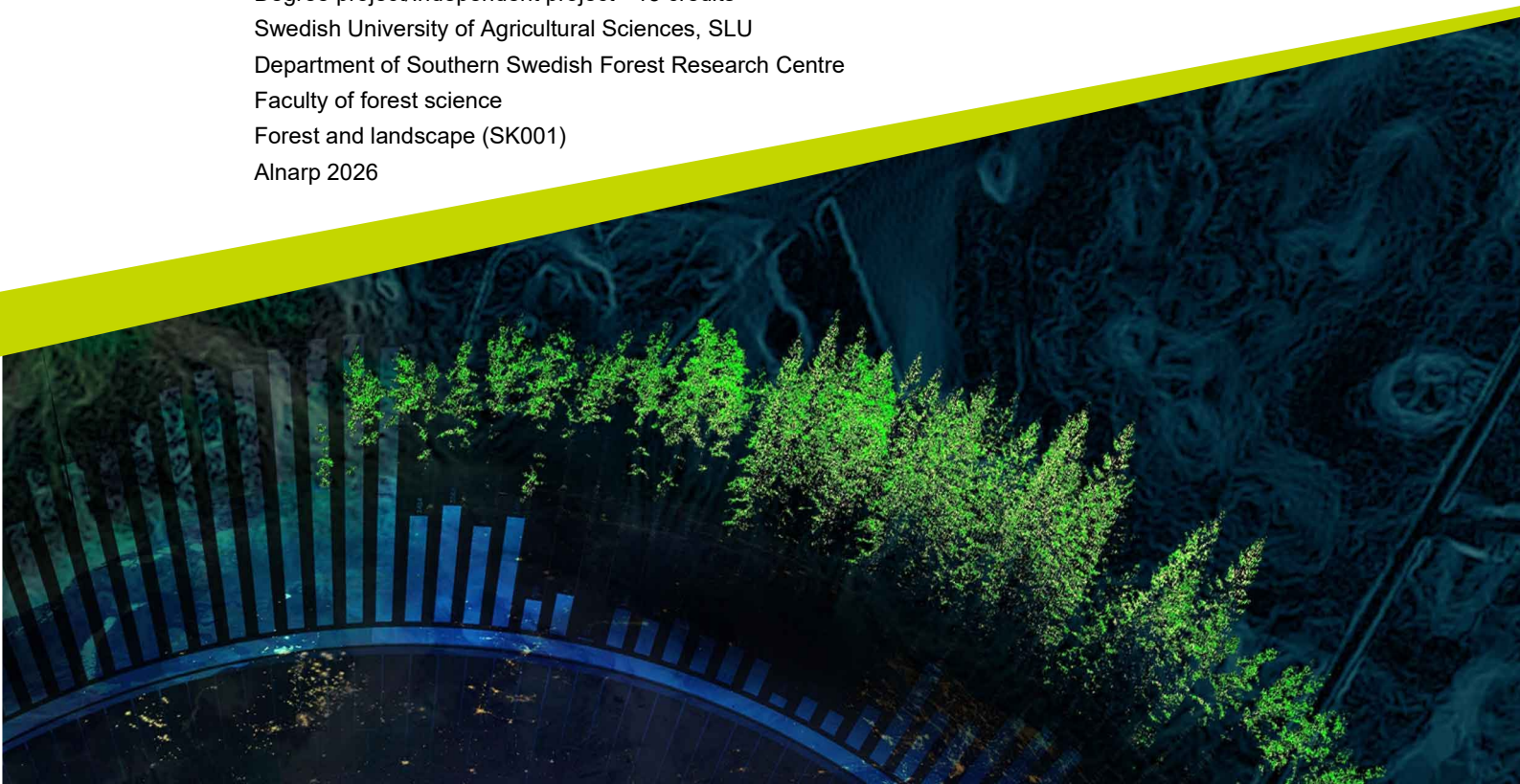




Through thorns to trees: regeneration pathways in Southern Swedish pasture landscapes

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Forest and landscape (SK001)
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Through thorns to trees: regeneration pathways in Southern Swedish pastures landscapes.

Genom törnen till träd: föryngringsvägar i sydsvenska betesmarker.

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Abstract

Wood-pastures in Europe are shaped by the interaction between grazing, shrub dynamics, and tree regeneration. In these landscapes, thorny shrub patches have been proposed to function as protective refugia that facilitate tree regeneration establishment and browsing escape. This study investigated regeneration pathways in grazed pastures in Southern Sweden and evaluated whether shrub characteristics influence the establishment and survival of tree regeneration under herbivore pressure. Field data were collected in eight cattle-grazed pasture systems differing in woodland structure and connectivity to surrounding forest. Shrub patch size, shrub species composition, distance to forest edge, and regeneration characteristics were measured along transects. Generalized Additive Mixed Models (GAMMs) and Linear Mixed Effect Models (LMMs) were used to assess relationships between shrub structure, regeneration establishment, and browsing escape thresholds. Tree regeneration establishment is positively associated with shrub patch size. In pastures bordering forests, regeneration probability declined with increasing distance from the forest edge, indicating spatial limitations in dispersal and establishment. Larger shrub patches partially compensated for this effect, allowing regeneration to establish at greater distances from forest edges. Shrub patch size requirements increased substantially between demographic stages: larger shrub patches were required for saplings to reach browsing escape heights than for initial establishment. Shrub species composition also influenced regeneration patterns. Patches containing *Rubus* and *Juniperus* were associated with significantly higher regeneration probabilities, suggesting that structural and defensive shrub traits play an important role in browsing protection. These findings indicate that thorny shrub patches are strongly associated with regeneration establishment and allow regeneration to escape grazing/browsing in wood-pasture systems. I conclude that shrubs provide an important pathway for tree regeneration under grazing/browsing pressure, with shrub establishment and growth strongly shaping woodland dynamics in semi-open landscapes.

Sammanfattning

Europeiska trädbärande betesmarker betesmarker formas genom samspelet mellan bete, buskdynamik och trädförnyring. I dessa landskap har taggiga och täta buskage föreslagits fungera som skyddande refugier som underlättar etablering av trädförnyring och hjälper unga träd att undkomma betning. Denna studie undersökte förnyrningsprocesser i betade hagmarker i södra Sverige och utvärderade om buskarnas egenskaper påverkar etablering och överlevnad hos trädförnyring under betestryck.

Fältdata samlades in från åtta nötkreatursbetade betesmarker som skilde sig åt i skogsstruktur och konnektivitet till omgivande skog. Buskagens storlek, buskartsammansättning, avstånd till skogskant samt förnyringens egenskaper registrerades längs transekter. Generalized Additive Mixed Models (GAMM) och Linear Mixed Effect Models (LMM) användes för att analysera sambanden mellan buskstruktur, etablering av trädförnyring och tröskelvärden för att undkomma betning.

*Sannolikheten för etablering av trädförnyring ökade med buskagens storlek. I betesmarker som gränsade till skog minskade sannolikheten för förnyring med ökande avstånd till skogskanten, vilket tyder på rumsliga begränsningar i spridning och etablering. Större buskage kunde delvis kompensera för denna effekt genom att möjliggöra etablering längre från skogskanter. Kraven på buskagens storlek ökade dessutom mellan olika utvecklingsstadier; större buskage krävdes för att unga träd skulle nå höjder där de kunde undkomma betning än för den initiala etableringen. Buskartsammansättningen påverkade också förnyrningsmönstren. Buskage som innehöll *Rubus* och *Juniperus* var förknippade med signifikant högre sannolikhet för förnyring, vilket tyder på att buskarnas struktur och försvarsegenskaper spelar en viktig roll för skydd mot betning.*

Resultaten visar att taggiga och täta buskage är starkt associerade med etablering av trädförnyring och möjligheten att undkomma betning i trädbärande betesmarker betesmarker. Studien stödjer hypotesen att buskförmedlat skydd kan utgöra en viktig förnyrningsmekanism under betestryck och visar hur buskars rumsliga struktur kan påverka dynamiken i halvöppna landskap.

Keywords: Wood-pastures, tree regeneration, shrub protection, shrub facilitation, pasture dynamics, regeneration dynamics, grazing ecology, browsing pressure

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Abbreviations

BJO	Björnö
BRB	Brösarps backar
GAM	Generalised additive model
HRF	Humlarödshus fålad
KNV	Knivsås-Borelund
KVS	Kronovalls store vång
LMEM	Linear mixed-effects model
NR	<i>Naturreservat</i>
SAR	Shrub-assisted regeneration
SMR	Standing mature regeneration
SSR	Spontaneous sapling regeneration
SBC	Stiby Backe canopy
STB	Stiby Backe
VRS	Värnanäs

1. Introduction

The generally accepted theory on succession, initially formulated by Clements (1916), has long dominated ecological theory and nature restoration. The theory states that vegetation development ultimately converges toward a stable climax community that persists over time (Clements, 1916). In the temperate zone, including Europe, this climax has generally been assumed to consist of closed-canopy forest. Support for this view came from regions with minimal human influence that were dominated by long-lived tree species and featured continuous canopy cover (Clements, 1916; Vera, 2002). Watt later expanded succession theory by introducing the gap-phase model. In this model, disturbances such as tree fall and decay create canopy openings that allow regeneration to occur (Watt, 1925; Tian et al., 2023). Gap dynamics therefore became the main explanation for regeneration processes in temperate forests.

