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Ungulate browsing blocks restoration of coniferous European Sand Belt forests into a broadleaved state

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ABSTRACT

Tree browsing by ungulates may act as a strong biotic filter on forest regeneration. In the western part of the so-called European sand belt, browsing is believed to block restoration of coniferous forests into a broadleaved-dominated state, but this process remains poorly documented. The aim of this study was to better understand the dynamics of tree recruitment in a forest landscape at the European sand belt, using food selection and apparent competition via shared natural enemies as frameworks. We monitored tree regeneration and browsing during 2012–2024 in permanent plots across De Hoge Veluwe National Park (the Netherlands) in transects as well as in exclosures paired with control plots. We found that food selection was not mediated by landscape-level characteristics, but rather by tree species identity. Tree species preferred by ungulates had less height growth when subject to browsing. Exclusion of ungulates led to a substantial increase in height growth of preferred species, while the relative height of avoided species was reduced, indicating apparent competition. Forest regeneration inside exclosures converged to a community of mixed broad-leaved species. These results confirm that browsing in this system indeed hampers the restoration of coniferous forest towards a broadleaved forest. Attempts to diversify these forests and increase resilience to climate change cannot succeed under current ungulate densities.

1. Introduction

Tree browsing by ungulates may act as a strong biotic filter on the composition and growth of tree seedlings and saplings during the establishment phase of forest regeneration. This can have long-lasting consequences for forest ecosystem functioning (Reed et al., 2022; Ramirez et al., 2021; Gill and Beardall, 2001; Hobbs, 1996). For example, browsing by ungulates may limit the extent and species composition of natural regeneration (Ammer, 1996; Gill and Beardall, 2001), and affect nutrient cycling (Ramirez et al., 2021; Sitters and Andriuzzi, 2019). It may cause loss of plant species and its dependents directly (Schulze et al., 2014; Allombert et al., 2005) or indirectly through structural changes of the habitat (Holt et al., 2010, 2013). And it may limit the potential of forests to adapt to climate change (Iverson and Prasad, 2001; Dyderski et al., 2018; Hanewinkel et al., 2013).

Ungulate browsing is particularly problematic in the so-called European sand belt (Koster, 2009), a region in northern European Lowlands. Here, most soils are susceptible to desiccation during drought periods and are strongly acidified due to accumulated sulphur and nitrogen deposition which further impoverished the already nutrient-poor soils (De Vries et al., 1995; Skidmore et al., 2024). Large-scale afforestation of heathlands and drift sands during the 19th and 20th century has created forest landscapes that are dominated by – mainly coniferous – plantations. These are typically species-poor and lack many of the native broadleaved species that would normally occur on these sites. This makes these forest ecosystems particularly vulnerable to climate change (Schueler et al., 2014; Saenz-Romero et al., 2019).

To enhance forest resilience in this system, managers nowadays aim

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to convert conifer stands to stands dominated by broadleaved species (Knoke et al., 2008) through natural regeneration and enrichment planting, introducing broadleaved species now lacking in the plantations and species that are expected to be more drought resistant. Yet, the success of these efforts has been limited, supposedly due to ungulate browsing that shifts the tree community towards the least-preferred or most browse-resistant species (Reed et al., 2022; White, 2012; Pastor et al., 1993; Rooney et al., 2015). Ungulates appear to block restoration of these forests into a broadleaved-dominated state (Kuiters and Slim, 2002) and instead prolong the existing dominance of coniferous species. While widely acknowledged among forest managers, this process remains poorly documented in the scientific literature.

Two well-established scientific frameworks are particularly useful for understanding successional patterns in forests in the European Sand Belt. The first concerns food selection and the feeding preferences that underlie ungulate-induced compositional and structural changes in forest (Augustine and McNaughton, 1998; Hedwall et al., 2018). Food selection by ungulates follows a hierarchical pattern within a region, with choices made on the scale of a landscape, community, and patch (Senft et al., 1987). On the landscape level, in the absence of overriding constraints, ungulates are expected to select areas of highest productivity or diversity (Ohse et al., 2017; Bobrowski et al., 2015). Within a plant community, ungulates select those patches with highest nutritional value or quantity (Bergqvist et al., 2012; Ohse et al., 2017) or with structural characteristics related to hiding or thermal cover (Vospernik and Reimoser, 2008; Nopp-Mayr et al., 2011; Gerhardt et al., 2013). For example, canopy gaps and low-density forests may be visited more often (Ohse et al., 2017; Kuijper et al., 2009) and browsing may affect seedling densities more strongly here than under closed canopy (Tilghman, 1989; Ammer, 1996). And within patches, they select plants to maximize nutrient intake, resulting in preference of certain species and the avoidance of others (Ohse et al., 2017: Boulanger, et al., 2009; Kuiters and Slim, 2002). The extent by which species are actually browsed depends on the species composition of the patch itself, leading to either associational resistance or associational susceptibility or palatability (Atsatt and O'Dowd, 1976). For example, Barbosa et al. (2009) found that the presence of unpalatable species generally results in less browsing of the neighbouring plants. This associational-resistance effect is stronger when browsing pressure is lower (Smit et al., 2007). On the other hand, high-diversity patches may increase overall browsing – an example of associational palatability - although the per capita browse probability for the species present may still be lower (Ohse et al., 2017). Thus, while ungulate browsing can induce compositional change towards unpalatable species, the actual outcome may be context-dependent on a scale ranging from landscape to patch level.

