Pastures facilitate the establishment of light-demanding tree species

Regeneration pathways in grazed pasture habitats in Southern Sweden

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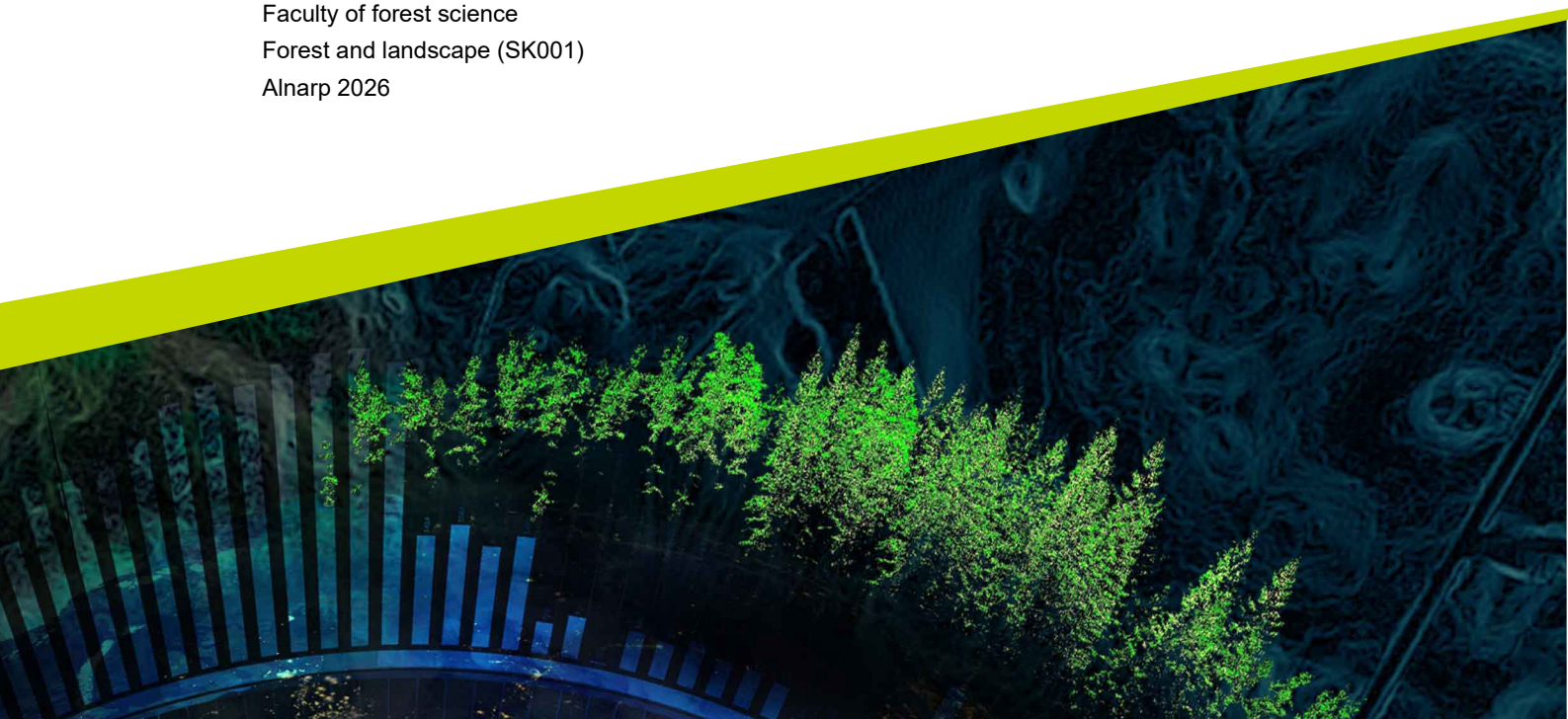

Pastures facilitate the establishment of light-demanding tree species; regeneration pathways in grazed pasture habitats in Southern Sweden

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Abstract

In the lowlands of Europe, grazed wood-pasture landscapes are highly valuable habitat types, with high amounts of biodiversity and other ecosystem services. This study tries to parameterise the dynamics between thorny scrub and tree crown, and the differences in the species composition of pastures and adjacent forests. Field observations were taken at seven protected grazed pastures in southern Sweden. Shrub patches were measured in terms of area, height and species composition, while tree regeneration was measured by height, stem diameter, and crown diameter. The frequency of shrub shoots was measured underneath free-standing mature trees. In adjacent forests, tree regeneration and basal area was measured in thirty meter transects. The results were analysed with a generalised additive mixed model (GAMM) and non-metric multidimensional scaling (NMDS).

There was a significant difference between the relative species abundance and the relative basal area per species between pastures and adjacent forests, with a greater number of light-demanding species regenerating in the pastures. The dynamics between the size of the tree crown and the occurrence of shrubs beneath it follows an S-curve, whilst the shrub shoot density decreases with the size of the tree crown. These results show that grazed wood-pastures can give regeneration pathways to tree species that would have a difficult time growing underneath closed canopies. Due to the value of wood-pastures as a habitat, it is of vital importance that these highly complex ecosystems are fully understood and modelled, so that they can be protected better in future. These parameterisations could be used in the future to create a robust model of these ecosystems.

Keywords: Wood-pasture, tree regeneration, tree crown shrub dynamics, southern Sweden, habitat protection

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Abbreviations

Abbreviation	Description
BJO	Björnö naturreservat
BRB	Brösarps backar naturreservat
GAMM	Generealised additive mixed model
HRF	Humlarödshus fälad naturreservat
KNV	Knivsås naturreservat
KVS	Kronovalls store vång naturreservat
NMDS	Non-metric multidimensional scaling
SAR	Shrub assisted regeneration
SBC	Stiby backe canopy
SMR	Standing mature regeneration
SSR	Spontaneous sapling regeneration
STB	Stiby backe naturreservat
TCTV	The theory of the cyclical turnovers of vegetation
VRS	Värnanäs naturreservat

1. Introduction

Few areas in the world have been more cultivated than the European lowlands. Currently, agricultural land makes up 40% of the territory of the European union member states, reaching over 50% in lowland countries (European Union, 2026). The situation puts the ecosystem services of natural ecosystems at risk, and resulted in the introduction of the EU restoration law (European Environment Agency, 2025) and numerous national level regulations to preserve the remains of the natural vegetation cover. However, the definition of the reference conditions that could potentially both guide the restoration measures and gauge their effectiveness remains the subject of ongoing debate.

For most of the 20th century, the general consensus on the state of European lowland vegetation before the advent of humanity was that it was a close-canopy deciduous forest (Harris & Harris, 1991; Watt, 1947), where the climax ecosystems were wholly dependent on the vegetation and the ecology of the plants (Iversen, 1960). This theory of succession states that the plant community develops from bare ground to a climax ecosystem following successive stages, with these stages being determined by the prevailing climatological conditions. The plants that thrive in these stages are always the tallest plants, because they are the strongest in the competition for light (Clements, 1916). An alternative view, "the theory of the cyclical turnovers of vegetation" (TCTV) (Vera 2000) has proposed that the lowlands of Europe were more open and park-like, and that large herbivores played an integral part in how the landscape and ecosystem operated. The closest modern analogy to these lost landscapes is wood pastures, an ecosystem composed of discontinuous forest canopy and bush vegetation.

