E+00
		Bird cherry - Rowan	1.6296879	0.4813484	3.385671888	1.26E-02
		Hazel - Oak	11.1979429	599.2932666	0.018685247	1.00E+00
		Hazel - Poplar	5.9776502	464.210917	0.012877013	1.00E+00
		Hazel - Rowan	-0.9415661	0.6517867	-1.444592202	7.77E-01
		Oak - Poplar	-5.2202926	758.0526232	-0.006886452	1.00E+00
		Oak - Rowan	-12.1395089	599.2932746	-0.020256374	1.00E+00
		Poplar - Rowan	-6.9192163	464.2109273	-0.014905328	1.00E+00
Figure 22	**Sapling ~HC * Habitat**	(1 Bramble-Alder New) - (3 Poplar-Hazel-Alder Old)	-1.47E+01	1481.979384	-9.95E-03	1
		(2 Bramble-Alder New) - (3 Bramble-Alder New)	-2.88E-01	2.5336199	-1.14E-01	1

		(2 Bramble-Alder New) - (1 Oak-Hazel-Alder New)	-3.78E+00	1.9370427	-1.95E+00	0.95948824
		(2 Bramble-Alder New) - (2 Oak-Hazel-Alder New)	-2.23E+00	2.0152284	-1.11E+00	0.99999138
		(2 Bramble-Alder New) - (3 Oak-Hazel-Alder New)	-1.47E+00	2.1247642	-6.90E-01	0.999999999
		(2 Bramble-Alder New) - (1 Oak-Poplar-Hazel New)	-2.44E+00	2.0363161	-1.20E+00	0.999964498
		(2 Bramble-Alder New) - (2 Oak-Poplar-Hazel New)	-3.04E+00	1.9824582	-1.54E+00	0.998066616
		(2 Bramble-Alder New) - (3 Oak-Poplar-Hazel New)	-2.56E+00	2.0227153	-1.27E+00	0.999907098
		(2 Bramble-Alder New) - (1 Poplar-Hazel-Alder New)	4.97E-14	2.5336199	1.96E-14	1
		(2 Bramble-Alder New) - (2 Poplar-Hazel-Alder New)	-5.60E-01	2.2891456	-2.44E-01	1
		(2 Bramble-Alder New) - (3 Poplar-Hazel-Alder New)	-4.05E-01	2.3456762	-1.73E-01	1
		(2 Bramble-Alder New) - (1 Bramble-Alder Old)	-2.20E+00	1.9468956	-1.13E+00	0.999988019
		(2 Bramble-Alder New) - (2 Bramble-Alder Old)	-1.28E+00	1.9934415	-6.43E-01	1
		(2 Bramble-Alder New) - (3 Bramble-Alder Old)	-3.36E-01	2.110488	-1.59E-01	1
		(2 Bramble-Alder New) - (1 Oak-Hazel-Alder Old)	-2.24E+00	1.9455589	-1.15E+00	0.999982725
		(2 Bramble-Alder New) - (2 Oak-Hazel-Alder Old)	-5.31E-01	2.0773658	-2.55E-01	1
		(2 Bramble-Alder New) - (3 Oak-Hazel-Alder Old)	6.93E-01	2.422604	2.86E-01	1
		(2 Bramble-Alder New) - (1 Oak-Poplar-Hazel Old)	-2.54E+00	1.9356482	-1.31E+00	0.999830828
		(2 Bramble-Alder New) - (2 Oak-Poplar-Hazel Old)	-1.78E+00	1.9589358	-9.07E-01	0.999999812
		(2 Bramble-Alder New) - (3 Oak-Poplar-Hazel Old)	-1.10E+00	2.0003994	-5.49E-01	1
		(2 Bramble-Alder New) - (1 Poplar-Hazel-Alder Old)	-2.64E+00	1.9379029	-1.36E+00	0.999696757
		(2 Bramble-Alder New) - (2 Poplar-Hazel-Alder Old)	-1.67E+00	1.9741807	-8.48E-01	0.999999951
		(2 Bramble-Alder New) - (3 Poplar-Hazel-Alder Old)	-4.42E-01	2.110488	-2.09E-01	1
