Trophic rewilding with red deer in Het Groene Woud, the Netherlands

Photo: Diana Parkhouse, Unsplash

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Abstract

The aim of this study was to investigate what vegetation changes have occurred in the 300 ha red deer enclosure of Het Groene Woud, the Netherlands, and if these changes in vegetation can attributed to area usage by red deer. This is a quantitative study which hopes to add to the current body of literature concerning rewilding, much of which consists of qualitative research. This study conducted fieldwork in which vegetation functional groups, mature trees and saplings up to 1.5m within the enclosure were measured in summer 2019. The fieldwork data was combined with GPS data from deer collars to relate the field layer and saplings with deer intensity of use. The vegetation change within the area between 2017 and 2019 was also analysed using data from a winter 2016/17 study of the area prior to red deer reintroduction. I found that deer intensity of use was lower in areas with more deadwood, that the amount of debarking of mature trees increased in areas of high deer intensity of use, and that bramble height was lower in areas of high deer intensity of use. Most other vegetation functional groups showed no relationship to deer intensity; forb height showed some showed a trend towards a relationship with deer intensity of use, however extensive further research is needed to eliminate any seasonal effects between the 2017 and 2019 studies. Saplings numbers were highest in areas of low and high deer intensity of use, and also showed some response to other vegetation structure parameters, such as the amount of lying deadwood.

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1. Introduction

The creation of protected natural landscapes and the abandonment of the fringes of agricultural land provides a unique opportunity for ecological restoration. This restoration may take many forms, for instance reforestation or the reconnection of habitats, and also the reintroduction of key species into an ecosystem. Rewilding is a branch of conservation biology which attempts to restore trophic interactions as a core of ecosystem functioning (Corlett, 2016). In trophic rewilding, species are deliberately reintroduced to restore their top-down trophic effects and induce trophic cascades in order to enable self-regulating, biodiverse ecosystems (Svenning et al, 2016). As the awareness of the increasing pressure we put on our ecosystems has become increasingly apparent in the last decade, more rewilding projects have been carried out (Perino et al, 2019).

One of the most well-known rewilding projects is the reintroduction of grey wolves (*Canis lupus*) back into Yellowstone National Park. In 1995 and 1996, 31 wolves were reintroduced after a 70-year absence from the park. Through the local extinction of wolves in the park, the trophic cascade was disrupted; without a top predator, elk (*Cervus canadensis*) numbers grew and they were able to intensely browse on plant species in certain habitats. This affected other animal species at lower trophic levels and caused soil degradation (which is linked to ecological processes such as nutrient cycling (Hunter et al, 2018)). The reintroduction of wolves meant that the elk population was regulated through predation, and therefore plant populations within parts of the landscape were able to recover due to decreased levels of herbivory (Ripple & Beschta, 2012). Many early rewilding projects focused on the role of large carnivores, however many modern-day projects also focus on the role of megafaunal herbivores, such as red deer. The reintroduction of herbivores is as important as the reintroduction of carnivores as herbivores are also able to shape landscapes. Through reducing the encroachment of woody species, a more diverse ecosystem and self-regulating trophic interactions can emerge from a more open landscape which is maintained by large herbivores (Cromsigt et al, 2018).

Due to historic and present-day interactions between humans and the environment (such as urbanisation, agriculture and hunting), many megafaunal species which fulfil a role within the ecosystem have become increasingly rare, or went (locally) extinct. If one (or more) megafaunal species is removed from an ecosystem, the lower trophic levels may be directly influenced; removal of a large carnivore species can lead to increases in their main prey, which could lead to cascading effects on the main plant food items of that prey (Ripple & Beschta, 2012). Through the removal of one or more species, and as the trophic cascade is disrupted, an ecosystem can become less resilient; it can no longer bounce back from perturbations and the desired ecosystem state may be lost (Elmqvist et al, 2003). Trophic cascades are a common theoretical framework used when constructing and analysing rewilding projects (Svenning et al, 2016); a trophic cascade refers to the interactions that occur over multiple trophic levels of an ecosystem (the levels within a food web) which, by extension, influence the properties and dynamics of the system (Pace et al, 1999).

The interaction of fauna with an ecosystem or trophic cascade also has an effect on the vegetation and landscape. The 'wood-pasture hypothesis' (Vera, 2000, p.85, p.102; Birks, 2005) states that mosaics of grasslands, regenerating shrubs and forests forming an open landscape are maintained by large grazing herbivores at the end of the Last Glacial Period. According to this hypothesis, initial gaps are created in the canopy through disturbances such as wind or insects, and these gaps are maintained by grazers, which as a result form a more open landscape. In this more open landscape shrub land is able to form, this provides an area in which tree seedlings and saplings can grow successfully and develop into new forest (Vera, 2000; Birks, 2005).

In the face of climate change, experimental restoration efforts are needed (Perino et al, 2019) which are flexible, protect biodiversity and consider the landscape. A project has been established in Het Groene Woud, in the Dutch province of Noord-Brabant, in which a small group of red deer (*Cervus elaphus*) have been reintroduced to the area to aid habitat restoration, namely maintaining the openness of the former agricultural landscape and creating more gradual forest boundaries (figure 1). This study shall examine the impact of this rewilding project. By the 1950s red deer had almost completely disappeared from the Dutch landscape, but protective laws and rewilding projects have seen their numbers rise in recent years. It is hypothesised that deer maintain an open landscape through grazing, browsing and particular behaviours (mud rolling, trampling and sweeping of antlers along trees), both of which create gradual forest boundaries in which other mammals and insects can also thrive (Svenning, 2002; Fenton, 2008; Dekker & Houben, 2018).

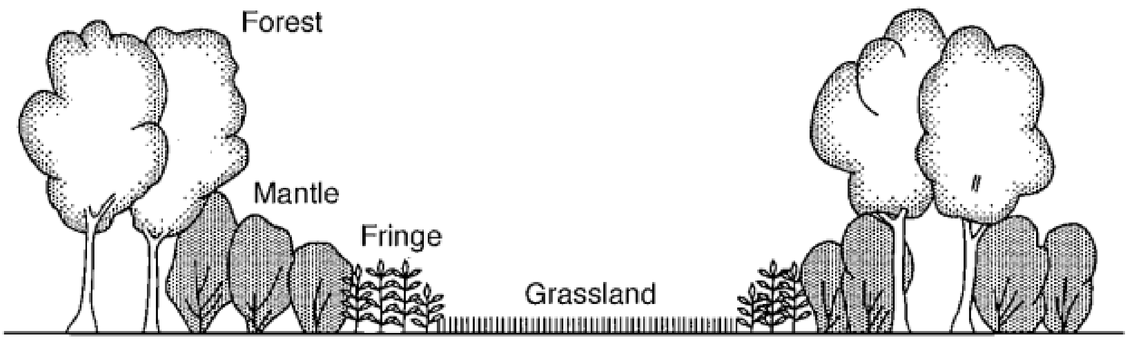

Figure 1. Schematic example of a gradual forest boundary, in which grasslands, fringe and mantle vegetation and forest create a gradual stepped boundary. This differs to a traditional agricultural landscape where meadows/grasslands are edged with a sharp treeline. In more gradual boundaries, more plant species are able to grow and can therefore support other animal species (depending on the ecosystem in place). *Source: Vera, 2000, p.87*

We propose the following research questions:

How is the vegetation structure in the Groene Woud deer enclosure linked to area usage by red deer? What changes can be observed in the vegetation structure since 2017?

Sub-question 1: How has the vegetation structure, namely the %cover and height of shrubs and herbaceous plants changed in the area since the reintroduction of deer in 2017?

Sub-question 2: How is the deer intensity of use and area usage linked to the abundance and height of tree saplings?

By answering this research question, it is hoped that a contribution can be made to the body of empirical studies that exist concerning the topic of rewilding. At present there are many opinion articles and essays which exist on the topic of rewilding, but more scientific, empirical studies are needed (Svenning et al, 2016). By conducting an empirical study in Het Groene Woud we hope to contribute to this body of knowledge which can then be used to understand rewilding as an ecological conservation method and potentially to help the planning of other, self-sustaining, rewilding projects.

This study also has a significant societal relevance. The United Nations (UN) General Assembly has designated the years between 2021 and 2030 as the “decade of ecological restoration” in an effort to combat climate change and ecosystem degradation, and also to promote food and water security (UN environment, 2019). By restoring ecosystems, we can create a more resilient socio-ecological system and the material and non-material ecosystem services on which we rely can be re-established. Considering the large-scale deforestation occurring for beef farming in Brazil (World Wildlife Fund, 2019a), and in South East Asia for palm oil (World Wildlife Fund, 2019b), present-day mass-extinction of many species and the imminent threat of climate change (Centre for Biological Diversity, 2019), rewilding projects are of high importance. This initiative by the UN encourages policy-makers to consider the importance of the environment in their decision making and in achieving the UN Sustainable Development Goals (UN Sustainable Development, 2019).

2. Methods

2.1 Research area

Het Groene Woud is a 300 ha area between Eindhoven, Tilburg and s' Hertogenbosch (figure 2). Het Groene Woud acts as a greenbelt (Kühn, 2013), preventing urban sprawl of the three cities by protecting a designated nature area of heathland, marsh, fens and forest on loam soils (soil of approximately 40% sand, 40% silt and 20% clay (World Atlas, 2019)). Having a higher amount of clay makes the soil very nutrient rich and therefore popular for agricultural use (Brabant Landschap, 2019). This soil is also ideal for certain plant species which are otherwise disappearing in Brabant such as the cowslip (*Primula veris*), European white elm (*Ulmus laevis*) and wood anemone (*Anemone nemorosa*) among others.

However, the area has been heavily influenced by past human activities. Large drainage ditches are present throughout the area, clear byways and paths run through the Groene Woud deer enclosure and many mature trees are found in neat rows, purposefully planted by humans. There are also some non-native tree species which were purposefully introduced by humans; Norwegian Spruce (*Picea abies*) (Caudullo et al, 2016), Canadian Poplar (*Populus canadensis)* and Canadian Maple (*Acer saccharum*).

In 2017, a herd of 13 red deer (*Cervus elaphus*), consisting of nine hinds and four stags, were released into a 300ha enclosure within de Scheeken part of Het Groene Woud, between the towns of Best and Liempde. These original deer had varied backgrounds to ensure healthy genetic variation; they originated from the Belgian Ardennes, Germany, Croatia and France. It was ensured that they had no elk or wapiti genes (*Cervus canadensis*) (Brabants Landschap 2016). Following introduction, the herd naturally grew and as of September 2019 the herd consisted of six males aged 2-5 years, four males less than 2 years, twelve hinds aged 2-8 years, four hinds aged less than 2 years, and eight calves. The management objective is to allow the size of the deer herd to slowly grow as the area of the enclosure is expanded over time, with a carrying capacity calculated at 15 deer per 100ha (Tielemans, 2017). The area in which the deer were released is secured using fences (which are passable for smaller mammals) and cattle grids, so that the red deer are confined to this area but can move freely within it (figure 3). In addition to the deer, 55 Aberdeen Angus cattle also roam in the same enclosure from spring until autumn, and an undefined number of roe deer also have year-round access to the enclosure (Brabant Landschap 2016, Tielemans, 2017, Dekker & Houben, 2018).

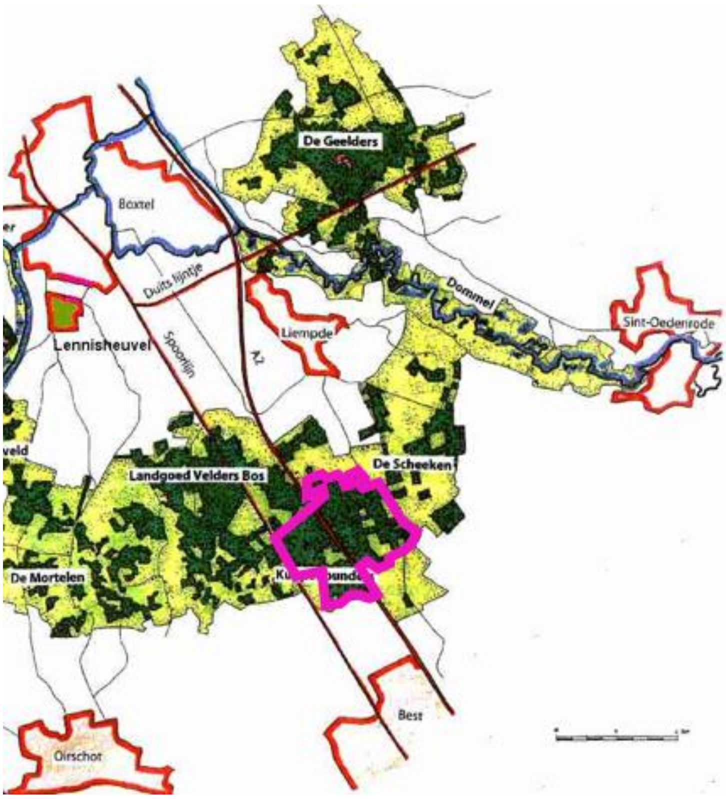

Figure 2. Location of the study area (shown outlined in pink) in relation to the two nearest towns of Boxtel, Liempde and Best. Source: lennisheuvel.nl

Figure 3. Some features of the area which control the extent of the movement of the red deer and other animals. (*A)* Cattle grid to prevent cattle and red deer leaving the enclosure. To the left of the grid is a gate which allows horse riders to pass through. *(B)* Deer gate which allows the smaller roe deer to pass through the area. The dimensions of these gates are 30cm wide by 40cm high. Image from Dekker & Houben, 2018. *(C)* Enclosure fencing. *(D)* The ecoduct over the A2 motorway. Image from: beeldbank.rws.nl (Meander A2 natuurbrug Best ID472848).

These 300 ha straddle the A2 motorway, where the 2 sides are connected by a 50m wide ecoduct (also known as a ‘wildlife crossing’) which is utilised by deer, badgers, beech martens, slow worms, butterflies and the northern crested newt (Dekker & Houben, 2018). In addition to the reintroduction of the red deer, small pools have been created in the area for amphibians, with particular consideration for the tree frog, which was reintroduced in 2011 (Brabants Landschap 2016). There is a planned extension of the deer enclosure which was opened in December 2019 after the completion of a new ecoduct over the railway line (figure 4).

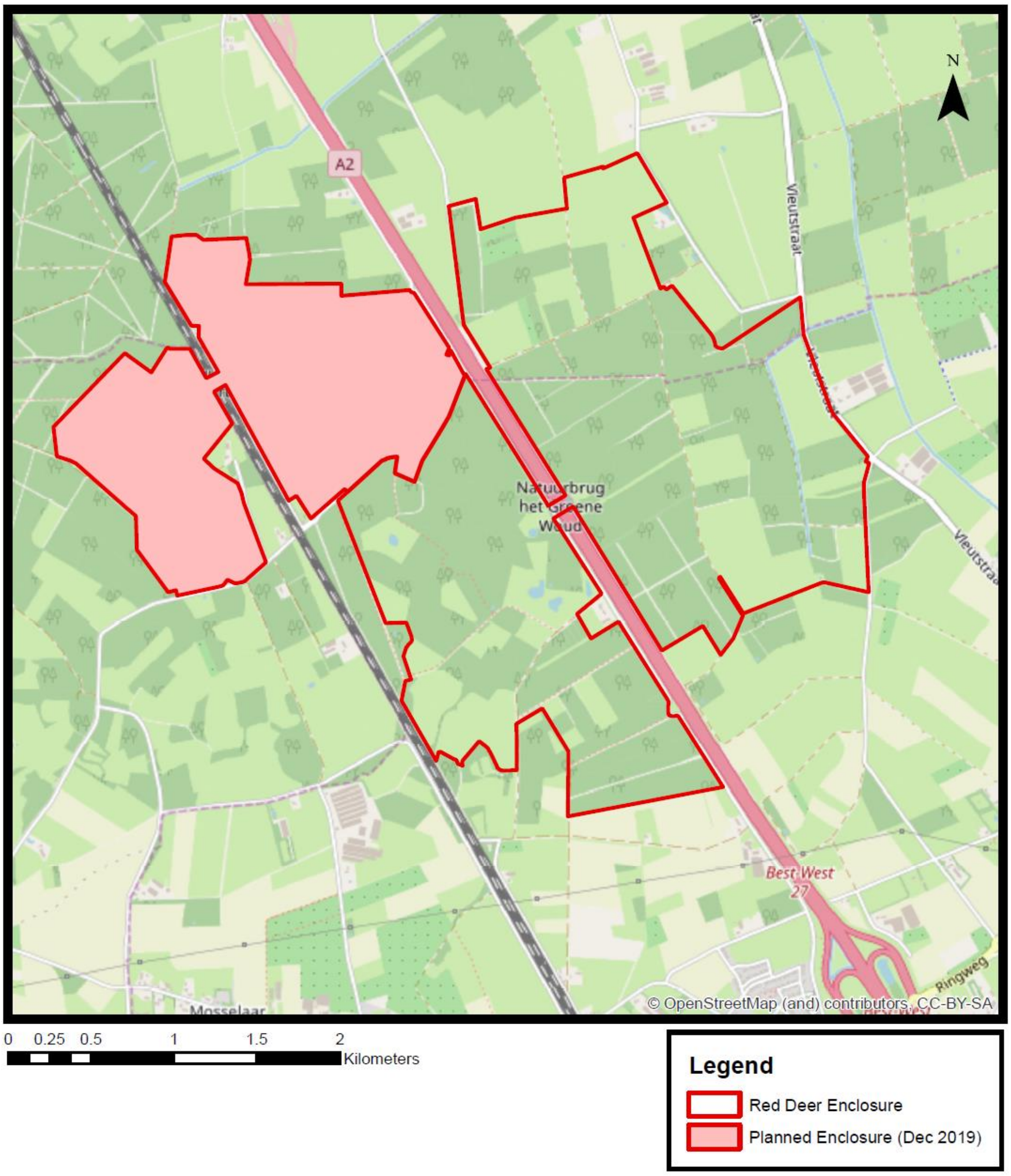

Figure 4. The extent of the present and the planned deer enclosures. At time of writing, Brabants Landschap are discussing the possibility of purchasing additional land to the north-east of the current enclosure.

2.2 Research design

2.2.1 Field survey

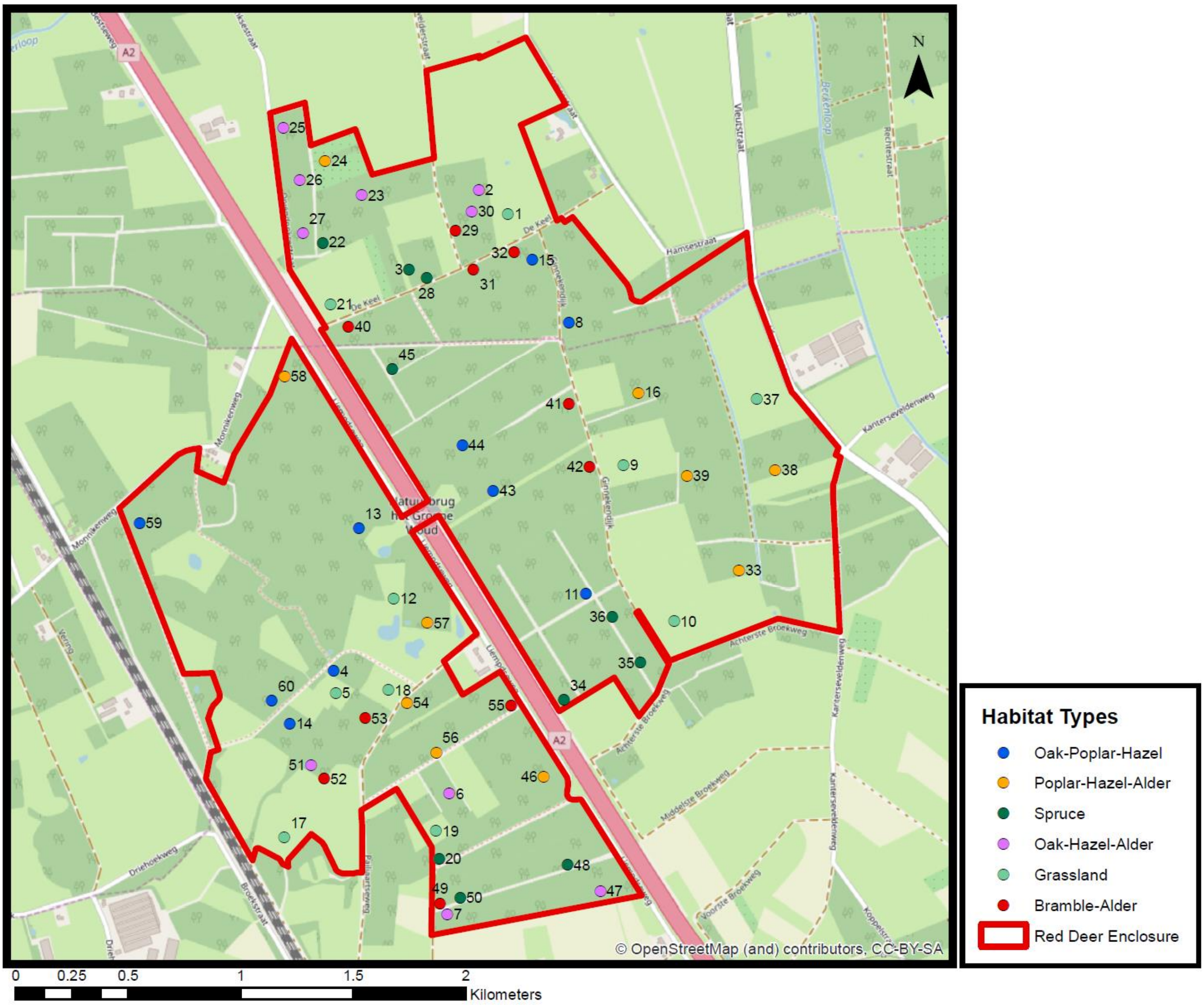

Figure 5. Map showing the location of each plot within the 3km², fenced of area within Het Groene Woud in which the red deer are found. The 6 habitat types are described in the legend. Adapted from Tielemans, 2017

The first step of this research was to re-measure the vegetation structure recorded by Tielemans (2017). I re-measured all plots in July and August 2019. The initial measurements performed by Tielemans were carried out in December and January 2016/17, therefore my measurements (particularly of herbaceous species) will form a new summer baseline. The fieldwork form used to record the data is shown in appendix 1. A full list of the observed plant species is shown in appendix 2 (with the scientific Latin, common English and common Dutch names given). Tielemans laid out and measured 60 plots of 20x20m divided over 6 habitat types (figure 5). The plots were partly distributed via random sampling; once the 6 habitat types were distinguished (table 1), 10 plots were randomly distributed throughout each habitat. Tielemans marked each plot with a pole in the southwest corner and provided GPS coordinates of the location of the pole (Rijksdriehoek/Dutch Grid coordinates). Only two of these poles remained therefore GPS coordinates were used during this study. For the full list of plots, see appendix 4.