The TCTV posits that the vegetation, of any particular area of lowland Europe before the advent of humanity, follows a cycle consisting of three modules. The first module is the open grassland, where grazers facilitate the arrival of thorny bushes, like hawthorn (*Crataegus spp.*) and blackthorn (*Prunus spinosa*). Within and on the fringes of this scrub are the only places in the grassland where trees will be able to grow. The seeds of these trees will end up in these bushes by the wind, or by animals like the Eurasian jay (*Garrulus glandarius*) and the northern nutcracker (*Nucifraga caryocatactes*) for oak (*Quercus spp.*) and common hazel (*Corylus avellana*) respectively (Vera, 2000).

Over time, the trees will outcompete the scrub that they grew in and form a grove. There is no change in the composition of the vegetation, since large herbivores stifle the regeneration of any shade-tolerant tree-species. At this stage, regeneration is limited to the fringes of these groves, where there is no competition for light and where there is still spiky shrub. In the third and last module the canopy of the grove opens up due to storm or disease. Due to the fact

that there is more light on the ground, but not enough light for the thorned shrubs, it will cause an increase in grasses and herbaceous plants, attracting the specialised grazers. The grazers cause the open spot in the grove to increase in size, until eventually it will become large enough to support the light-demanding thorny scrub. At the time scale beyond the lifespan of dominant tree species, grasslands and forests alternate each other, the system being modulated by grazers and thorned scrub (Schalk, 1990; Spiecker & Spiecker, 1988; Vera, 2000).

The wood pasture, despite the fact that these landscapes are highly valuable in terms of cultural and biodiversity values, is a very threatened habitat in Europe (Bergmeier & Roellig, 2014). The wood-pastures of today have many threats, including overgrazing, disease and abandonment. The intena

sification of agriculture in Europe is the main driver of most of these threats, placing many low-intensive agricultural habitats in jeopardy (Bergmeier et al., 2010). In concurrence with this, many light demanding tree species are becoming rarer, many failing to properly regenerate in the modern closed-canopy forest (Vera, 2000).

Whilst TCTV has been extensively researched in other European countries, in Sweden the research has always stayed limited (Oldén et al., 2017). The research into TCTV has always been smaller scale however, focussing on a singular or a few variable(s); a cohesive model is something that does not exist. This research gap is unfortunate for three reasons: (a) it is likely that TCTV dynamics were the prehistoric conditions of southern Sweden (Vera, 2000), (b) areas governed by TCTV dynamics, like wood pastures, are high in biodiversity (Bergmeier et al., 2010), and (c) spatially integrated models are a tool of increasing importance in the field of nature conservation (Campbell, 2025).

I studied the dynamics of pasture vegetation on eight sites in seven southern Swedish nature reserves, representing different stages of succession from open pastures towards close-canopy forests. With a focus on understanding the role of pastures in tree species diversity at a landscape level and the dynamics that govern shrub-tree relations, I formulated two null hypotheses:
(NullH1) Composition of tree species in semi-natural pasturelands is the same as the composition in adjacent closed-canopy forests.
(NullH2) There is no effect of the crown size on the density of thorny scrub underneath the crown in semi-natural pasturelands in Southern Sweden.

The alternative hypothesises to these null hypotheses are that the species compositions is different between forest and pasture, and that there is an effect of the crown size on the shrub density. The ultimate goal of this study was to contribute to process-based modelling of vegetation dynamics in wood pastures and to provide a parameterisation of TCTV on modern day ecosystems.

2. Methods

2.1 Data collection

The data were collected in eight grazed pastures in seven nature reserves, located in the provinces of Skåne, Blekinge and Kalmar (Fig 1. & Table 1).

Figure 1: map showing the study sites. The data were collected on eight grazed pastures in seven nature reserves, located in the provinces of Skåne, Blekinge and Kalmar.

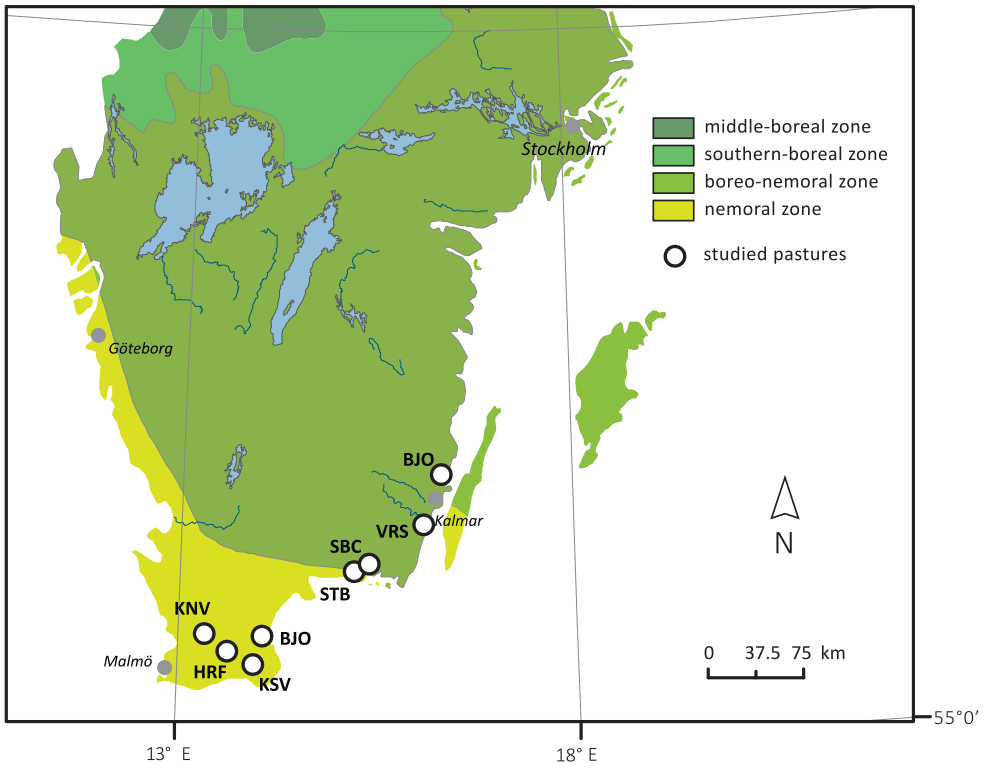


Table 1: Studied pastures and their ID, location and size.