		(3 Bramble-Alder New) - (1 Oak-Hazel-Alder New)	-3.49E+00	1.683776	-2.07E+00	0.924777713
		(3 Bramble-Alder New) - (2 Oak-Hazel-Alder New)	-1.95E+00	1.7731645	-1.10E+00	0.999992812
		(3 Bramble-Alder New) - (3 Oak-Hazel-Alder New)	-1.18E+00	1.8967315	-6.21E-01	1
		(3 Bramble-Alder New) - (1 Oak-Poplar-Hazel New)	-2.15E+00	1.797095	-1.20E+00	0.999964717
		(3 Bramble-Alder New) - (2 Oak-Poplar-Hazel New)	-2.76E+00	1.7358306	-1.59E+00	0.996867409
		(3 Bramble-Alder New) - (3 Oak-Poplar-Hazel New)	-2.28E+00	1.781669	-1.28E+00	0.999893743
		(3 Bramble-Alder New) - (1 Poplar-Hazel-Alder New)	2.88E-01	2.3456762	1.23E-01	1
		(3 Bramble-Alder New) - (2 Poplar-Hazel-Alder New)	-2.72E-01	2.0792197	-1.31E-01	1
		(3 Bramble-Alder New) - (3 Poplar-Hazel-Alder New)	-1.18E-01	2.1412996	-5.50E-02	1
		(3 Bramble-Alder New) - (1 Bramble-Alder Old)	-1.91E+00	1.6951016	-1.13E+00	0.999988412
		(3 Bramble-Alder New) - (2 Bramble-Alder Old)	-9.93E-01	1.7483638	-5.68E-01	1
		(3 Bramble-Alder New) - (3 Bramble-Alder Old)	-4.88E-02	1.880725	-2.59E-02	1
		(3 Bramble-Alder New) - (1 Oak-Hazel-Alder Old)	-1.95E+00	1.6935662	-1.15E+00	0.999982318

		(3 Bramble-Alder New) - (2 Oak-Hazel-Alder Old)	-2.43E-01	1.8434792	-1.32E-01	1
		(3 Bramble-Alder New) - (3 Oak-Hazel-Alder Old)	9.81E-01	2.2253038	4.41E-01	1
		(3 Bramble-Alder New) - (1 Oak-Poplar-Hazel Old)	-2.26E+00	1.6821716	-1.34E+00	0.999763486
		(3 Bramble-Alder New) - (2 Oak-Poplar-Hazel Old)	-1.49E+00	1.7089169	-8.71E-01	0.999999915
		(3 Bramble-Alder New) - (3 Oak-Poplar-Hazel Old)	-8.11E-01	1.756293	-4.62E-01	1
		(3 Bramble-Alder New) - (1 Poplar-Hazel-Alder Old)	-2.35E+00	1.6847655	-1.40E+00	0.999550505
		(3 Bramble-Alder New) - (2 Poplar-Hazel-Alder Old)	-1.39E+00	1.726371	-8.03E-01	0.999999984
		(3 Bramble-Alder New) - (3 Poplar-Hazel-Alder Old)	-1.54E-01	1.880725	-8.20E-02	1
		(1 Oak-Hazel-Alder New) - (2 Oak-Hazel-Alder New)	1.54E+00	0.6906642	2.23E+00	0.853313604
		(1 Oak-Hazel-Alder New) - (3 Oak-Hazel-Alder New)	2.31E+00	0.9646216	2.39E+00	0.753513684
		(1 Oak-Hazel-Alder New) - (1 Oak-Poplar-Hazel New)	1.33E+00	0.7499699	1.78E+00	0.98591754
		(1 Oak-Hazel-Alder New) - (2 Oak-Poplar-Hazel New)	7.32E-01	0.5882282	1.24E+00	0.999932559
		(1 Oak-Hazel-Alder New) - (3 Oak-Poplar-Hazel New)	1.21E+00	0.7122141	1.70E+00	0.992020975
		(1 Oak-Hazel-Alder New) - (1 Poplar-Hazel-Alder New)	3.78E+00	1.683776	2.24E+00	0.848534567
		(1 Oak-Hazel-Alder New) - (2 Poplar-Hazel-Alder New)	3.22E+00	1.2868797	2.50E+00	0.676253155