Recent research increasingly challenges both the concept of a single forest climax and the assumption that gap dynamics alone drive regeneration (Pickett & White, 1985; Attiwill, 1994; Vera, 2002). Long-term pollen records raise particular doubts about whether closed-canopy forests dominated European landscapes throughout the Holocene. Pollen diagrams from across Europe show the persistent presence of many tree species over the last 13,000 years (Huntley, 1990). Traditional interpretations assumed that these species coexisted and regenerated together within dense forests through gap-phase dynamics (Clements, 1916; Watt, 1925). However, the pattern of regional abundance of light-demanding tree species exposed a major inconsistency in this interpretation. In particular, oaks (*Quercus sp.*) have been found to be abundant in European pollen records (Huntley, 1990; Vera, 2002). However, experimental and observational studies have shown that for successful establishment oak regeneration requires high light availability, disturbances, an overall low basal area and little competition from shade tolerant species. Although oak seedlings survive under a wider range of conditions, oak saplings require increased light and reduced competition (Annighöfer et al., 2015). Studies suggested that oak regeneration depends on disturbances that create spatial and temporal canopy discontinuities and reduce competition (Bobieć, 2011). Many old oaks that persist within modern dense forests likely established during earlier periods of stronger anthropogenic disturbance (Bernadzki et al., 2009). Therefore, oak ultimately fails to regenerate in dense forests (Vera, 2002; Götmark et al., 2005; Bernadzki et al., 2009; Bobieć, 2018). These findings contradict expectations derived from classical succession theory and the gap-phase model, both of which assume that regeneration continuously replaces the existing canopy composition (Watt, 1925; Vera, 2002; Bobieć, 2018). The evidence instead suggests that European landscapes

historically contained substantial semi-open landscapes rather than continuous closed forest (Plieninger et al., 2015).

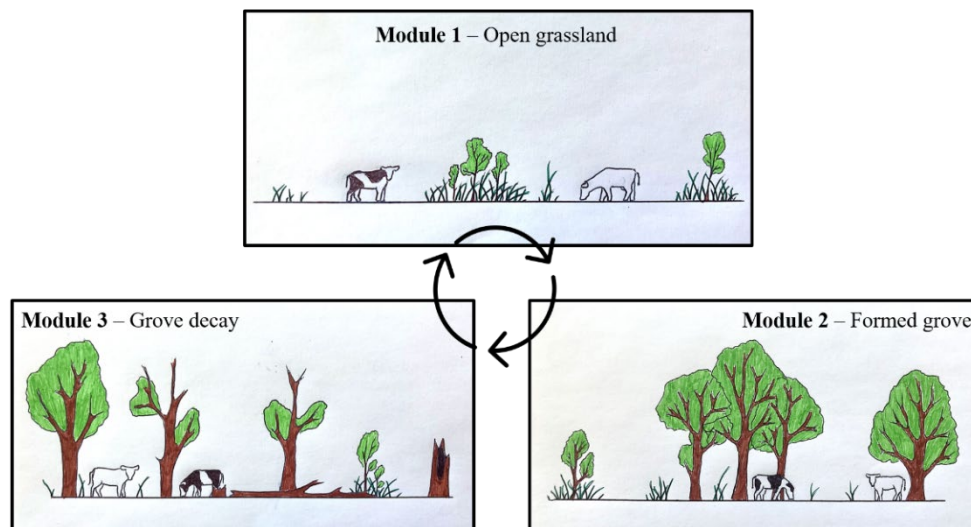
These inconsistencies stimulated alternative theories of forest dynamics. Vera (2002) proposed the theory of cyclical turnover of vegetation as an alternative to classical succession theory and the climax concept. His framework emphasized dynamic processes, landscape heterogeneity, large herbivores, and disturbances, all of which earlier theories largely overlooked despite their demonstrated importance in natural forests (Brumelis et al., 2011; Carvalho et al., 2020). Rather than interpreting all tree species as components of dense forest, Vera grouped species according to their habitat requirements and landscape positions (Vera, 1997, 2002) and pointed to the presence of light-demanding tree species in pollen records as an indication of open and wooded grazed landscapes (Vera, 2002). These landscapes offer favourable conditions for light demanding species, in particular pedunculate oak (*Quercus robur*) by combining low canopy closure, reduced competition from shade-tolerant species, small-scale disturbances by herbivore activities and open conditions that support sapling development (Vera, 2002; Bobiec et al., 2011; Annighöfer et al., 2015).

Thorny shrub forms a central component of Vera's theory because it provides regeneration pathways for trees in grazed landscapes by protecting saplings from herbivory (Vera, 2002). Based on this mechanism, Vera proposed that much of prehistoric Europe consisted not of continuous closed forest, but of semi-open, savanna-like landscapes maintained through the interaction between vegetation dynamics and large herbivores. Within these landscapes, tree regeneration was assumed to occur primarily inside thorny shrub patches, where saplings remain protected from grazing long enough to develop into groves. Large herbivores, including aurochs, tarpan, European bison, deer species, and elk, maintained these open systems by suppressing widespread canopy closure and sustaining a shifting mosaic of grassland, shrub, and woodland (Vera, 2002). Historical reconstructions render support for this interpretation and suggest that Europe hosted abundant herbivore populations prior to the onset of the major human expansion (Sandom et al., 2014). The replacement of wild herbivores by livestock has been shown to allow thorny and spiky shrubs to expand in present day pastures (Bergmeier, 2010; Oldén, 2016), a resemblance aligning with Vera's theory on the role of herbivores and the resemblance between pastures and prehistoric landscapes.

Vera explained the long-term dynamics of these landscapes through a cyclical process driven by grazing and vegetation succession, which I visualised with the drawing in figure 1. The first phase consists of open grassland, where selective grazing and high light availability allow thorny shrubs to establish and expand. Inside these protected shrub patches, tree saplings escape browsing pressure and gradually develop into small stands or groves. As canopy cover increases, the system enters the second phase, during which the developing trees suppress the shrub layer through shading. Grazing nevertheless continues beneath the canopy, and because protective shrub no longer persists, shade-tolerant species fail to regenerate successfully. Consequently, the oldest trees occupy the centre of the grove. The third phase begins when aging canopy trees die and create openings within the stand that are not replaced by new tree regeneration. Grasses and herbs then colonize these openings, which increases grazing activity and accelerates canopy decline. As the grove gradually opens, light availability eventually becomes sufficient for thorny shrub to re-establish, thereby recreating the protected conditions necessary for tree regeneration and initiating a new cycle (Vera, 2002).

Figure 1

The three modules of the theory of cyclical turnover of vegetation



Note. Three drawings showing the successive modules as proposed by Vera in the theory of cyclical turnover of vegetation. Module 1 shows the open grassland, where tree regeneration can establish in shrub patches. Module 2 shows the formed grove by the mature trees. Under this grove no regeneration can take place due to low light availability and grazing. Module 3 shows the decay of the grove, where light can reach the understory again, aiding in the establishment of grasses and herbs and ultimately thorny shrubs and regeneration again (module 1). Drawings made by author.

While it is increasingly recognized that shrubs provide regeneration pathways in grazed landscapes, important uncertainties remain. Many existing studies are observational and do not integrate grazing pressure, shrub characteristics, and tree regeneration within the same system. It remains unclear what shrub patch size is sufficient to provide protection against herbivory, and how canopy development influences shrub persistence. Furthermore, although Vera's theory and the importance of wood pastures are increasingly acknowledged, they have not yet been extensively tested through structured empirical studies.

The current study aims to model tree regeneration dynamics in wood pastures in Southern Sweden, while focusing on the interaction between shrub structure and grazing pressure. This will be used to assess dynamics of pastures under various management regimes and test Vera's theory of the cyclical turnover of vegetation. To explore Vera's theory more in depth and assess its consequences for future nature management, it is important to move beyond theory, literature reviews and debate. This paper presents a case study in the regions Skåne, Blekinge and Kalmar (Småland) in Southern Sweden. I focused on module one in Vera's cyclical turnover of vegetation theory, therefore I hypothesized that spiky shrub patches function as protective refuges that enhance establishment probability of tree regeneration and increased the likelihood of regeneration to escape browsing pressure. To test this hypothesis, I addressed the following research questions:

(Q1) how does shrub patch size influence the establishment probability of tree regeneration in pastures?

(Q2) how does the distance between a shrub patch and the bordering forest influence the establishment probability of tree regeneration?

(Q3) what is the minimum size of shrub patches to allow for regeneration to escape and ultimately survive grazing?

(Q4) how does the species composition of the shrub patch influence establishment probability of tree regeneration?

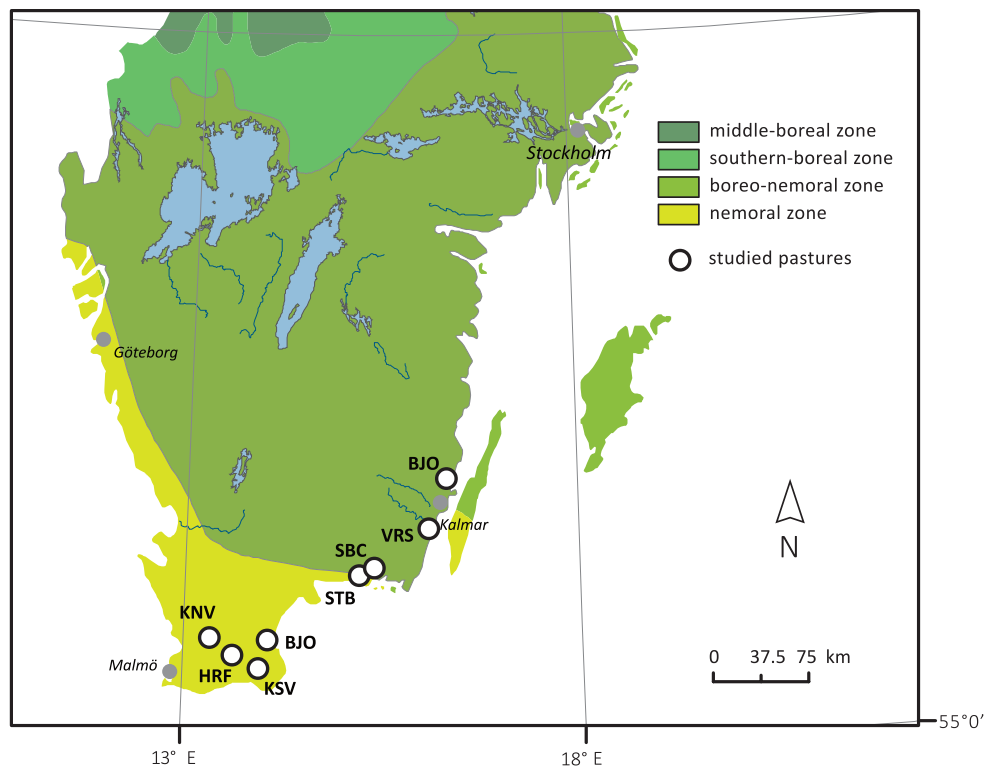
2. Methods

Study sites, pasture selection and definitions

Over the course of three to four weeks in April 2026, I surveyed eight pastures located in Southern Swedish provinces of Skåne, Blekinge and Kalmar (Småland). Figure 2 shows a map with the locations of the 8 studied pastures.