The second framework is that of apparent competition via shared natural enemies (Connell, 1990; Holt and Bonsall, 2017). Connell (1990) has shown that interactions between plants that are often described as direct or indirect interference (the classic competition effects) might as well be cases of apparent competition. Holt and Bonsall (2017) expanded the concept, describing asymmetrical apparent competition in cases where one plant species is affected much less by the herbivore than the other, leading to different outcomes of their interaction then when the herbivore is absent. Selective browsing will induce growth losses in preferred species, while leaving the avoided species unaffected (Bödeker et al., 2023). This leads to differential height growth among species in communities subject to browsing: avoided species gain a competitive advantage over preferred species, mediated by light availability, even though such species may not have inherently higher height growth rates. This apparent competition has been implicated (Ammer, 1996; Schulze et al., 2014) but not explicitly investigated in the context of ungulate and tree community dynamics.

The aim of this study was to better understand the dynamics of tree recruitment in the forest landscape of the European Sand Belt, using the general insights and principles outlined above. Specifically, we tested the idea that ungulates, through their foraging preferences for native broadleaved species, block restoration of these conifer-dominated forests into a broadleaved-dominated state. Our approach was to monitor browsing levels and compositional changes of tree recruits in regeneration patches accessible to ungulates, and inside exclosures and their control plots. Monitoring spanned multiple years within a single protected area that contained forest landscapes representative for the European Sand Belt.

We tested three predictions. First, we tested whether browsing intensity is scale dependent, following the idea that ungulate choices are made on the scale of a landscape, community and patch (Senft et al., 1987). If so, browsing levels should be highest in the most productive habitats (better soils, more food available), and in patches of highest food quality and quantity within those habitats. Simultaneously, overall browsing levels should increase with ungulate density. Second, we tested whether ungulates select the more palatable broadleaved species over conifers. Third, we tested whether preferential ungulate browsing alters the competitive positioning of species, leading to apparent competition. In the presence of ungulates, preferred species should have reduced plant height relative to surrounding avoided species. Conversely, in absence of browsing, the competitive positioning of these two groups should change.

2. Methods

2.1. Study site

Measurements were conducted in De Hoge Veluwe National Park (henceforth ‘the Park’), a fenced 53 km^2 protected area located in the centre of the Netherlands, within the European Sand Belt. The Park consists of a mosaic of forests (29 km^2), dry and wet heathlands (13 km^2), open or sparsely vegetated drift sands (8 km^2) and grasslands (3 km^2) (Bijlsma et al., 2015). Climate is temperate, without a dry season and with warm summers (Cfb), with an average yearly temperature of 10.1 °C and a mean annual precipitation of 869 mm (KNMI, 2024).

The Park is situated on the flank of a large push moraine and its glacial outwash, for the largest part blanketed by cover sands during the last ice age. Most cover sands eroded during the Holocene to drift sands that were consolidated for the most part in the previous centuries. Soil substrate is sandy, ranging from fluvial sands of variable texture and silt content to fine, well-sorted aeolian sands with no silt. Soil types vary accordingly, with inceptisols on loamy substrates, spodosols on cover sands and entisols on drift sands. Small parts of the area were cultivated in the previous centuries for agricultural use, but most of the fields were abandoned and reforested in the last century. Groundwater is generally not available to plants, so vegetation relies on water holding capacity of the topsoil. Soil quality varies but is generally low, with the most fertile areas in the northern and southern parts of the Park, and the central part as least fertile.