		(1 Oak-Hazel-Alder New) - (3 Poplar-Hazel-Alder New)	3.37E+00	1.3849436	2.43E+00	0.725576022
		(1 Oak-Hazel-Alder New) - (1 Bramble-Alder Old)	1.58E+00	0.454174	3.48E+00	0.083361723
		(1 Oak-Hazel-Alder New) - (2 Bramble-Alder Old)	2.50E+00	0.624244	4.00E+00	0.013648186
		(1 Oak-Hazel-Alder New) - (3 Bramble-Alder Old)	3.44E+00	0.9327546	3.69E+00	0.042128596
		(1 Oak-Hazel-Alder New) - (1 Oak-Hazel-Alder Old)	1.54E+00	0.4484094	3.43E+00	0.097629874
		(1 Oak-Hazel-Alder New) - (2 Oak-Hazel-Alder Old)	3.25E+00	0.8551727	3.80E+00	0.028946015
		(1 Oak-Hazel-Alder New) - (3 Oak-Hazel-Alder Old)	4.47E+00	1.5115825	2.96E+00	0.322300884
		(1 Oak-Hazel-Alder New) - (1 Oak-Poplar-Hazel Old)	1.23E+00	0.4032441	3.06E+00	0.258480106
		(1 Oak-Hazel-Alder New) - (2 Oak-Poplar-Hazel Old)	2.00E+00	0.5032905	3.97E+00	0.014958894
		(1 Oak-Hazel-Alder New) - (3 Oak-Poplar-Hazel Old)	2.68E+00	0.6461188	4.14E+00	0.007626997
		(1 Oak-Hazel-Alder New) - (1 Poplar-Hazel-Alder Old)	1.14E+00	0.4139317	2.75E+00	0.477617025
		(1 Oak-Hazel-Alder New) - (2 Poplar-Hazel-Alder Old)	2.10E+00	0.5596974	3.76E+00	0.03323161
		(1 Oak-Hazel-Alder New) - (3 Poplar-Hazel-Alder Old)	3.33E+00	0.9327546	3.58E+00	0.061285148
		(2 Oak-Hazel-Alder New) - (3 Oak-Hazel-Alder New)	7.67E-01	1.113331	6.89E-01	0.999999999
		(2 Oak-Hazel-Alder New) - (1 Oak-Poplar-Hazel New)	-2.09E-01	0.9335234	-2.24E-01	1
		(2 Oak-Hazel-Alder New) - (2 Oak-Poplar-Hazel New)	-8.11E-01	0.8093352	-1.00E+00	0.999998694
		(2 Oak-Hazel-Alder New) - (3 Oak-Poplar-Hazel New)	-3.31E-01	0.9034711	-3.67E-01	1
		(2 Oak-Hazel-Alder New) - (1 Poplar-Hazel-Alder New)	2.23E+00	1.7731645	1.26E+00	0.999917044
		(2 Oak-Hazel-Alder New) - (2 Poplar-Hazel-Alder New)	1.67E+00	1.4018097	1.19E+00	0.999967128

		(2 Oak-Hazel-Alder New) - (3 Poplar-Hazel-Alder New)	1.83E+00	1.4923403	1.23E+00	0.999948665
		(2 Oak-Hazel-Alder New) - (1 Bramble-Alder Old)	3.64E-02	0.7178336	5.07E-02	1
		(2 Oak-Hazel-Alder New) - (2 Bramble-Alder Old)	9.53E-01	0.8358778	1.14E+00	0.999985692
		(2 Oak-Hazel-Alder New) - (3 Bramble-Alder Old)	1.90E+00	1.0858371	1.75E+00	0.988764643
		(2 Oak-Hazel-Alder New) - (1 Oak-Hazel-Alder Old)	-7.12E-03	0.7142003	-9.97E-03	1
		(2 Oak-Hazel-Alder New) - (2 Oak-Hazel-Alder Old)	1.70E+00	1.0199663	1.67E+00	0.993771621
		(2 Oak-Hazel-Alder New) - (3 Oak-Hazel-Alder Old)	2.93E+00	1.6105567	1.82E+00	0.981774059
		(2 Oak-Hazel-Alder New) - (1 Oak-Poplar-Hazel Old)	-3.10E-01	0.6867437	-4.52E-01	1
		(2 Oak-Hazel-Alder New) - (2 Oak-Poplar-Hazel Old)	4.57E-01	0.7498749	6.10E-01	1