Table 1. The size and %cover of the 6 habitat types found in the study area of Het Groene Woud. Adapted from Tielemans, 2017.

Habitat type	**Size (ha)**	**Cover (%)**
Grassland	70.57	27.1
Bramble, alder forest	8.13	3.1
Poplar, hazel, alder forest	55.22	21.2
Oak, hazel, alder forest	19.26	7.4
Oak, poplar, hazel forest	96.72	37.2
European spruce forest	10.41	4
Total	260.3	100

To repeat Tielemans' method, the entire 20x20m plot was considered. Within each plot, the % aerial cover of the herb layer, the shrub layer and the deadwood were estimated. The average height of the herb and shrub layers for the whole plot were also taken through 6 random samples using a tape measure. Tielemans also broke down the herbaceous and shrub layers, stating which species were found in each category and what the % aerial cover of those species was within its respective layer. Tielemans also noted which tree species were observed in the plot and what percentage they formed out of the total number of trees. However, Tielemans considered all shrubs and trees smaller than 10m to be a shrub. For this study all single-stemmed woody species, regardless of size, were considered to be trees. Multiple-stemmed woody plants were classed as shrubs (see appendix 2 for observed shrub and tree species species).

I also recorded additional new data to get a more detailed insight into the impact of red deer on the cover of the field layer and recruitment of trees and shrubs. Within each 20x20m plot, I laid out 5 circles with a 2m radius, each subdivided into 4 quadrants, (figure 6). The circles were made by placing a pole in the central point of the circle. Using a rope, I traced a circle with a 2m radius and poles were placed at the 4 cardinal points to mark the extent of the 4 quadrants. In each plot I measured the trees above and below 150cm separately. For each tree above 150cm within the 20x20m plot, I recorded the species, height (m), diameter (cm, diameter breast height, DBH) and if debarking occurred. DBH was recorded using a measuring stick, height was estimated visually. Trees below 150cm within the 5 circles were also measured. The species of each individual and its height were recorded, and whether it displayed signs of debarking or browsing by red deer. The height was recorded in centimetres using a measuring pole. Furthermore, I also measured the amount of deadwood. I counted the number of standing deadwood individuals within the 20x20m plot, and also the number of lying deadwood individuals with dimensions of over 50cm high x 50cm wide x 100cm long. Lying deadwood of this size and over are considered to be escape impediments for deer because they may block their views and potential escape routes (Kuijper et al, 2013).

I then estimated the % aerial cover and measured the height of 8 functional groups in each quadrant. I also noted if the functional groups displayed evidence of browsing. The functional groups are as follows:

- Brambles
- Graminoids
- Other shrubs
- Common rush
- Forbs
- Mosses
- Ferns
- Bare soil (non-vegetation functional group, height measurement not applicable)

I measured the height of the 7 functional vegetation groups (in centimetres) using the 'drop disc' method (Stewart et al, 2001). A 30cm diameter cardboard disc, through which a measuring stick was placed, was dropped onto the shrub layer. The height at which the disc came to rest relative to the measuring stick was recorded as the height of the layer. The height for each functional group within a circle is the average of the 4 measurements from the quadrants. Height measurements were taken from the centre of the quadrants; if there were no individuals of a group at the centre of the quadrant, the closest individual(s) were measured.

Also note that whilst Tielemans recorded grass and forb cover, the heights of these groups were not specifically recorded. Instead, these were combined to make a single herbaceous layer %cover, the overall height of which was also recorded. I did not compare my woody shrub layer measurements to those of Tielemans (2017) since they used a different definition of a shrub. However, I did compare the height and cover of the bramble layer, which is the most dominant herbaceous shrub species.

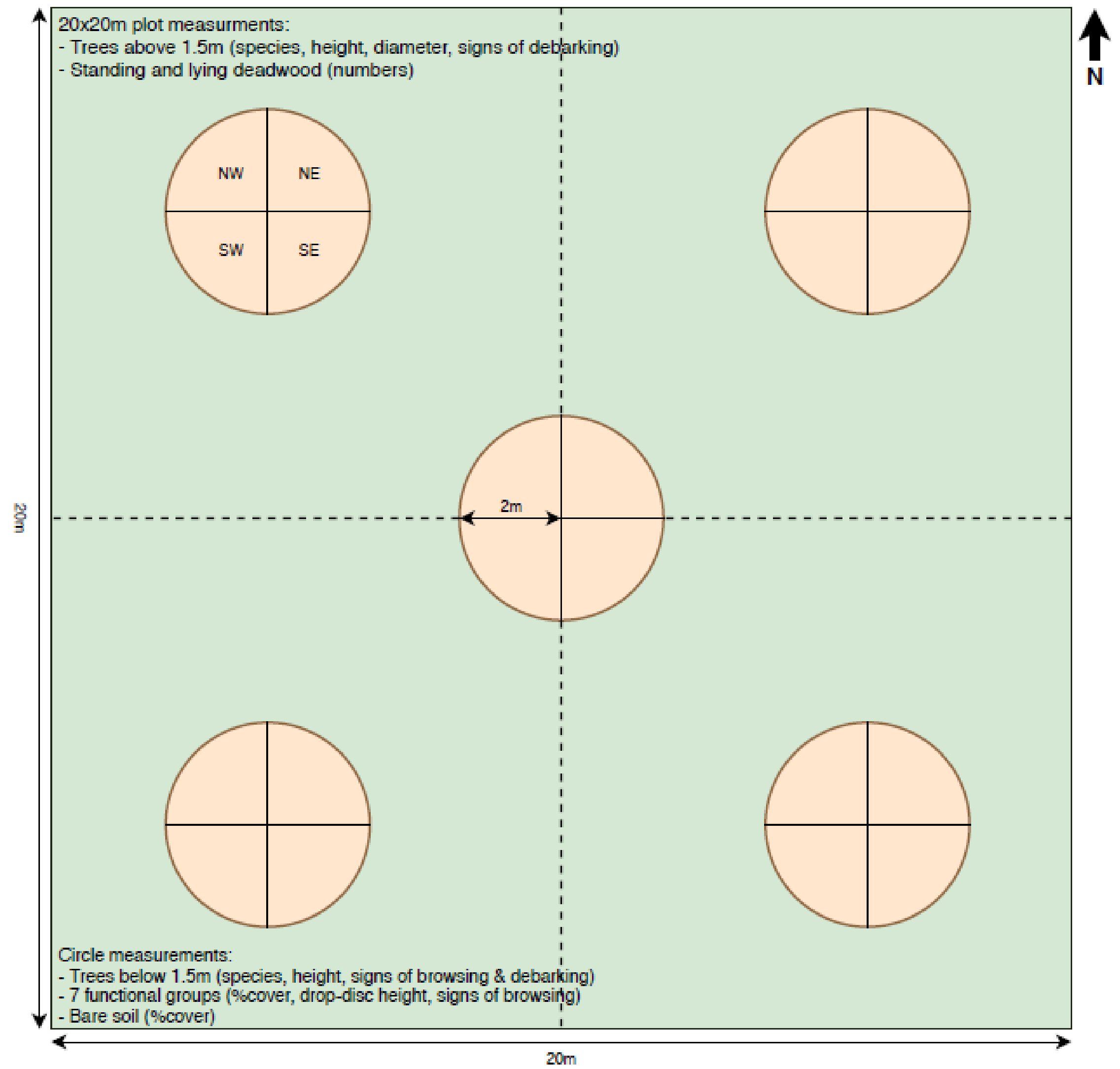

Figure 6. Layout of the 20x20m plot and the locations of the four circles within it, with solid lines marking the boundaries of the quadrants (with the orientations NW, NE, SW and SE). Also noted within the diagram are the tasks performed in the 20x20m plot and in the 5 sample circles.

2.2.2 GPS collar data analysis

In addition to assessing the change in vegetation, I also analysed deer spatial use. When the project started, 4 deer (2 males and 2 females) were released wearing GPS collars (Dekker & Houben, 2018). There was data available from the collars for the period of February 2017 until April 2019, giving a total of 79,029 data points for the study period. Between September 2018 and April 2019, the batteries of the GPS devices started to run out and the collars started falling off the deer. The data from the GPS collars were mapped in ArcGIS.

There were four collars which are as follows:

- 22295 – Hind 1: 20,112 data points from 07/11/2016 until 27/03/2019
- 22296 – Hind 2: 21,758 data points from 07/11/2016 until 03/06/2019
- 22297 – Stag 1: 17,798 data points from 07/11/2016 until 25/09/2018
- 22298 – Stag 2: 19,361 data points from 07/11/2016 until 09/12/2019

The GPS collars were mapped as points on a map. Grid layers of 4 different resolutions (20x20m, 50mx50m, 100mx100m and 200mx200m) for the deer enclosure were then created. For each grid cell that contained a sample plot, the number of GPS points within that grid cell was summed and assigned to the sample plot to give the deer density per plot (plot use density).

The GPS points were summed per grid cell in the following variables:

- All deer collar locations (all year)
- All deer collar locations for summer (1st April - 30th September)
- All deer collar locations for winter (1st October - 31st March)
- Hind locations (all year)
- Hind summer locations (1st April - 30th September)
- Hind winter locations (1st October - 31st March)
- Stag locations (all year)
- Stag summer locations (1st April - 30th September)
- Stag winter locations (1st October - 31st March)

It is important to note that there is less data for stag localities in winter, as both stag collars ended prematurely, running for only one full winter, whilst both hind collars ran for two full winter seasons.

The 20x20m resolution most closely represents the resolution of most modern GPS devices. However, when used to represent the data, many grid cells appeared empty or showed low values (see figure 8 for deer space use maps). In the 20x20m grid, the majority of grid cells represent between 0 and 2 GPS points per cell. Plot use density is severely under-represented in the 20x20m resolution, with at least 22 out of 60 plots having a plot use density of 0. This resolution underperforms particularly when presenting stag movements in winter (due to the lack of data), in which many of the grid cells carried a value of 0. If the GPS collars were worn for a longer duration, or if more individuals were wearing collars, this could be a more appropriate resolution to use.

Conversely, the 200x200m resolution over-inflated the density data, as there were a high number of GPS points per grid cell. Because of the small size of the enclosure and the number of sample plots within it, multiple sample plots fell within one grid cell, therefore this resolution was not able to accurately tell us the plot use densities. The 50x50m and 100x100m grids provided more accurate representations of the deer densities. The data did not appear over- or under-represented. The 50x50m resolution was used to analyse deer density in the statistical analysis as it is closer to the resolution of modern GPS devices whilst also providing a fair representation of deer density throughout the enclosure. The plot use density data was used for statistical analysis.

2.2.3 Combining field data and ArcGIS data

Plot use densities were exported from ArcGIS into Excel. Data from the fieldwork was compiled into a single spreadsheet. All the variables from the fieldwork form were represented in this spreadsheet. The % aerial cover and height (cm) of the 8 functional groups was averaged across the 5 circles (the average of each circle being derived from the combined averages of the 4 quadrants). Additionally, some new categories were calculated in Excel retrospectively at the individual plot scale:

- Browsing of Brambles, Graminoids, Other Shrubs, Forbs and Ferns – This value was derived from the number of circles which display browsing e.g. if 4 of 5 circles showed evidence of browsing on the nettles, Forb Browsing = 80%
- Number of Tree Stems (>1.5m)
- %Trees Debarked (>1.5m)
- Average Height of Trees Debarked (m) (>1.5m)
- Average DBH of Trees Debarked (cm) (>1.5m)
- Number of trees (<50cm, 51-100cm and 101-150cm)
- %Browsed Trees (<50cm, 51-100cm and 101-150cm)
- Number of hazel, rowan, oak, poplar, alder, bird cherry, silver birch individuals in each height class (<50cm, 51-100cm and 101-150cm)

The deer plot use density data from ArcGIS was also input into this spreadsheet. The plot use densities were not normally distributed; the data showed a bias towards lower density. 38 of 60 plots had a maximum plot use density of 15 or fewer GPS points, whilst only 7 plots had maximum plot density of 50 or more points, and 2 plots had a maximum plot density of over 100 GPS points. Therefore, the plot use densities were divided into quartiles to represent four deer intensity of use levels; low (25th quartile), medium-low (50th quartile), medium-high (75th quartile) and high (100th quartile) (table 2). This comprehensive spreadsheet was then imported into SPSS for statistical analysis.

Table 2. Maximum number of GPS points per quartile per deer density variable. Note that all deer density variables had at least one sample plot which had 0 GPS points, therefore the minimum bound for the 25th quartile is 0 in all cases.

		Deer Density Variables								
		All Deer	All Deer Sum	All Deer Win	Hinds	Hinds Sum	Hinds Win	Stags	Stags Sum	Stags Win
Quartile	25th	3	1.25	1	1	0	1	0.25	0	0
	50th	11	4.5	5	8	2	3	2.5	2	1
	75th	24.75	11.75	12.5	15.75	5	10	7	5	2
	100th	176	68	117	150	38	112	46	45	15

2.2.4 Statistical analysis

An ANOVA model was used to evaluate the variation in the means of selected variables across the four intensity of use levels. The nine deer density variables (all of which had been split into the four intensity of use levels) were used as fixed factors (predictors), whilst the following were dependent (response) variables:

a. Bramble height
b. Bramble cover
c. Forb height
d. Forb cover
e. Graminoid height
f. Graminoid cover
g. Bramble browsing
h. Forb browsing
i. Debarking

Additionally, the following variables were tested in a general linear model as predictors, for their effect on deer intensity of use as a response variable:

j. Number of lying deadwood
k. Number of tree stems <1.5m
l. Percentage of bare soil cover

Furthermore, 7 dominant woody species were identified and the estimated marginal means were calculated through a general linear model to inform us how these species are affected across the four deer density levels. LSD post-hoc tests were performed on significant results (those with significant p-values) so that the mean number of individuals from each species could be numerically compared across the deer intensity of use levels. There were not enough data points on an individual species level for these tests to yield reliable results. Therefore, all saplings (regardless of species) were grouped into their height classes and their response to deer intensity of use was tested with an ANOVA model. A linear regression model was also used to briefly investigate if there were any relationships between certain vegetation variables (those which showed a significant relationship with deer intensity of use) and tree saplings. This was performed to investigate whether certain parameters protect saplings from deer herbivory.

3. Results

3.1 ArcGIS maps and deer activity

The GPS collar points were converted into density maps according to the nine density variables at four resolutions (figure 8 and 9). The maps for all collars show that activity is concentrated mainly in the north and west of the enclosure (figure 8). Hind activity is mainly concentrated in the west, however they additionally utilise the south and the north of the enclosure in the winter months (figure 9). Meanwhile, stags gathered mainly in the east and south although they move into the west a little more during the winter season (figure 9).

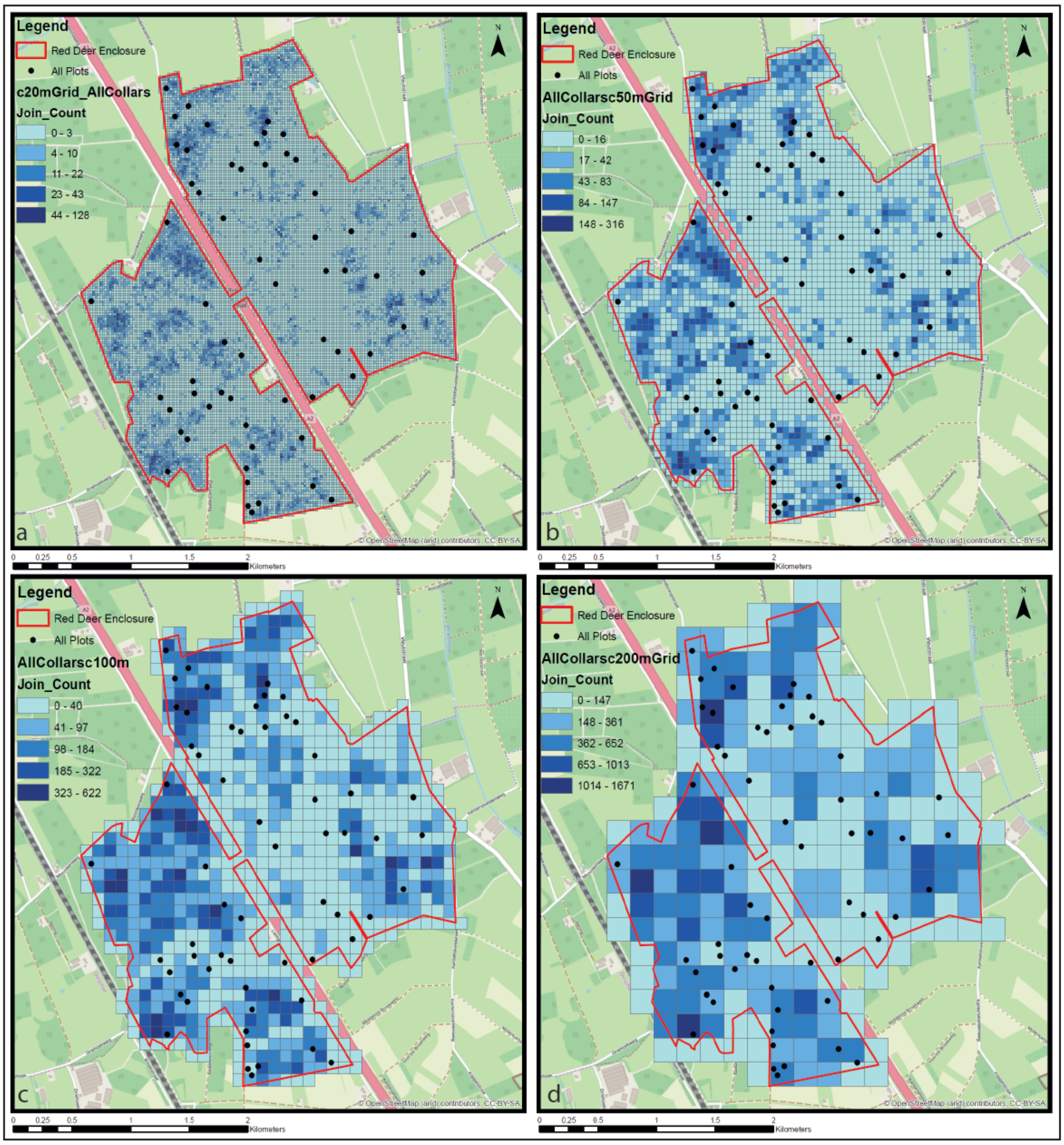

Figure 8. Comparison of the four grid resolutions for all four deer collars for the entire study. These maps also display the plot locations. *a*) represents the 20x20m gird, *b*) shows the 50x50m grid, *c*) displays the 100x100m grid, and *d*) shows the 200x200m grid. Note how in the 20x20m grid, many of the plots appear to be in areas where the usage has a value of almost 0, which cannot be possible as this is a small enclosure in which a herd of deer have been roaming for two years. Meanwhile, in the 200x200m grid, many of the plot points fall within the same grid square, therefore being assigned the same usage value.

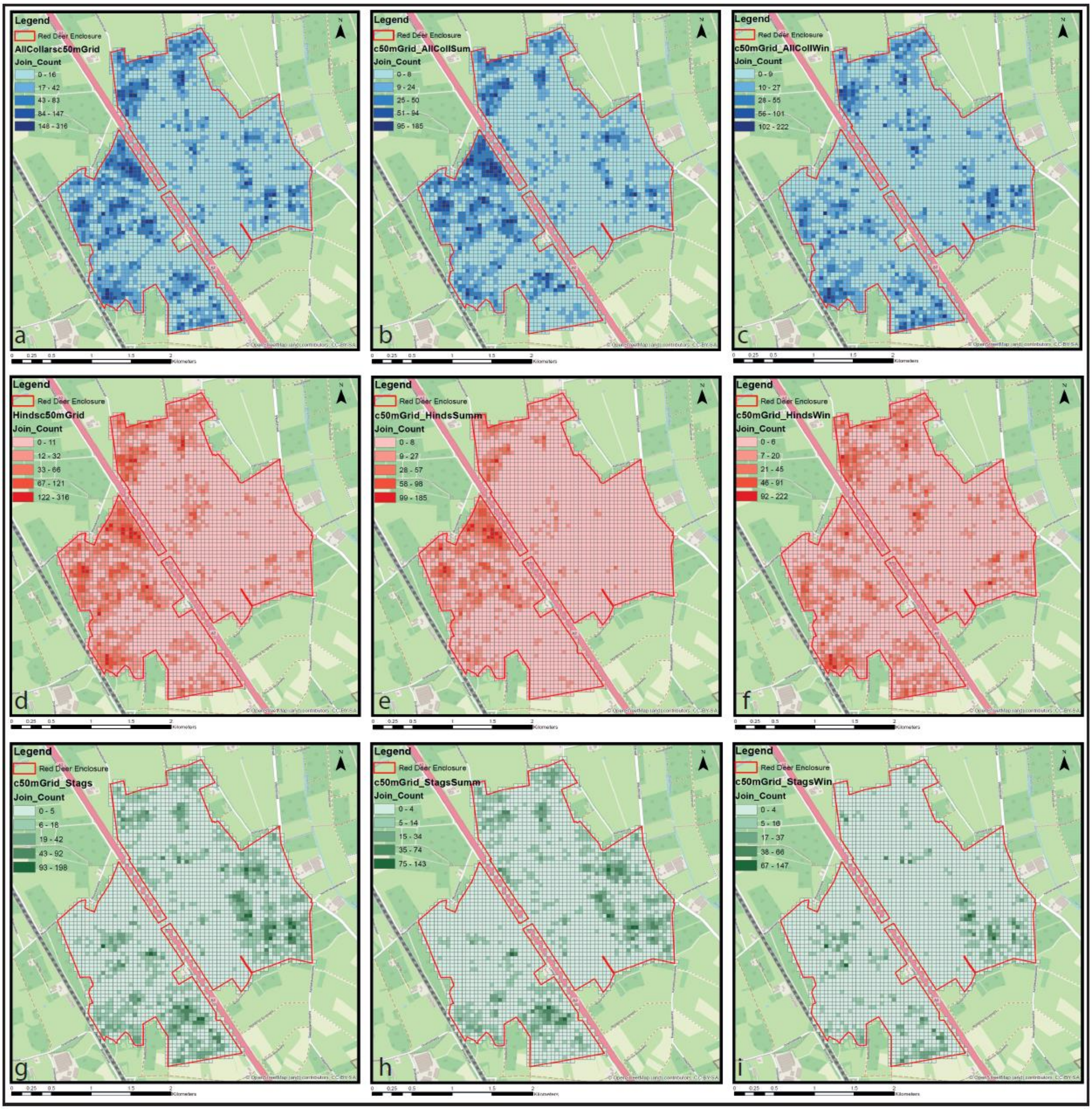

Figure 9. Density maps at the 50x50m resolution. *a*) represents the density of all four collars over the full duration of the study, *b*) represents all four collars over the summer period (April 1st until September 30th), *c*) represents all four collars over the winter period (October 1st until March 31st). *d*) shows the two hind densities for the whole duration of the study, *e*) shows the hinds in summer and *f*) in winter. *g*) shows the two stag densities for the whole duration of the study, *h*) the stag density in summer and *i*) in winter.