Most forests in the Park are dominated by *Pinus sylvestris* (66 % of the forest area), either planted or naturally established from the surrounding forest cultures. The northern and southern sections of the Park include plantations, predominantly monocultures planted as a second generation after *P. sylvestris,* with broadleaved species like *Quercus robur, Q. rubra* and *Fagus sylvatica* (23 % of the forest area) and the conifers like *Pseudotsuga menziesii* and *Larix kaempferi* (9 % of the forest area) as most common species. Some patches of old *Q. robur* woodland are found scattered throughout the Park. The forest floor is usually sparsely covered by ground vegetation, mainly consisting of species from the previous landscape (*Molinia*, *Calluna*), and *Vaccinium myrtillus*.

2.2. Ungulate community

Four species of ungulates are present in the Park. As the area is entirely fenced, ungulate population densities are known relatively precisely. For this study we used spring counts of (sub)adults as a measure of population density, that is all individuals present before birth of the new generation (Fig. 1).

Red deer (*Cervus elaphus*) is the dominant cervid present, an intermediate feeder with a diet mostly consisting of grasses, dwarf shrubs and tree leaves, twigs and bark (Groot Bruinderink and Hazebroek, 1995). Red deer population density is assessed by yearly vantage point counts in late February/early March, providing accurate estimates of red deer numbers present in the Park (Dijkhuis et al., 2023). In 2015–2017, a few fallow deer entered the Park, and were counted in a similar manner.

Roe deer (*Capreolus capreolus*) is a typical browser with a broad diet of forbs, bramble and tree leaves and twigs (Tixier and Duncan, 1996). Numbers of the highly territorial roe deer are assessed in each of three subdivisions of the Park, where game warden map all individuals during their inspection rounds at the end of winter and early spring.

European mouflon (*Ovis aries musimon*) is a grazer, mainly feeding on grasses, and also forbs and dwarf shrubs (Marchand et al., 2013). Total numbers, sex, and age class of mouflon are assessed in spring, when the sheep form a large herd in open area, independently by two or three game wardens. Directly following herd assessment, game wardens cross the entire Park and count stray animals that are added to the total. To obtain spring counts of (sub)adults, new-born lambs were subtracted from the total. In 2021, wolf (*Canis lupus*) established in the Park and decimated the mouflon population (Fig. 1) with no free-roaming animals sighted in the Park since December 2022.

To relate browsing levels on trees to the abundance of ungulates, we estimated the total metabolic weight of red deer, roe deer, mouflon and fallow deer from the yearly counts in the Park. Body mass of the animals was assessed using data of culled adult animals from the game administration in the period 2010–2021, averaged over males and females (See supplementary material Table S1). Metabolic weight was calculated as body mass raised to the power 0.67 (White and Seymour, 2003) and summed over all species within each year (Fig. 1). Also wild boar (*Sus scrofa*) is present in the Park. As this species is not directly involved in tree browsing, we did not include it in the total ungulate density estimates. A total of 11.1 km^2 of animal refuge areas is distributed over the Park, restricting public access to allow animals to be left undisturbed during the opening hours of the Park. All ungulate species, except roe deer, are culled by hunting based on a preset target of spring counts per species.

2.3. Measurements

We measured vegetation composition and browsing during 2012–2024 in permanent plots that were scattered among the forests in the Park. We had two types of plots: (1) 40–80 transect plots of 3 × 24 m, which we used to assess height, composition and browsing of tree regeneration related to ungulate density and site conditions, and the probability of tree species to grow to > 5 cm dbh under browsed conditions; and (2) 5–20 fenced and paired control plots of 10 × 10 m each, which we used to evaluate the species composition and relative heights of forest regeneration under browsed and unbrowsed conditions.

2.3.1. Browsing incidence in transects

The transects (3 ×24 m) were established between 2012 and 2017, permanently marked, and monitored yearly for browsing until 2019. 40 transects were installed in 2012, and 10 were added in each of the following years (except 2016) to a total of 80 transects. Transects were installed in locations with recent tree recruitment so sufficient individuals of woody species were available to assess browsing. Due to this plot selection the density and composition in the transects were not representative for the average regeneration status in the Park and biased towards broadleaved species. Most transects were positioned in recently cleared areas, or under an open canopy of mature trees. Stand types were classified as Scots pine stands (*Pinus sylvestris*; 67 % of transects), stands of other conifers (mostly *Pseudotsuga menziesii, Pinus nigra* and *Larix kaempferi*; 22 % of transects) and broadleaved stands (mostly *Quercus robur* and *Betula pendula*; 11 % of transects). The transects were distributed over the entire Park area and fairly proportional across the different stand age classes present in the Park. Over the years, several transects were lost due to severe damage by management activities. Such transects were used for the assessment of browsing but were not used in the analysis of patterns in browsing or plot dynamics over multiple years.