Pasture name	Pasture ID	Forest adjacent	Coordinates	Size (ha)	County
Björnö	BJO	No	56.77147028512293, 16.371629231102933	103.5	Kalmar
Brösarps backar	BRB	No	55.71926332967376, 14.131151850862185	58	Skåne
Humlarödshus Fälad	HRF	Yes	55.600945545684894, 13.6686129112441	16	Skåne
Kronovalls store vång	KNV	Yes	55.63881032175975, 14.043130907524459	50	Skåne
Knivsås-Borelund	KVS	Yes	55.68726187494841, 13.510474796882216	159	Skåne
Stiby Backe Canopy	SBC	No	56.019783334473416, 14.685813879396925	131.5	Blekinge
Stiby Backe	STB	Yes	56.02598878883427, 14.706383051104904	131.5	Blekinge
Värnanäs	VRS	No	56.485952914464534, 16.140661023393033	239	Kalmar

I selected sites that had (1) patches of thorny scrub, (2) evidence of (cattle) grazing, (3) the absence of (major) human disturbance and (4) the absence of large rock formations, due to the protection effect they provide. This set of selection criteria resulted in a selection of sites which likely featured intermediate levels of browsing and grazing pressures that allowed the regeneration of bushes and associated dynamics of tree regeneration. Despite this observation, the sites nevertheless represented the gradients of grazing intensity and shrub cover. I noted two different categories of pasture; Pastures with forest adjacent to the site, and forests without an adjacent forest. These categories were named “forested” and “unforested”.

In sites with an adjacent forest, the pasture was surveyed using a transect, moving from the “forested side” to the other side of the pasture. In pastures where there was no forest adjacent or in close proximity of the pasture, a transect was made from the entrance of the pasture, either straight or perpendicular to the entrance. The width of transect was based on the density and size of shrubs in the pasture, ensuring that enough data were gathered in every site. In these transects, all shrub patches and trees that met the requirements were measured, unless there were either signs of human disturbance or large rocks. This filtering was done to reduce the background noise of the data.

In the field, I measured the size of shrub patches, the height and diameter of tree regeneration, and the basal area and frequency of regeneration in the forests adjacent to surveyed pastures. The location of the centre of the shrub patch was measured using Emlid RX GPS unit for each shrub patch.

Shrub patches were defined as a patch of thorny scrub that is clearly defined in its size, and that has a density that would protect small trees against the predation of large grazers. The large grazer in our study was the cow (*Bos taurus*); therefore, the borders of the patch were determined by assessing the possibility for a cow to move in a space which can be a potential "separator" of two patches. The site criteria were also used to choose the shrub-patch measured, as some sites had local variation in rockiness, or human disturbance. The species that we considered eligible for this shrub, regardless of height and size, are in accordance with Vera (2000, pg. 342): hawthorn, blackthorn, blackberry (*Rubus fruticosus*), wild roses (*Rosa spp.*), and juniper (*Juniperus communis*). Additionally, we added European wild apple (*Malus sylvestris*), European raspberry (*Rubus idaeus*), and gooseberry (*Ribes uva-crispa*) to the list, as they behaved similarly to the species above, or because they often added to the protection effect of other, more dominant shrubs.

For each shrub patch, I measured two diameters using a five-metre-long ruler, assuming its shape to be an ellipse, and height. The height was taken from the ground to the highest shrub. I noted all bush and tree species.Tree regeneration was defined as any tree, no matter the size or age, that grew in the pasture. This regeneration was classified in three categories, based on their appearance in the field. The first is "shrub-assisted regeneration" (SAR). These are all trees that stand within a shrub patch. These trees can be any size, or age, as long as they stand within a shrub patch, as specified above. The second is "standing mature regeneration" (SMR). These account for mature trees that have no shrub patch beneath. They still can have shrubs beneath their crown; however, these do not protect the tree anymore, due to either a low density or being not around the trunk of the tree. Lastly there is the "Spontaneous sapling regeneration" (SSR). These account for saplings, that have regenerated outside of a shrub patch, without protection from grazing. Sapling is here defined as a tree of which the crown can still fully be grazed, which is around 2.5 metres in height (Van Uytvanck et al., 2010).

For all tree classes, I measured the stem diameter just above ground level, due to the fact that that the measured trees would not be uniform in height. The stem diameter was measured using a calliper. I measured the crown size with one diameter, with the assumption that the crown was circular in shape, due to the fact that the trees would grow up in environments with minimal light competition. Trees that were made up of multiple stems, like for instance hazel or coppice oaks, were counted as one tree with X number of stems. For these trees, I measured only the dominant stem for height and stem diameter, whilst taking all

stems into account for the crown size. I counted the frequency of shrub shoots beneath SMR. The location of SMR and SSR were measured using a GPS unit, while SAR used the location data of the shrub patch they were a part of.

In the adjacent forests of “forested” sites Three transects were done in random locations in each of the forests. These transects were thirty metres long and four metres wide. In each transect I counted the frequency of tree regeneration and measured the basal area of mature trees. The basal area was individually measured for each species using a relascope at the start of the transect, using mature canopy trees both within and outside of the transect. The frequency of tree regeneration consisted of counting saplings and noting their species. Sapling was defined the same as the saplings in SSR.

2.2 Statistical analyses

Two separate datasets were created: shrub data and tree regeneration data. These datasets were linked to each other using a code indicating which shrub patch each tree belonged to. This was done due to the fact that the majority of shrub patches had multiple tree species in it. The shrub species data were simplified into six categories: Rosa, Crataegus, Prunus_spinosa, Juniperus, Rubus and Other, with the Other category encompassing gooseberry and European wild apple. The stem density for shrubs underneath the tree crowns of SMR was calculated by dividing the crown size of these trees by the number of shrub stems. The data was analysed using RStudio (version 4.4.1), using the packages: tidyverse, mgcv, patchwork, dlplyr, tidyr, ggplot2, stringr and scam.

I analysed the dynamics of tree crown size and the density of shrub shoots beneath the tree crown using a gaussian generalised additive mixed model framework (GAMM). Gaussian GAMM is a modelling technique which allows for the modelling of normally distributed non-monotonic relationships. They allow the data to determine the relationship between the response and the explanatory variables, instead of assuming some form of a parametric relationship (Guisan et al., 2002). It allows the use predictor variables, and random variables, which was necessary to look at the differences between sites. A gaussian GAMM was used, as only the SMR with shrub shoots beneath their crowns were used for the test, which followed a normal distribution.

The conditional shrub shoot density was analysed for free-standing trees which had shrub shoots beneath their crowns. A Gaussian GAMM was used for this analysis, after the shrub shoot density was transformed using ln(x+1). The diameter of the tree crown was used as a smooth predictor using penalised regression splines, while the pasture ID was used as a random-effect smooth predictor, to account for the variation between sites. The tree crown diameter was also transformed, prior to analysis, using ln(x+1), to account for the strong right-skew in the distribution. The fit of the GAMM was checked using a gam check function.