		(2 Oak-Hazel-Alder New) - (3 Oak-Poplar-Hazel Old)	1.13E+00	0.8523383	1.33E+00	0.999789652
		(2 Oak-Hazel-Alder New) - (1 Poplar-Hazel-Alder Old)	-4.05E-01	0.6930732	-5.85E-01	1
		(2 Oak-Hazel-Alder New) - (2 Poplar-Hazel-Alder Old)	5.60E-01	0.7888424	7.09E-01	0.999999999
		(2 Oak-Hazel-Alder New) - (3 Poplar-Hazel-Alder Old)	1.79E+00	1.0858371	1.65E+00	0.994682502
		(3 Oak-Hazel-Alder New) - (1 Oak-Poplar-Hazel New)	-9.76E-01	1.151062	-8.48E-01	0.999999951
		(3 Oak-Hazel-Alder New) - (2 Oak-Poplar-Hazel New)	-1.58E+00	1.0528538	-1.50E+00	0.998648573
		(3 Oak-Hazel-Alder New) - (3 Oak-Poplar-Hazel New)	-1.10E+00	1.1268264	-9.75E-01	0.999999227
		(3 Oak-Hazel-Alder New) - (1 Poplar-Hazel-Alder New)	1.47E+00	1.8967315	7.73E-01	0.999999993
		(3 Oak-Hazel-Alder New) - (2 Poplar-Hazel-Alder New)	9.07E-01	1.5551682	5.83E-01	1
		(3 Oak-Hazel-Alder New) - (3 Poplar-Hazel-Alder New)	1.06E+00	1.6372408	6.48E-01	1
		(3 Oak-Hazel-Alder New) - (1 Bramble-Alder Old)	-7.31E-01	0.9842575	-7.43E-01	0.999999997
		(3 Oak-Hazel-Alder New) - (2 Bramble-Alder Old)	1.85E-01	1.0733916	1.73E-01	1
		(3 Oak-Hazel-Alder New) - (3 Bramble-Alder Old)	1.13E+00	1.277701	8.84E-01	0.999999886
		(3 Oak-Hazel-Alder New) - (1 Oak-Hazel-Alder Old)	-7.74E-01	0.9816108	-7.89E-01	0.999999989
		(3 Oak-Hazel-Alder New) - (2 Oak-Hazel-Alder Old)	9.36E-01	1.2222148	7.66E-01	0.999999994
		(3 Oak-Hazel-Alder New) - (3 Oak-Hazel-Alder Old)	2.16E+00	1.745672	1.24E+00	0.999939199
		(3 Oak-Hazel-Alder New) - (1 Oak-Poplar-Hazel Old)	-1.08E+00	0.9618184	-1.12E+00	0.999989539
		(3 Oak-Hazel-Alder New) - (2 Oak-Poplar-Hazel Old)	-3.10E-01	1.0078642	-3.08E-01	1
		(3 Oak-Hazel-Alder New) - (3 Oak-Poplar-Hazel Old)	3.68E-01	1.0862589	3.39E-01	1
		(3 Oak-Hazel-Alder New) - (1 Poplar-Hazel-Alder Old)	-1.17E+00	0.9663479	-1.21E+00	0.9999564
		(3 Oak-Hazel-Alder New) - (2 Poplar-Hazel-Alder Old)	-2.08E-01	1.0371837	-2.00E-01	1
		(3 Oak-Hazel-Alder New) - (3 Poplar-Hazel-Alder Old)	1.02E+00	1.277701	8.02E-01	0.999999984
		(1 Oak-Poplar-Hazel New) - (2 Oak-Poplar-Hazel New)	-6.02E-01	0.8605006	-7.00E-01	0.999999999
		(1 Oak-Poplar-Hazel New) - (3 Oak-Poplar-Hazel New)	-1.23E-01	0.9495777	-1.29E-01	1
		(1 Oak-Poplar-Hazel New) - (1 Poplar-Hazel-Alder New)	2.44E+00	1.797095	1.36E+00	0.999706547

		(1 Oak-Poplar-Hazel New) - (2 Poplar-Hazel-Alder New)	1.88E+00	1.4319596	1.31E+00	0.999829465
		(1 Oak-Poplar-Hazel New) - (3 Poplar-Hazel-Alder New)	2.04E+00	1.5206964	1.34E+00	0.999768407