For each woody individual in a transect the species identity, height class and browsing damage to the leader shoot were recorded. Leader shoot browsing is representative for general browsing of shoots on a seedling, directly determines height growth and ultimately affects sapling mortality (Eiberle and Nigg, 1987). Height classes were 10–40 cm, 40–80 cm, 80–120 cm, 120–160 cm, 160–200 cm and

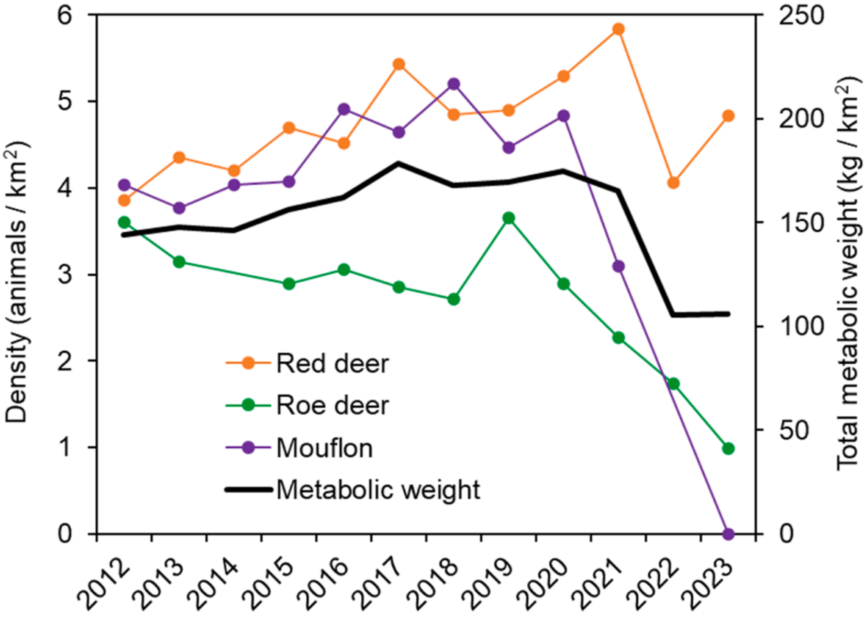

Fig. 1. Population densities (number of individuals per km^2) of the major ungulate species contributing to tree browsing in De Hoge Veluwe National Park in the period 2012–2023. The total metabolic weight includes red deer, roe deer, mouflon and fallow deer (*Dama dama*; densities not shown as this involves a few animals in the period 2015–2017). Data from the Park game administration, based on spring counts of (sub)adult individuals.

> 200 cm. All measurements were done in September/October prior to leaf fall. After 2019, no further assessment of browsing was done as the leader shoots of most of the trees in the transects had grown to heights out of reach of ungulates, leaving only a few smaller individuals vulnerable to leader shoot browsing. Between 2019 and 2024, ingrowth of individuals into the tree layer was assessed in the transects by determining species, diameter, and height for all individuals with a diameter at breast height (1.30 m) of more than 5 cm.

Browsing damage was marked when the leader shoot of the current year was bitten off by ungulates, as judged by the typical frayed edges of the bite marks left on the remaining shoot. Occasionally also bite marks of lagomorphs or mice were identified on small seedlings. To prevent inclusion of leader shoot damage by mammals other than ungulates, and because the largest ungulate, red deer, has a reach of approximately 150 cm, we limited the calculation of browsing percentages to plants with a height between 40 and 160 cm.

The habitat features of each plot location were characterized by estimating the percentage cover of the most dominant vegetation layers in a 25 m radius circle around the centre of the plot. Estimates included canopy cover (percentage of ground covered by the vertical projection of the tree crowns) of mature trees, ground cover of *Vaccinium myrtillus*, and ground cover of grasses (mostly *Molinia caerulea* and *Avenella flexuosa*). Cover was estimated to the nearest 5 % when cover was > 10 %, and to the nearest 1 % when cover was < 10 %. In the analyses, cover percentages were grouped into two classes: *V. myrtillus* cover: 1 = 0–5 %, 2 = >5 %; grass cover: 1 = 0–25 %, 2 = >25 %.

Biomass of the broadleaved individuals was used as a proxy of browse availability in the transect plots. Above-ground biomass of the tree individuals was estimated using the generic biomass equations of Annighöfer et al. (2016) for broadleaved and conifers, using the height class midpoints as input variable. For the height class > 2 m, biomass was calculated assuming a height of 2.5 m.