3.2 Relation between deer space use and vegetation variables

It was found that there was a significant relationship between red deer and bramble height (table 3, $F = 1.6$, $p = 0.001$). Bramble height decreased from the 25th to the 75th deer intensity quartiles, but did not differ between the 75th and 100th deer intensity quartiles (figure 10). Figure 10 displays the results for all deer over the whole study period; the two seasons and the two genders also showed the same trends. Bramble cover was related to intensity of use for some deer density variables (all deer, hinds and stags year-round and during summer, and hinds year-round) but not for others (namely all deer winter and hind summer densities) (table 3). Concerning mean bramble cover, there was little difference between the 25th, 50th and 100th deer intensity quartiles, meanwhile the 75th intensity quartile has the lowest mean bramble cover (full results for all post-hoc tests are presented in appendix 5, tables 7-16). Tests between bramble browsing and deer intensity of use, and between forb browsing and deer intensity of use showed no significance. The amount of bramble browsing per plot was generally the same regardless of plot usage, and forb browsing was higher in low intensity areas (figure 11).

Table 3. P-values and F-values resulting from general linear models which investigate the effect on vegetation structure by the red deer. P-values that are highlighted green indicate a significant result, red indicates an insignificant result, whilst yellow indicates that there is a statistical trend.

		Density Cluster																	
		All Deer		All Deer Sum		All Deer Win		Hinds		Hinds Sum		Hinds Win		Stags		Stags Sum		Stags Win	
Response	**Predictor**	***p*-value**	**F-value**	***p*-value**	**F-value**	***p*-value**	**F-value**	***p*-value**	**F-value**	***p*-value**	**F-value**	***p*-value**	**F-value**	***p*-value**	**F-value**	***p*-value**	**F-value**	***p*-value**	**F-value**
Bramble Height	Deer Density	0.001	1.60	0.001	1.79	0.09	0.73	0.001	2.18	0.03	1.06	0.001	1.86	0.00	1.78	0.001	2.91	0.001	2.24
Bramble Cover	Deer Density	0.01	1.21	0.01	1.22	0.20	0.48	0.03	0.98	0.78	0.12	0.34	0.30	0.001	2.39	0.001	3.53	0.07	0.78
Forb Height	Deer Density	0.13	1.98	0.26	1.39	0.46	0.87	0.13	1.96	0.03	3.09	0.37	1.07	0.64	0.57	0.56	0.70	0.07	2.50
Forb Cover	Deer Density	0.35	1.13	0.22	1.47	0.78	0.37	0.28	1.43	0.47	0.86	0.89	0.22	0.08	2.35	0.71	0.47	0.07	2.52
Graminoid Height	Deer Density	0.33	1.18	0.33	1.16	0.17	1.72	0.46	0.88	0.30	1.24	0.56	0.63	0.38	1.04	0.31	1.22	0.69	0.49
Graminoid Cover	Deer Density	0.10	2.18	0.18	1.68	0.82	0.30	0.97	0.07	0.87	0.24	0.97	0.08	0.08	2.37	0.04	2.95	0.44	0.91
Bramble Browsing	Deer Density	0.69	0.50	0.88	0.22	0.84	0.28	0.69	0.49	0.51	0.79	0.92	0.16	0.71	0.47	0.66	0.54	0.35	1.11
Forb Browsing	Deer Density	0.07	2.45	0.14	1.92	0.51	0.79	0.05	2.73	0.28	1.30	0.19	1.64	0.37	1.07	0.62	0.59	0.03	3.35
Debarking	Deer Density	0.001	3.28	0.02	6.66	0.03	3.64	0.03	6.73	0.04	8.68	0.03	3.37	0.02	2.22	0.05	3.47	0.09	1.03
Deer Density	Lying Deadwood	0.001	1.12	0.00	0.74	0.001	1.01	0.001	0.70	0.01	0.68	0.00	0.78	0.001	1.13	0.01	1.10	0.08	0.65
Deer Density	Mature Tree Stems	0.001	4.28	0.06	2.42	0.05	2.46	0.22	1.55	0.45	1.11	0.40	1.18	0.11	1.91	0.06	2.36	0.65	0.88
Deer Density	Bare Soil Cover	0.001	1.87	0.12	1.72	0.25	1.38	0.20	1.48	0.22	1.43	0.56	0.96	0.26	1.35	0.25	1.36	0.30	1.29
#Trees <50cm	Deer Density	0.048	2.81	0.057	2.65	0.064	2.56	0.121	2.02	0.074	2.44	0.092	2.25	0.27	3.28	0.036	3.06	0.661	0.53
#Trees 51-100cm	Deer Density	0.007	4.43	0.018	3.66	0.008	4.36	0.014	3.88	0.2	1.60	0.046	2.84	0.087	2.30	0.029	3.24	0.545	0.72
#Trees 101-150cm	Deer Density	0.003	5.10	0.001	5.89	0.01	4.18	0.012	4.02	0.039	2.98	0.032	3.15	0.028	3.25	0.026	3.31	0.049	2.79

The relationships between deer intensity of use and forb height, forb cover, graminoid height and graminoid cover are shown to be insignificant across almost all deer density variables (*p*-values presented in table 3). Conversely, figure 10 demonstrates that there is a general decrease in mean forb height with increasing deer intensity. There is little variance in forb height between the 25th and 50th intensity quartiles, however the mean forb height decreases in the 75th intensity quartile, and again in the 100th intensity quartile. However, each intensity level shows a high amount of overlap in the range of forb heights, particularly between the 25th and 50th intensity quartiles and between the 75th and 100th intensity quartiles. The graminoid height and bramble cover boxplots (figure 10) also show a high amount of overlap between all intensity levels. There is little variance in mean bramble cover and mean graminoid height across all intensity levels. Forb cover and graminoid cover vary across the intensity levels but in a non-linear pattern to increasing deer intensity of use. The marginal means table (appendix 5, table 6) presents the means and the upper and lower bounds of each vegetation variable per density quartile from the ANOVA test, and the LSD post-hoc test (appendix 5, tables 7-16) present the difference in mean variance between groups. Even in significant tests (table 3) and boxplots in which the mean value of each group show a significant pattern, there is much overlap between groups.

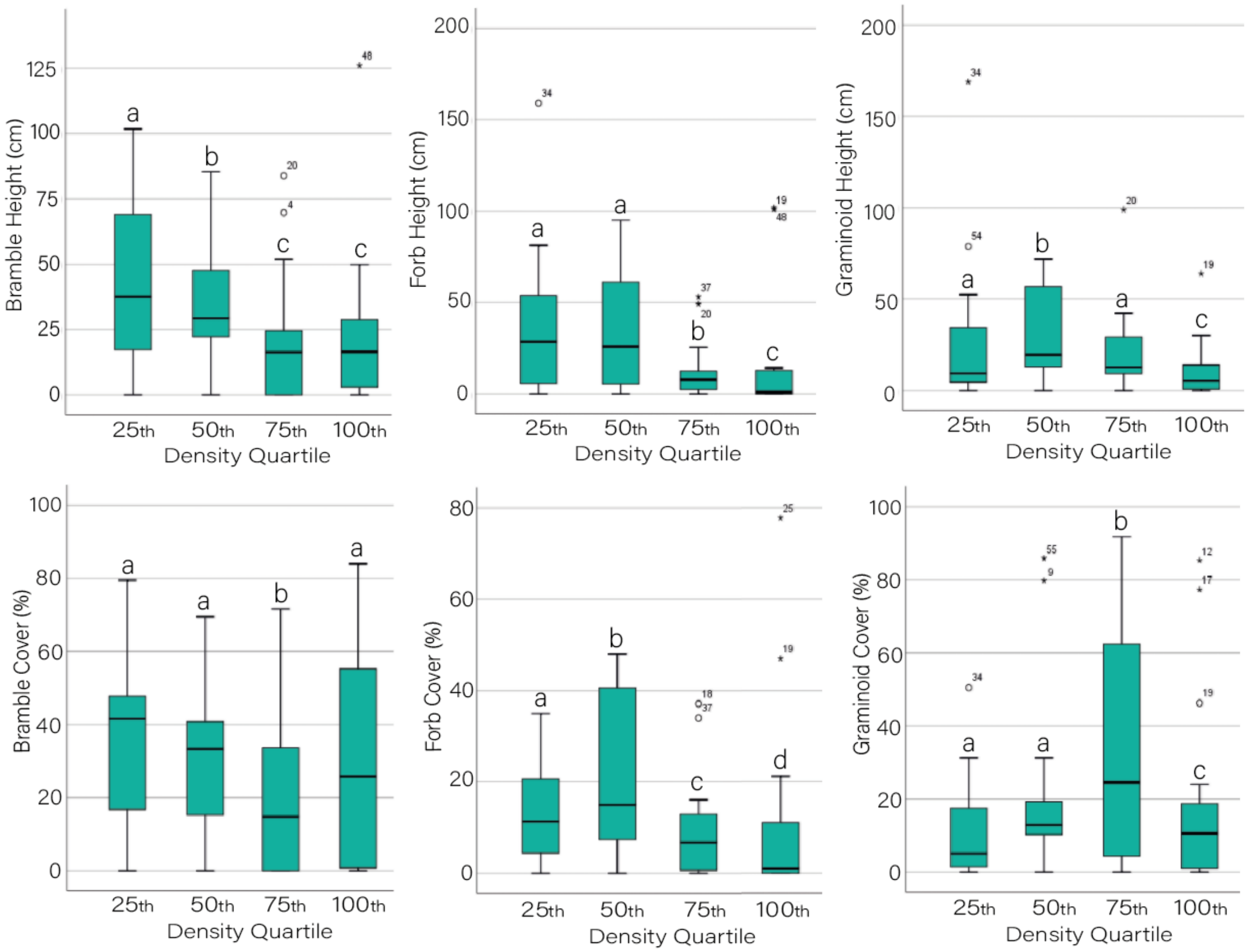

Figure 10. Box plots showing the overall mean effect of the deer intensity of use (density quartiles) on 6 vegetation structure parameters: bramble height (cm), forb height (cm), graminoid height (cm), bramble cover, (%) forb cover (%) and graminoid cover (%). These boxplots use the data for all four deer collars given over the whole study period (both genders over both seasons).

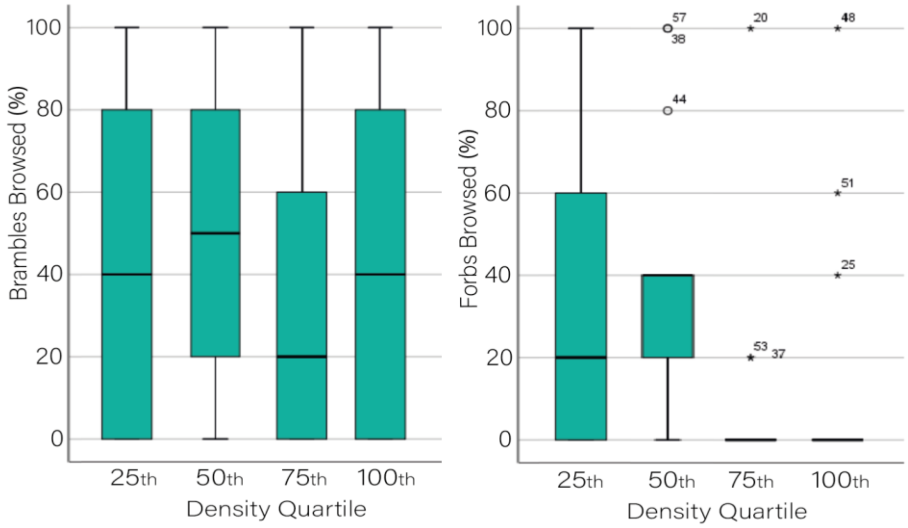

Figure 11. % of samples circles browsed per 20x20m sample plot. Bramble browsing and forb browsing show no relation to intensity of use (density quartiles). The amount of bramble browsing per sample plot is relatively constant across the intensity levels. Forb browsing is high in low intensity plots, but barely occurs in the medium-high and high intensity plots.

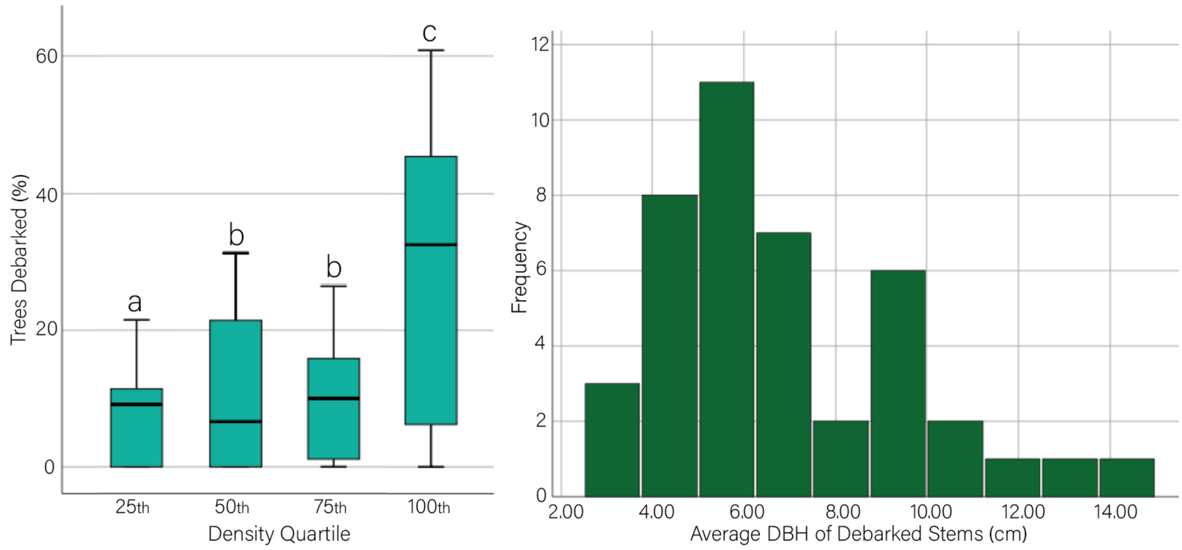

Figure 12. a) shows the relationship between deer intensity of use (density quartiles) and the percentage of trees that are debarked. There is a positive relationship between the two; areas of higher intensity show a higher number of debarked trees. *b*) is a histogram depicting the average diameter of debarked trees. Mature trees with a diameter over 14cm, and younger trees less than 3cm in diameter generally do not show evidence of debarking.

Additionally, lying deadwood, %bare soil cover and the number of mature tree stems over 1.5m were tested against deer density to see if they influence whether deer used a plot (figure 13). The number of mature tree stems over 1.5m and %bare soil cover showed no overall significance in influencing deer intensity of use (table 3 and figure 13), however the number of lying deadwood individuals showed a strong influence on deer intensity of use. As the amount of lying deadwood increases, deer usage decreases (table 3, table 4 and figure 13). There is a strong relationship between deer intensity and debarking (table 3), excluding stags in winter. Debarking increases with increasing deer intensity of use. The average DBH of debarked trees is 4.76cm, with the minimum DBH at 2.79cm and the maximum at 14cm (figure 12). The minimum DBH of all mature trees measured (mature trees being over a height of 1.5m) was 0.5cm, whilst the maximum was 133cm, and the average DBH was 15.706cm. The average heights of debarked trees have not been calculated as mature tree height was estimated (and often greatly underestimated), therefore any value given would be neither accurate or precise.

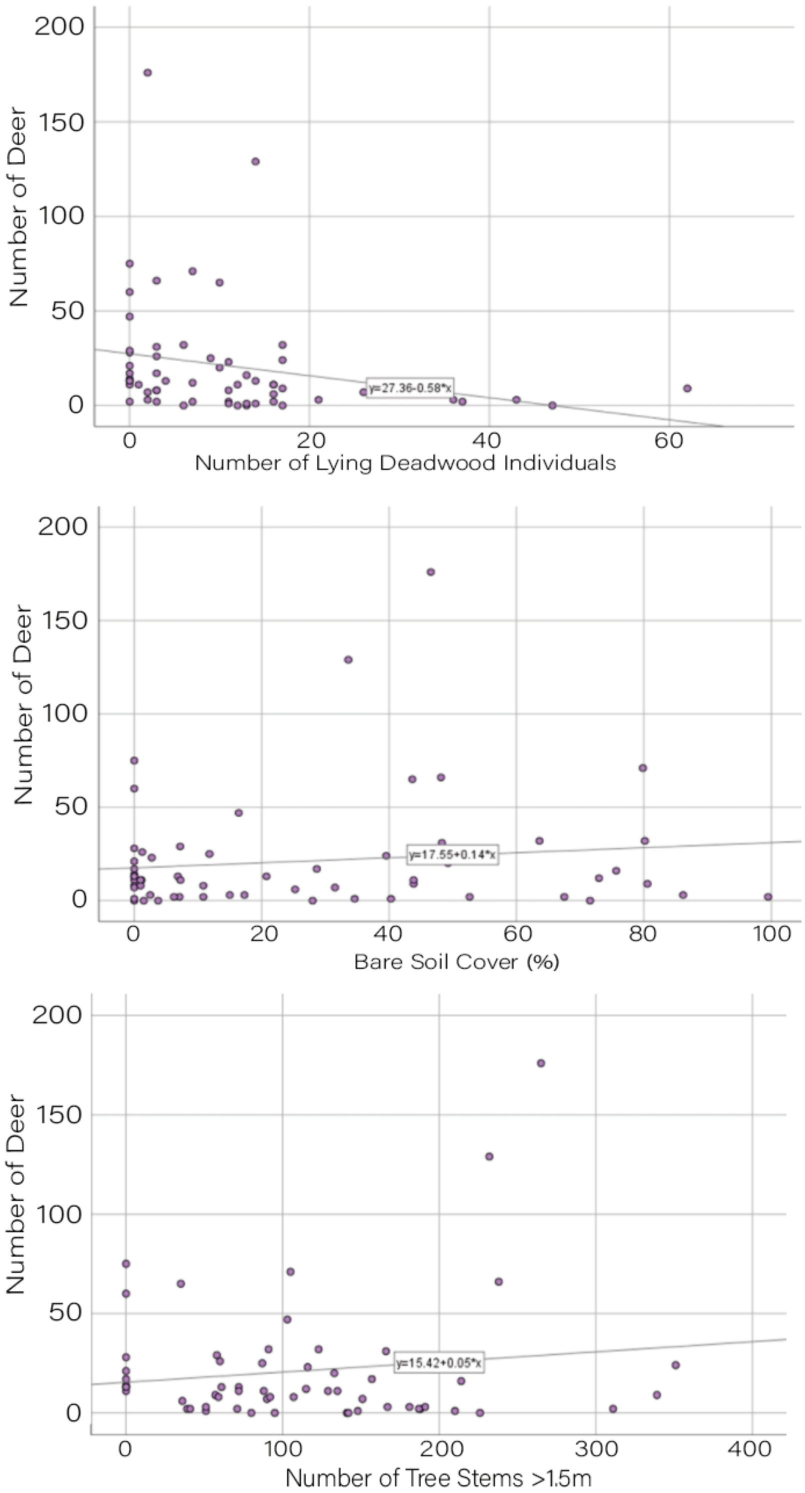

Figure 13. Scatter plots for tests in which deer density was the dependent variable. The number of lying deadwood vs. number of deer is the only test of these three which shows a discernible trend; as the amount of lying deadwood increases, the number of deer decreases. The line of slope for this test is -0.58. The other two test show no obvious trend. The line of slope for bare soil cover (%) vs. number of deer is +0.14, whilst the line of slope for the number of tree stems vs. number of deer is +0.05. For these results, the response variable is the absolute number of deer, not the density quartiles. This is because some levels of the predictor only had one response case.