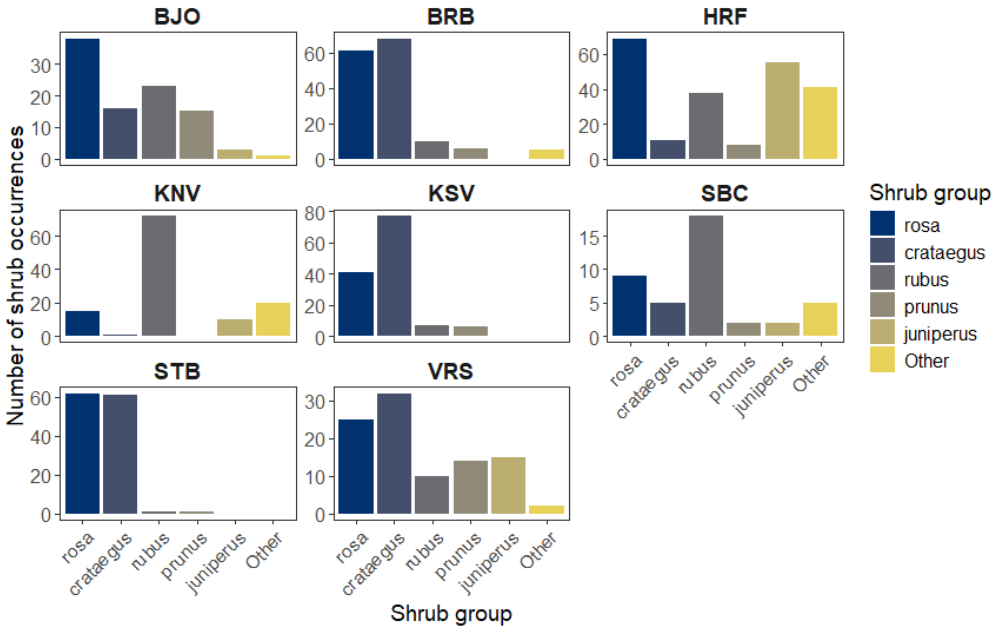
To compare differences in species composition between the canopy of the reference forests and the tree regeneration in the pastures, I used a non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarities. NMDS ordination was used here as the data collected was nonparametric, and because it can handle non-linear relationships. Bray-Curtis dissimilarities were used as it allowed the analysis of abundance based compositional data containing uneven species distributions and many zeros. The species composition data were converted to relative abundance within each site to amplify the proportional differences in the composition. Only species exceeding a minimum relative abundance threshold of 3% in at least one compartment were

retained. The NDMS was conducted using two ordination dimensions and iterative monotonic optimisation to preserve ranked dissimilarities among samples. Within this resulting ordination, the distances among points represented the relative difference in species composition, with points closer together being more similar of community structure. I relied on stress values to evaluate the ordination quality, with lower stress indicating a better representation of multivariate relationships in reduced dimensional space. The ordinations were visualised separately for tree regeneration in pastures and the canopy of the adjacent forest and ordered by shade-tolerance (Den ouden et al., 2023; Niinemets & Valladares, 2006; Vera, 2000) to assess the extent to which the tree regeneration in the pasture reflects the composition of adjacent forest canopies.

3. Results

The diversity of shrub species varied among pastures. Overall, roses and hawthorn were dominant on most sites, followed up by blackberry. Most other species were seen in far fewer quantity, with most sites having very little of them. The sites of BJO, HRF, and VRS seemed to have a more even distribution of shrub occurrence, while KNV, BRB and STB were more dominated by one or two species (Fig. 2)

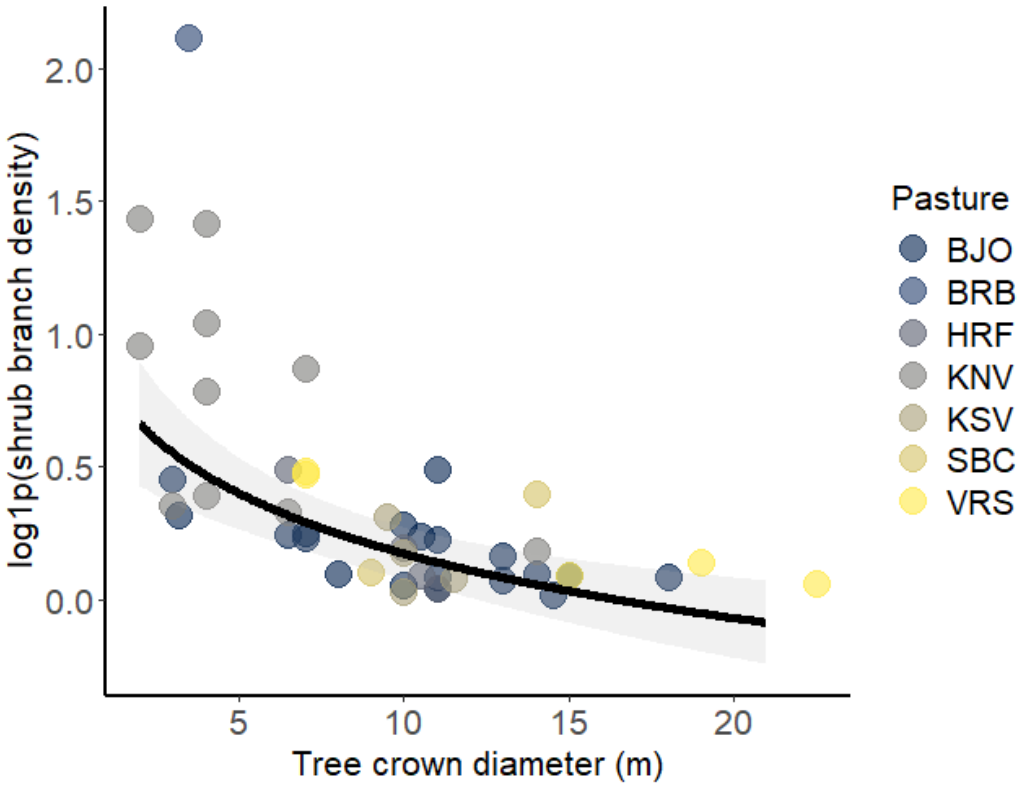
Figure 2: Shrub occurrence per shrub group, categorised by pasture ID. The presence per shrub group is treated independently from shrub patches, as most shrub patches have multiple species within them. The category "other" encompasses the species of Malus sylvestris and Ribes uva-crispa.



Note: n=981

The size of the tree crown has a significant negative effect on the density of shrub branches (Table 2). The greatest effect seems to be below five metres, with the effect gradually bottoming out (Fig. 3). The pasture ID however is a significant variable for this effect, meaning that this effect is dependent on the site and that these results should be interpreted cautiously.

Figure 3: The relationship between tree crown diameter and shrub shoot density (shrub branch density) conditional on shrub presence. Shrub shoot density was calculated as the number of shrub shoots beneath a tree crown divided by crown area, assuming a circular crown. The response variable was transformed using "ln(1+x)" prior to analysis and modelled using a Gaussian GAMM. Only trees with shrub presence under the tree crown were included in the conditional density analysis. The solid black line is the fitted GAMM relationship; the shaded ribbon is a 95% confidence interval. The colour of the points indicates pasture ID in both panels.