Figure 2

Map with locations of the studied pastures



Note. This map shows the locations of the nature reserves in which the studied pastures are located. The pastures in Skåne are located in Knivsås-Borelund NR (KNV), Humlarödshus Fälad NR (HRF), Kronovalls Store Vång NR (KSV), and Brösarps backar NR (BRB). The pastures in Blekinge are both located in Stiby backe NR (STB + SBC). The pastures in Småland are located in Björnö NR (BJO) and Värnanäs NR (VRS).

The selected pastures span gradients of grazing intensity, shrub cover and pasture age. In order for a pasture to be suitable for our research, the pasture had to meet the four conditions. First, either seasonal or year-round grazing had to be present. The cow (*Bos taurus*) has been found to have a similar ecological impact on natural landscapes as traditional occurring species such as the aurochs, tarpan, European bison, deer species and the elk (Allred et al., 2011; Vera 2002). Therefore, I determined cattle must play a role in the grazing and maintenance of the pasture. This means the pasture must be fenced, but grazing by wild animals

(e.g. boars, roe deer, red deer, fellow deer, rabbits or moose) does not have to be ruled out. Second, shrub patches which can provide regeneration pathways have to be present. I defined a shrub patch as “a patch of thorny shrub that is clearly defined in its size, and that is able to protect small trees against the predation of large grazers.” For a shrub to serve as protection, the first criterion for the shrub is to consist of (a combination of) species that are in possession of spikes or thorns. I considered the following species as protecting shrub; Blackberry (*Rubus fruticosus*), Blackthorn (*Prunus spinosa*), Dog Rose (*Rosa canina*), Eglantine (*Rosa rubiginosa*), Gooseberry (*Ribes uva-crispa*), Hawthorn (*Crataegus sp.*), European raspberry (*Rubus udaeus*), and European wild apple (*Malus sylvestris*).

The second criterion for the shrub is to be dense enough to deter grazing. Because cattle function as large grazers in our system, shrub density must be high enough to restrict their access. I defined the borders of the shrub as the transition from accessible, to inaccessible for cattle. I excluded pastures containing large, low-density shrub patches where cattle access was uncertain and patch boundaries were difficult to define.

Third, I excluded pastures that provide regeneration pathways by other means, e.g. when factors such as large rock formations, rather than spiky shrub patches, were providing protection from grazers/browsers. Lastly, I avoided pastures with considerable human interference. This was the case when shrub patches were mowed, fresh and not yet overgrown tree stumps were visible, or dead wood and cuttings were deliberately piled up, resulting in man-made protection provided by dead wood. For a detailed list of the selected nature reserves in which I studied one or more pastures, see table A1 in Appendix A.

Within each pasture, I set out a transect to measure shrubs and regeneration (see figure B1 in Appendix B). If the pasture was bordering a forest, the transect started at the edge of the forest and would continue into the pasture. If no forest was bordering the pasture, I placed the transect at the entrance of the pasture, following a course straight or perpendicular to the entrance. The width of the transect reflected the size of the pasture and the shrub patches present. In pastures that ran a long course, the transect was narrow with a singular line of shrub. In other pastures that ran wide rather than deep, the transect followed a wider course as well. Within the transect, all possible shrub patches, solitary trees, and regeneration were measured. I avoided inventory of the shrubs if they (a) showed clear signs of human interference; (b) held large rock formations allowing regeneration to take place; (c) were too large to map, or; (d) held unclear borders in relation to the ability for cattle to access. See figure 3 for unsuitable (left) and suitable (right) conditions in pastures.

Figure 3

Photographs of various pasture conditions



Note. The photograph on the left is taken in a pasture that did not meet the conditions to be included in the study. The area of the total pasture was covered with large thorny shrub patches that were both impenetrable and penetrable, rather than showing distinct, measurable, borders. The photograph on the right is taken in HRF, where the border between the grazed and traversed grassland and the shrub patches with regeneration is clear. Photographs taken by author.

I defined tree regeneration as any tree occurring within the pasture, regardless of age, size, or association with shrub. Because regeneration occurred under contrasting conditions, I divided all individuals into three categories: Shrub-assisted regeneration (SAR), standing mature regeneration (SMR), and spontaneous sapling regeneration (SSR). SAR were saplings and smaller trees located within the shrubs. SMR were solitary mature trees that effectively escaped grazing pressure. These trees occasionally contained shrub beneath the crown, but cattle could still access the stem. SSR were saplings regenerating outside shrub patches. These saplings could reach a height of approximately 5 meters, and the crown can still be reached and grazed by cattle.

Vegetation surveys

I mapped shrub patches and tree regeneration using an Emlid Reach RX GPS unit. I approximated each shrub patch as an ellipse and therefore measured two perpendicular diameters to estimate patch area. I also measured patch width, length, and height using a 5 m telescopic ruler, while larger patches required additional pacing measurements. I measured patch height from ground level to the highest point of the shrub canopy and recorded the shrub species composition within each patch. I used these measurements to assess how shrub patch size, structure, and composition influenced tree regeneration.

Each category of tree regeneration followed a different measuring protocol. I recorded SAR individuals as part of the associated shrub patch and identified tree species, height, stem diameter above ground, stem number, and crown diameter, assuming a circular crown. I measured these variables using a telescopic ruler and callipers. For multi-stemmed individuals, I measured the dominant stem height and diameter while including all stems when estimating crown diameter. For the SMR group, I measured the same variables as for SAR individuals and recorded the number and species composition of thorny shrubs occurring beneath the crown. I also counted the number of spiky shrub plants present under the crown and recorded the species composition of the spiky shrub plants. Finally, For the SSR group, the measured aspects were the same as for the SAR classified trees, but independent of shrub presence.

To record canopy composition in nearby mature forests, I randomly selected three sampling points and established 50×2 m² transects from each point. At the transect origin, I measured species-specific basal area using a relascope. Along each transect, I recorded all regeneration per species, defining regeneration as trees ≤ 5 m in height. These data allowed comparison of regeneration patterns between forests and pastures and assessment of the relative abundance of potential seed-source species (see Bachelor project of Theun Blaauw for further details and results of this analysis).

Statistical methods

I divided the sampled pastures into two systems based on the presence or absence of bordering mature closed-canopy forest. System 1 includes pastures directly bordering a mature forest, allowing analyses of distance-dependent regeneration patterns. The pastures assigned to this system were Knivsås-Borelund (KNV) *naturreservat* (NR), Kronovalls Store Vång NR (KSV), and a pasture in Stiby backe NR (STB). System 2 includes pastures lacking a bordering mature forest, where analyses related to seed-source distance were not applicable. The pastures assigned to this system were in Björnö NR (BJO), Brösarps backar NR (BRB), Humlarödshus Fälad NR (HRF), another pasture in Stiby backe NR (SBC), and a pasture in Värnanäs NR (VRS).

In system 1 I analysed the probability of establishment of regeneration in relation to the shrub size and the distance to the forest edge, while in system 2, I analysed the probability of establishment of regeneration in relation to the shrub size without looking at distance relationships.

To evaluate how shrub refugia and landscape position (distance to the forest edge) jointly influenced tree regeneration establishment, I modelled the probability of regeneration presence as a function of shrub patch size and distance

to the nearest forest edge. Analyses were restricted to regeneration-stage individuals (tree height ≤ 5 m) to minimize confounding effects associated with large established trees, whose canopy development may suppress shrub growth and thereby obscure facilitative shrub effects. Only observations with available measurements of shrub area and forest-edge distance were included. To analyze establishment probability, I used generalized additive mixed models (GAMMs) with a binomial error distribution and logit link. Since I didn't expect perfect linear relationships, using a GAMM seemed the best option, as a GAMM is a model which allows for modelling non-linear and non-constant variance datasets. 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). The response variable represented establishment occurrence (presence/absence of tree regeneration within shrub patches). The shrub area was a log-transformed predictor ($\log_{10}(\text{shrub area})$) and distance to forest edge was modelled as a smooth non-linear term. I fitted models separately for pastures with in system 1 (KNV, KSV, and STB) and for the pastures in system 2 (BJO, BRB, HRF, SBC, and VRS), I used only the shrub area as the predictor.

I analysed shrub-size effects on regeneration and escape thresholds using a sequential two-stage modelling framework. First, I fitted GAMMs describing the relationship between shrub area and the probability of regeneration establishment or escape into successive height classes. I analysed 3 different escape thresholds; 1.3, 1.5, and 2.0 meters. Which are found to be standard escape thresholds for deer (1.3 meters) (Barrere et al., 2024), and (a combination with) cattle (2.0 meters) (Whistance, 2018). These models were fitted at the individual shrub-patch level using binomial error distributions and smooth terms for shrub area. To reduce potential confounding caused by mature canopy trees suppressing shrub development, I excluded regeneration patches containing trees taller than 5 m. This filtering step was intended to focus the analyses on regeneration stages still likely interacting directly with shrub protection rather than on mature tree-shrub associations, likely dominated by negative effect of crown shade upon shrub development. Second, I extracted shrub-area threshold estimates from the fitted GAMMs. For each pasture, regeneration process, and target probability level (0.25, 0.50, and 0.75), I calculated the shrub area required to achieve the specified probability of establishment or escape. I analysed derived threshold estimates using linear mixed-effects models (LMEM) with process and probability levels treated as fixed effects and pasture identity included as a random intercept. As a result, the mixed-effects models operated on summarized threshold estimates rather than on the original shrub-level observations.

To study the effect of shrub diversity and species composition, I grouped species, dividing them in the following categories; (1) *Rosa*; (2) *Rubus*; (3) *Crataegus*; (4) *Prunus*; (5) *Juniperus*, and (6) other.