Thermal cover was characterized for each transect by two canopy classes: 1 = canopy cover 0–25 %, and 2 = canopy cover > 25 %. Hiding cover was determined for each transect by the density of conifers > 160 cm tall.

For the landscape-level analysis, transects were assigned to one of three sections: (1) Hoenderloo Estate in the northern part, and (2) Kemperberg in the southern part of the Park. Both sections were afforested in the 19th century, and consist of a mosaic of stands of *Pinus sylvestris*, *Pseudotsuga menziesii*, *Fagus sylvatica*, *Quercus robur* and some other less frequent conifer and broadleaved species. These areas are of higher habitat quality due to the relatively more fertile soils, longer forest history and generally more productive understory vegetation (Bijlsma et al., 2015). (3) Wildbaan, the central part of the Park, which is mostly covered by drift sands, *P. sylvestris plantations* and naturally established *P. sylvestris* woodlands. These forests are less productive, dominated by pine, have only poorly developed organic soil layers and carry a sparse and unproductive ground flora.

Each transect and exclosure-control plot was assigned to a soil type, based on the 1:50,000 soil map of the Park (Wageningen Environmental Research, 2024). Soils were then classified (See supplementary material Table S2) into soil fertility classes, with 1 = poorest (entisols), 2 = intermediate (mainly spodosols), 3 = richest (mainly inceptisols). Note that overall soil fertility here is at the poor end of the soil fertility gradient. Additional habitat variables were stand type (3 levels: stands of *P. sylvestris*, other conifers or broadleaved) and animal refuge area (0/1).

2.3.2. *Vegetation in exclosures versus control plots*

The 20 exclosures and paired controls were established between 2014 and 2018 (five in winter 2014/2015, 5 in each of three successive winters). Plot pairs were established in similar conditions within recently cleared stands, at least 20 m apart, and then randomly assigned to the exclosure or control treatment. Exclosures were built using 2 m high metal mesh wire and were 12 × 12 m to allow a 1 m buffer around the 10 × 10 m experimental plot. Vegetation and browsing were measured until autumn 2022.

In 2015, the entire 10 × 10 m plots of the five first-established sites were inventoried for all woody regeneration. In 2016, woody regeneration was sampled in four 3 × 3 m subplots. From 2017 onwards, we followed a slightly modified protocol adopted from the German forest regeneration monitoring program (cf. Forstliche Gutachten, 2024). In each plot, all saplings > 50 cm tall were recorded on the entire 100 m^2 plots, and seedlings and saplings < 50 cm recorded in the four 3 × 3 m subplots, representing a total subplot area of 36 m^2 within each plot.

Height, browsing damage of the leader shoot and species was recorded for each woody individual in the (sub)plots. Cover of trees (> 5 cm dbh) and shrubs (woody individuals 50–500 cm high), cover of dwarf shrubs, grasses, herbs, and woody individuals (<50 cm in height), and cover of mosses. Cover was estimated for each vegetation layer and for each species within that layer.

The effect of shading on the composition of the regenerating tree community was assessed using a forest canopy cover index: each plot was assigned a canopy cover class, based on the cover of adult trees above the plot pair (control-exclosure). Two canopy cover classes were used: no or sparse canopy (0–25 %) and intermediate to dense canopy (>25 %).

Relative tree heights in the exclosure and control plots were characterized using the 95th percentile of heights per species or species group within each plot. This represented the most competitive individuals that were most likely to maintain themselves in the main canopy. To calculate the 95th percentile, heights of all individuals present were used, with the heights of plants < 50 cm entered 3-fold to compensate for the smaller area sampled in the plots. This implies that in plots with a low number of individuals of a species or species group, the 95th percentile was slightly underestimated. Only the most frequently occurring species were presented on the species level (*P. sylvestris*, *B. pendula* and *S. aucuparia*). The remaining species were lumped into a broadleaved or conifer group. Relative heights were calculated as the 95th percentile heights relative to the maximum 95th percentile height of a species or species group within a plot in a given sampling year.