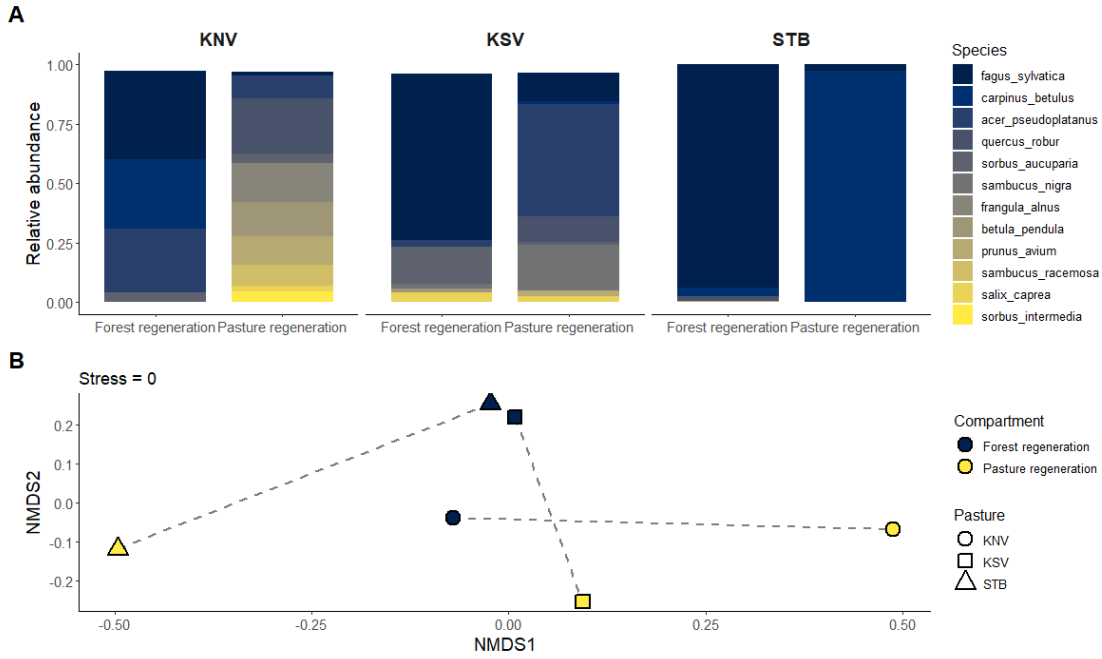
Note: n=45, k=4

Table 2: results of the Gaussian generalised additive mixed model (GAMM) testing for the shrub shoot density underneath the crown of trees. Shrub shoot density was calculated as the number of shrub shoots beneath a tree crown divided by crown area assuming a circular crown. The response variable was log-transformed as "ln(1+x)". The predictor variable was the tree crown diameter, and Pasture ID was a random effect. Only trees with shrub presence were included in the conditional density analysis.

Fixed effect				
Term	*Estimate*	*Std. error*	*t-value*	*p-value*
Intercept	0.592	0,2025	2.613	0.0129
Significance of smooth terms				
Group	*edf*	*Ref. df*	*F*	*p-value*
Tree crown diameter	1.000	1	19.495	8.46*10^-5
Pasture ID	5.684	6	7.725	1.16*10^-5
n = 45				
R^2(adj.) = 0.743				

The relative abundance of tree species on KNV, KSV and STB was different between forest and pasture environments. The effect seems to be the clearest on the site of KNV, with a greater percentage of species being light demanding. STB is a clear outlier in this regard, as it shows mostly hornbeam (*Carpinus betulus*), which is shade tolerant. Swedish whitebeam (Sorbus intermedia), both elder species (*Sorbus nigra/racemosa*), and alder buckthorn (*Frangula alnus*) only grow in the pasture. Though not exclusive, beech (*Fagus* sylvatica) and to a lesser extent birch are more common in forests and pastures respectively. When looking at the NMDS-analysis, it shows that all three sites had great differences between their pastures and forests (Fig. 4). The relative abundance of each pasture differed greatly from the other pastures, whilst the composition of the forests was more similar to each other.

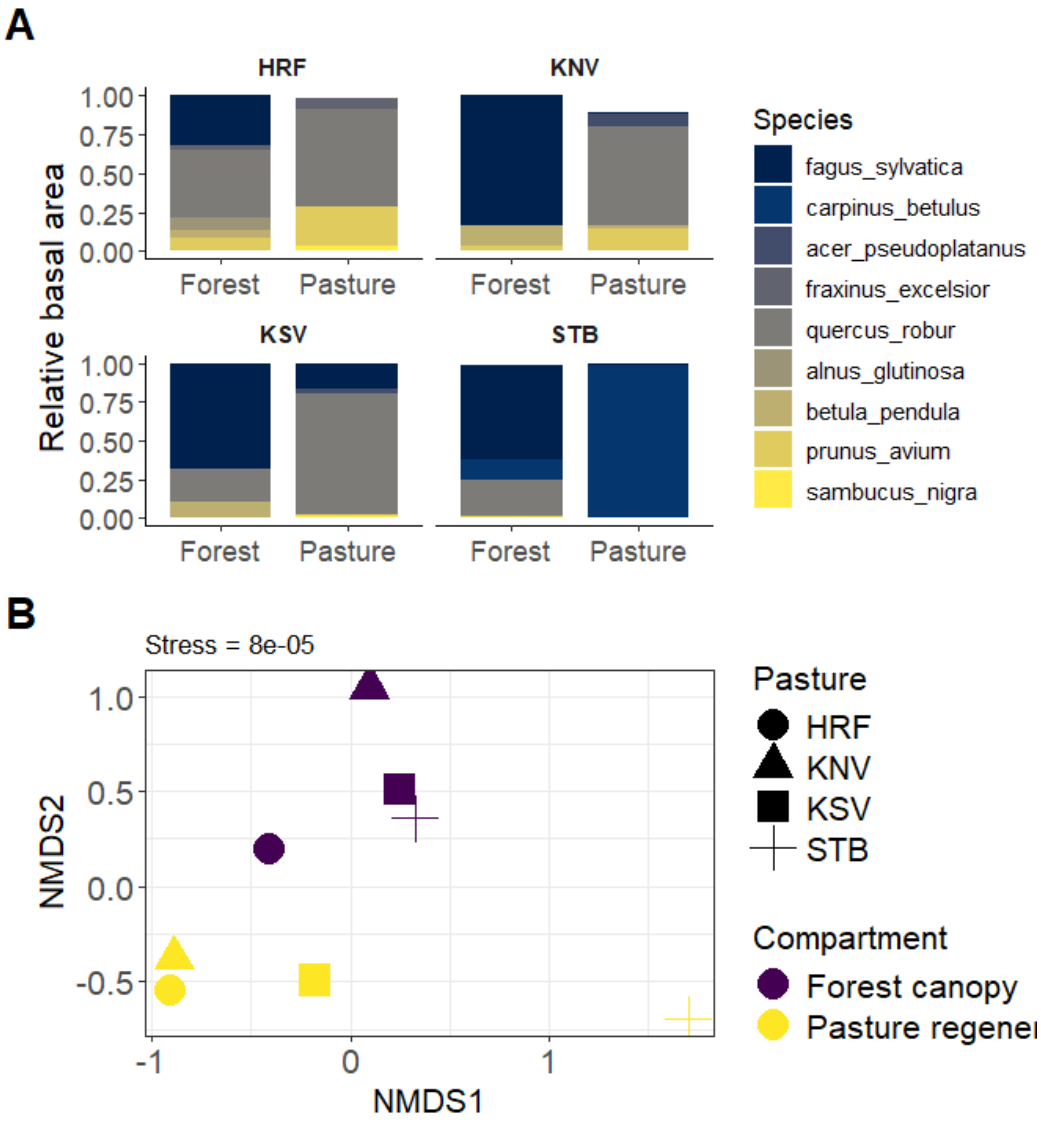
Figure 4: Relative species composition of tree regeneration recorded beneath forest canopies and within shrub patches in open grazed pasture areas across three sites (KNV, KSV, STB). (A) Species abundances are regeneration counts standardised within each habitat type to obtain relative abundances. Only species exceeding a minimum relative abundance threshold of 3% in at least one pasture were retained. Bars are proportional species composition within each contrast, with colours indicating tree species identity. Species were ordered according to ecological shade tolerance to facilitate comparison of compositional differences between two environments. (B) Non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarities of relative species composition. Points are individual site vs. compartment combinations, with symbol shape indicating pasture ID and colour indicating compartment type. Distances among points reflect compositional similarity in multivariate species space. NMDS was performed using two-dimensions. Stress values are shown within the ordination panel.