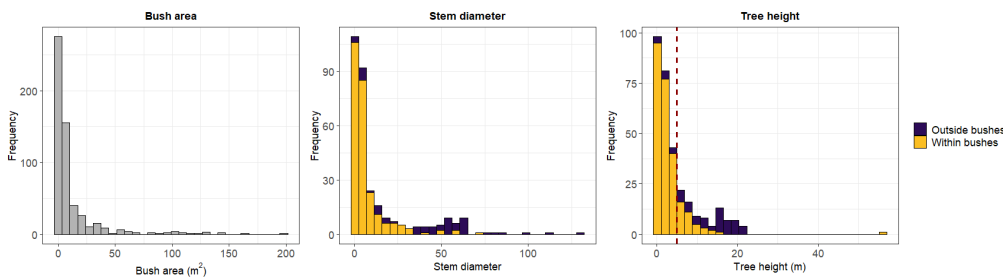
I fitted GAMMs with binomial error distribution and logit link. Response variable was tree regeneration in a shrub patch, which I converted into presence/absence (1/0) data. In this way, I represented tree regeneration as a binary outcome of its establishment and survival in a given patch. I included shrub area as a smooth term, shrub group presence/absence variables as fixed effects, and pasture identity as a random effect. Because sampling was targeted toward shrub patches and regeneration locations rather than random pasture microsites, I restricted the analyses of establishment and escape thresholds to observations containing shrub cover. The resulting models therefore quantify conditional regeneration dynamics within shrub refugia and not landscape-wide probabilities of recruitment.

3. Results

Figure 4 shows frequency distributions of the shrub area, stem diameter and tree height of the sampled shrub patches and trees. The data on the trees is partitioned into regeneration occurring within thorny shrubs and regeneration occurring outside shrubs. The graph shows the relative absence of regeneration before the sapling threshold (< 5 meters) occurring outside thorny shrub patches.

Figure 4

Frequency distributions of shrub and regenerating tree sizes.



Note. The graph shows 1 frequency distributions of shrub size (left), and 2 frequency distributions of regenerating trees (middle and right). Stem diameter and tree height distributions are partitioned into regeneration occurring within thorny shrubs and regeneration occurring outside shrubs. The dashed red line in the tree-height panel indicates the sapling threshold used in subsequent analyses (tree height < 5 m).

System 1 – shrub patch size and distance to forest

I analysed the probability of establishment of regeneration in relation to the shrub patch size and the distance to the forest edge.

I found that regeneration establishment in pastures adjacent to forests was significantly associated with both shrub patch area and distance from the forest edge (table A2 in Appendix A). The probability of regeneration presence varied significantly with log-transformed shrub area ($p = 0.002$) and with distance to the forest edge ($p = 0.001$).

The effect of distance to edge was non-linear (edf = 3.219), indicating that regeneration probability changed unevenly across the distance gradient. In contrast, the effect of shrub area was approximately linear (edf = 1.00).

The interaction between shrub area and distance to edge was not significant ($p = 0.474$), suggesting that the effect of shrub patch size on regeneration establishment did not depend on proximity to the forest edge.

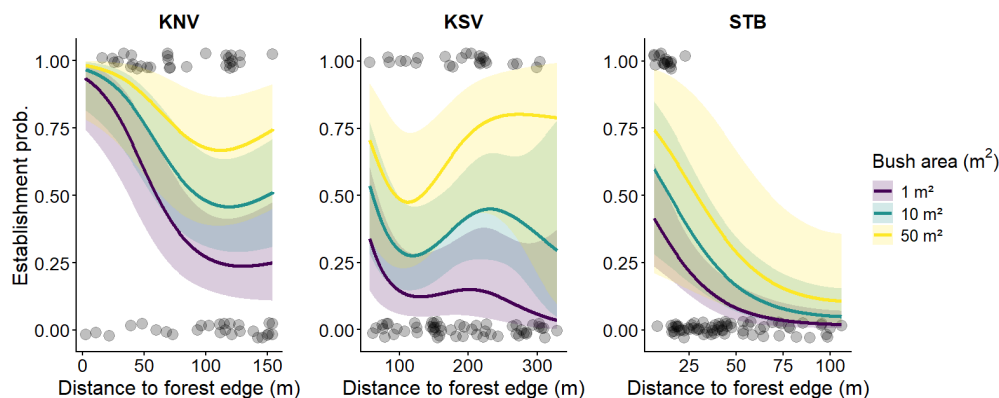
Significant variation among pastures was detected ($p < 0.001$).

Figure 5 shows the predicted establishment probability of regeneration across distance from forest edge. The predicted establishment probability of regeneration

seems to be largest at the edge of the forest but increases again as distance to forest border increases. Which can be seen first in pasture KNV, and then in pasture KSV, where the transact covered increasingly longer distances compared to pasture STB.

Figure 5

Establishment probability curves in relation to distance to forest edge across pastures bordering forest

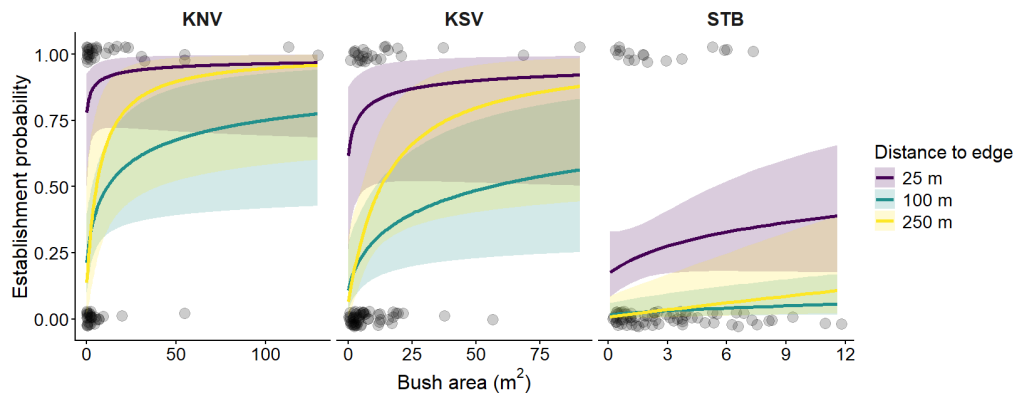


Note. Predicted probability of tree regeneration establishment along gradients of distance to forest edge in three wooded pastures (KNV, KSV, and STB), shown for shrub patches of different sizes (1, 10, and 50 m²). The predictions were derived from generalized additive models (GAMs) fitted separately across the observed environmental gradient while accounting for nonlinear responses. The coloured lines represent predicted establishment probability for shrub patches of different sizes (1, 10, and 50 m²). Shaded ribbons are 95% confidence intervals. Shrub patch area was log-transformed prior to analysis using $\log(1+x)$, but predictions are shown on the original area scale (m²). Gray points are observed binary establishment outcomes (presence/absence of tree regeneration). Shrub patch area was log-transformed prior to analysis using $\log(1+x)$, but predictions are shown on the original area scale (m²). Panels correspond to individual pastures.

The predicted establishment probability of regeneration increased exponentially with an increase in area of the shrub patch before reached a plateau.

Figure 6

Establishment probability curves in relation to shrub area across pastures bordering forests



Note. Predicted probability of tree regeneration establishment in relation to shrub patch size across three studied pastures (KNV, KSV, and STB). Predictions were generated from generalized additive models (GAMs) fitted to binary establishment data using a binomial error distribution and logit link function. The coloured lines represent predicted establishment probability at different distances from the forest edge (25, 100, and 250 m). Shaded ribbons are 95% confidence intervals. Gray points represent observed establishment outcomes (presence/absence of tree regeneration). Shrub patch area was log-transformed prior to analysis using $\log(1+x)$, but predictions are shown on the original area scale (m^2). Panels correspond to individual pastures and are displayed on their observed shrub-area ranges.

System 2 – shrub patch size

I analysed the probability of regeneration establishment internally in pastures, in relation to the size of the shrub (table A3 in Appendix A).

I found that regeneration establishment in pastures without bordering forests is significantly associated with shrub patch area. The probability of regeneration presence varies significantly with log-transformed shrub area ($p < 0.001$).

I found a linear effect of shrub area ($edf = 1.00$), indicating that regeneration probability changed linearly across shrub patch area gradients.

Here too did I detect a significant variation among pastures ($p < 0.001$).

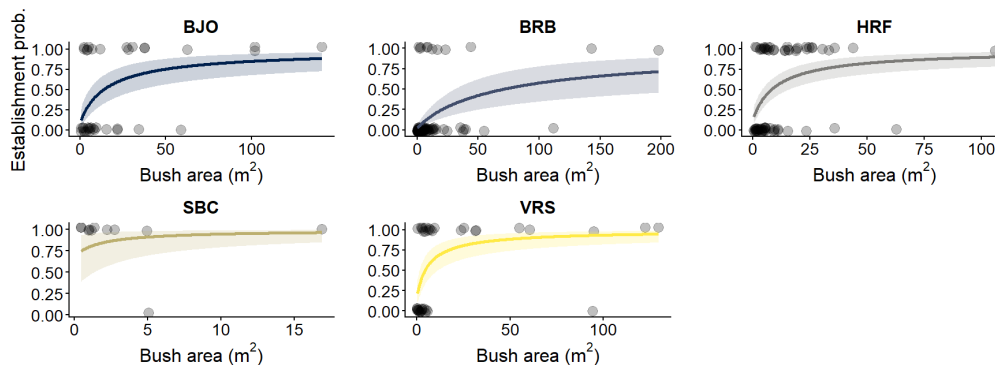
I analysed what shrub patch area is needed for a variation of regeneration probabilities (0.005, 0.1, 0.25, 0.5, 0.75, and 0.95) across the 5 pastures. The shrub patch area varied between $10 m^2$ to almost $200 m^2$ to secure regeneration to establish for 95%. The exact shrub area thresholds per probability and pasture are shown in table A4 in Appendix A.

Figure 7 shows the predicted probability of regeneration establishment across shrub patch sizes in the 5 pastures without forest edge relationships. The graphs show us that small shrub patches offer only a small establishment probability of

regeneration. But, in most cases, seems to increase to a maximum establishment probability before the effect plateaus.