2.4. *Food preference*

Food preferences of ungulates were derived from the transect data on terminal-shoot browsing. Specifically, we estimated Chesson's Index of Electivity (ε) (Chesson, 1983), using the R-package {electivity} (Quintans, 2025). ε is calculated for each species *i* as

$$\epsilon_i = \frac{m \times \alpha_i - 1}{(m-2) \times \alpha_i + 1}$$

where α_i is Manly's selection index (Manly et al., 1972) for species *i*, and m the total number of species in a plot. α is in turn calculated as

$$\alpha_i = \frac{r_i}{n_i} \times \frac{1}{\sum_{j=1}^{m} \frac{r_j}{n_j}}$$

where r_i and r_j = the proportions of species *i* and *j* browsed in a plot, n_i and n_j = the proportions of species *i* and *j* available in a plot. The electivity index takes values between −1 (avoided) and + 1 (preferred). The values of ε were calculated using all the individuals between 40 and 160 cm in height of a given species occurring in the plots in each sampling year. We then evaluated the indices of electivity per species for differences between years, Park sections and soil fertility classes. We calculated mean electivity values per species weighted by the square root of the number of individuals of that species in a plot. Values for ϵ_i were calculated only for those species that occurred as individuals 40–160 cm tall in at least 5 % of the transects in each census and were thus sufficiently represented in the dataset to obtain meaningful electivity estimates.

2.5. Analyses

All analyses were done in R 4.4 (R Core Team, 2024). The relationships between habitat- and patch level variables with the browsing index (i.e., the proportion of broadleaved individuals between 40 and 160 cm with their leader shoot browsed) were tested with generalized linear mixed models (GLMM) with a binomial error distribution and a logit link, using the package {lme4} (Bates et al., 2015). Sampling Year and Plot were included as random factors. At the habitat level, Section, Stand type, Refuge area and Soil fertility were included as fixed factors. At the patch level, Section, Forage quantity [Browse, Grass, Blueberry], Thermal cover [Canopy cover], and Conifer density were included as fixed factors. The Browse index, the availability of Browse and the density of Conifers were log-transformed prior to analyses. Best-fitting models were determined using a backward procedure by successively eliminating non-significant factors and selecting the models with lowest AIC.

Food preference (electivity) was compared between species using weighted GLMM with a binomial error distribution and a logit link. Electivity was converted to a proportion, and related to species with plot ID as random factor and the square root of the sample size as weight. Marginal means and significance were calculated using {emmeans}. This was done across all years as well as separately for plots grouped by year, by section of the Park and by soil type.

Community dynamics were analysed with Nonmetric Multidimensional Scaling (NMDS), using {vegan} (Oksanen et al., 2025). Census data were the counts of all individuals taller than 40 cm by species. Factors included were exclosure, presence of a canopy at the start, and soil fertility class. Different censuses of the same plots were included as separate observations, and vectors connecting these were added to the ordination plots using {ggplot2} as to visualize the development.

The likelihood of ingrowth of broadleaved species in 2024 in relation to the initial proportion in the seedling bank (average of 2012–2014) was analysed using binary logistic regression, with plots as replicates. Factors included in the model were the average percentage of browsed broadleaved individuals (40–160 cm in height) over the first three sampling years of the transects (arcsine-transformed), the percentage of all broadleaved individuals in the transects relative to conifers in the first three sampling years of the transects (arcsine-transformed), soil fertility using classes (See supplementary material Table S2) extremely poor (fertility class 1) and poor (fertility classes 2 and 3), and canopy classes open (0–25 % canopy cover) and closed (>25 % canopy cover).

We used a GLMM to test for differences in height between trees inside and outside exclosures. Rather than absolute height, we used relative height as response variable: the 95th percentile heights relative to the maximum 95th percentile height of a species or species group within a plot in a given sampling year (see 2.3.2). Relative heights were arcsine transformed prior to analysis. To make this a pairwise comparison, the exclosure – control pair ID was included as random factor.

3. Results

3.1. Browsing incidence

Browsing incidence varied considerably over the sampling years (See supplementary material Figure S1). Except for a peak in 2013, browsing generally increased between 2012 and 2017, and then sharply decreased the following two years (See supplementary material Figure S1). At the habitat level, variation in browsing was not explained by either stand type or whether the plot was located within an animal refuge area. The browsing index was lower in the section Kemperberg than in the section Hoenderloo Estate ($p < 0.01$), and also lower on soils of intermediate fertility ($p < 0.05$; See supplementary material Table S3). There were no significant interactions between sections and soil fertility class.

At the patch-level, we included section as an additional model factor, while we excluded hiding cover as this factor was strongly correlated with both the availability of browse and conifers. Section again explained most variation in browsing, in addition to the interaction between the availability of browse in broadleaved trees and shrubs, the abundance of grasses on the plot and the presence of thermal cover. The abundance of *V. myrtillus* (blueberry) or the density of larger (>160 cm) conifers did not explain variation in browsing index (See supplementary material Table S3). Overall, the amount of browse did not affect the browse index under both high and low canopy cover. Only when 0–25 % grass cover was present in the plots, the browsing index significantly decreased with increasing availability of browse in plots with low canopy cover (See supplementary material Figure S2).