		(1 Oak-Poplar-Hazel New) - (1 Bramble-Alder Old)	2.45E-01	0.7750632	3.16E-01	1
		(1 Oak-Poplar-Hazel New) - (2 Bramble-Alder Old)	1.16E+00	0.8855109	1.31E+00	0.999836266
		(1 Oak-Poplar-Hazel New) - (3 Bramble-Alder Old)	2.11E+00	1.124491	1.87E+00	0.974075041
		(1 Oak-Poplar-Hazel New) - (1 Oak-Hazel-Alder Old)	2.02E-01	0.7716994	2.61E-01	1
		(1 Oak-Poplar-Hazel New) - (2 Oak-Hazel-Alder Old)	1.91E+00	1.0610227	1.80E+00	0.983555291
		(1 Oak-Poplar-Hazel New) - (3 Oak-Hazel-Alder Old)	3.14E+00	1.6368661	1.92E+00	0.966571417
		(1 Oak-Poplar-Hazel New) - (1 Oak-Poplar-Hazel Old)	-1.01E-01	0.746361	-1.36E-01	1
		(1 Oak-Poplar-Hazel New) - (2 Oak-Poplar-Hazel Old)	6.66E-01	0.8048293	8.27E-01	0.99999997
		(1 Oak-Poplar-Hazel New) - (3 Oak-Poplar-Hazel Old)	1.34E+00	0.9010651	1.49E+00	0.998748733
		(1 Oak-Poplar-Hazel New) - (1 Poplar-Hazel-Alder Old)	-1.97E-01	0.752189	-2.62E-01	1
		(1 Oak-Poplar-Hazel New) - (2 Poplar-Hazel-Alder Old)	7.68E-01	0.8412551	9.13E-01	0.999999784
		(1 Oak-Poplar-Hazel New) - (3 Poplar-Hazel-Alder Old)	2.00E+00	1.124491	1.78E+00	0.985919052
		(2 Oak-Poplar-Hazel New) - (3 Oak-Poplar-Hazel New)	4.80E-01	0.8278015	5.79E-01	1
		(2 Oak-Poplar-Hazel New) - (1 Poplar-Hazel-Alder New)	3.04E+00	1.7358306	1.75E+00	0.988202912
		(2 Oak-Poplar-Hazel New) - (2 Poplar-Hazel-Alder New)	2.48E+00	1.3542768	1.83E+00	0.979556702
		(2 Oak-Poplar-Hazel New) - (3 Poplar-Hazel-Alder New)	2.64E+00	1.4477828	1.82E+00	0.981091245
		(2 Oak-Poplar-Hazel New) - (1 Bramble-Alder Old)	8.47E-01	0.6199036	1.37E+00	0.999678221
		(2 Oak-Poplar-Hazel New) - (2 Bramble-Alder Old)	1.76E+00	0.7534501	2.34E+00	0.790094918
		(2 Oak-Poplar-Hazel New) - (3 Bramble-Alder Old)	2.71E+00	1.023737	2.65E+00	0.560434642
		(2 Oak-Poplar-Hazel New) - (1 Oak-Hazel-Alder Old)	8.04E-01	0.6156926	1.31E+00	0.999848355
		(2 Oak-Poplar-Hazel New) - (2 Oak-Hazel-Alder Old)	2.51E+00	0.9535862	2.64E+00	0.567729811
		(2 Oak-Poplar-Hazel New) - (3 Oak-Hazel-Alder Old)	3.74E+00	1.5693591	2.38E+00	0.762737551
		(2 Oak-Poplar-Hazel New) - (1 Oak-Poplar-Hazel Old)	5.01E-01	0.5836199	8.58E-01	0.999999938
		(2 Oak-Poplar-Hazel New) - (2 Oak-Poplar-Hazel Old)	1.27E+00	0.6567402	1.93E+00	0.963532806
		(2 Oak-Poplar-Hazel New) - (3 Oak-Poplar-Hazel Old)	1.95E+00	0.7716708	2.52E+00	0.65929236