Figure 7

Establishment probability curves in relation to shrub area across internally wooded pastures



Note. Predicted probability of tree regeneration establishment in relation to shrub patch size across five studied pastures (BJO, BRB, HRF, SBC, and VRS). Predictions were generated from a generalized additive model (GAM) fitted to binary establishment data using a binomial error distribution and logit link function. The coloured line represents the predicted establishment probability for each pasture. Shaded ribbons are 95% confidence intervals. Gray points represent observed establishment outcomes (presence/absence of tree regeneration). Shrub patch area was log-transformed prior to analysis using $\log(1+x)$, but predictions are shown on the original area scale (m²). Panels correspond to individual pastures and are displayed on their observed shrub-area ranges.

Figure B2 in Appendix B shows how the required shrub area increases for higher establishment probabilities per pasture.

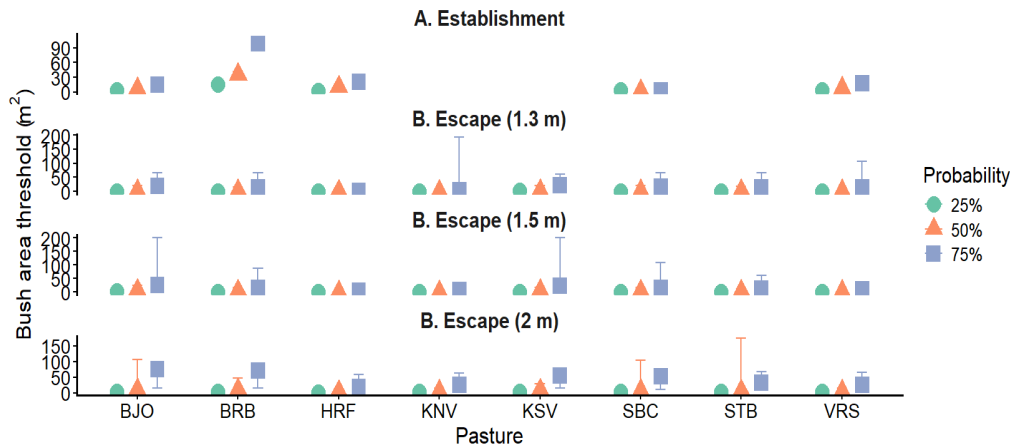
Escape probability

I analysed what shrub patch size is needed for regeneration not only to establish, but to survive long enough to escape grazing (table A5 in Appendix A).

Shrub patch area was significantly smaller for regeneration to reach 1.3 and 1.5, than it was for regeneration to establish at 25% ($p < 0.001$). The shrub patch area needed for regeneration to reach 2m was not significantly different from the shrub patch area needed to reach an establishment probability of 25% ($p = 0.895$).

Figure 8 shows the overall relationship between shrub size and escape probability across all pastures. The y-axis displays the shrub area needed for establishment or escape to take place at certain probability levels. The graph shows that larger shrub area is needed for trees to reach escape heights (B) than to establish (A).

Figure 8
Estimated shrub area required for establishment and escape at various probability levels



Note. Estimated shrub patch area required to meet target probability thresholds for; (A) tree regeneration establishment, and (B) browse escape at three height thresholds: 1.3 m, 1.5 m, and 2 m, across eight studied pastures. Threshold areas were estimated from generalized additive models (GAMs) fitted to binary outcome data using a binomial error distribution and logit link function. Point shapes and colours represent the three target probability levels (25%, 50%, and 75%). Error bars represent 95% confidence intervals. Shrub patch area was log-transformed prior to analysis using $\log(1+x)$, but estimates are shown on the original area scale (m^2). Where confidence intervals exceeded the observed shrub-area range of a pasture, they were truncated at the maximum observed value. Note

Figure B3 in Appendix B shows how large a shrub patch must be to achieve a given probability of establishment or escape.

I analysed whether the difference among demographic stages changed depending on the probability level. I found that the effect of demographic stage depends on the probability level.

I detected a significant interaction between demographic stage and probability level ($p = 0.008$), indicating that the magnitude of threshold differences among stages varied across probability levels. The separation among stages is not perfectly constant, but the effect may be biologically small.

The separation among demographic stages is essentially stable across probabilities.

Shrub diversity and its effects

I analysed whether regeneration establishment differs among shrub species, after accounting for shrub size and pasture effects (table A6 in Appendix A). I compared shrubs containing one of the following species: (1) *Rosa*; (2) *Rubus*; (3) *Crataegus*; (4) *Prunus*; (5) *Juniperus*, and; (6) Other. Figures B4 and B5 in Appendix B show the abundance of each species present per pasture. Shrub species identity influenced establishment probability. Shrub patches containing *Rubus* ($p < 0.001$), and *Juniperus* ($p < 0.001$) showed significantly higher establishment probabilities. *Crataegus*, *Rosa* and *Prunus* showed no significant effects. *Crataegus* showed the lowest establishment probability compared with other shrub groups. Results regarding *Crataegus* and *Malus sylvestris* might be affected by errors made during sampling, which suggests that these results should be regarded with caution. Figure B6 in Appendix B shows the establishment probability of tree regeneration over shrub patch area per species.

4. Discussion

Both shrub patch size and landscape context strongly influence regeneration dynamics. Overall, the results supported the hypothesis that shrub functioned as a protective refuge that enhance establishment probability and increase the likelihood of regeneration escaping browsing pressure.

Shrub patch size- and thresholds

I observed a positive relationship between shrub patch size and probability of regeneration establishment. Larger shrub patches increased the probability of successful establishment, both in edge-connected and edge-free pastures. This pattern aligned with ecological facilitation theory, which proposes that shrub can act as a protective refuge that enhance seedling survival under grazing pressure (Milewski et al., 1991; Smit et al., 2005; Smit et al., 2006; Van Uytvanck et al., 2008; van Klink et al., 2016). The small number of regeneration outside thorny shrub patches further showed the important role of shrub patches in creating regeneration pathways in pastures.

Small shrubs frequently lacked regeneration entirely, whereas establishment probability increased rapidly once shrub patches exceeded a certain size. These sizes depended strongly on the pasture and could range from 10 m² to almost 200 m². Variability in the effect across pastures suggested differences in their grazing intensity, vegetation structure, soil moisture, and seed availability.

Required shrub-area thresholds increased strongly with target regeneration probability, indicating that higher probabilities of establishment were associated with progressively larger shrub patches. Threshold estimates also differed significantly among regeneration-height criteria, reflecting differences in the fitted establishment and escape probability functions across regeneration stages.

Distance to forest relationships

Spatial context influenced regeneration patterns. In pastures with a bordering forest, distance to forest edge was negatively correlated with establishment probability. Regeneration generally declined with increasing distance from the forest edge, likely reflecting dispersal limitation.

Several studies have shown that distance to seed source affects regeneration across a range of landscapes (Stevens-Rumann & Morgan, 2019; Axer et al., 2021a; Axer et al., 2021b; Ursell & Safford, 2022). However, shrub size partially compensated for this effect, suggesting that sufficiently large shrubs can function as a protective refuge even in more distant locations.

The shrub area and distance to edge influence regeneration independently, indicating that the effect of shrub patch area on regeneration establishment does

not significantly change with distance from the forest edge. Shrub size remained the dominant predictor of establishment in internally wooded systems where distance to edge, or seed source adjacency, was not considered.

Escape size- and thresholds

I then analysed the probability of regeneration to reach a given escape height in relation to shrub patch size. I used a threshold analysis to estimate shrub size required to achieve different probabilities of reaching escape height. After establishing, regeneration escapes the risk of being browsed at so-called escape height. These heights differ per grazer species but is usually dominated by the tallest grazer (Walters et al., 2020). I analysed 3 different escape thresholds; 1.3, 1.5, and 2.0 meters. Whereas the 1.3 meter is the standard escape threshold for deer (Barrere et al., 2024), and 2.0 meters for cattle (Whistance, 2018).

The browsing escape analyses showed that across all tested escape thresholds (1.3 m, 1.5 m, and 2.0 m), larger shrubs were associated with higher escape probabilities. I found that the probabilities of reaching the 1.3 m and 1.5 m browsing escape thresholds were consistently lower than the probability of initial establishment, whereas no significant difference was detected for the 2 m threshold. This indicates that facilitating initial recruitment is easier than sustaining saplings long enough to reach early escape heights. This supports the interpretation that browsing pressure represents a secondary demographic bottleneck following establishment. Even when seedlings successfully germinate beneath shrubs, larger or denser shrub structures may be necessary to provide sufficient long-term protection for saplings to reach escape height.

Shrub patch species composition

Shrub functional traits is an important predictor of tree regeneration in the grazed landscapes since they differed in thorniness, shrub canopy density, controlling light conditions at the ground, level of grazing protection, and likely also microclimate within the shrub. *Juniperus* and *Rubus* function as strong protective refuges. Previous studies have showed that Juniper acts as a protective shrub due to its unpleasantness for grazers (Oldén et al., 2016; Olf et al., 1999). Other shrub species showed no significant association with regeneration establishment. Previous studies showed a positive relationship between the occurrence of *Quercus robur* and *Prunus spinosa* (Bakker et al., 2004). Although I recorder *Prunus spinosa* during pasture inventories, this shrub did not show a significant effect on establishment probability. This might be caused by the low number of recorded *Prunus spinosa*. Although the GAM framework accounts statistically for unequal sample sizes through estimation uncertainty, rare shrub groups such as *Prunus spinosa* may still result in less precise estimates and should therefore be interpreted cautiously.

These findings emphasize that shrub functional traits may be more important than shrub presence alone when evaluating facilitative interactions in grazed landscapes.

Limitations and implications for future studies

Shrub composition data limited the species-level interpretation of the results. I did not record shrub dominance within individual shrub patches and instead treated all recorded shrub species equally, regardless of abundance. Rare species therefore contributed equally to dominant species, which likely reduced the ability to detect species-specific effects on regeneration establishment. Field identification also introduced uncertainty because sampling took place in early spring, when many shrubs remained in bud or only partially leafed out. In particular, I occasionally struggled to distinguish *Malus sylvestris* from *Crataegus* species, which may have introduced classification errors into the dataset. These uncertainties may partly explain the weak or absent relationships between shrub composition and establishment probability.