Note: n=635

The composition of relative basal areas on the sites of HRF, KNV, KSV, and STB also show that there is a difference between the forest and the pasture. Overall, the pasture sites, besides STB, have more light-demanding tree species, like pedunculate oak (*Quercus robur*) and wild cherry (*Prunus avium*), than the forests. This trend is, again, missing with STB, where both forest and pasture only seem to grow shade-tolerant species, like beech and hornbeam. When looking at the NMDS-analysis, it shows that KNV and STB have the largest difference between forest and pasture, followed by KSV. HRF seems to have the most similarity between its pasture and forest. (figure 5).

Figure 5: Comparison of tree species composition between the tree regeneration of pastures and the canopy of the adjacent forests across four sites (HRF, KNV, KSV, and STB). (A) The relative basal area composition of mature forest canopies ("forest") and regenerating trees recorded in open pasture habitats ("pasture"). Species abundances were standardised within each compartment to obtain relative basal area proportions. Only species exceeding a minimum relative abundance threshold of 3% in at least one compartment were retained. Species were ordered according to ecological shade tolerance to facilitate comparison among compartments and sites. (B) Non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarities of relative species composition. Points are individual site vs. compartment combinations, with symbol shape indicating pasture ID and colour indicating compartment type. Distances among points reflect compositional similarity in multivariate species space. NMDS was performed using two-dimensions. Stress values are shown within the ordination panel.



Note: n=802

4. Discussion

I observed significant difference in the composition of both relative abundance and relative basal area of trees, between the pastures and their adjacent forests. Pastures generally contained more tree species, and more light-demanding tree species than their adjacent forests. The forests had more shade-tolerant species, with beech being the dominant species on most sites. The density of shrub shoots decreased with the size of the tree crown above it, showing the suppression effect that the tree crowns have on the shrubs below them.

Shrub-assisted regeneration in pasturelands provides a pathway for many species to maintain their presence in the modern southern Swedish landscape. Many species of light-demanding tree species are unable to regenerate properly in closed-canopy forests, due to (a) competition by shade-tolerant tree species and (b) the overgrazing of browsers in gaps (Kuijper et al., 2009; Vera, 2000).

The modern closed-canopy forest inherently favours shade-tolerant species for regeneration. In the closed-canopy forest system, following the principles of the classical forest model, tree species germinate under the canopy, and only grow dominant when a gap forms in this canopy (Watt, 1947). While light-demanding tree species, like wild cherry, are often able to germinate in low-light conditions, they are outclassed in terms of growth by shade-tolerant species (Schalk, 1990; Spiecker & Spiecker, 1988). This principle holds true for oak as well, with seedlings being able to survive for up to four years under the canopy, but often being outcompeted (Annighöfer et al., 2015; Lemée, 1987). This means in practice that when a gap forms the shade-tolerant species have a headstart and thus can grow dominant quicker.

Light-demanding species that regenerate in gaps are often victim to heavy browsing. The browsing pressure is heightened by forest gaps, due to the increase in biomass production caused by the increase in the light intensity (Kuijper et al., 2009). This increase in browsing pressure is felt more heavily by light demanding tree species, as shade-tolerant species like beech have been noted to be less browsed than their light-demanding counterparts (Boulanger et al., 2009; Ohse et al., 2017). The abundance of light in open pastures, in combination with browsing protection provided by the thorned scrub, allows these species to regenerate in a natural capacity. This is especially true for rarer tree species like European wild apple or wild pear (Pyrus pyraster), where wood-pastures are some of the habitats where they appear most commonly (Höltken et al., 2014; Rackham, 1980; Rodwell, 1991).

Species like Swedish whitebeam and alder buckthorn were absent in surveyed forests. This can be explained by the fact that these species are light-demanding species and are thus only on the pastures and the fringes of woodlands (Den

ouden et al., 2023; Namvar & Spethmann, 1985; Vera, 2000). The fact that hornbeam was prevalent on STB can be explained by the fact that hornbeams can regenerate well in hawthorn or blackthorn scrub, the former of which is quite numerous on site STB (Pott & Hüppe, 1991). Hornbeam is also resistant to browsing, being able to regenerate well after damage (Rubner, 1960). The absence of hornbeam on other hawthorn dominated sites can be explained by the absence of the species on adjacent forests. The forest adjacent to site STB was less diverse in tree species than the other Overall, the documented pattern of the presence and absence of light-demanding and shade-tolerant tree species broadly supports the notion of a browsers-controlled regeneration bottleneck in canopy forests (Salek et al., 2019; Vera, 2000).

Beech trees were dominant in the forest habitats (fig. 4 & 5), while being almost completely absent in the pastures. The prevalence of beech in the forests is easily explained by their shade tolerance (Den ouden et al., 2023). Their near complete absence in the pasture can be explained by a few factors. (1) Beech has a smaller dispersion area than species like oak or cherry. Acorns and cherry seeds are dispersed by birds which can cover great distances. The main dispersers of beech are rodents, which only disperse over small distances, severely limiting their dispersion into a pasture (Nilsson, 1985). (2) beech is sensitive to damage by rodents. While the thorny scrub may protect the beech from large grazers, they also protect grasses and herbaceous plants, which provide perfect cover for mice and voles (von Lüpke, 1987). (3) young beech is more sensitive to late frost (Den ouden et al., 2023; von Lüpke, 1987).