Animal density, expressed as the total metabolic weight of red deer, roe deer and mouflon, also varied over the years (Fig. 1). The level of terminal shoot browsing correlated positively with animal density, correlated negatively with hiding cover, but was not related to browse availability (See supplementary material Figure S3, Table S4).

3.2. Food preference

Ungulates had a strong preference for four broadleaved species: *S. aucuparia*, *R. frangula, B. pubescens* and *Q. rubra*. All four coniferous species were strongly avoided. Two broadleaved species (*F. sylvatica* and *B. pendula*) were also avoided, but to a much lesser degree (Fig. 2). The ranking in preference was generally constant over the sampling years, Park sections and soil fertility classes (See supplementary material Figure S4, Figure S5, Figure S6).

3.3. Community dynamics in transects

The species composition of tree recruitment in the transects during 2012 – 2019 clearly shifted from mixed cohorts of broadleaves and conifers to heavily conifer-dominated thickets. *B. pendula* was the single broadleaved species maintaining itself (Fig. 3). In time, the densities of the regenerating cohorts in the transects decreased. All other broadleaved species remained present but only as small individuals. The height distributions of all conifers and *B. pendula* gradually shifted to the higher height classes (Fig. 3).

The representation of broadleaved species in the ingrowth (individuals with dbh > 5 cm in 2024) increased with the proportion of broadleaved species among seedlings in 2012–2014 (logistic regression; Fig. 4). Substantial ingrowth was dominated by broadleaved species only when the regeneration in the establishment phase was composed of more than 50–80 % of broadleaved species, with the highest thresholds under closed canopy and on the poorest soils (See supplementary material Figure S5 for model output). Beyond the thresholds, *B. pendula* was the dominant broadleaved species in the ingrowth.

3.4. Exclosure-control plots

The tree species composition diverged strongly from paired control plots after exclusion of ungulates (Fig. 5). Only the presence of an exclosure significantly correlated with the ordination (See supplementary material Table S6). Exclusion of ungulates led to a regeneration that was more represented by broadleaved species. Exclosure plots clustered more – i.e. were more similar – than control plots. Canopy cover and Soil fertility did not explain variation among the plots. The Euclidean distances between exclosure-control plot pairs were not related to the time since establishment of the exclosure-control plot pairs (See supplementary material Table S7).

Relative heights were significantly larger in exclosures than in control plots for *S. aucuparia*, *B. pendula* and the group of other broadleaved trees, lower for *P. sylvestris* (Fig. 6; Table 1), and not significantly different for other conifers. These differences were similar between cohorts for the broadleaved species, while for the coniferous species the two youngest cohorts of exclosure-control plots significantly differed from the two oldest cohorts (See supplementary material Table S8).