The analytical framework constrained direct comparisons between demographic stages. Establishment models included all shrub patches, whereas browsing escape models only included patches that already contained regeneration. Escape thresholds therefore describe post-establishment survival and growth rather than transitions across the continuous gradient in shrub sizes. Differences between establishment and escape thresholds should consequently be interpreted with caution.

The observational design of the study limited its causal inference. I collected all data within a three-week sampling period and relied exclusively on observational data. Although the analyses revealed strong associations between shrub structure and regeneration, they effectively disregarded other likely important predictors such as soil conditions, moisture availability, management history, or historical and current grazing pressure. Shrub patches may therefore occur preferentially in microsites already favorable for regeneration, which could partly confound facilitative effects.

Pasture heterogeneity may also influence the model estimates. The sampled pastures differed substantially in structure, connectivity, and surrounding vegetation. I attempted to account for this variation by separating forest-adjacent pastures from internally wooded systems, yet the number of sampled pastures remained limited. Some relationships may therefore reflect pasture-specific conditions rather than broader ecological patterns.

The study represented a temporal snapshot rather than a long-term assessment. Regeneration establishment and browsing escape likely varied through time with fluctuations in herbivore pressure, climate, mast years, and disturbance regimes. This study did not capture such temporal dynamics.

To overcome these limitations, I suggest future studies to take additional factors into account and consult detailed historical and site condition maps. These might help in understanding shrub establishment and regeneration dynamics. To extend the scope of the study beyond just a snapshot, future studies should focus on long-term monitoring methods and include grazing pressure, shrub, regeneration, and age data. This will allow researchers to reconstruct size dynamics and determine whether the observed establishment patterns will ultimately turn into successful tree survival and form so-called groves. Including temporal, grazing and age data will significantly strengthen this study by enabling researchers to find thresholds under various grazing patterns and reconstruct the time of shrub establishment, regeneration establishment, grove forming, and grove decay. This will ultimately assist in reconstructing the three models proposed by Frans Vera in his cyclical vegetation turnover theory.

Ecological implications

Wood pastures provide habitat to a unique variety and composition of species, rarely found in either woodlands or grasslands (Bergmeier et al., 2010; Lindenmayer et al., 2014). The coexistence of old trees, deadwood, disturbance by large grazers, and high light availability creates structurally heterogeneous environments that support high biodiversity (Bergmeier et al., 2010; Bergmeier et al., 2014; Plieninger et al., 2015; Oldén, 2016; Lőrincz et al., 2024). Light demanding tree species, such as oak, can regenerate and escape competition in pastures due to the combination of high light availability, small scale disturbances and open conditions with low competition from shade-tolerant species (Annighöfer et al., 2015).

Studies in Sweden show that old trees in open landscapes provide habitat for red-listed epiphytic lichen species (Paltto et al., 2011) and an increased openness around oaks is found to positively influence species richness and abundance of oak-associated beetles (Wilderberg et al., 2012). Maintaining this successional pathway ensures preservation of species which are otherwise disfavoured in the modern forest and are highly dependent on the specific conditions provided by wooded pastures.

This study demonstrates a strong association between shrubs and tree regeneration establishment and browsing escape in grazed wood-pasture systems. These findings suggest that shrub-mediated regeneration pathways can emerge under ongoing grazing conditions without direct human intervention, indicating that such processes may operate naturally within semi-open landscapes.

While shrub-mediated protection may represent an important regeneration pathway, it is unlikely to have been the sole mechanism maintaining landscape and forest dynamics and biodiversity in historical European landscapes. Other

disturbances, including windthrow and fire, likely created additional regeneration opportunities and habitats.

Alongside herbivory, fire likely played a key role in shaping historical landscape structure and species composition (Bond, 2005). Recent research from Scandinavia has demonstrated that low-severity fires can promote oak regeneration by reducing competition and creating favourable establishment conditions (Drobyshev et al., 2021).

Abandonment of traditional practices like forest grazing, selective cutting, and low-intensity fires, and the introduction of large-scale production forests resulted in a shift from open forests to dense and dark forests. This shift reduces natural oak regeneration opportunities, which can explain the observed steep decline of natural oak regeneration over the past few decades (Petersson et al., 2019).

Although additional factors such as fire impact, small herbivores, local site conditions, shifts in land-use type and variation in grazing intensity were not explicitly quantified, the observed regeneration patterns indicate that structurally heterogeneous pasture systems can maintain regeneration dynamics under extensive grazing regimes and may contribute to improving conditions for natural oak regeneration. The coexistence of grazing, shrub refuges, and tree regeneration suggests that regeneration and herbivory need not be viewed as mutually exclusive processes, but can coexist within dynamic semi-open landscapes.

Practical implications

In addition to their ecological importance, wood pastures represent a historical form of land use in Europe (Bergmeier et al., 2010; Hartel et al., 2013) and are highly valued cultural landscapes in Sweden (Garrido, 2017). This further highlights the importance of maintaining these unique and diverse landscapes.

The challenge of maintaining both open habitat conditions and continuous tree regeneration has long complicated the management of wood pastures. Since wood pastures cannot be effectively managed solely through either conventional forest or grassland management approaches (Bergmeier et al., 2010), rewilding-based management may provide an alternative framework capable of maintaining both openness and regeneration processes simultaneously.

Rewilding approaches in Europe frequently aim to restore the ecological functions of large herbivores, which can act as keystone species maintaining structurally diverse vegetation mosaics (Lorimer et al., 2015; Oldén et al., 2016; Mitchell & Kirby, 1990). Several studies have proposed the use of domestic herbivores as ecological replacements for extinct or functionally reduced native herbivore communities, providing a pragmatic approach for initiating rewilding processes (Gordon et al., 2021a; Gordon et al., 2021b; van Wieren, 1995; Garrido, 2017). Because all wood pastures included in this study were grazed by cattle,

either seasonally or year-round, these systems may provide useful models for grazing-based rewilding initiatives.

From this perspective, wood pastures and grazing-based rewilding systems can be viewed as complementary approaches that sustain semi-open landscapes through naturalistic grazing dynamics.

Planting or promoting tree regeneration near thorny or structurally dense shrub patches may provide an effective management tool in landscapes exposed to intense browsing pressure. Such shrubs can function as natural protective shelters, allowing saplings to establish and survive where regeneration would otherwise fail. Consequently, thorny shrub patches should not automatically be regarded as undesirable encroachment within wooded pastures, but may represent an important component of regeneration dynamics. At the same time, the removal or heavy trimming of shrub patches may reduce regeneration success and interrupt long-term woodland continuity. Management strategies such as rotational grazing may help maintain the balance between disturbance and regeneration within pasture systems (Aidarov et al., 2019). Long-term planning and ecological monitoring remain essential, as excessive grazing may suppress regeneration entirely, while insufficient grazing may lead to canopy closure and the decline of open-habitat biodiversity (Bergmeier et al., 2010).

Overall, maintaining a mosaic of open pasture, shrub patches, scattered mature trees, and regenerating woodland may be central to both conservation-oriented pasture management and future rewilding initiatives in Southern Sweden.

5. Conclusion

My study suggests that the mechanisms proposed in module 1 of Vera's theory of cyclical vegetation turnover can plausibly operate in wooded pastures. While this study did not test the complete temporal cycle, the findings supported the idea that thorny shrub patches function as protective refuges that facilitate regeneration under herbivore pressure. With further studies investigating the subsequent modules and long-term vegetation dynamics, wooded pastures may increasingly be understood not merely as transitional landscapes, but as long-term dynamic systems capable of maintaining woodland continuity within open grazing environments. Ultimately, this can support development of a new management paradigm relying on herbivore-mediated tree regeneration pathways that contribute to long-term structural heterogeneity in lowland European landscapes.

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Popular science summary

Across Europe, many traditional wood-pastures are disappearing due to land-use change, shrub removal, and forest intensification. At the same time, natural regeneration of trees such as oak species is often difficult in grazed landscapes because young saplings are heavily browsed by livestock and wild herbivores. Yet in many pastures, young trees can still be found growing within thorny shrub patches. This thesis investigated how shrubs may help trees regenerate in cattle-grazed pastures in Southern Sweden.

Fieldwork was carried out in eight semi-natural pasture systems. Shrub patches and tree regeneration were measured along transects, focusing on shrub size, shrub species composition, distance to forest edges, and the height of regenerating trees. The study explored whether shrubs function as protective refuges that shelter young trees from browsing.

The results showed that larger shrub patches were consistently associated with higher probabilities of tree regeneration establishment. In pastures connected to forests, regeneration also became less likely further away from the forest edge, suggesting that seed dispersal and landscape structure influence where trees establish. However, sufficiently large shrub patches could partially compensate for this effect. The study also found that much larger shrub patches were needed for trees to grow tall enough to escape browsing than for initial establishment, highlighting browsing as a major bottleneck in tree development. Shrub species composition mattered as well: patches dominated by *Rubus* and *Juniperus* were particularly effective in supporting regeneration.

These findings suggest that thorny shrubs can play an important ecological role in maintaining tree regeneration within grazed wood-pasture landscapes. Rather than being obstacles to biodiversity, shrubs may help sustain long-term woodland continuity and structural diversity in semi-open ecosystems. The study contributes to our understanding of how grazing, shrubs, and tree regeneration interact and provides insights relevant to pasture restoration, biodiversity conservation, and future nature management.

Appendix A

Table A1

List of the studied sites

Nature reserve	Pasture ID	Forest bordering	Coordinates	Size (ha)	County
Björnö	BJO	No	56.77147028512293, 16.371629231102933	103.5	Kalmar
Brösarps backar	BRB	No	55.71926332967376, 14.131151850862185	1424	Skåne
Humlarödshus Fälä	HRF	No	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	STB SBC	Yes	56.02598878883427, 14.706383051104904	131.5	Blekinge
Värnanäs	VRS	No	56.485952914464534, 16.140661023393033	344	Kalmar

Note. List of the 7 nature reserves, in which the studied pastures are located. The pasture ID, location, size and county are given. Whether the pasture was or was not bordering a forest determines what analyses can be done.