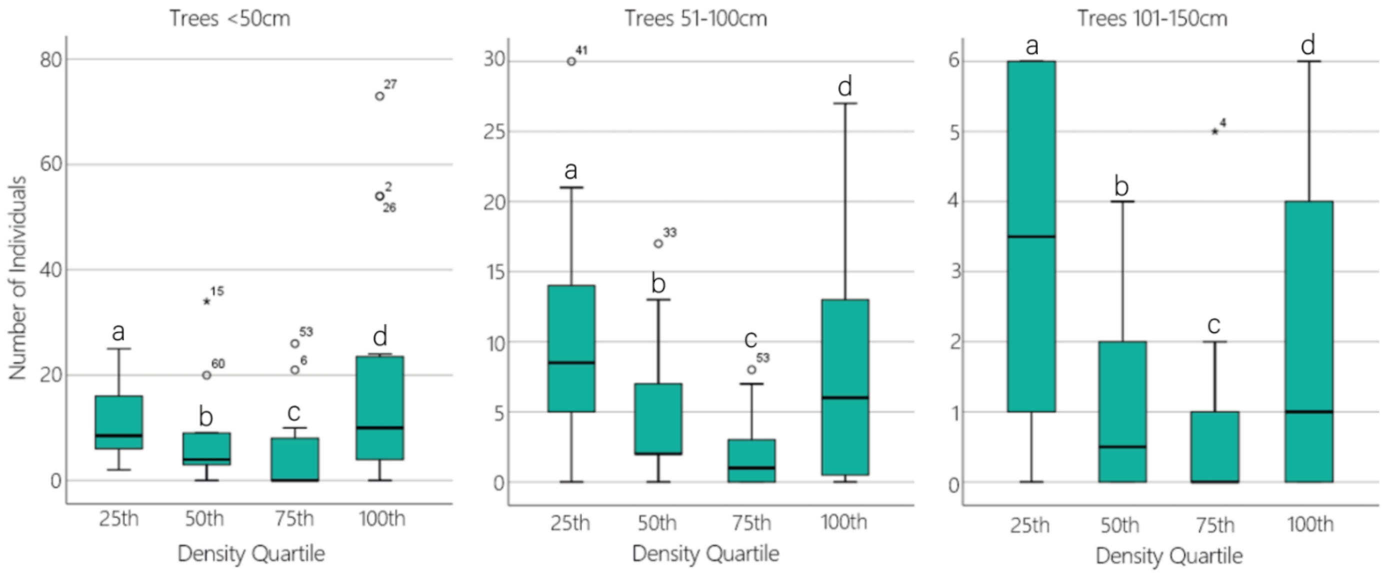

Figure 14. Boxplots showing the number of tree saplings per deer intensity of use level (density quartiles) across the 3 height classes.

The number of sapling individuals per density quartile presents a U-shaped boxplot across all height classes (figure 14). For all three height classes, the number of sapling individuals was highest for the low and high deer intensity of use, and lowest for the two intermediate deer intensity of use classes.

Analysis of how individual species responded to deer intensity of use was performed but yielded no significant results in this study as all species except hazel (*Corylus avellana*) had too few data points to run a valid, reliable test. The analysis of the number of hazel saplings as a response to deer intensity of use (figure 15) also showed a similar pattern to that shown in figure 14. The number of sapling individuals was highest in the low and high deer intensity of use areas, particularly in the <50cm and 51-100cm height classes, however the 101 -150cm height class does show a decrease in individuals with increasing deer density. Oak saplings (*Quercus robur)* appeared in significant numbers only in the <50cm height class and were most numerous in the high intensity areas. Similar to oak, rowan (*Sorbus aucuparia*) also appeared in significant numbers in the high intensity areas.

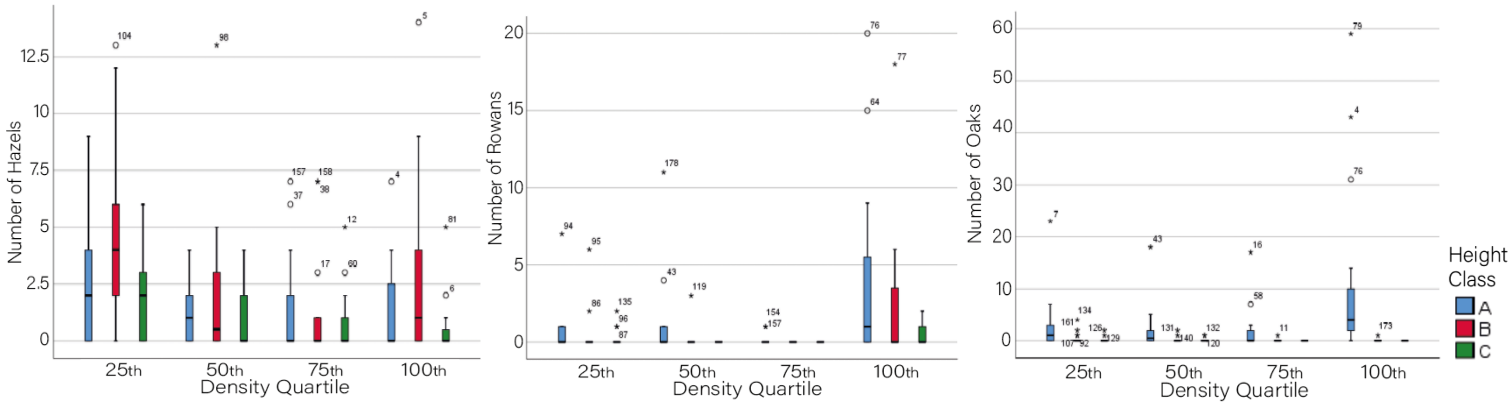

Figure 15. Boxplots displaying how the number of hazel, rowan and oak saplings at different height classes responds deer intensity of use (density quartiles). Blue bars represent individuals <50cm, red represents individuals 51-100cm, green represents those 101-150cm. The 25th density quartile (lowest intensity of use) is on the left side of each graph, and the 100th density quartile (high intensity of use) is on the right side of each graph.

Bramble height and the number of lying deadwood individuals both showed a significant relationship to deer intensity of use. These two parameters were then tested as predictor variables, with tree saplings as a response variable. It was found that there was a marginal relationship between saplings <50cm and the number of lying deadwood; numbers of saplings <50cm are slightly higher in areas of higher deadwood, however this is not a significantly clear relationship. Analysis of all height classes combined also showed this pattern; that increased lying deadwood does allow for higher rates of sapling establishment. Other tests, particularly tree saplings against bramble height proved to be insignificant.

Table 5. p-values and regression slope values for sapling height as a response to the number of lying deadwood individuals and bramble height.

Response	**Predictor**	***p*-value**	**Regression line of slope**
Trees <50cm	Lying Deadwood	0.086	y=10.08+0.1*x
Trees 51-100cm	Lying Deadwood	0.185	y=5.51+0.11*x
Tress 101-150cm	Lying Deadwood	0.211	y=1.53+0.04*x
All Trees <150cm	Lying Deadwood	0.166	y=16.99+0.26*x
Trees <50cm	Bramble Height	0.123	y=13.42-0.07*x
Trees 51-100cm	Bramble Height	0.492	y=6.48-5.72E-3*x
Tress 101-150cm	Bramble Height	0.275	y=1.28+0.02*x
All Trees <150cm	Bramble Height	0.316	y=21.31-0.04*x

3.3 Comparison with 2017 data

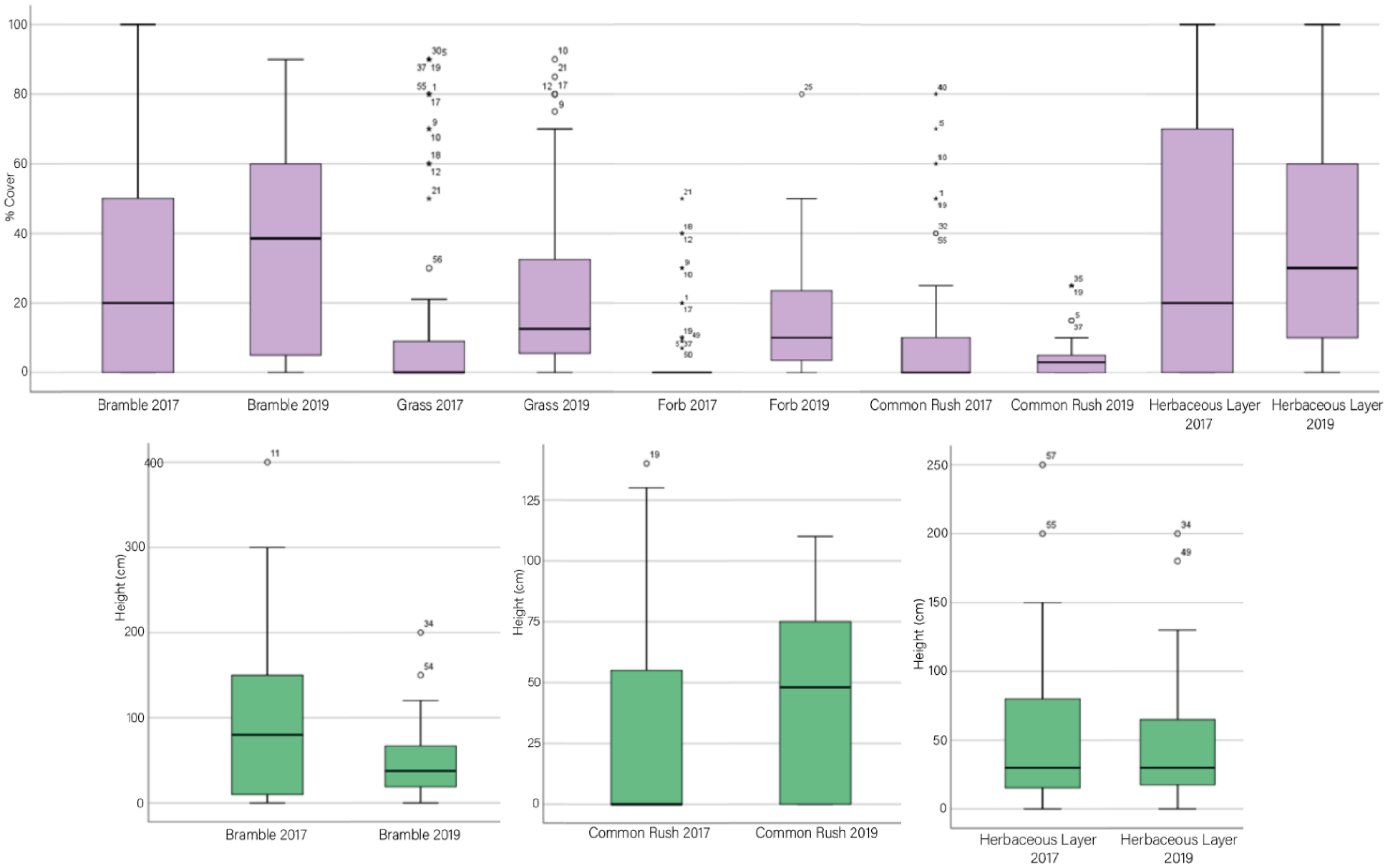

Figure 16. Boxplots showing the changes in selected vegetation parameters between 2017 and 2019.

Between 2017 and 2019, the mean cover of brambles, grasses and forbs have increased. The mean cover of common rush and the herbaceous layer have also increased, but the overall variance has decreased. The height of bramble has decreased significantly since 2017; both the mean and the overall variance show a decrease. The herbaceous layer shows no overall change from 2017 to 2019.

T-test results (see appendix 5, table 18) support the variance and mean decrease for bramble between 2017 and 2019, and also support the increase in graminoids and forbs between 2017 and 2019. The t-test also shows that the herbaceous layer height mean is marginally lower in 2019, and the variance is also marginally lower. Bramble and herbaceous layer cover both show a small increase in the mean value, but no overall change in variance between 2017 and 2019.

4. Discussion

4.1 Results summary

The results of this study tell us that there is a significant relationship between bramble height, the number of trees debarked, and the number of lying deadwood individuals with deer intensity. There is a trend towards a relationship between forb height and deer intensity. For this relationship to be understood, any seasonal vegetation effects should be eliminated. There is a trend toward a relationship between saplings <50cm, saplings 51-100cm and deer intensity, however a relationship does occur between saplings 101-150cm and deer intensity. An unexpected pattern occurred in the analysis (see the ‘U-shaped’ boxplots in figure 14) for which there may be a few explanations. This study has found that bramble and herbaceous layer height have both decreased since 2017, although other vegetation variables show no change. However, changes and patterns in vegetation cannot necessarily be linked to deer. Analysis of vegetation variables with the 9 deer density variables show that season and gender showed no differing influence on vegetation overall.

4.2 Significant results

4.2.1 Bramble height (*Rubus fruticosus*)

This study found that the height of bramble decreased between 2017 and 2019, and that the decrease in bramble height was also linked to deer intensity; areas of higher deer intensity were linked to lower bramble heights. Whilst the test of bramble browsing against deer intensity did not yield a significant result, it may be likely that bramble height has decreased due to bramble browsing. Bramble height decreases with increasing deer intensity and, furthermore, bramble height has significantly decreased since 2017, although the seasonal effect would cause bramble to increase from 2017 to 2019. It is likely that there was an error of some kind in the methodology for measuring levels of browsing; the methodology of this study recorded simply ‘yes’ or ‘no’ if a sample circle was browsed, it would be more effective to measure the level of browsing within each sample circle, i.e. how many quadrants within each sample circle were browsed. However, we still cannot eliminate the possibility that deer actively select areas with lower, thin-stemmed brambles, and avoid areas of high, dense brambles. Dense brambles could create an escape impediment, therefore such areas would be avoided. We may also consider that browsing of brambles by cattle and roe deer can also occur.

Other studies commonly find that bramble grows continuously, often up to 2m in height, in exclosures, whereas areas that deer can access often see a stable or declining bramble height (depending on the amount of available bramble and the size of the deer herd) (Kirby, 2001; Morecroft et al, 2001; Cooke, 2003; Joys et al, 2010). Therefore, we could also attribute the decline in bramble height over time in Het Groene Woud to deer browsing. It is also worth noting that the decrease in bramble height did not occur with a change in bramble cover; the %cover stayed relatively constant between 2017 and 2019. This could be because deer do not function to thin the bramble cover, they only browse the tips of bramble stems, preventing them from growing higher (Cooke, 2003).

4.2.2 Herbaceous layer height

It was found that the herbaceous layer height decreased between 2017 and 2019. The comparative decrease was marginal (figure 16), with mean and the variance in 2019 being only very slightly lower than in 2017. However, given the seasonal difference between the two studies, we would expect the 2019 herbaceous layer to be noticeably higher than the 2017 measurement, as the former study was performed in summer and the latter in winter. Therefore, it is possible that the herbaceous layer height is linked to deer intensity. Further research is need to support this, and to eliminate the seasonal effect. The statistical analysis was somewhat inconclusive. Other studies have found that deer contribute to a reduction in the herbaceous layer height and cover (Anderson, 1994; Kirby, 2001; Webster, 2005). One particular study found an initial increase in forb cover as a response to deer herbivory of bramble and ferns, however this was later followed by a noticeable decline in the herbaceous layer (Perrin et al, 2011). Studies have also found that deer will avoid tall forbs and grasses, as these have relatively low nutritional value, therefore continue to reduce the pre-existing low growing herbaceous plants (Smit et al, 2015). Furthermore, the pre-existing species composition within an area will dictate which species are preferentially browsed, and therefore species may either decline or thrive under deer herbivory (Virtanen et al, 2002).

The herbaceous layer is broken down into forbs and graminoids for the purpose of this study, whereas Tielemans (2017) combined these two into one layer. Whilst we see a change in the herbaceous layer between the two studies which we could potentially link to deer browsing, the forb and graminoid %cover and height showed no relationship with deer intensity. Furthermore, the test between forb browsing and deer density had no significance. Therefore, we cannot confidently conclude that the deer are browsing the herbaceous layer, however other factors which were not measured (namely cattle and roe deer grazing) may show a relationship with the herbaceous layer that we do not yet understand. Note that roe deer may enter and leave the enclosure freely, therefore we cannot fully know the number of roe deer in the enclosure or the amount of browsing they cause. For cattle, the number of cattle in the enclosure is kept relatively constant. But similarly to the methodology for bramble browsing, it is also likely that there was an error when measuring the level of forb browsing per plot (the level of browsing was recorded per sample circle, rather than per sample quadrant).

The interaction between deer and the herbaceous/forb/graminoid layers needs significant amounts of further testing and re-examination of the methodology. It is documented in literature that deer generally cause a reduction in herbaceous species, which also affects soil properties and nutrient cycling (Russell et al, 2001). It may be of further interest to understand which herbaceous understory species are affected by deer browsing; for instance nettles were commonly browsed within the area (personal observation), whereas other species are actively avoided, such as ground ivy (*Glechoma hederacea*) which is considered toxic and is too low to the ground to be affected by red deer browsing (Anderson, 1994; Cooke, 2003). This creates the potential for changes in fringe and mantle vegetation structure and species composition; the vegetation structure may become more open, which allows for more species richness and may aid the encroachment of some woody species saplings, or selective deer browsing may facilitate the certain species becoming dominant. Re-examining the herbaceous species observable in sample plots over time, and recording their dominance, will create further understanding of the true effect of deer on the herbaceous layer. Simply measuring %cover and height of selected functional groups may not be specific enough to fully understand changes in an area which has a diverse range of herbaceous species.

4.2.3 Tree debarking

One of the most significant tests of this study showed that there was a clear relationship between debarking and deer density. Higher levels of deer density corresponded to higher levels of debarking. Furthermore, debarking occurred on trees between 4cm and 10cm. Through my personal observations I noted that hazel (*Corylus avellane*) and rowan (*Sorbus aucuparia*) were the most commonly debarked trees, followed by bird cherry (*Prunus padus*), however further statistical analysis is needed to support this. Other studies have found that *Pinaceae* family and *Acer* genus species to be most commonly debarked, which was not found in this study (perhaps mainly as there were few individuals of these species in the study area), however of the deciduous species, hazel and rowan were the next most preferable species to debark (Jamrozy, 1980; Feher et al, 2016).

Figure 67. Bark stripping of a birch tree in the Groene Woud deer enclosure.

Bark stripping can leave a mature tree vulnerable to a weakened stem and fungal growth (Verheyden et al, 2006). Bark stripping may occur to compensate for mineral or roughage deficiencies, particularly in winter (when resources are low) and in areas to which deer have been confined (Gill, 1992; Verheyden et al, 2006). However, bark stripping can account for up to 10% of a deer's diet (Verheyden, 2006) and has been found to occur with a heavily browsed herbaceous understory (Feher et al, 2016). The high levels of debarking observed in the Groene Woud enclosure, particularly in areas of high deer intensity of use, are consistent with the literature, however links between debarking and herbaceous browsing in the area cannot be analysed as there is not sufficient data to perform any analysis.

4.2.4 Lying deadwood

The influence of the amount of lying deadwood on deer intensity of use also proved significant; deer avoided areas of high lying deadwood. Lying deadwood over 50x50x100cm are considered to be escape impediments for deer because they may block their views and potential escape routes (Kuijper et al, 2013), hence deer avoid areas of abundant lying deadwood.

4.2.5 Tree saplings

The interaction between tree saplings and deer intensity of use was interesting and presented us with further questions. The 'U-shaped' box plots in figure 14 are not what we would expect to see, given what is written in the literature; areas with a high deer intensity of use have caused reduced growth rates and establishment of saplings elsewhere (Gill & Beardall, 2001; Russel et al, 2001; Götmark et al, 2005). In my study, the abundance of saplings was highest in the high intensity of use areas; it is possible that deer seek out these areas of numerous saplings, and that the two-year study period is not long enough to show decline in sapling numbers that has been associated with high deer intensity in other studies (Gill & Beardall, 2001; Russel et al, 2001; Götmark et al, 2005). This pattern of higher abundance in the high deer intensity areas was consistent across all height classes of all combined trees below 1.5m, and is clearly visible in rowans and oak saplings (figure 15).

The <50cm height class had the highest total number of recorded individuals, and the 101-150cm height class had the fewest recorded individuals. This study found that high numbers of saplings occurred in high deer intensity of use areas; this is contradictory of the literature. Literature suggests that tree regeneration in the areas of high deer herbivory is found to be minimal for certain preferred species (Virtanen et al, 2002; Koda & Fujita, 2011), particularly for trees over 50cm, with individuals often being unable to grow taller than 200cm (Churski et al, 2016). However, herbivory of palatable species improves chances of successful recruitment of other, less-palatable species due to reduced competition for resources. Deer browsing of tree species often changes the inter-species competition dynamics (Gill & Beardall, 2001). If the recruitment success of certain species is reduced, the species composition of newly-regenerated forest will differ considerably from before the introduction of deer. However, seedlings below 50cm can also be affected by other parameters such as soil fertility or herbaceous plant cover (Kuijper et al, 2010), which also prevents them growing into the 51-100cm height class.

It was also found that sapling establishment did show a relationship to the number of lying deadwood individuals. Areas of high lying deadwood are avoided by deer, the number of tree saplings below 50cm also showed a trend to increase in areas of high lying deadwood abundance. Areas of high deadwood abundance show potential to create 'nurseries' for saplings, and protect them from herbivory by red deer (de Chantal & Granström, 2007). This is consistent with other studies and available literature; aggregations of deadwood can prevent deer herbivory of saplings and can also promote the growth of thicker, more sturdy stems (de Chantal & Granström, 2007). However, as a mechanism to exclude deer from the area, this does depend on the quantity and layout of the deadwood (de Chantal & Granström, 2007; Hagge et al, 2019). As a way to promote heterogeneity in forests, to increase sapling recruitment and to encourage forest regeneration, areas of deadwood (created naturally or man-made) have been citied in other studies as a successful management strategy (de Chantal & Granström, 2007; Hagge et al, 2019). By employing this as a natural or man-made strategy, or by creating exclosures, it is possible to create areas in which the abundance of saplings is higher, and in which the number of saplings reaching maturity without herbivory damage increases.

Interestingly, this study found that whilst there was a relationship between bramble height and deer intensity of use (see 4.2.1), it did not find any significant relationship between bramble height and sapling establishment. Literature can be contradictory on this subject; sapling establishment of particular species which are not reliant on high amounts of light to grow, can establish themselves successfully in bramble thicket areas which provide protection from herbivory as they are less frequented than areas of lower bramble height and cover (Harmer et al, 2010). However too much bramble reduces the amount of light reaching the forest floor, which can also negatively impact sapling recruitment, particularly into the upper height classes (van Uytvanck & Hoffmann, 2009; Harmer et al, 2012); moreover, increased bare soil cover can increase seedling establishment in lower height classes of species which require more light, but protection from deer herbivory is not provided (Kirby, 2001).