The decrease of the shrub shoot density underneath growing tree crowns (fig. 3) shows the suppression effect these crowns have on the shrub underneath, as most of the shrub species are light-demanding, and they will not survive well in the shade (Coops, 1988; Ellenberg, 1986; Vera, 2000). The fact that these shrubs are underneath the tree crown to begin with seems to point at the fact that these tree regenerated within the shrubs, which is line with the TCTV (Vera, 2000). This is speculatory however, as there is no concrete proof that these trees were regenerated in shrub patches.

4.1 Management implications

Noble broadleaf species like oak and wild cherry regenerate well in these pasturelands indicating that it may be an effective way for landowners to convert grasslands in to wood-pastures or broadleaf forests, especially if it is already adjacent to one. Oaks seem especially receptive to this, with case studies showing that natural regeneration by Eurasian jays can be a more cost effective measure than conventional regeneration methods (Bobiec & Rotherham, 2024). There are some caveats to this regeneration however: (A) that the large grazers need to be fenced in, which can be very expensive, (B) that, due to the low amounts of

intraspecific competition, the trees will grow quite branched and wide, making them unsuitable for commercial timber production (Den ouden et al., 2023), and (C) that small grazers can still browse on small trees, despite the protection of shrubs (Uytvanck et al., 2008). One posited solution to the last problem on floodplains in the Netherlands is by periodically flooding the pasture to drown small grazers (Bakker et al., 2004). This however will likely not be feasible in most of southern Sweden, as the area lacks major floodplains of river deltas.

Wood pastures are great stores of biodiversity, since they offer four habitat types in a relatively small amount of space. These habitat types (grasslands, solitary trees, forests and forest edges) provide a large variety in different micro-habitats and structural elements, which can benefit certain species groups. An example of a species group that benefits from such diversity is arthropods. Ants especially make great use of the diversity of microclimates and habitat structures, with a great variety of species as a result (Lőrincz et al., 2024). Grasshoppers also benefit from TCTV management, with wood-pastures housing more species diversity than forests and similar species diversity to open grasslands (Rösch et al., 2019).

Plant, bird and bat species exhibit a great functional diversity in wood pastures. This diversity increases with the structural complexity of the habitat (Jakobsson et al., 2020). What can be concluded by this is that wood pastures give more diversity as they age, as long as the different habitat types keep getting maintained by grazers.

Wood pastures can be a viable alternative to open pastures for the commercial production of livestock. Dairy cows specifically produce slightly more milk on hot days when shaded by trees (Fisher et al., 2008). The loss of grasses and herbaceous plants, due to shading effect of trees is offset by the increase in livestock production, keeping the overall livestock production the same (Tölgyesi et al., 2023). Landowners can use this principle to capture carbon on grazed pasturelands, mitigating climate effects and allowing them to neutralise their own carbon footprint.

Wood pastures can provide local communities with many woody and non-woody plant products, in addition to livestock products (Moreno et al., 2018; Torralba et al., 2018). In central Europe, wood-pastures are often used for foraging by local communities, as most wild fruit trees are light-demanding species and grow well on them. This use of the wood-pasture promotes the use of local ingredients and a sense of a communal use (Varga et al., 2022). These agroforestry systems generally lead to greater regulating ecosystem services than conventional forestry or agriculture (Moreno et al., 2018).

4.2 Future studies

Several limitations in terms of sites and protocol have impacted this study. In ideal circumstances, the density of grazing would have been parameterised for this study. The fact that this could not be done is a major drawback, as grazing is the factor on which the TCTV hinges on. There were multiple reasons why this was more difficult than previously thought and subsequently dropped: (1) the lack of a complete grazing history for the pastures, and (2) the lack of time; the scope of a bachelor thesis is quite small and so is the timeframe to complete this study. This meant that there was no time to ask for cattle data from local governments. The grazing history of the pasture we deemed especially important as the number of animals and subsequently the grazing pressure could fluctuate heavily over time, making the possibility for drawing the wrong conclusion very reasonable.

For future studies, it is vital that this herbivory gap is filled. Studies should focus on three aspects of herbivory: (1) large grazers, (2) wild browsers, and (3) small herbivores. These three aspects encompass different niches within the TCTV, and they cover different stages in the lifecycle of the trees. Especially the effect of smaller browsers, like rabbits or rodents, that can circumvent the protection of thorny scrub are seemingly more as important in the control of the establishment of trees as larger grazers (Bakker et al., 2004; von Lüpke, 1987). Together, these three forms of herbivory form the controlling factor that shapes the ecosystems governed by the TCTV, and they therefore should be studied in great detail.

Another limitation of the protocol is that there is no randomised design for the choosing of sites. The reasons for this are, again the time constraints, and the lack of sites that adhered to our conditions stated in the methods. This meant that all sites that we found suitable were chosen for inventory.

Lastly, while the effect of the pasture was considered as a random effect in the models, there was no exploration of the actual differences the pastures held. This is especially pressing, considering the fact that Pasture ID was a significant effect. The reason for this difference can likely be explained by, again, the absence of any data on herbivory. We simply do not know if the browsing pressure is comparable between sites. Another reason could be the large differences in size between the pasture, as this could have an effect on how far into the pasture the seeds can rain.

4.3 Conclusion

TCTV governed wood pastures support biodiversity and other ecosystem services, and it is vital that these threatened habitats are preserved and expanded.

Mechanistic understanding of the successional dynamics of these systems should support its preservation as one of the reference successional pathways in lowland European forests. Specifically, future studies should parameterise the grazing pressure and history of the sites, as they hold the key role in the top-down control of these habitats. Extra regard should be given to the role of smaller herbivores, as their bypassing of the scrub's protection means that they play a far greater role in the survival of seedlings than the large grazers.