Table A2

GAMM results testing the effects of shrub area and distance to the forest edge on establishment probability of regeneration

Parametric coefficients					
<i>Term</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>z value</i>	<i>p-value</i>	
(Intercept)	-0.780	0.931	-0.838	0.402	
Smooth terms					
<i>Term</i>	<i>edf</i>	<i>Ref.df</i>	χ^2	<i>p-value</i>	
s(log_shrub_area)	1.000	1.000	9.474	0.002	**
s(distance.edge)	3.219	3.688	17.876	0.001	**
ti(log_shrub_area, distance.edge)	1.328	1.575	0.712	0.474	
Random effects					
<i>Term</i>	<i>edf</i>	<i>Ref.df</i>	χ^2	<i>p-value</i>	
s(pasture)	1.854	2.000	22.702	<0.001	***
Adj. R ² = 0.203 Deviance explained = 20.2% n = 217					

*Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1*

Note. Results of the generalized additive mixed model (GAMM) testing the effects of shrub area and distance to the forest edge on establishment probability of regeneration. The response variables are log-transformed shrub area, distance to the forest edge, and an interaction term. Process and probability are fixed effects, while pasture identity is a random effect. edf = estimated degrees of freedom; χ^2 = chi-square test statistic.

Table A3

GAMM results testing the effect of shrub area on regeneration presence, without distance to edge

Parametric coefficients					
<i>Term</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>z value</i>	<i>p-value</i>	
(Intercept)	-0.017	0.841	-0.020	0.984	
Smooth terms					
<i>Term</i>	<i>edf</i>	<i>Ref.df</i>	χ^2	<i>p-value</i>	
s(log_shrub_area)	1.000	1.000	31.91	<0.001	***
Random effects					
<i>Term</i>	<i>edf</i>	<i>Ref.df</i>	χ^2	<i>p-value</i>	
s(pasture)	3.740	4.000	39.34	<0.001	***
Adj. R ² = 0.331 Deviance explained = 28.2% n = 243					

*Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1*

Note. Results of the generalized additive mixed model (GAMM) testing the effect of shrub area on regeneration presence, without distance to edge. The response variable is log-transformed bush area. Process and probability are fixed effects, while pasture identity is a random effect. edf = estimated degrees of freedom; χ^2 = chi-square test statistic.

Table A4*Shrub area thresholds over various probabilities for the 5 internally wooded pastures*

<i>Pasture</i>	<i>Threshold probability</i>	<i>Shrub area threshold (m²)</i>	<i>Predicted probability</i>
BJO			
	0.005	0.613	0.118
	0.100	0.613	0.118
	0.250	3.433	0.250
	0.500	13.870	0.500
	0.750	49.131	0.750
	0.950	141.372	0.885
BRB			
	0.005	0.314	0.026
	0.100	5.462	0.101
	0.250	20.510	0.251
	0.500	71.199	0.500
	0.750	197.920	0.714
	0.950	197.920	0.714
HRF			
	0.005	0.471	0.160
	0.100	0.471	0.160
	0.250	1.740	0.251
	0.500	8.298	0.502
	0.750	29.875	0.749
	0.950	106.029	0.902
SBC			
	0.005	0.471	0.746
	0.100	0.471	0.746
	0.250	0.471	0.746
	0.500	0.471	0.746
	0.750	0.504	0.750
	0.950	10.603	0.950
VRS			
	0.005	0.283	0.215
	0.100	0.283	0.215
	0.250	0.542	0.244
	0.500	4.429	0.502

	0.750	17.126	0.750
	0.950	129.591	0.947

Note. Estimated shrub-area thresholds and predicted probabilities of regeneration presence for the 5 pasture without bordering forest at six target threshold probabilities. Shrub area thresholds are expressed in m². Where the model could not reach a given probability within the observed range, the maximum observed shrub area is reported.

Table A5*LMM results showing the variation in various escape heights.*

Fixed effects						
<i>Term</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>df</i>	<i>t value</i>	<i>p-value</i>	
(Intercept) (Establishment at probability: 0.25)	1.132	0.211	26.53	5.352	<0.001	***
process: Escape_1.3	-1.119	0.177	75.78	-6.317	<0.001	***
process: Escape_1.5	-1.042	0.177	75.78	-5.886	<0.001	***
process: Escape_2	0.023	0.177	75.78	0.132	0.895	
Establishment at probability: 0.5	1.002	0.137	74.12	7.313	<0.001	***
Establishment at probability: 0.75	2.343	0.137	74.12	17.100	<0.001	***
Random effects						
<i>Group</i>	<i>Variance</i>	<i>Std. Dev.</i>				
pasture (Intercept)	0.148	0.384				
Residual	0.272	0.522				
Type III ANOVA (Satterthwaite's method)						
<i>Term</i>	<i>NumDF</i>	<i>DenDF</i>	<i>F value</i>	<i>p-value</i>		
process	3	74.83	31.08	<0.001	***	
probability	2	74.12	147.23	<0.001	***	
n = 87 Groups (pasture) = 8 REML criterion = 155.7						

*Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1*

Note. Results of the linear mixed-effects model (LMM) testing how shrub-area escape thresholds vary among regeneration processes and target probabilities. The response variable is log-transformed shrub-area threshold. Process and probability are fixed

effects; pasture identity is a random intercept. Degrees of freedom and p-values estimated using Satterthwaite's method.

Table A6

GAMM results testing the effect of shrub group and shrub area on regeneration presence

Parametric coefficients					
Term	Estimate	Std. Error	z value	p-value	
(Intercept) (<i>Crataegus</i>)	-0.656	0.149	-4.400	<0.001	***
shrubs group: <i>Juniperus</i>	1.086	0.317	3.427	<0.001	***
shrubs group: <i>Prunus</i>	0.604	0.357	1.692	0.091	.
shrubs group: <i>Rosa</i>	0.203	0.199	1.016	0.310	
shrubs group: <i>Rubus</i>	1.037	0.244	4.255	<0.001	***
Approximate significance of smooth terms					
Term	edf	Ref.df	Chi.sq	p-value	
s(area.pred)	1.000	1.001	71.89	<0.001	***
Parametric terms (ANOVA)					
Term	df	Chi.sq	p-value		
shrubs group	4	26.78	<0.001	***	
n = 734 Adj. R ² = 0.153 Deviance explained = 12.3% -REML = 446.06					

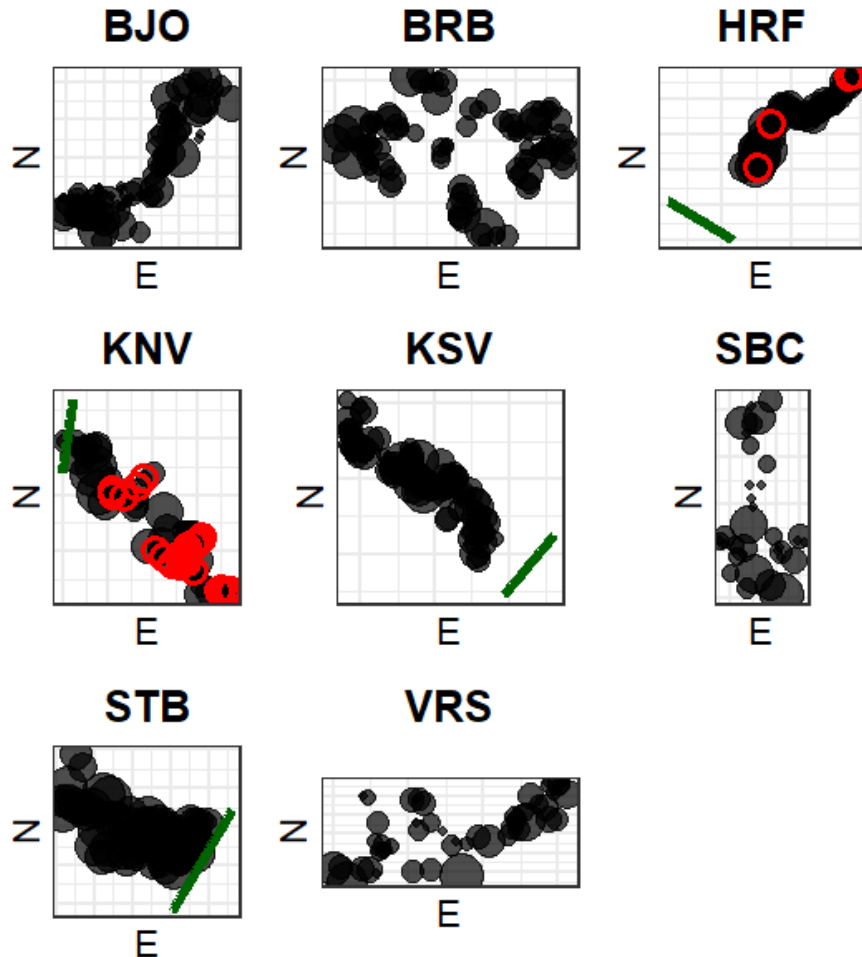
*Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1*

Note. Results of the generalized additive mixed model (GAMM) testing the effect of shrub group and shrub area on regeneration presence. The response variable is regeneration presence (binary), modelled with a binomial family and logit link. Shrub group is a parametric fixed effect; shrub area is included as a smooth term s(area.pred). p-values for parametric coefficients are based on z-tests; significance of terms from Type III ANOVA (Chi-square tests).

Appendix B

Figure B1

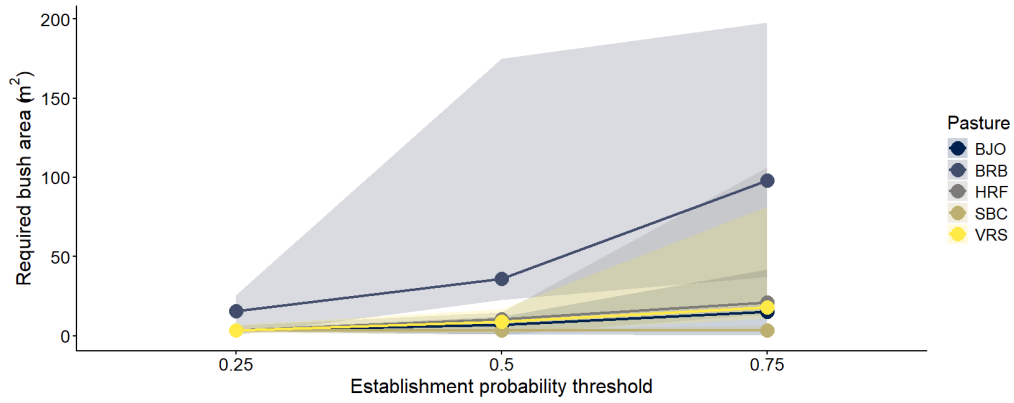
Maps showing the transects in each studied pasture.