4.3 Limitations and future improvements

Some limitations of this study are related to the methodology and experimental design; more sample plots are needed in the forested area between plots 13 and 58-60. By placing more sample plots in this area we can hope to understand how deer may be impacting the deeper forest vegetation within the enclosure. Furthermore, the methodology concerning saplings may need to be revised; if small exclosures were installed in the area, we would then be able to experimentally exclude browsing and therefore could test effect of browsing on saplings, this would also enable us to understand the causal link between deer space use and sapling density. Additionally, field observations indicated that nettles (*Urtica dioica*, figure 18) were a commonly occurring and heavily browsed group, therefore future studies may wish to add an additional nettle functional group which would be analysed separately to the broad forb functional group, in which nettles were placed for this study. The method of measuring bramble and forb browsing should also be adjusted; the methodology of this study indicated if browsing of a functional group occurred per sample circle, this should be recorded per quadrant.

The method of this study should be repeated in the future; two years may not be a long enough study period for the effects of deer density on vegetation to become fully clear. In particular, the groups shaped by and used by deer should be monitored; namely brambles, forbs and saplings. Furthermore, by repeating this study in the future, any early warnings of over-utilization of the food source may become apparent.

It should also be noted that Aberdeen Angus cattle (*Bos taurus taurus*) are also in the Red Deer enclosure in Het Groene Woud from spring through to autumn. It is difficult to determine which grazing/browsing effects are caused by cattle and which are caused by the deer. Deer are browsers and intermediate feeders (animals that consume predominantly forbs and woody species, but also grasses if necessary) whilst cattle are grazers (animals that consume graminoids and locally available forbs, but avoid woody species) (Hoffman, 1989; Sankey et al. 2006), however in a small area the amount of dietary overlap is unclear, particularly around forest boundaries. It may be of interest to investigate how much dietary and spatial overlap occurs and if there is high competition between the deer and the cattle (Lovari et al, 2014). The movements of the cattle within the enclosure and their eating behaviours are poorly understood. Through personal field observations, cattle were seen to graze in fields and at forest boundaries (figure 19), never venturing into deeper forest, however further research is needed before any conclusions can be made on the bovine impact on vegetation within the enclosure. GPS collars on cattle and field observations on their behaviour may provide useful insights. It may be of interest to understand the impacts of cattle, not

Figure 18. Browsing of nettles in the Grone Woud enclosure. It was highly common to observe the tips of nettle plants to be browsed.

only for understanding vegetation structure, but also for understanding their relationship with the red deer.

Figure 19. Some Aberdeen Angus cows observe fieldwork from the comfort of the shady path. Cattle were often seen along the pathways and forest boundaries, whilst the deer were more often seen deeper in the forest.

5. Conclusion

The three clear results of this study are that high amounts of lying deadwood reduce area usage by red deer, that increased amounts of mature tree debarking occurs with increased levels of deer intensity of use, and that bramble height reduces with increasing deer intensity of use. It could be that deer prefer to visit areas of lower bramble height, however the overall bramble height has decreased between 2017 and 2019, despite ant possible seasonal effect, therefore it is most likely that the reduction in bramble height is caused by red deer browsing. Relationships between other vegetation functional groups and deer intensity of use could not be determined. It is possible that there may be a relationship between deer intensity of use and the height of the forb, graminoid and general herbaceous layers, but for this to be determined, future studies will need to eliminate any seasonal effects. No relationships were found between %cover of any of the vegetation functional groups and deer intensity of use. This may be because deer browse the tips of vegetation, rather than causing thinning of the layer.

There was also no strong relationship found between tree saplings and deer intensity of use. The abundance, height and establishment of saplings showed no significant relationship to deer intensity of use and is more likely to be controlled by and mixture of herbivory other contributing factors, such as resource availability and other limiting factors. It is possible that deer seek out areas of high sapling abundance as certain sapling species are a favoured food source, and there is evidence that sapling establishment is somewhat facilitated by areas of abundant deadwood providing protection from herbivory. At present there is no evidence to suggest that deer directly facilitate or restrict sapling establishment, or that they have any effect on the abundance or height of saplings within the Groene Woud enclosure. By installing small exclosures in the area, it may be possible to investigate the relationship between sapling height, abundance and establishment, and deer intensity of use.

There are some changes within the Groene Woud enclosure since 2017, however few of these changes can be linked to area usage by red deer, and are more likely to be related to seasonal effects. With further research over a longer time period, any effects by red deer on vegetation may become more evident. Additionally, as the deer herd grows there may also be more pressure on resource availability and the vegetation structure. With the new extension of the red deer enclosure in Het Groene Woud, it may be of interest in the future to see how the red deer interact with this new space, and how this influences the vegetation in the original study area. There are some patterns emerging which inform us about how deer are interacting with the landscape within the enclosure in Het Groene Woud, however further research is needed to address the knowledge gaps found by this study and the study by Tielemans, 2017. Re-examining the methodology and the locations of the sample plots should occur in future studies. Whilst trends do appear, they are not consistent across density groups or throughout the enclosure, therefore other variables may be controlling the vegetation structure which have not yet been identified. Previous studies have indicated that during the early years following reintroduction of red deer, forest dynamics are constantly shifting as the deer shape the vegetation structure and the landscape (Gill & Beardall, 2001).

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Picture Sources

Many of the figures and photographs provided in this thesis are by the author. Those taken from other sources, with permission, are listed here.

Title Page: Parkhouse, D. (2018) Sepia photograph of brown deer eating grass. *Unslpash*. https://unsplash.com/photos/sR7bgUjMt0w [accessed 26-01-2020]

Figure 1: Vera, F. W. M., (2000) Schematic transverse section of the structure of a grazed park-like landscape with mantle and fringe vegetation. *Grazing ecology and forest history*. CABI publishing.

Figure 3b: Dekker, J., & Houben, B. (2018) Figure 3: Reeënpoortje in het raster van het edelhertengebied. TERREINGEBRUIK VAN EDELHERTEN IN HET GROENE WOUD. Een analyse van het eerste half jaar in de Brabantse natuur (*English Translation*: Terrain use of red deer in Het Groene Woud. An analysis of the first half year in nature in Brabant). Report. *ARK Natuurontwikkeling en Brabants Landschap*

Figure 3d: Joop van Houdt (2014) Meander A2 natuurbrug Best ID472848. *Rijkswaterstaat*. https://beeldbank.rws.nl/MediaObject/Details/Meander%20A2%20%20%20natuurbrug%20Best_472848 [accessed 28-08-2019]

Appendix 1

Fieldwork form

Plot number		**Coordinates**		**Observer**	
Plot description		**Date**			

Madelon's data

Herbaceous layer				
Total species	**Plot cover (%)**	**Average height (cm)**	**Forb/herb cover (%)**	**Grass cover (%)**

Shrub layer		
Total species	**Plot cover (%)**	**Average height (cm)**

	Cover (%)	**Average height (cm)**
Bramble		
Common rush		

Deadwood cover (%)	

Plot number		**Coordinates**		**Observer**	
Plot description		**Date**			

New Data

	Number		**Number (over 50x50x100cm)**
Standing deadwood		**Lying deadwood**	

Trees above 1.50m in 20x20m plot			
Species	**Height (m)**	**Diameter (cm, DBH)**	**Debarking? (yes/no)**

Plot number		Coordinates		Observer	
Plot description		Date			

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

Circle 1

Functional group	% Cover				Drop-disc height (cm)				Browsing? (yes/no)
	NE	SE	SW	NW	NE	SE	SW	NW	
Bramble									
Common rush									
Graminoids									
Other shrubs									
Forbs									
Mosses									
Ferns									
Bare soil									

Circle 2

Functional group	% Cover				Drop-disc height (cm)				Browsing? (yes/no)
	NE	SE	SW	NW	NE	SE	SW	NW	
Bramble									
Common rush									
Graminoids									
Other shrubs									
Forbs									
Mosses									
Ferns									
Bare soil									

Circle 3

Functional group	% Cover				Drop-disc height (cm)				Browsing? (yes/no)
	NE	SE	SW	NW	NE	SE	SW	NW	
Bramble									
Common rush									
Graminoids									
Other shrubs									
Forbs									
Mosses									
Ferns									
Bare soil									

Plot number		Coordinates		Observer	
Plot description		Date			

Circle 4

Functional group	% Cover				Drop-disc height (cm)				Browsing? (yes/no)
	NE	SE	SW	NW	NE	SE	SW	NW	
Bramble									
Common rush									
Graminoids									
Other shrubs									
Forbs									
Mosses									
Ferns									
Bare soil									

Circle 5

Functional group	% Cover				Drop-disc height (cm)				Browsing? (yes/no)
	NE	SE	SW	NW	NE	SE	SW	NW	
Bramble									
Common rush									
Graminoids									
Other shrubs									
Forbs									
Mosses									
Ferns									
Bare soil									

Trees below 1.50m within the 5 circles				
Circle no.	Species	Height (cm)	Browsing? (yes/no)	Debarking? (yes/no)

Appendix 2

Common names (in English and Dutch) and Latin names of observed tree, shrub and herbaceous species.

Shrub Species

Latin	*English*	*Dutch*
Rubus fruticosus	Bramble	Braam
Lonicera periclymenum	Honeysuckle	Kamperfoelie
Ribes nigra	Blackcurrant	Zwarte bes
Ribes rubrum	Redcurrant	Rode bes
Ilex aquifolium	Holly	Hulst

Tree Species

Latin	*English*	*Dutch*
Populus canadensis	Canadian Poplar	Canadese populier
Quercus robur	Oak	Eik
Corylus avellana	Hazel	Hazel
Sorbus aucuparia	Rowan	Wilde lijsterbes
Betula pendula	Silver Birch	Zilverberk/Zilveren berk
Salix cinerea	Grey Willow	Grijze wilg
Salix alba	White Willow	Witte wilg
Fraxinus excelsior	Ash	Es
Prunus serotina	American Black Cherry	Amerikaanse vogelkers
Frangula alnus	Alder Buckthorn	Sporkehout
Crataegus monogyna	Hawthorn	Eenstijlige meidoorn
Pinus sylvestris	Scots Pine	Grove den
Picea abies	Norwegian Spruce	Noorse fijnspar
Acer saccharum	Canadian Maple	Canadese esdoorn
Carpinus betulus	Hornbeam	Haagbeuk
Alnus rhombifolia	White Alder	Amerikaanse Witte els
Alnus glutinosa	Alder (European)	Els
Prunus padus	Bird Cherry	Gewone vogelkers

Herbaceous Species

Latin	**English**	**Dutch**
Dactylis glomerata	Cock's foot grass	Kropaar
Agrostis capillaris	Brown top grass	Gewoon struisgras
Holcus lanatus	Common velvet grass	Gestreepte witbol
Poaceae	Other grasses/common grass	Gras
Hedera helix	Common ivy	Klimop
Glechoma hederacea	Ground ivy (alehoof)	Hondsdraf
Juncus effusus	Common rush	Pitrus
Carduus acanthoides	Thistle	Langstekelige distel
Urtica dioica	Nettle	Grote brandnetel
Rumex obtusifolius	Dock	Ridderzuring

Rumex acetosa	Sorrel	Veldzuring
Convolvulus arvensis	Bindweed	Akkerwinde
Stachys sylvatica	Hedge woundwort	Bosandoorn
Jacobaea vulgaris	Ragwort	Jakobskruiskruid
Mentha longifolia	Mint	Munt
Lapsana communis	Common nipplewort	Akkerkool
Myosotis scorpioides	Forget-me-not	Vergeet-me-nietje
Bellis perennis	Daisy	Margrietjes
Silene dioica	Red campion	Dagkoekoeksbloem
Anthriscus sylvestris	Cow parsley	Fluitenkruid
Maianthemum bifolium	False lily of the valley	Dalkruid
Hypericum perforatum	St John's wort	Sint-janskruid
Eupatorium cannabinum	Boneset/hemp-agrimony	Koninginnekruid
Geum urbanum	Herb Bennet	Geel nagelkruid
Lythrum salicaria	Purple loosestrife	Grote kattenstaart
Ononis spinosa	Spiny restharrow	Kattendoorn
Polygoratum multiflorum	Solomon's seal	Gewone salomonszegel
Galeopsis tetrahit	Brittle-stemmed hemp-nettle	Gewone hennepnetel
Prunella vulgaris	Heart-of-the-Earth/All-heal	Gewone brunel
Taraxacum officinale	Dandelion	Paardenbloem

Appendix 3

Plots: habitat type and location

Plot no.	WGS84 coordinates	Grassland	Bramble-Alder	Poplar-Hazel-Alder	Oak-Hazel-Alder	Oak-Poplar-Hazel	Spruce
1	N51° 32.834' E005° 22.859'	■					
2	N51° 32.842' E005° 22.754'				■		
3	N51° 32.733' E005° 22.586'						■
4	N51° 32.129' E005° 22.417'					■	
5	N51° 32.093' E005° 22.414'	■					
6	N51° 31.943' E005° 22.687'				■		
7	N51° 31.766' E005° 22.692'				■		
8	N51° 32.656' E005° 22.986'					■	
9	N51° 32.445' E005° 23.104'	■					
10	N51° 32.218' E005° 23.234'	■					
11	N51° 32.240' E005° 23.013'					■	
12	N51° 32.238' E005° 22.559'	■					
13	N51° 32.353' E005° 22.437'					■	
14	N51° 32.052' E005° 22.312'					■	
15	N51° 32.725' E005° 22.853'					■	
16	N51° 32.557' E005° 23.144'			■			
17	N51° 31.880' E005° 22.016'	■					
18	N51° 32' 05.500'' E005° 22' 34.000''	■					
19	N51° 31.886' E005° 22.663'	■					
20	N51° 31.853' E005° 22.676'						■
21	N51° 32.671' E005° 22.384'	■					
22	N51° 32.775' E005° 22.386'						■
23	N51° 32.846' E005° 22.468'				■		
24	N51° 32.884' E005° 22.397'			■			
25	N51° 32.944' E005° 22.289'				■		
26	N51° 32.861' E005° 22.327'				■		
27	N51° 32.785' E005° 22.338'				■		
28	N51° 32.723' E005° 22.641'						■
29	N51° 32.807' E005° 22.739'				■		
30	N51° 32.782' E005° 22.700'		■				
31	N51° 32.724' E005° 22.738'		■				
32	N51° 32.746' E005° 22.821'		■				
33	N51° 32.284' E005° 23.378'			■			
34	N51° 32.105' E005° 22.947'						■
35	N51° 32.133' E005° 23.153'						■
36	N51° 32.208' E005° 23.083'						■
37	N51° 32.535' E005° 23.411'	■					
38	N51° 32.431' E005° 23.439'			■			
39	N51° 32.419' E005° 23.269'			■			
40	N51° 32.646' E005° 22.439'		■				
41	N51° 32.517' E005° 22.968'		■				
42	N51° 32.433' E005° 23.027'		■				

43	N51° 32.398' E005° 22.793						
44	N51° 32.478' E005° 22.724'						
45	N51° 32.591' E005° 22.548'						
46	N51° 31.979' E005° 22.882'						
47	N51° 31.804' E005° 23.003'						
48	N51° 31.824' E005° 22.931'						
49	N51° 31.775' E005° 22.677'						
50	N51° 31.791' E005° 22.746'						
51	N51° 31.988' E005° 22.367'						
52	N51° 31.960' E005° 22.406'						
53	N51° 32.054' E005° 22.499'						
54	N51° 32.070' E005° 22.578'						
55	N51° 32.068' E005° 22.824'						
56	N51° 32.011' E005° 22.664'						
57	N51° 32.204' E005° 22.636'						
58	N51° 32.559' E005° 22.307'						
59	N51° 32.345' E005° 21.946'						
60	N51° 32.102' E005° 22.260'						

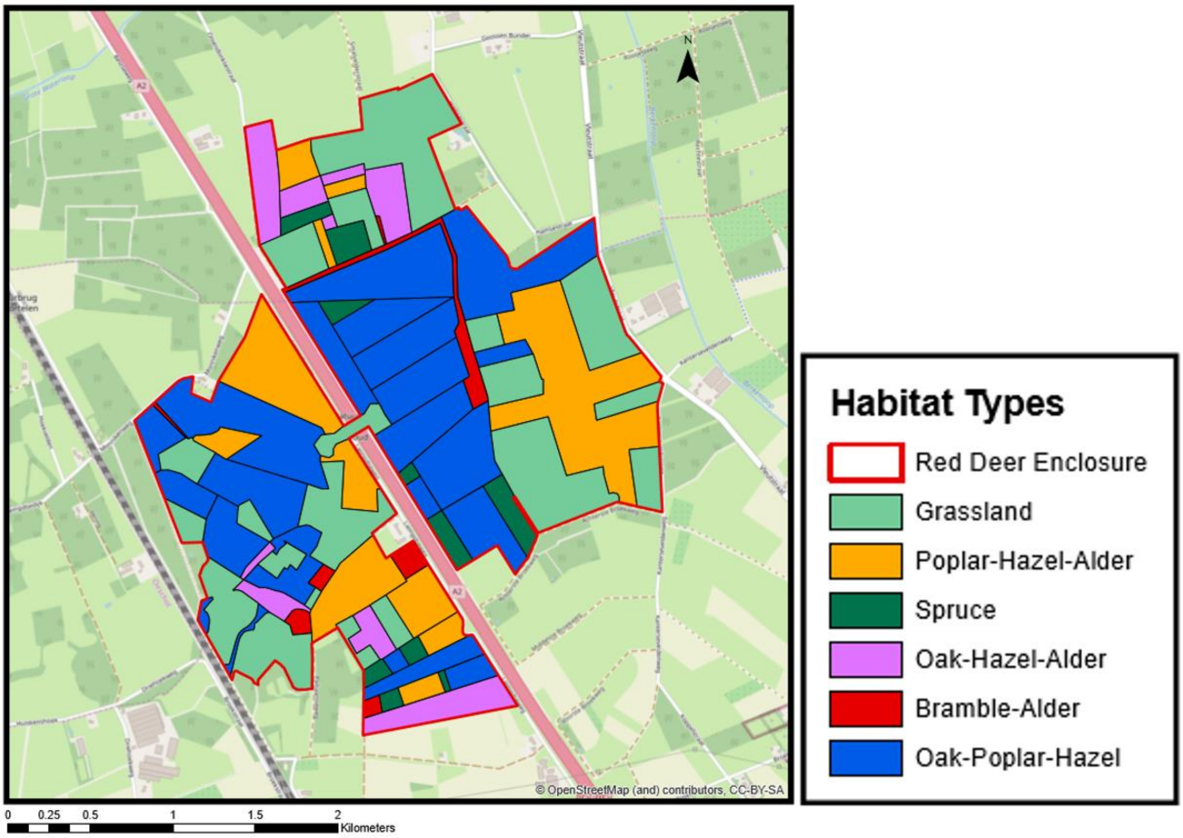


Figure 20. Habitat types and distribution throughout the enclosure.

Appendix 4

In this section, I shall very briefly report some the data collected from fieldwork performed in July and August 2019. This shall be a visual representation of the data so that the reader may have an up-to-date picture of the current vegetation structure of the deer enclosure.

Figures 21 and 22 provide a visual representation of the functional group composition per plot. Field observations showed grassland plots to be the most homogenous, whereas spruce plots showed the most variety in functional group composition. The values given here for the % aerial cover of the functional groups are derived from the averages of the 5 circles within each study plot. The habitat type for each plot is displayed in figure 20 and in appendix 3. I have also presented the number of freestanding and lying deadwood individuals per plot in figure 23. Tielemans (2017) presented deadwood per plot as an %estimate of the whole plot. I, however, found this to be an inaccurate technique that did not provide detail on the type of deadwood found in each plot, therefore I counted each deadwood individual.

The number of trees above 1.5m are displayed in figure 24, canopy height is presented in figure 25. Trees below 1.5m are shown in figure 26. There have been some limitations within the fieldwork method, particularly concerning the height of the mature trees. The height of the canopy is considerably underestimated; the true height of the canopy is likely to be 50-100% more than the value given. The canopy height may be a useful figure for calculating plot openness however in terms of deer browsing behaviour, this measure is not vital; mature trees are not affected by deer browsing.

The heights of the bramble, graminoid and forb functional groups per plot are presented in figure 27. I shall present these three groups only as these are the most susceptible to browsing, and are also the three most dominant groups. Brambles, graminoids and forbs are the 3 most common vegetation functional groups. As a comparison, bramble forms 29.77% of the area vegetation structure, graminoids form 22.53%, and forbs form 13.09% of the area vegetation structure (in terms of cover, not height). The next dominant functional group is ferns, which make up only 3.12% of the total vegetation (note that 26.13% of the area is bare soil). These groups may also be a limiting factor on woody species recruitment, therefore it is important to know the average height of each of these groups per plot. The heights for the function groups are derived from the averages of the 5 circles within each study plot. It should be noted that ferns were also browsed in 5 of the plots, despite ferns generally being deer-resistant.