Table D4 – Pairwise comparison of the means subquestion 2, comparing 2019 and 2021. The comparisons were done using Tukey's method with the *emmeans* package, version 1.6.1 (Lenth et al., 2020). Significant differences ($p \leq 0.05$) are marked in green, insignificant differences ($p > 0.05$) are marked in red. In the Comparison column, the numbers "1", "2", and "3" depict the different height classes of saplings: height class 1 includes saplings <50 cm, height class 2 includes saplings of 51-100 cm, and height class 3 includes saplings of 101-150 cm. Also in the Comparison column, brackets clarify the names of the habitat types. The difference in mean is estimated by subtracting the second category from the first category, as stated in the Comparison column.

Figure in thesis	Model	Comparison	Estimated difference in means	SE	t ratio	p value
Figure 27	Change ~ HC * RPU	1 - 2	-58.079242	24.69931	-2.3514524	0.05165196
		1 - 3	-62.263954	24.69931	-2.5208787	0.03363752
		2 - 3	-4.184712	24.69931	-0.1694263	0.98430095
Figure 28	Change ~ HC * Habitat	(Bramble-Alder) - Grassland	-1.458333	4.961265	-0.2939439	0.99970047
		(Bramble-Alder) - (Oak-Hazel-Alder)	8.275	4.961265	1.6679214	0.55501561
		(Bramble-Alder) - (Oak-Poplar-Hazel)	-2.518939	4.860004	-0.5182999	0.99539448
		(Bramble-Alder) - (Poplar-Hazel-Alder)	-4.013889	5.082289	-0.7897797	0.96891231
		(Bramble-Alder) - Spruce	-6.691667	4.961265	-1.3487824	0.75721024
		Grassland - (Oak-Hazel-Alder)	9.733333	4.677525	2.0808724	0.30271292
		Grassland - (Oak-Poplar-Hazel)	-1.060606	4.569982	-0.232081	0.99990638
		Grassland - (Poplar-Hazel-Alder)	-2.555556	4.8057	-0.5317759	0.99480519
		Grassland - Spruce	-5.233333	4.677525	-1.1188252	0.87296381
		(Oak-Hazel-Alder) - (Oak-Poplar-Hazel)	-10.793939	4.569982	-2.3619218	0.17631682
		(Oak-Hazel-Alder) - (Poplar-Hazel-Alder)	-12.288889	4.8057	-2.5571483	0.11436262
		(Oak-Hazel-Alder) - Spruce	-14.966667	4.677525	-3.1996976	0.02032604
		(Oak-Poplar-Hazel) - (Poplar-Hazel-Alder)	-1.494949	4.70109	-0.3180006	0.99955984
		(Oak-Poplar-Hazel) - Spruce	-4.172727	4.569982	-0.9130731	0.94268154
		(Poplar-Hazel-Alder) - Spruce	-2.677778	4.8057	-0.5572086	0.99353927

Table D5– Pairwise comparison of the means subquestion 3. The comparisons were done using Tukey's method with the *emmeans* package, version 1.6.1 (Lenth et al., 2020). Significant differences ($p \leq 0.05$) are marked in green, insignificant differences ($p > 0.05$) are marked in red.

Figure in thesis	Model	Comparison	Estimated difference in means	SE	t ratio	p value
Figure 31A	Bramble Height ~ Year	2017 - 2019	15.871667	6.381481	2.4871448	0.03659579
		2017 - 2021	14.2757	6.381481	2.2370513	0.06781785
		2019 - 2021	-1.595967	6.381481	-0.2500935	0.96611489