Note. Sampled pasture in Björnö nature reserve. The dots show the sampled features, the size of the dots show the approximate size of sampled shrubs. The green line shows the edge of the nearby/adjacent forest. The transect follows the approximate direction from either the edge of the pasture, or the border of the bordering (nearby in the case of HRF) forest toward the centre of the pasture. Only representative shrubs, regeneration, or mature trees are included in the dataset. Shrubs were skipped that; (a) showed clear signs of human interference; (b) held large rock formations allowing regeneration to take place; (c) were too large to map, or; (d) held unclear borders in relation to the ability for cattle to access. The red circles are missing coordinates, which are recovered using interpolation or extrapolation.

Figure B2

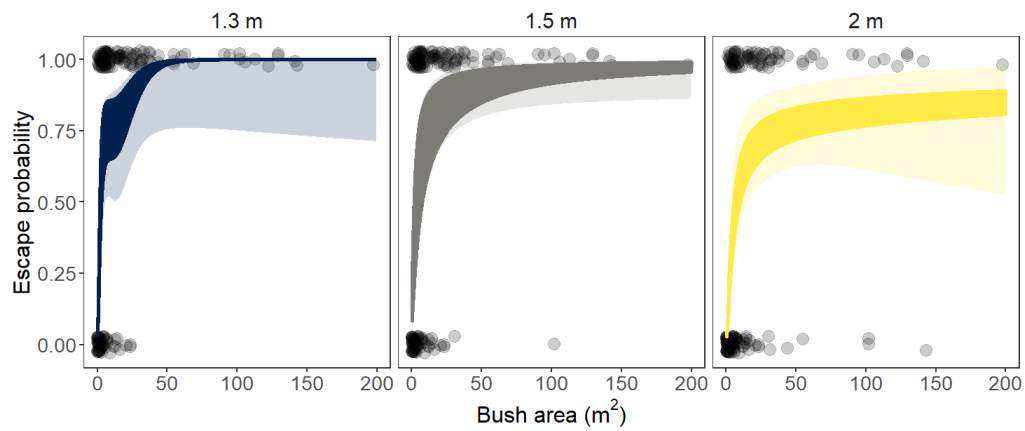
Graph showing the required shrub area for different establishment probabilities per internally wooded pasture



Note. Required shrub patch area to meet target tree regeneration establishment probability thresholds across five studied pastures (BJO, BRB, HRF, SBC, and VRS). For each pasture, the shrub area required to reach establishment probability thresholds of 0.25, 0.50, and 0.75 was estimated from generalized additive models (GAMs) fitted to binary establishment data using a binomial error distribution and logit link function. Lines connect threshold estimates for each pasture across the three probability levels. Shaded ribbons represent 95% confidence intervals. Shrub patch area was log-transformed prior to analysis using $\log(1+x)$, but estimates are shown on the original area scale (m^2). Where the upper confidence interval exceeded the observed shrub-area range of a pasture, it was truncated at the maximum observed value.

Figure B3

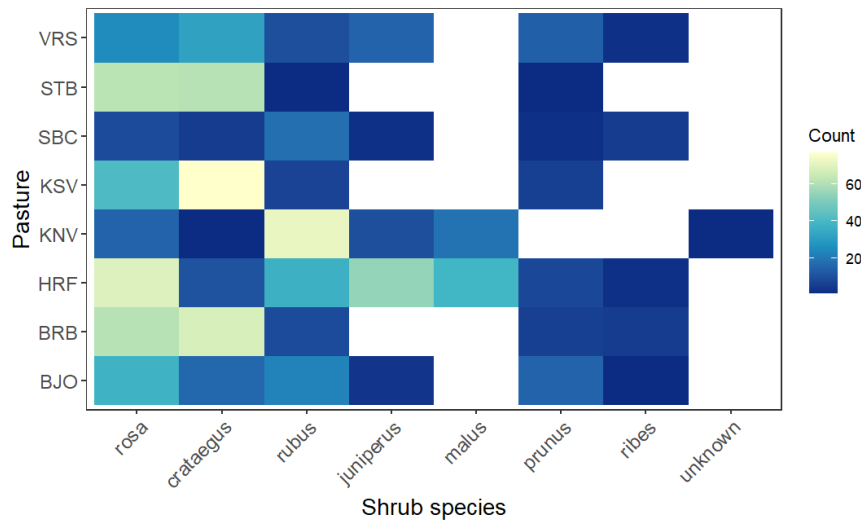
Graph showing the probability of reaching various escape heights over shrub area



Note. Predicted probability of tree regeneration escaping browse at three height thresholds (1.3 m, 1.5 m, and 2 m) in relation to shrub patch size. Predictions were generated from generalized additive models (GAMs) fitted to binary escape data using a binomial error distribution and logit link function. The coloured line represents the predicted escape probability for each height threshold. Shaded ribbons are 95% confidence intervals. Gray points represent observed escape outcomes (presence/absence of tree regeneration exceeding the height threshold). Shrub patch area was log-transformed prior to analysis using $\log(1+x)$, but predictions are shown on the original area scale (m²). Panels correspond to individual height thresholds and share a common x-axis range.

Figure B4

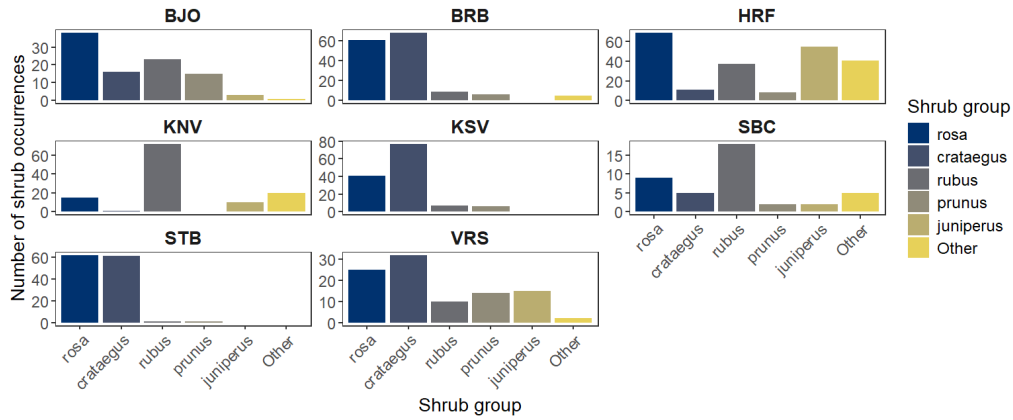
Heatmap showing the presence of different shrub specie groups per pasture



Note. Heatmap showing the abundance of shrub species recorded across eight studied pastures. Cell colour indicates the count of shrub patches of each species per pasture, ranging from dark blue (low counts) to light yellow (high counts). White cells indicate that a species was not recorded in that pasture. Shrub species are shown on the x-axis and pastures on the y-axis.

Figure B5

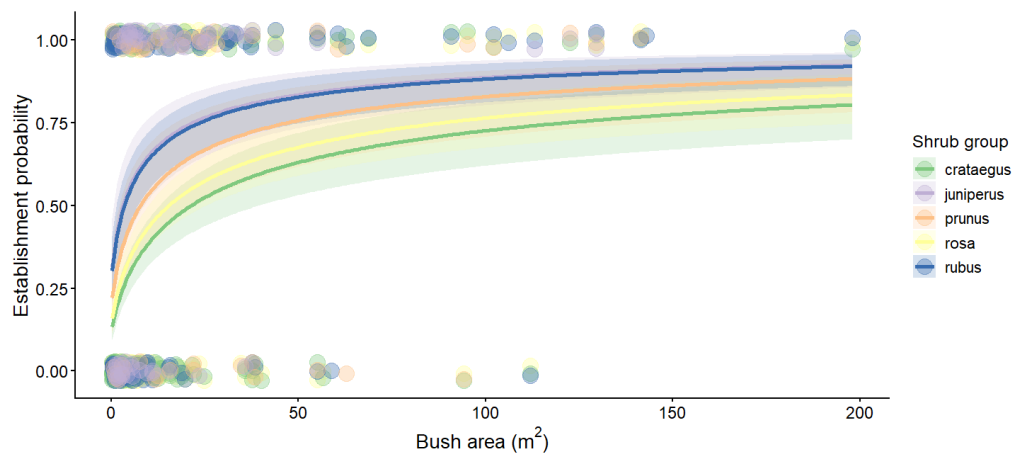
Bar chart showing the number of detected shrubs per shrub group per pasture



Note. Number of shrub occurrences by shrub group across eight studied pastures (BJO, BRB, HRF, KNV, KSV, SBC, STB, and VRS). Bars show the count of recorded shrub patches belonging to each shrub group (*Rosa*, *Crataegus*, *Rubus*, *Prunus*, *Juniperus*, and other) within each pasture. Colours correspond to shrub groups as indicated in the legend. Panels correspond to individual pastures and share a common set of shrub groups on the x-axis, but y-axis scales differ among panels to reflect variation in total shrub abundance.

Figure B6

Graph showing the probability of regeneration establishment for various shrub groups



Note. Predicted probability of tree regeneration establishment in relation to shrub patch size across five shrub groups (*Crataegus*, *Juniperus*, *Prunus*, *Rosa*, and *Rubus*). Predictions were generated from a generalized additive model (GAM) fitted to binary establishment data using a binomial error distribution and logit link function. The coloured lines represent predicted establishment probability for each shrub group. Shaded ribbons are 95% confidence intervals. Points represent observed establishment outcomes (presence/absence of tree regeneration), coloured by shrub group. Shrub patch area was log-transformed prior to analysis using $\log(1+x)$, but predictions are shown on the original area scale (m^2).

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