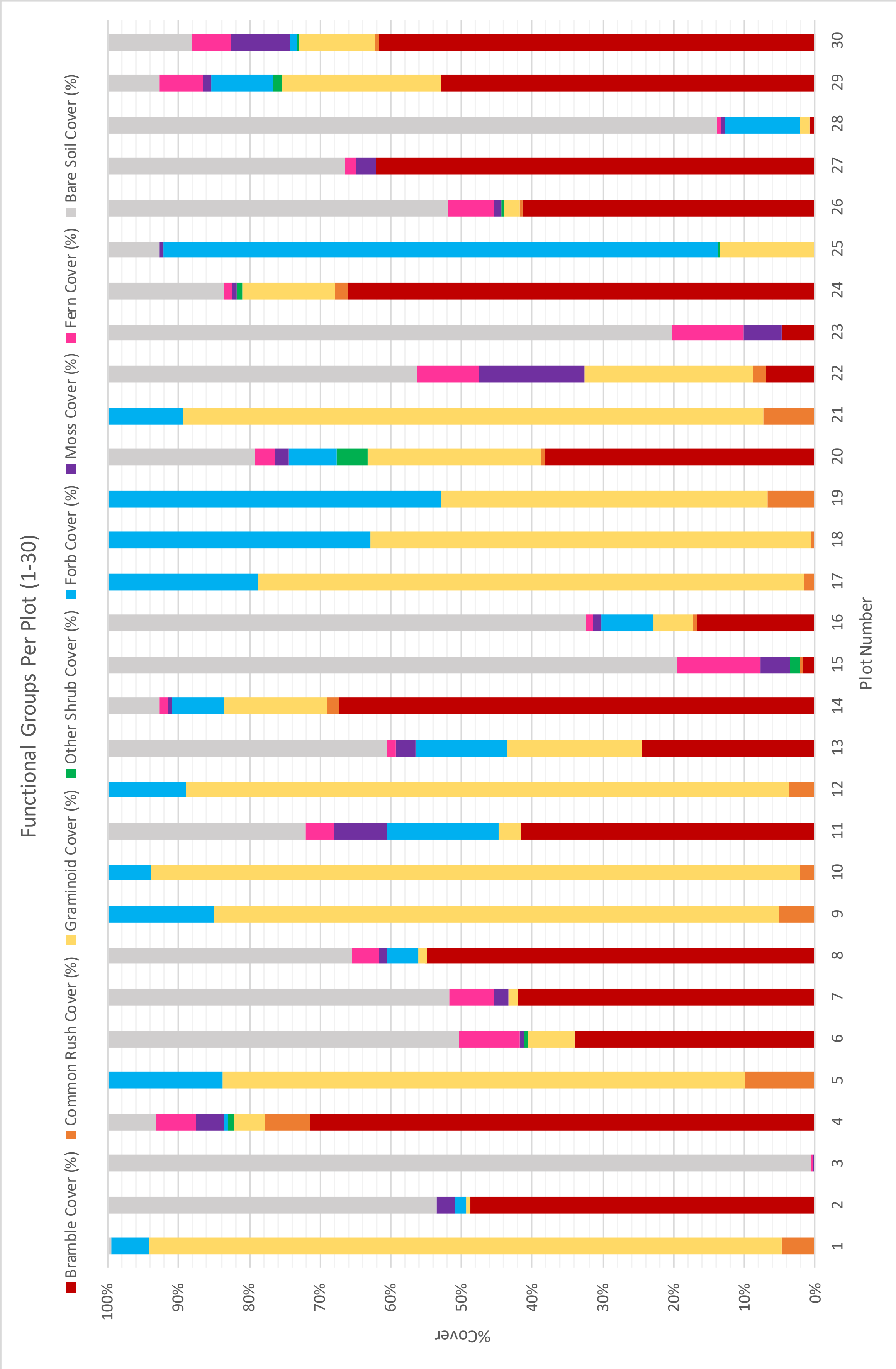


Figure 21. Functional group composition for plots 1 to 30.

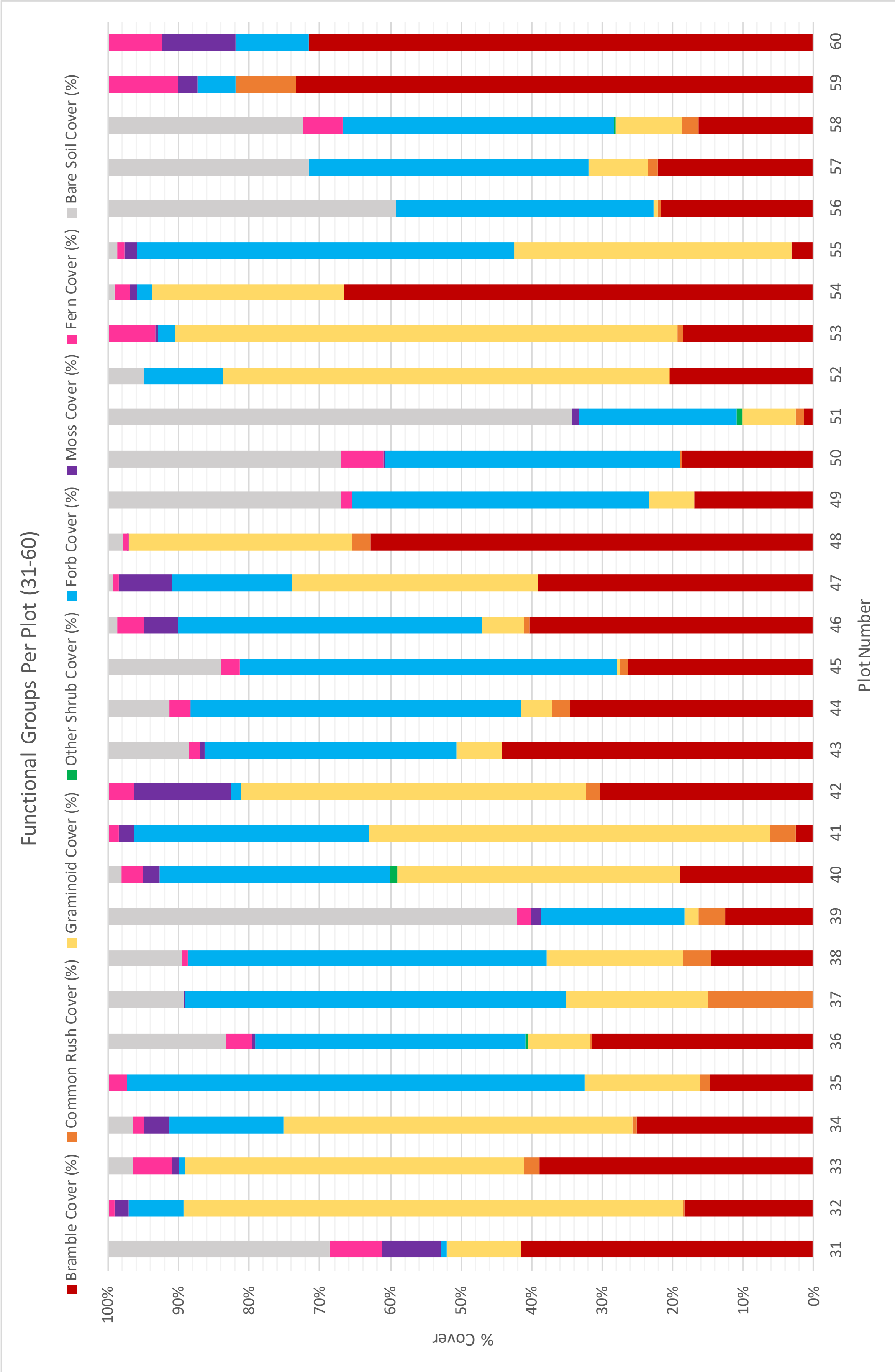


Figure 22. Functional group composition for plots 31 to 60.

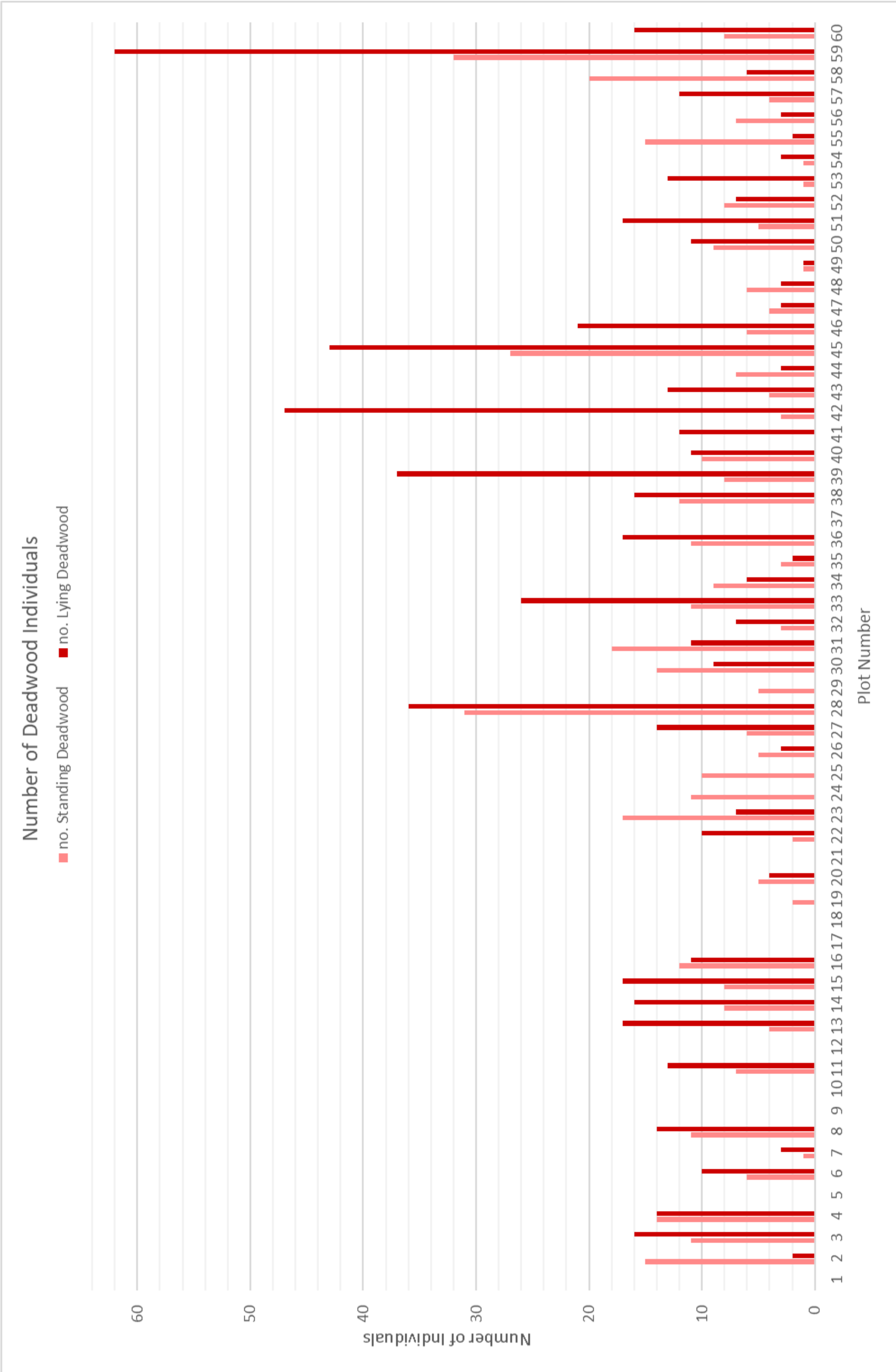


Figure 23. Amount of standing and lying deadwood per plot.

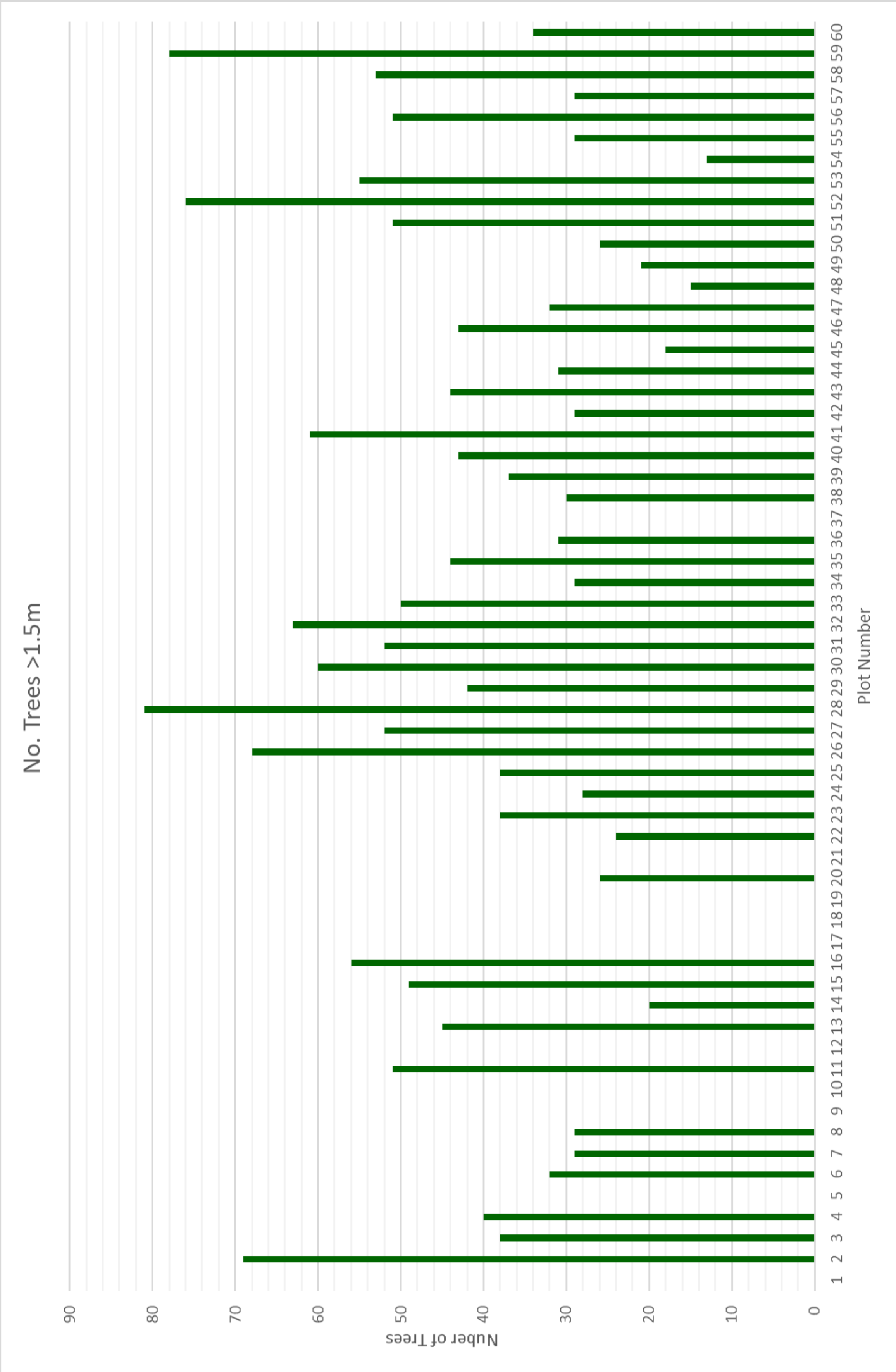


Figure 24. Number of trees higher than 150cm per plot.

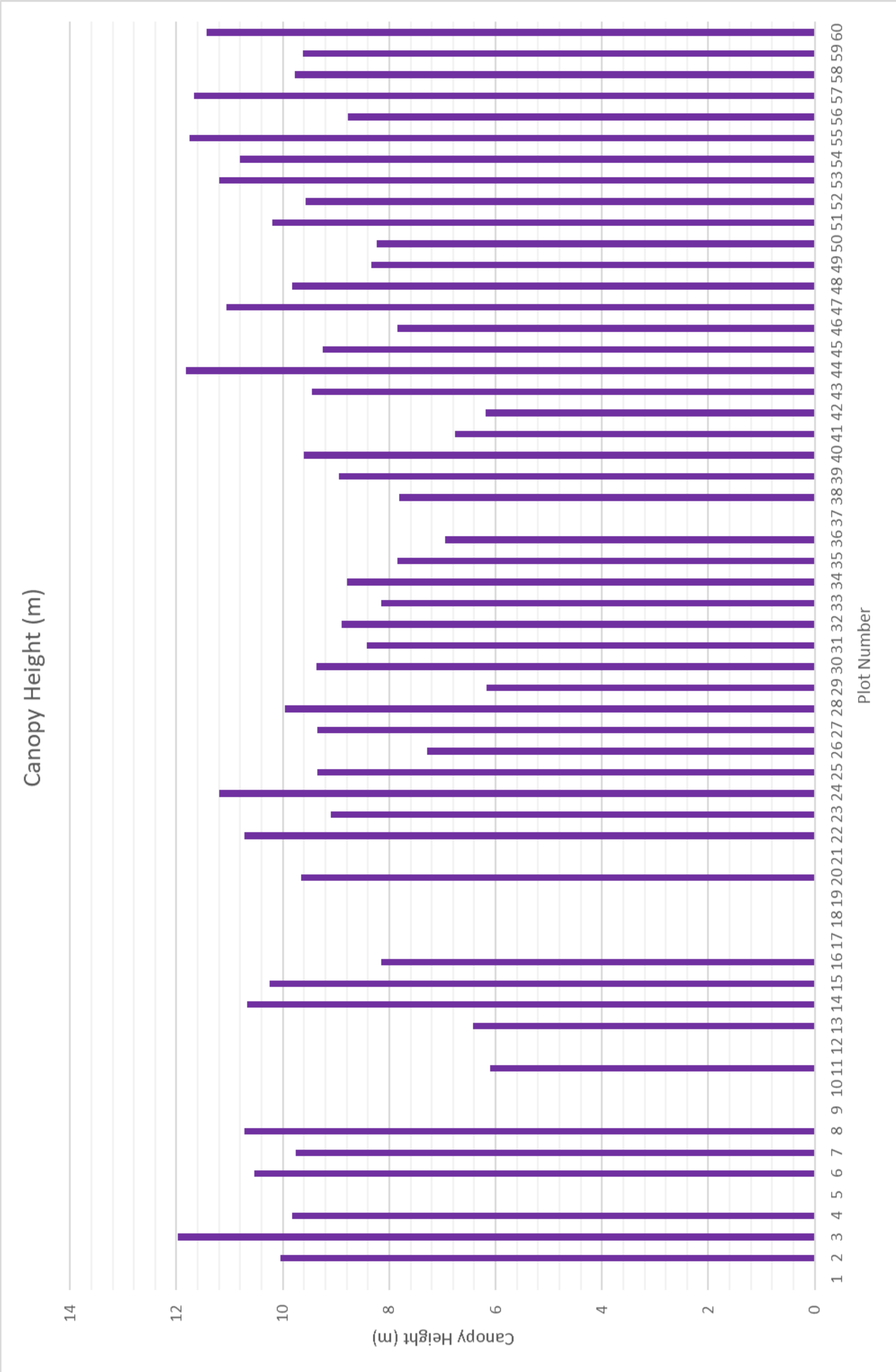


Figure 25. Canopy height (in metres) per plot. Note that these figures have likely been vastly underestimated.

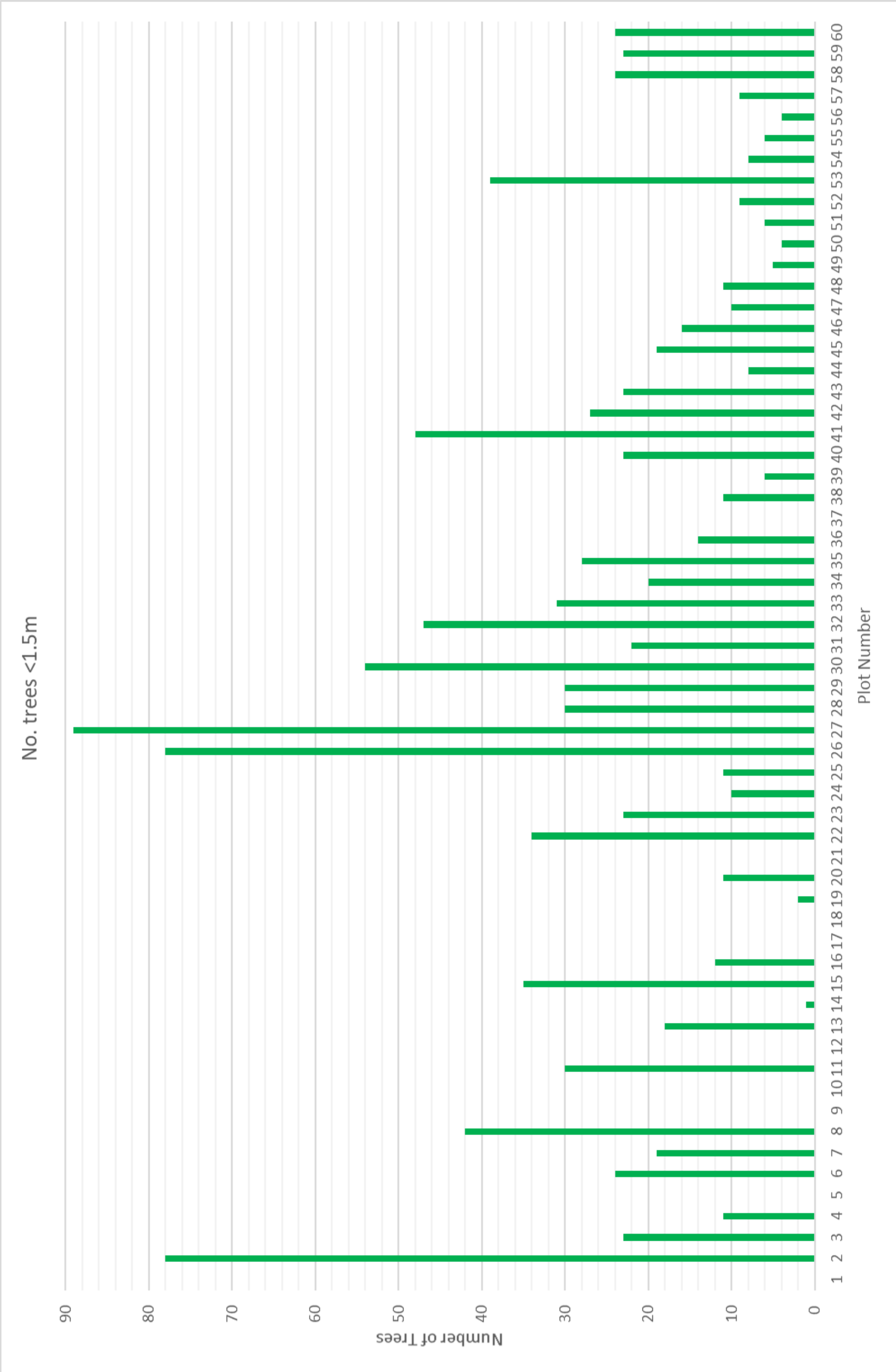


Figure 26. Number of trees below 150cm per plot.