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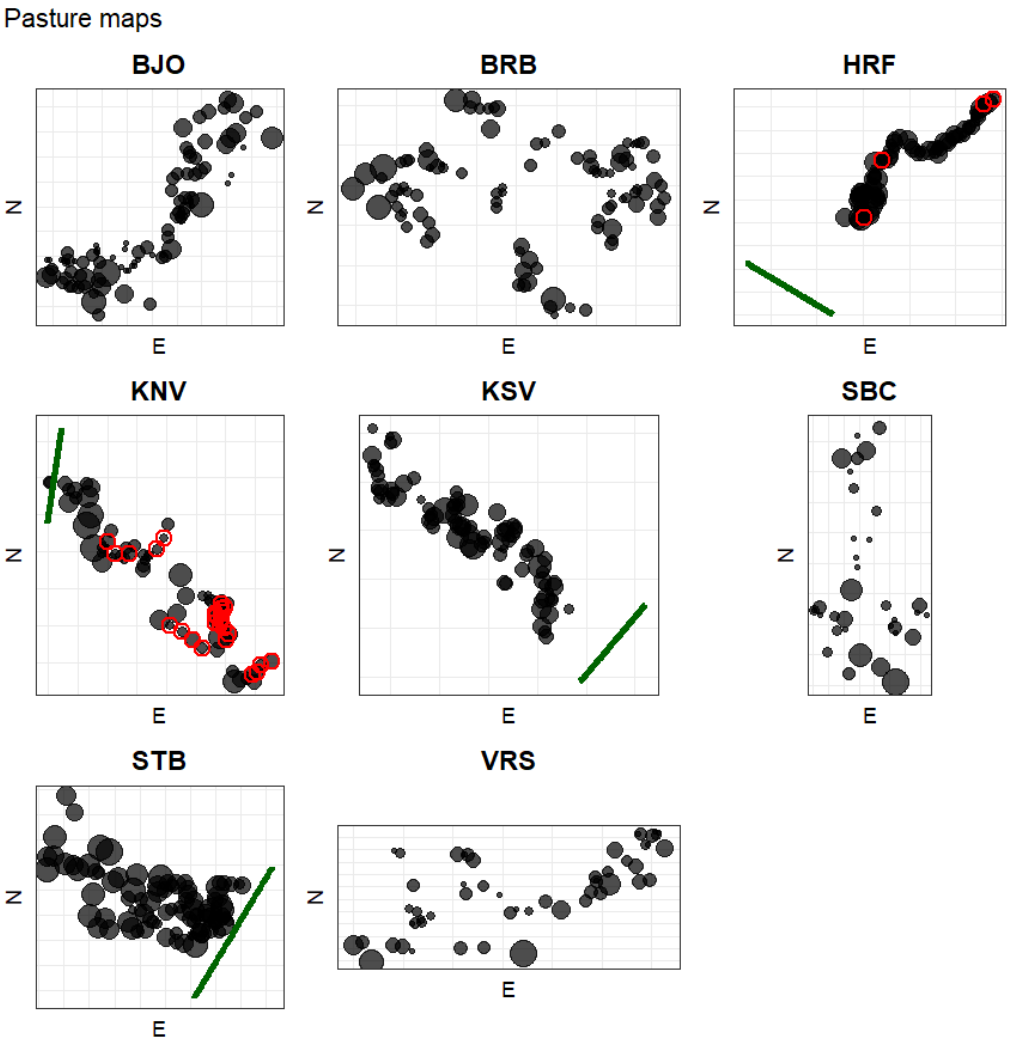
Appendix

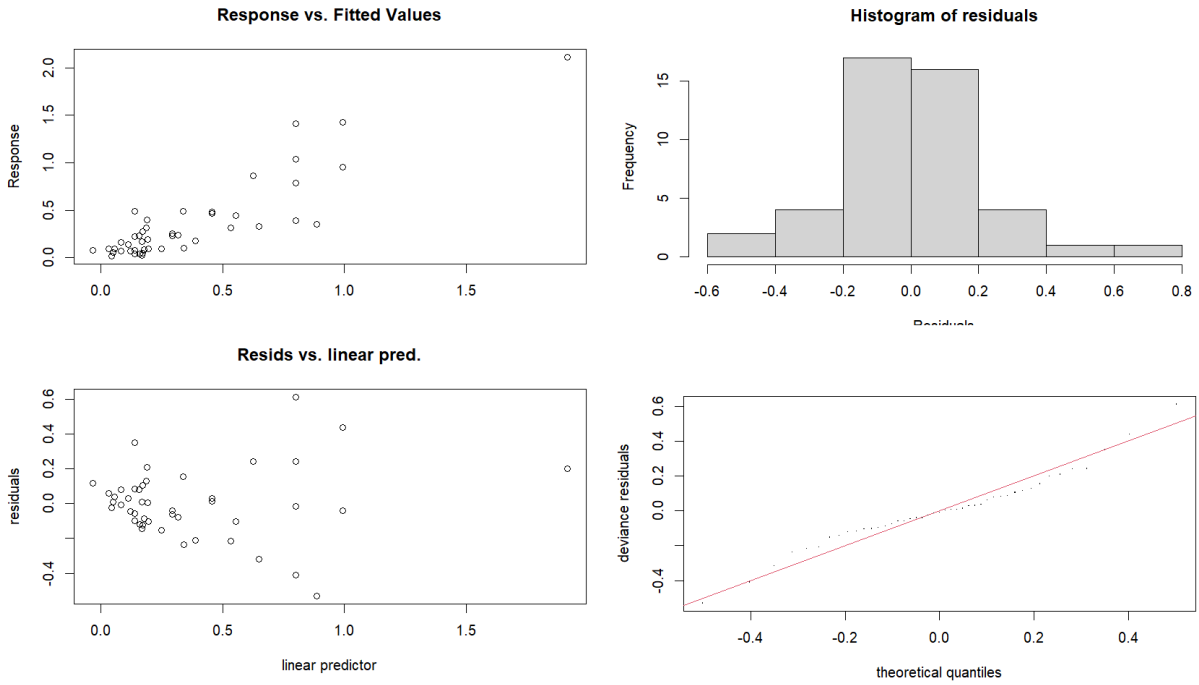
This appendix contains figures and tables that give extra context and information about the data gathering.

Appendix figure 1: plot showing the spatial data of the pastures. Black dots are clusters of shrub patches, mature trees or sapling clusters, with larger dots representing larger clusters of data points. Red data points show corrupted spatial data, due to GPS errors. These points have been regained using a coordinate recovery function. These coordinates were not used in any statistical analyses. The green line shows the forest edge; what should be noted here is that the forest edge is a fenced border, and not where the tree crowns start.



Note: n=617

Appendix figure 2: Results of the GAM check function.



Appendix table 1: Summary of shrub patch data per pasture ID.

Pasture ID	Shrub patch frequency (n)	Mean shrub diameter 1 (m)	Mean shrub diameter 2 (m)	Mean shrub height (m)
BJO	97	4,76	4,56	1,97
BRB	94	3,32	3,34	1,92
HRF	87	4,03	3,74	2,29
KNV	75	3,36	3,19	1,13
KSV	84	3,15	3,23	2,30
SBC	35	2,55	2,56	1,52
STB	92	1,68	1,80	2,04
VRS	61	3,45	3,43	2,32
Total	617			

Appendix table 2: Summary of tree regeneration data per Pasture ID

Pasture ID	Tree regeneration frequency (n)	Mean stem diameter (cm)	Mean height (m)	Mean tree crown diameter (m)	Frequency of SMR (n)
BJO	258	7,57	2,92	1,35	27
BRB	60	4,09	1,74	0,70	1
HRF	187	6,89	3,01	1,57	4
KNV	140	5,03	2,39	1,41	13
KSV	83	5,66	2,05	1,31	4
SBC	434	1,60	0,75	0,32	6
STB	80	2,82	1,21	0,47	1
VRS	164	4,95	2,17	0,98	5
Total	1278				

Appendix table 3: Summary of the tree regeneration frequency and basal area in the forests adjacent to pastures.

Pasture ID	Tree regeneration frequency (n)	Mean basal area (m^2/ha)
HRF	133	27
KNV	78	18
KSV	104	19
STB	170	22

Appendix table 4: Results of the GAM check function. The p-value being high means that the basis dimension "k" has not been set to low.

Variable	*k*	*edf*	*k-index*	*p-value*
Tree crown diameter	3.00	1.00	1.12	0.72
Pasture ID	7.00	5.65	NA	NA

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