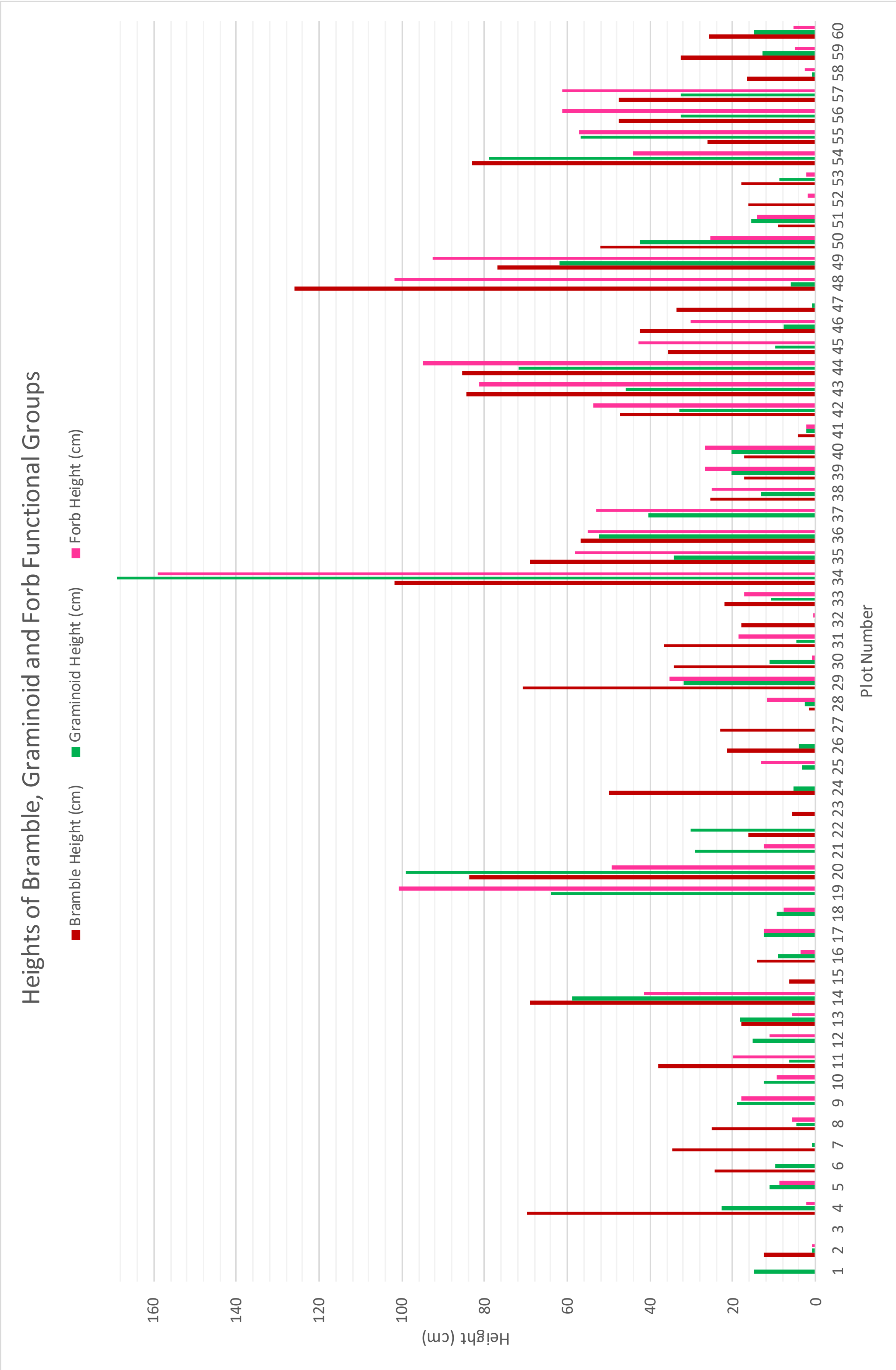


Figure 27. Heights of the bramble, graminoid and forb functional groups per plot.

Appendix 5

Here, I shall present some extra statistical results. The first table (table 6) shows the marginal means for the ANOVA tests presented in Figure 10 in the main section of the paper. The following figure (figure 28) shows the results of the individual species analysis for trees below 1.5m. As is visible here, there is not enough data, for a pattern to form, for almost all species. Third, I shall present the results of the post-hoc test which relate to the tests which were significant overall (mainly significant p-vales, presented in table 3). Partial Eta squared denotes the effect size. A larger effect size denotes a larger difference between the group means. LSD post-hoc tests were performed for bramble height, bramble cover, %trees debarked, and for the 3 sapling height classes relative to the 4 deer density groups. LSD could not be performed for lying deadwood, mature tree stems or bare soil cover as some groups had only one case. However, the partial Eta squared is still available for these. The Diff. (I-J) column is used for understanding differences between groups. A negative results means that the value of the J column is higher than that of the I column, and a positive result means that the J column has a lower value than the I column. The closer the Diff. (I-J) column is to 0, the less significant the mean difference between groups is. What is visible in both figure 10 and tables 7-16, is that there is lots of overlap between groups, even in the significant tests. Finally, table 18 presents the t-tests needed for comparisons of the 2017 and 2019 vegetation data (shown in the main text in section 3.3, figure 16). The t-tests show that bramble height, forb cover and graminoid cover show significant changes between 2017 and 2019 (not considering the seasonal effect).

Table 6. Moving means for each vegetation variable per deer density variables. These were calculated as part of the ANOVA tests. These are averaged means. Total mean is calculated as an average of the "all deer", "hinds" and "stags" GPS groups. Summer mean is calculated from "all deer summer", "hinds summer" and "stags summer". Similarly, the Winter mean is calculated from "all deer winter", "hinds winter" and "stag winters". The 95% confidence interval is not presented in this table, but we can still observe how each vegetation variable is affected by deer density.

Model	Mean	Density Quartile			
		25.00	**50.00**	**75.00**	**100.00**
Density vs. Bramble Height (cm)	**Total**	41.85	34.89	27.70	22.05
	Summer	41.08	34.86	25.79	21.80
	Winter	36.77	27.59	40.47	21.77
Density vs. Bramble Cover (%)	**Total**	36.53	29.63	23.25	29.82
	Summer	36.32	28.31	23.65	28.77
	Winter	32.40	26.62	31.10	29.48
Density vs. Forb Height (cm)	**Total**	36.29	32.15	19.92	19.41
	Summer	35.60	29.99	23.45	14.02
	Winter	31.03	22.68	40.08	14.15
Density vs. Forb Cover (%)	**Total**	13.32	16.58	13.36	11.29
	Summer	12.96	17.27	15.93	14.37
	Winter	13.72	15.19	15.04	12.08
Density vs. Graminoid Height (cm)	**Total**	30.16	26.65	22.61	12.50
	Summer	29.27	27.17	22.79	11.29
	Winter	28.08	18.04	27.86	14.53
Density vs. Graminoid Cover (%)	**Total**	13.89	18.94	30.48	21.85
	Summer	13.65	21.51	32.26	19.87
	Winter	18.58	22.85	22.89	23.85
Density vs. Bramble Browsing (%)	**Total**	41.09	41.49	36.22	43.90
	Summer	39.18	48.95	36.36	37.75
	Winter	40.64	35.66	43.89	51.30
Density vs. Forb Browsing (%)	**Total**	30.99	30.19	20.54	9.74
	Summer	26.98	31.94	19.27	12.39
	Winter	28.23	19.58	38.33	8.49
Density vs. Debarking (%)	**Total**	9.88	10.09	11.55	25.06
	Summer	9.40	11.18	9.47	27.23
	Winter	12.20	10.71	9.70	25.10

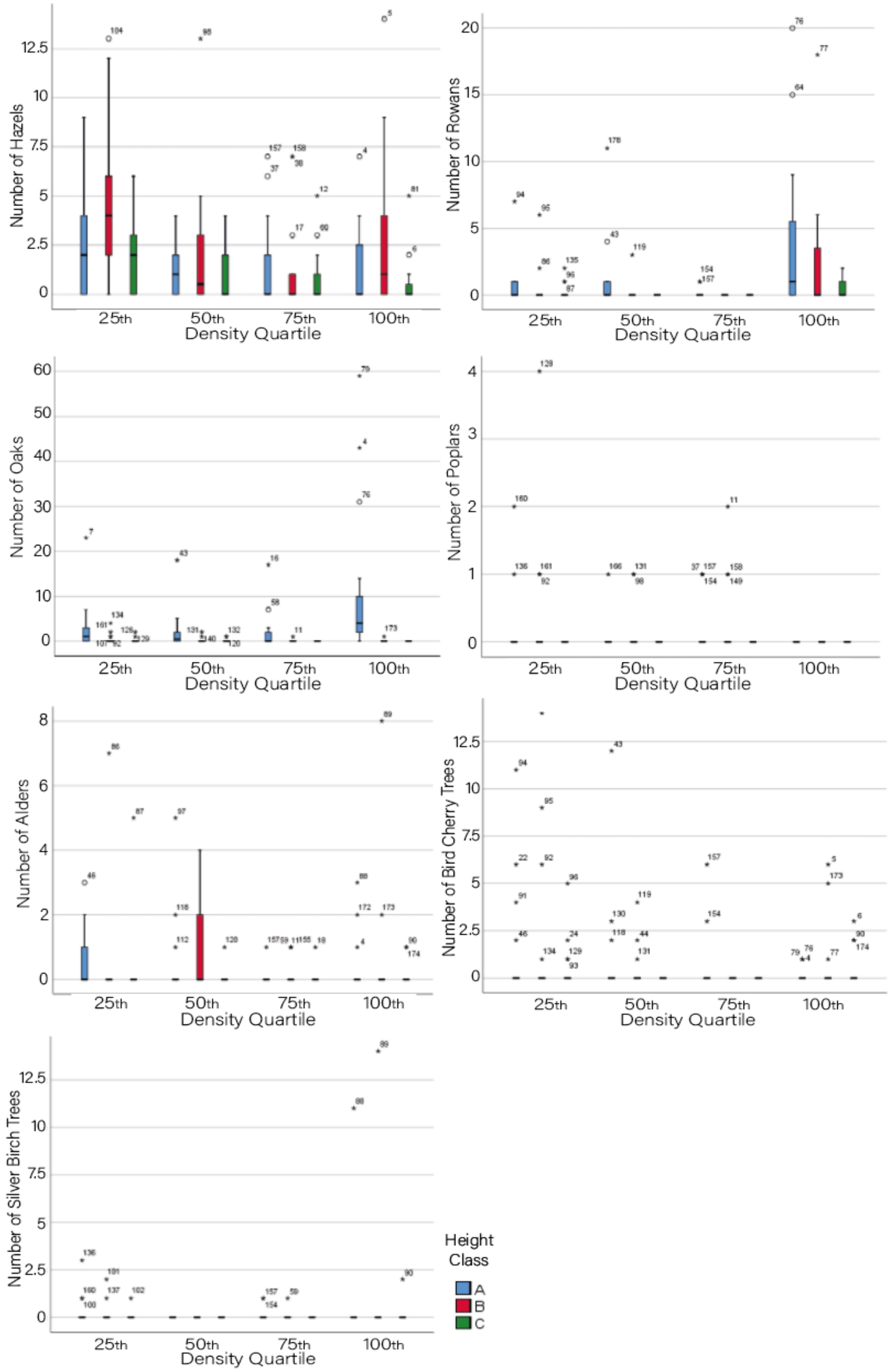


Figure 28. Box plots showing the numbers of individuals in each height category across the 4 density levels, for each of the 7 dominant species. Hazel, rowan and oak appeared in significant numbers in a larger proportion of plots. The 7 dominant species were determined to be species appearing in at any height in over 50% of plots. Species such as poplar, bird cherry and silver birch were commonly found as mature trees, although few were found as saplings below 1.5m. Though not observed to be widespread across the area (as hazel, rowan and oak appear to be), these species could still be found in higher numbers in concentrated patches.

Table 7. LSD post-hoc multiple comparison test for bramble height against deer density.

Dependent Variable: Bramble Height (cm) Predictor: Deer Density						
LSD Post-Hoc Multiple Comparisons						
(I) QuartileAllDeer	(J) Quart	Diff. (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower	Upper
25	50	4.5599	10.47908	0.665	-16.4322	25.552
	75	18.5759	10.70339	0.088	-2.8656	40.0173
	100	18.1461	10.28072	0.083	-2.4486	38.7409
50	25	-4.5599	10.47908	0.665	-25.552	16.4322
	75	14.0159	11.32647	0.221	-8.6737	36.7056
	100	13.5862	10.92792	0.219	-8.3051	35.4775
75	25	-18.5759	10.70339	0.088	-40.0173	2.8656
	50	-14.0159	11.32647	0.221	-36.7056	8.6737
	100	-0.4297	11.1432	0.969	-22.7523	21.8928
100	25	-18.1461	10.28072	0.083	-38.7409	2.4486
	50	-13.5862	10.92792	0.219	-35.4775	8.3051
	75	0.4297	11.1432	0.969	-21.8928	22.7523

Table 8. LSD post-hoc multiple comparison test for bramble cover against deer density.

Dependent Variable: Bramble Cover (%) Predictor: Deer Density						
LSD Post-Hoc Multiple Comparisons						
(I) QuartileAllDeer	(J) Quart	Diff. (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower	Upper
25	50	5.3381	8.75227	0.544	-12.1948	22.871
	75	16.909	8.93962	0.064	-0.9992	34.8172
	100	6.8167	8.5866	0.431	-10.3844	24.0177
50	25	-5.3381	8.75227	0.544	-22.871	12.1948
	75	11.5709	9.46002	0.226	-7.3798	30.5216
	100	1.4786	9.12715	0.872	-16.8053	19.7625
75	25	-16.909	8.93962	0.064	-34.8172	0.9992
	50	-11.5709	9.46002	0.226	-30.5216	7.3798
	100	-10.0923	9.30696	0.283	-28.7364	8.5518
100	25	-6.8167	8.5866	0.431	-24.0177	10.3844
	50	-1.4786	9.12715	0.872	-19.7625	16.8053
	75	10.0923	9.30696	0.283	-8.5518	28.7364

Table 9. LSD post-hoc multiple comparison test for forb height against deer density.

Dependent Variable: Forb Height (cm) Predictor: Deer Density						
LSD Post-Hoc Multiple Comparisons						
(I) Quartil	(J) Quartil	Diff. (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower	Upper
25	50	-0.08532	11.65491	0.994	-23.4329	23.2623
	75	22.32265	11.90439	0.066	-1.5247	46.17
	100	18.87778	11.43429	0.104	-4.0279	41.7834
50	25	0.08532	11.65491	0.994	-23.2623	23.4329
	75	22.40797	12.59739	0.081	-2.8276	47.6436
	100	18.9631	12.15412	0.124	-5.3845	43.3107
75	25	-22.3227	11.90439	0.066	-46.17	1.5247
	50	-22.408	12.59739	0.081	-47.6436	2.8276
	100	-3.44487	12.39356	0.782	-28.2721	21.3824
100	25	-18.8778	11.43429	0.104	-41.7834	4.0279
	50	-18.9631	12.15412	0.124	-43.3107	5.3845
	75	3.44487	12.39356	0.782	-21.3824	28.2721

Table 10. LSD post-hoc multiple comparison test for forb cover against deer density.

Dependent Variable: Forb Cover (%) Predictor: Deer Density						
LSD Post-Hoc Multiple Comparisons						
(I) Quartil	(J) Quartil	Diff. (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower	Upper
25	50	-7.99206	5.78419	0.173	-19.5792	3.5951
	75	2.24722	5.90801	0.705	-9.5879	14.0824
	100	0.85056	5.6747	0.881	-10.5172	12.2184
50	25	7.99206	5.78419	0.173	-3.5951	19.5792
	75	10.23929	6.25193	0.107	-2.2848	22.7634
	100	8.84262	6.03195	0.148	-3.2408	20.9261
75	25	-2.24722	5.90801	0.705	-14.0824	9.5879
	50	-10.2393	6.25193	0.107	-22.7634	2.2848
	100	-1.39667	6.15077	0.821	-13.7181	10.9248
100	25	-0.85056	5.6747	0.881	-12.2184	10.5172
	50	-8.84262	6.03195	0.148	-20.9261	3.2408
	75	1.39667	6.15077	0.821	-10.9248	13.7181

Table 11. LSD post-hoc multiple comparison test for graminoid height against deer density.

Dependent Variable: Graminoid Height (cm)						
Predictor: Deer Density						
LSD Post-Hoc Multiple Comparisons						
(I) Quartil	(J) Quartil	Diff. (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower	Upper
25	50	-0.52817	10.52048	0.96	-21.6032	20.5469
	75	5.13803	10.74568	0.634	-16.3881	26.6642
	100	17.15778	10.32134	0.102	-3.5183	37.8339
50	25	0.52817	10.52048	0.96	-20.5469	21.6032
	75	5.66621	11.37122	0.62	-17.1131	28.4455
	100	17.68595	10.9711	0.113	-4.2918	39.6637
75	25	-5.13803	10.74568	0.634	-26.6642	16.3881
	50	-5.66621	11.37122	0.62	-28.4455	17.1131
	100	12.01974	11.18723	0.287	-10.391	34.4305
100	25	-17.1578	10.32134	0.102	-37.8339	3.5183
	50	-17.686	10.9711	0.113	-39.6637	4.2918
	75	-12.0197	11.18723	0.287	-34.4305	10.391

Table 12. LSD post-hoc multiple comparison test for graminoid cover against deer density.

Dependent Variable: Graminoid Cover (%)						
Predictor: Deer Density						
LSD Post-Hoc Multiple Comparisons						
(I) Quartil	(J) Quartil	Diff. (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower	Upper
25	50	-10.8655	9.23812	0.245	-29.3717	7.6407
	75	-23.95064*	9.43587	0.014	-42.853	-5.0483
	100	-7.89833	9.06325	0.387	-26.0542	10.2575
50	25	10.86548	9.23812	0.245	-7.6407	29.3717
	75	-13.0852	9.98516	0.195	-33.0878	6.9175
	100	2.96714	9.63381	0.759	-16.3317	22.266
75	25	23.95064*	9.43587	0.014	5.0483	42.853
	50	13.08516	9.98516	0.195	-6.9175	33.0878
	100	16.05231	9.8236	0.108	-3.6267	35.7313
100	25	7.89833	9.06325	0.387	-10.2575	26.0542
	50	-2.96714	9.63381	0.759	-22.266	16.3317
	75	-16.0523	9.8236	0.108	-35.7313	3.6267

Table 13. LSD post-hoc multiple comparison test for trees debarked against deer density.

Dependent Variable: Trees Debarked (%) Predictor: Deer Density						
LSD Post-Hoc Multiple Comparisons						
(I) QuartileAllDeer	(J) Quart	Diff. (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower	Upper
25	50	-2.6478	5.25209	0.616	-13.169	7.8734
	75	-3.0186	5.36452	0.576	-13.765	7.7278
	100	-15,1892*	5.15268	0.005	-25.5113	-4.8672
50	25	2.6478	5.25209	0.616	-7.8734	13.169
	75	-0.3708	5.6768	0.948	-11.7428	11.0012
	100	-12,5414*	5.47706	0.026	-23.5133	-1.5696
75	25	3.0186	5.36452	0.576	-7.7278	13.765
	50	0.3708	5.6768	0.948	-11.0012	11.7428
	100	-12,1706*	5.58495	0.034	-23.3586	-0.9826
100	25	15,1892*	5.15268	0.005	4.8672	25.5113
	50	12,5414*	5.47706	0.026	1.5696	23.5133
	75	12,1706*	5.58495	0.034	0.9826	23.3586

Table 14. LSD post-hoc multiple comparison test for number of trees <50cm against deer density.

Dependent Variable: NoTreeslt50cm Predictor: Deer Density						
LSD Post-Hoc Multiple Comparisons						
(I) QuartileAllDeer	(J) QuartileAllDeer	Diff. (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower	Upper
25	50	3.4286	4.84385	0.482	-6.2748	13.132
	75	5.3077	4.94754	0.288	-4.6034	15.2188
	100	-8.2667	4.75216	0.087	-17.7864	1.2531
50	25	-3.4286	4.84385	0.482	-13.132	6.2748
	75	1.8791	5.23555	0.721	-8.6089	12.3672
	100	-11,6952*	5.05133	0.024	-21.8143	-1.5762
75	25	-5.3077	4.94754	0.288	-15.2188	4.6034
	50	-1.8791	5.23555	0.721	-12.3672	8.6089
	100	-13,5744*	5.15084	0.011	-23.8927	-3.256
100	25	8.2667	4.75216	0.087	-1.2531	17.7864
	50	11,6952*	5.05133	0.024	1.5762	21.8143
	75	13,5744*	5.15084	0.011	3.256	23.8927

Table 15. LSD post-hoc multiple comparison test for number of trees 51-100cm against deer density.

Dependent Variable: NoTrees51cm100cm Predictor: Deer Density						
LSD Post-Hoc Multiple Comparisons						
(I) QuartileAllDeer	(J) QuartileAllDeer	Diff. (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower	Upper
25	50	5,7063*	2.38815	0.02	0.9223	10.4904
	75	8,1239*	2.43927	0.002	3.2375	13.0104
	100	2.0778	2.34294	0.379	-2.6157	6.7713
50	25	-5,7063*	2.38815	0.02	-10.4904	-0.9223
	75	2.4176	2.58126	0.353	-2.7533	7.5885
	100	-3.6286	2.49044	0.151	-8.6175	1.3604
75	25	-8,1239*	2.43927	0.002	-13.0104	-3.2375
	50	-2.4176	2.58126	0.353	-7.5885	2.7533
	100	-6,0462*	2.5395	0.021	-11.1334	-0.9589
100	25	-2.0778	2.34294	0.379	-6.7713	2.6157
	50	3.6286	2.49044	0.151	-1.3604	8.6175
	75	6,0462*	2.5395	0.021	0.9589	11.1334

Table 16. LSD post-hoc multiple comparison test for number of trees 101-150cm against deer density.

Dependent Variable: NoTrees101cm150cm Predictor: Deer Density						
LSD Post-Hoc Multiple Comparisons						
(I) QuartileAllDeer	(J) QuartileAllDeer	Diff. (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower	Upper
25	50	2,1190*	0.72081	0.005	0.6751	3.563
	75	2,6410*	0.73623	0.001	1.1662	4.1159
	100	1.3333	0.70716	0.065	-0.0833	2.7499
50	25	-2,1190*	0.72081	0.005	-3.563	-0.6751
	75	0.522	0.77909	0.506	-1.0387	2.0827
	100	-0.7857	0.75168	0.3	-2.2915	0.7201
75	25	-2,6410*	0.73623	0.001	-4.1159	-1.1662
	50	-0.522	0.77909	0.506	-2.0827	1.0387
	100	-1.3077	0.76649	0.094	-2.8432	0.2278
100	25	-1.3333	0.70716	0.065	-2.7499	0.0833
	50	0.7857	0.75168	0.3	-0.7201	2.2915
	75	1.3077	0.76649	0.094	-0.2278	2.8432

Table 17. Effect size tables (partial Eta squared) for deer density as a dependent factor, with number of lying deadwood individuals, number of mature tree stems (>1.5m) and %bare soil cover as the predictors. Post-hoc test were not available for these, as some predictor groups had fewer than two cases (which is needed for a post-hoc comparison).

Dependent Variable: QuartileAllDeer50m						
Fixed Factor/Predictor: Lying Deadwood						
Source	df	Mean Sq.	F	Sig.	Partial Eta Squared	
Corrected Model	21	916.541	1.119	0.371	0.382	
Intercept	1	98756.109	120.6	0	0.76	
no.LyingDeadwooc	21	916.541	1.119	0.371	0.382	
Error	38	818.874				
Total	60					
Corrected Total	59					
a R Squared = ,382 (Adjusted R Squared = ,041)						

Dependent Variable: QuartileAllDeer50m						
Fixed Factor/Predictor: No. Mature Tree Stems						
Source	df	Mean Sq.	F	Sig.	Partial Eta Squared	
Corrected Model	48	995.877	4.275	0.006	0.949	
Intercept	1	168541.5	723.495	0	0.985	
NumberofTreeSter	48	995.877	4.275	0.006	0.949	
Error	11	232.955				
Total	60					
Corrected Total	59					
a R Squared = ,949 (Adjusted R Squared = ,727)						

Dependent Variable: QuartileAllDeer50m						
Fixed Factor/Predictor: %Bare Soil Cover						
Source	df	Mean Sq.	F	Sig.	Partial Eta Squared	
Corrected Model	43	977.125	1.873	0.087	0.834	
Intercept	1	163282.5	312.944	0	0.951	
BareSoilCover	43	977.125	1.873	0.087	0.834	
Error	16	521.763				
Total	60					
Corrected Total	59					
a R Squared = ,834 (Adjusted R Squared = ,389)						

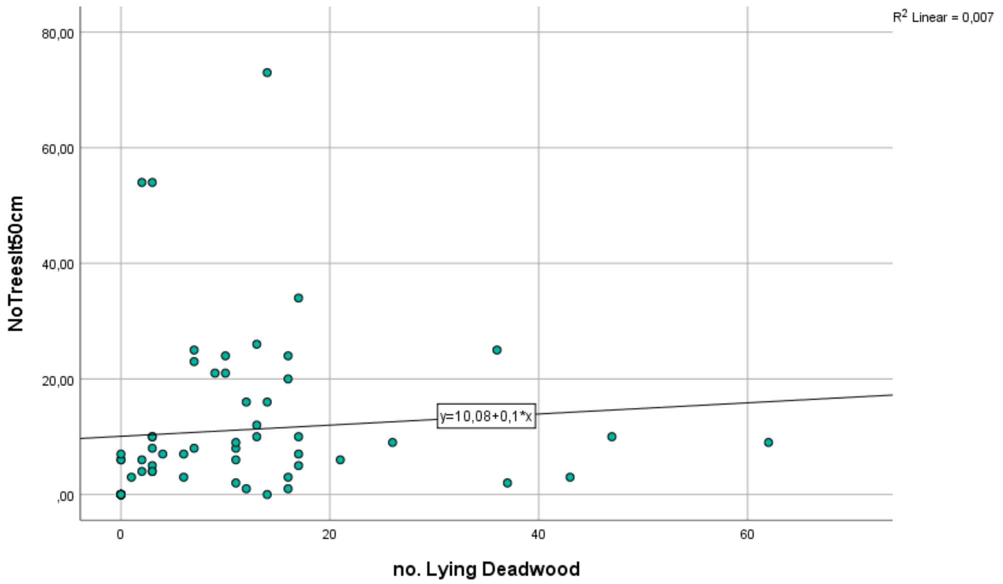
Table 18. T-test values and mean differences between related vegetation functional groups in 2017 and 2019.

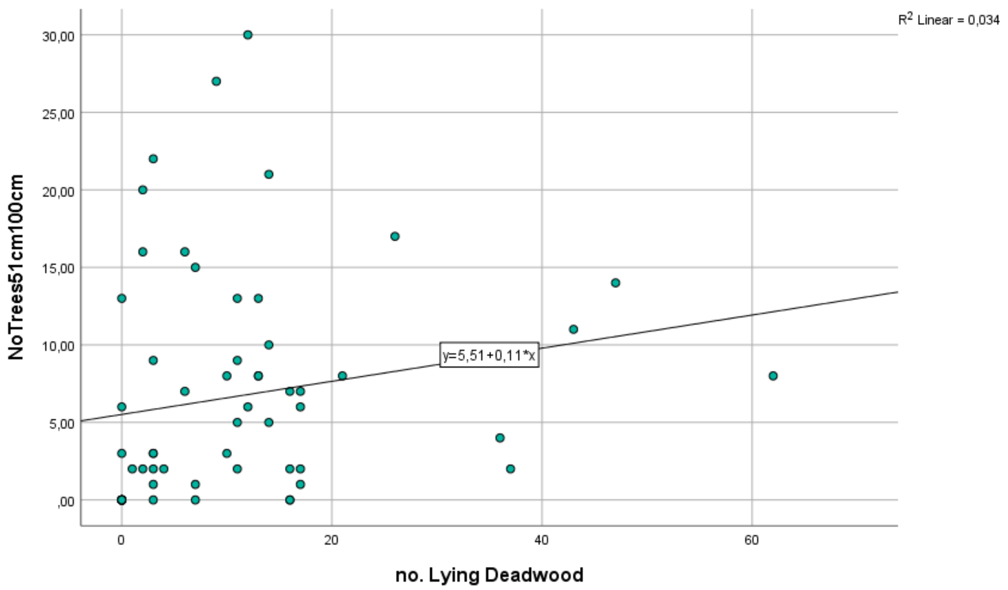
Bramble Cover 2017-2019							
	N	**Mean**	**Std. Dev.**	**Std. Error Mean**			
BrambleCover2017	60	31.08	34.087	4.401			
BrambleCover2019	60	35.35	27.507	3.551			
	t	**df**	**Sig.**	**Mean Diff.**	**95% Confidence Interval of the Difference**		
					Lower	**Upper**	
BrambleCover2017	7.063	59	0	31.083	22.28	39.89	
BrambleCover2019	9.955	59	0	35.35	28.24	42.46	
Graminoid Cover 2017-2019							
	N	**Mean**	**Std. Dev.**	**Std. Error Mean**			
GrassCover2017	60	16.32	31.025	4.005			
GrassCover2019	60	24.25	25.174	3.25			
	t	**df**	**Sig.**	**Mean Diff.**	**95% Confidence Interval of the Difference**		
					Lower	**Upper**	
GrassCover2017	4.074	59	0	16.317	8.3	24.33	
GrassCover2019	7.462	59	0	24.25	17.75	30.75	
Forb Cover 2017-2019							
	N	**Mean**	**Std. Dev.**	**Std. Error Mean**			
ForbCover2017	60	4.6	11.245	1.452			
ForbCover2019	60	16.47	16.3	2.104			
	t	**df**	**Sig.**	**Mean Diff.**	**95% Confidence Interval of the Difference**		
					Lower	**Upper**	
ForbCover2017	3.169	59	0.002	4.6	1.7	7.5	
ForbCover2019	7.825	59	0	16.467	12.26	20.68	
Common Rush Cover 2017-2019							
	N	**Mean**	**Std. Dev.**	**Std. Error Mean**			
CommonRushCover2017	57	9.82	18.992	2.516			
CommonRushCover2019	60	4.22	5.39	0.696			
	t	**df**	**Sig.**	**Mean Diff.**	**95% Confidence Interval of the Difference**		
					Lower	**Upper**	
CommonRushCover2017	3.906	56	0	9.825	4.79	14.86	
CommonRushCover2019	6.06	59	0	4.217	2.82	5.61	
Herbaceous Cover 2017-2019							
	N	**Mean**	**Std. Dev.**	**Std. Error Mean**			
HerbCover2017	60	35.82	38.481	4.968			
HerbCover2019	60	39.13	32.464	4.191			
	t	**df**	**Sig.**	**Mean Diff.**	**95% Confidence Interval of the Difference**		
					Lower	**Upper**	
HerbCover2017	7.21	59	0	35.817	25.88	45.76	
HerbCover2019	9.337	59	0	39.133	30.75	47.52	

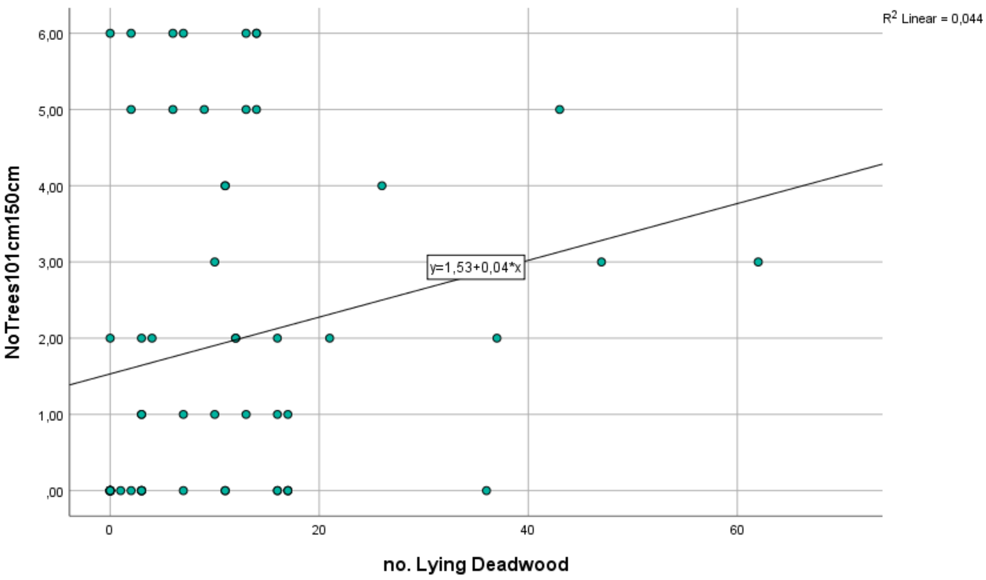
Bramble Height 2017-2019								
	N	**Mean**	**Std. Dev.**	**Std. Error Mean**				
BrambleHeightcm2017	60	95	90.544	11.689				
BrambleHeightcm2019	60	47.45	42.825	5.529				
	t	**df**	**Sig.**	**Mean Diff.**	**95% Confidence of the Difference**			
					Lower	**Upper**		
BrambleHeightcm2017	8.127	59	0	95	71.61	118.39		
BrambleHeightcm2019	8.583	59	0	47.45	36.39	58.51		
Common Rush Height 2017-2019								
	N	**Mean**	**Std. Dev.**	**Std. Error Mean**				
CommonRushHeightcm2(	60	30.42	42.269	5.457				
CommonRushHeightcm2(	60	40.68	35.168	4.54				
	t	**df**	**Sig.**	**Mean Diff.**	**95% Confidence Interval of the Difference**			
					Lower	**Upper**		
CommonRushHeightcm2(	5.574	59	0	30.417	19.5	41.34		
CommonRushHeightcm2(	8.961	59	0	40.683	31.6	49.77		
Herbaceous Layer Height 2017-2019								
	N	**Mean**	**Std. Dev.**	**Std. Error Mean**				
HerbHeightcm2017	60	51.47	49.453	6.384				
HerbHeightcm2019	60	46.38	42.754	5.52				
	t	**df**	**Sig.**	**Mean Diff.**	**95% Confidence Interval of the Difference**			
					Lower	**Upper**		
HerbHeightcm2017	8.061	59	0	51.467	38.69	64.24		
HerbHeightcm2019	8.404	59	0	46.383	35.34	57.43		

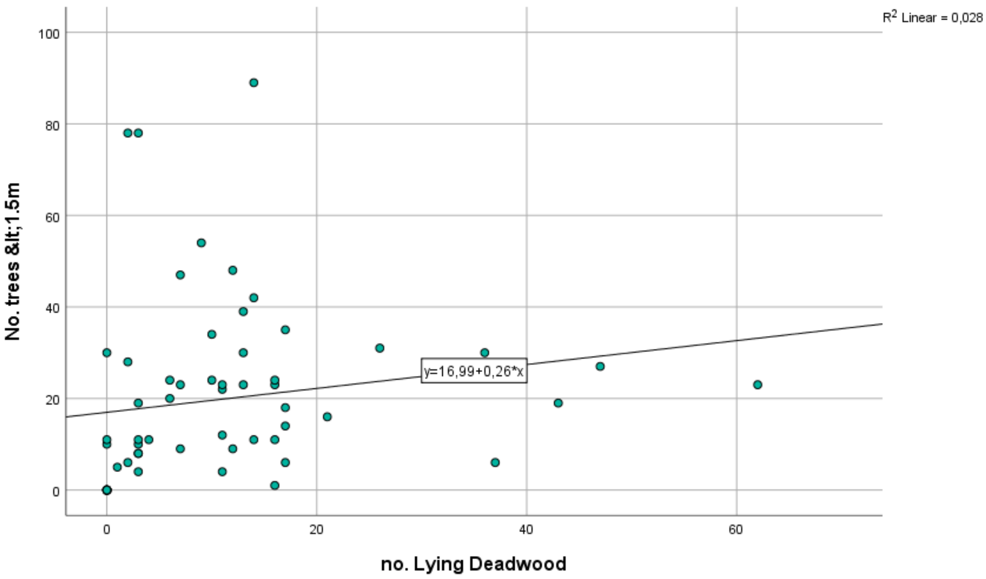
Appendix 6

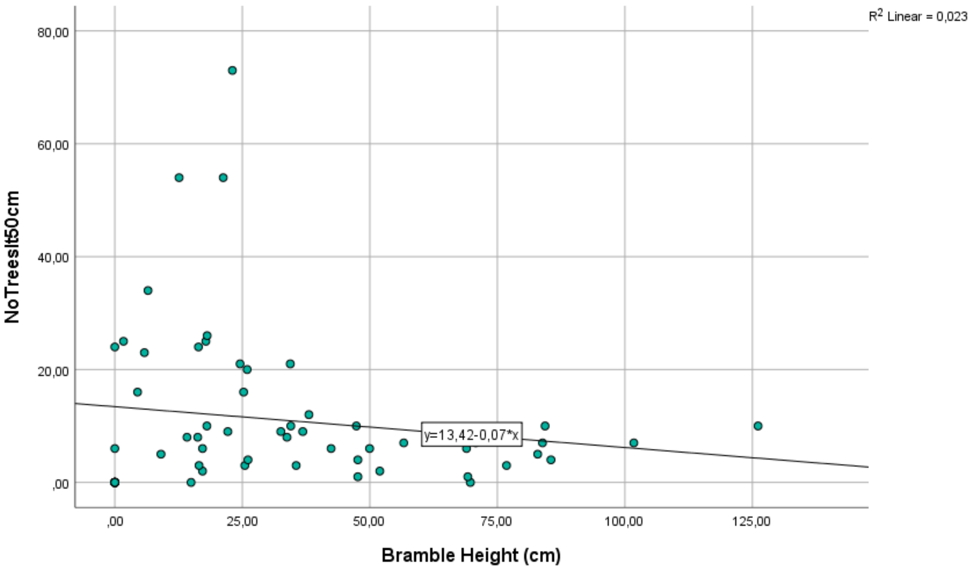
This section presents the linear regression scatter plots for the tests of tree saplings again lying deadwood and bramble height. These scatter plots correspond to table 5 in the main text.

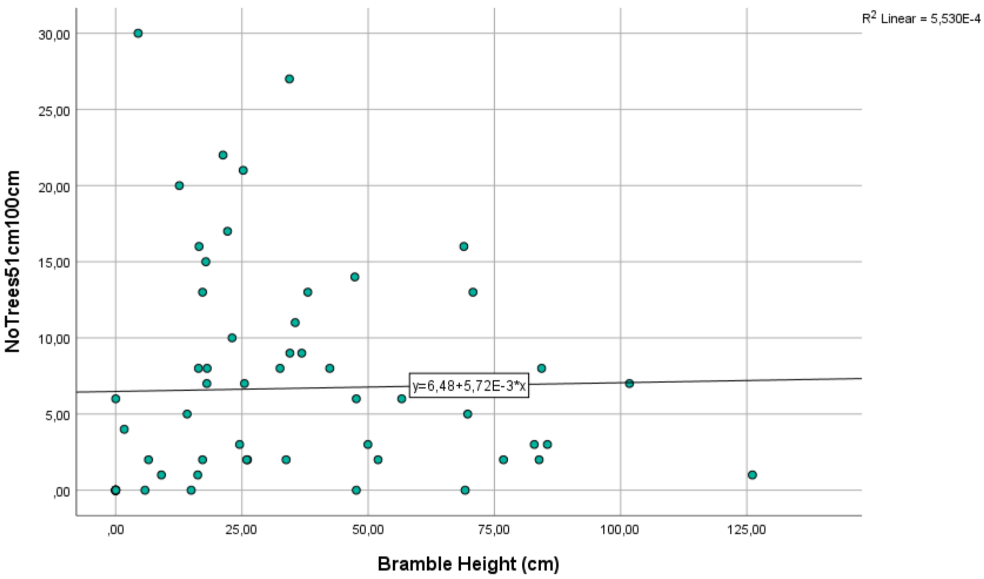


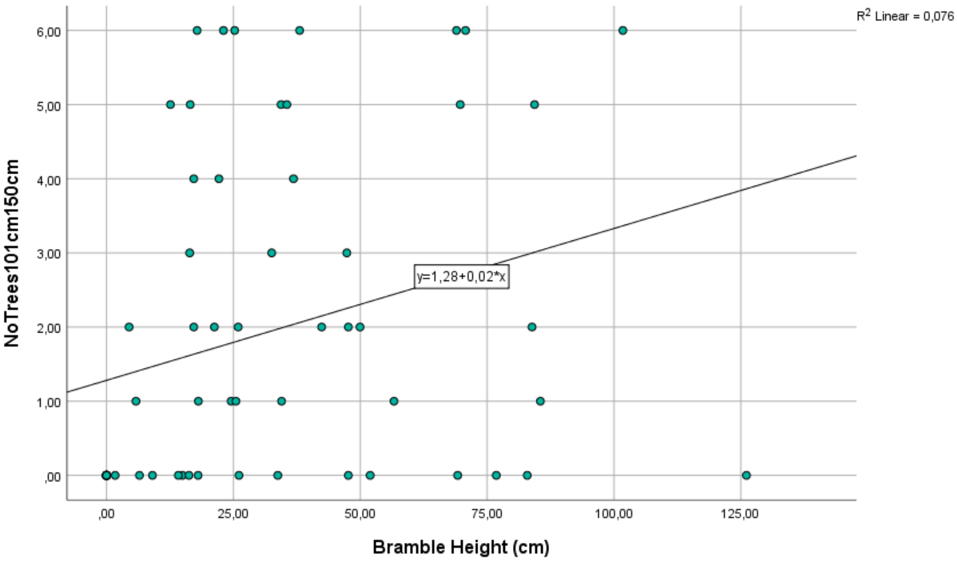


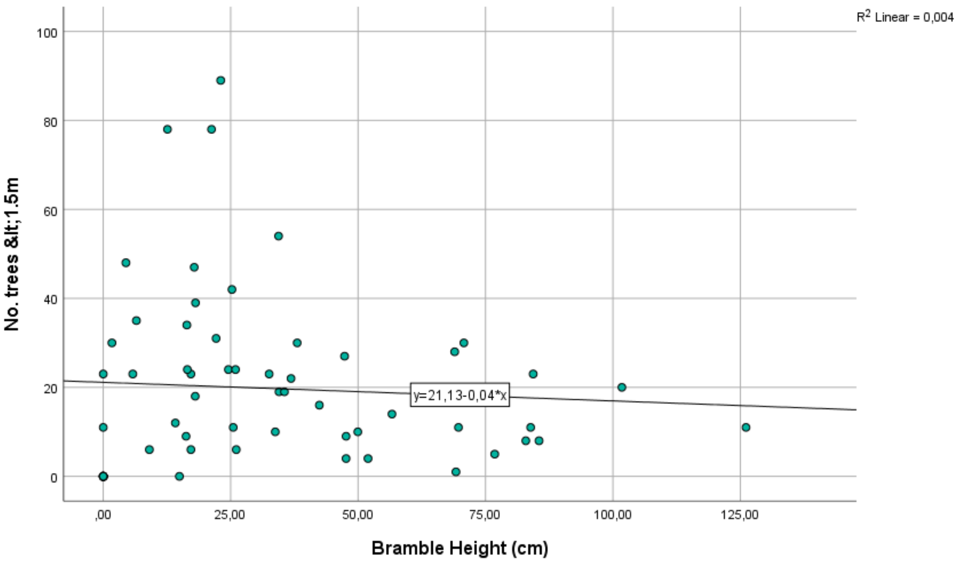

R2 Linear = 0,044
6,00
5,00
4,00
3,00
2,00
1,00
,00
NoTrees101cm150cm
y=1,53+0,04*x
0
20
40
60
no. Lying Deadwood


R2 Linear = 0,028
100
80
60
40
20
0
No. trees <1.5m
y=16,99+0,26*x
0
20
40
60
no. Lying Deadwood


R2 Linear = 0,023
80,00
60,00
40,00
20,00
,00
NoTreeslt50cm
y=13,42-0,07*x
,00
25,00
50,00
75,00
100,00
125,00
Bramble Height (cm)


R2 Linear = 5,530E-4
y=6,48+5,72E-3*x
NoTrees51cm100cm
Bramble Height (cm)


R2 Linear = 0,076
y=1,28+0,02*x
NoTrees101cm150cm
Bramble Height (cm)


R2 Linear = 0,004
y=21,13-0,04*x
No. trees <1.5m
Bramble Height (cm)