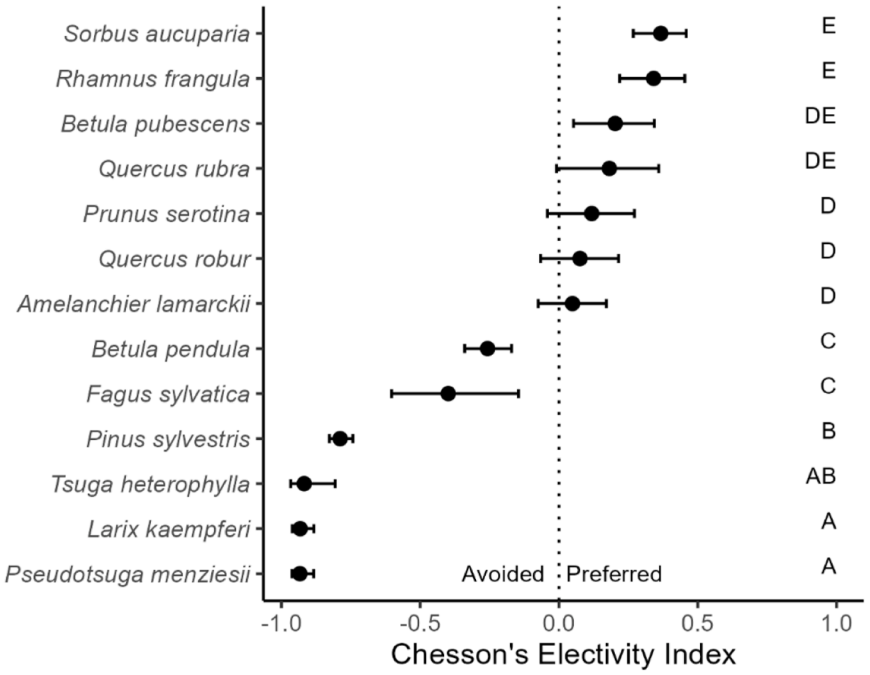

Fig. 2. Browsing preference of ungulates for 13 tree species at De Hoge Veluwe National Park, the Netherlands. Chesson's indices for electivity (square-root weighted means ± 95 % CI) for the most frequent species in the transect study, based on individuals occurring in the transects between 40 and 160 cm in height. Species with different letters have significantly different electivity indices. Only species with a frequency of occurrence in the plots > 5 % were included. Data were pooled over all census years (2012–2019).

4. Discussion

Ungulate browsing in the western part of the European Sand Belt is widely believed to block restoration of coniferous forests into a broadleaved-dominated state (Kuiters and Slim, 2002; Heinze et al., 2011), instead prolonging the existing dominance of coniferous species, but this process remains scantly documented in the scientific literature. Our multi-year study within the enclosed area of De Hoge Veluwe National Park, The Netherlands, clearly indicated that ungulate browsing indeed has the perceived effects. We found that strong browsing preferences reduced the competitive ability of broadleaved tree species, leading to an apparent competitive advantage of – unpalatable – conifers that gradually gained dominance in the early stages of forest regeneration. Browsing was related to the total density of ungulates and hiding cover. Thus, ungulates indeed block restoration of these forests into a broadleaved state, instead pushing forests into an alternative, coniferous state.

4.1. Spatial scale of browsing

Browsing intensity varied widely among the plots, and some of this was in line with the prediction that ungulate food selection is scale dependent (cf Senft et al., 1987). Browsing incidence did vary at the landscape level, i.e., between the different sections within the Park, but was not explained by stand type or animal refuge areas. Browsing incidence also varied at the patch level, but this was poorly explained by the availability of food or hiding cover. Within patches, finally, species identity clearly affected browsing incidence.

Our finding that percentage browsing was not generally mediated by landscape features or environmental variables is in line with previous studies (Kuijper et al., 2010; Bobrowski et al., 2015; Möst et al., 2015). The latter found that deer management measures in the Bayerische Wald National Park (Germany), such as the distance to winter exclosures and deer control areas, were the best predictors of the probability of browsing in *S. aucuparia*, *Abies alba* and *Fagus sylvatica*. We found that browsing incidence was not higher inside the animal refuge areas than outside, despite the fact that refuge areas maintain elevated ungulate densities during the day (Rowcliffe et al., 2026).

4.2. Ungulate density effects

During our study, there was little variation in ungulate density over the years (total metabolic weight ranging from 144 to 178 kg km^{-2} between 2012 and 2019, see Fig. 1). Nevertheless, we found a significant correlation between ungulate density and terminal shoot browsing of broadleaved species, which is in line with studies in other systems (e.g. Borowski et al., 2021; Horsley et al., 2003). This correlation existed even though the general browsing index was considerably lower in the last two census years which had relatively high ungulate densities (See supplementary material Figure S1). The relationship between ungulate density and browsing index appeared to be mediated by the density of tree individuals > 160 cm in the plots, where increased hiding cover resulted in less browsing.

The amount of available browse did not explain any variation in terminal shoot browsing, except in clearings and in combination with a low grass cover (See supplementary material Table S3). A higher density of tree saplings > 160 cm could have had several effects: it would increase competitive pressure on the smaller plants reducing their number and thus availability of terminal shoots (on which browsing was measured), while offering alternative browse on lateral branches. The reduced browsing incidence with increasing hiding cover therefore cannot be directly related to a lower activity of ungulates in dense thickets but rather could have shifted browsing from terminal shoots to lateral branches. Likewise, the lack of a grass cover would shift the attention of ungulates to higher vegetation levels, ignoring low terminal shoots and focus browsing on lateral branches within easy reach.

This points to a constraint on the use of terminal shoot loss as a measure of browsing incidence. Browsing incidence is commonly assessed as the fraction of plants with the terminal shoot removed by browsing as this directly impacts height growth and thus competitive strength (Eiberle and Nigg, 1987; Bödeker et al., 2021). This would only apply to those individuals with terminal shoots accessible to ungulates

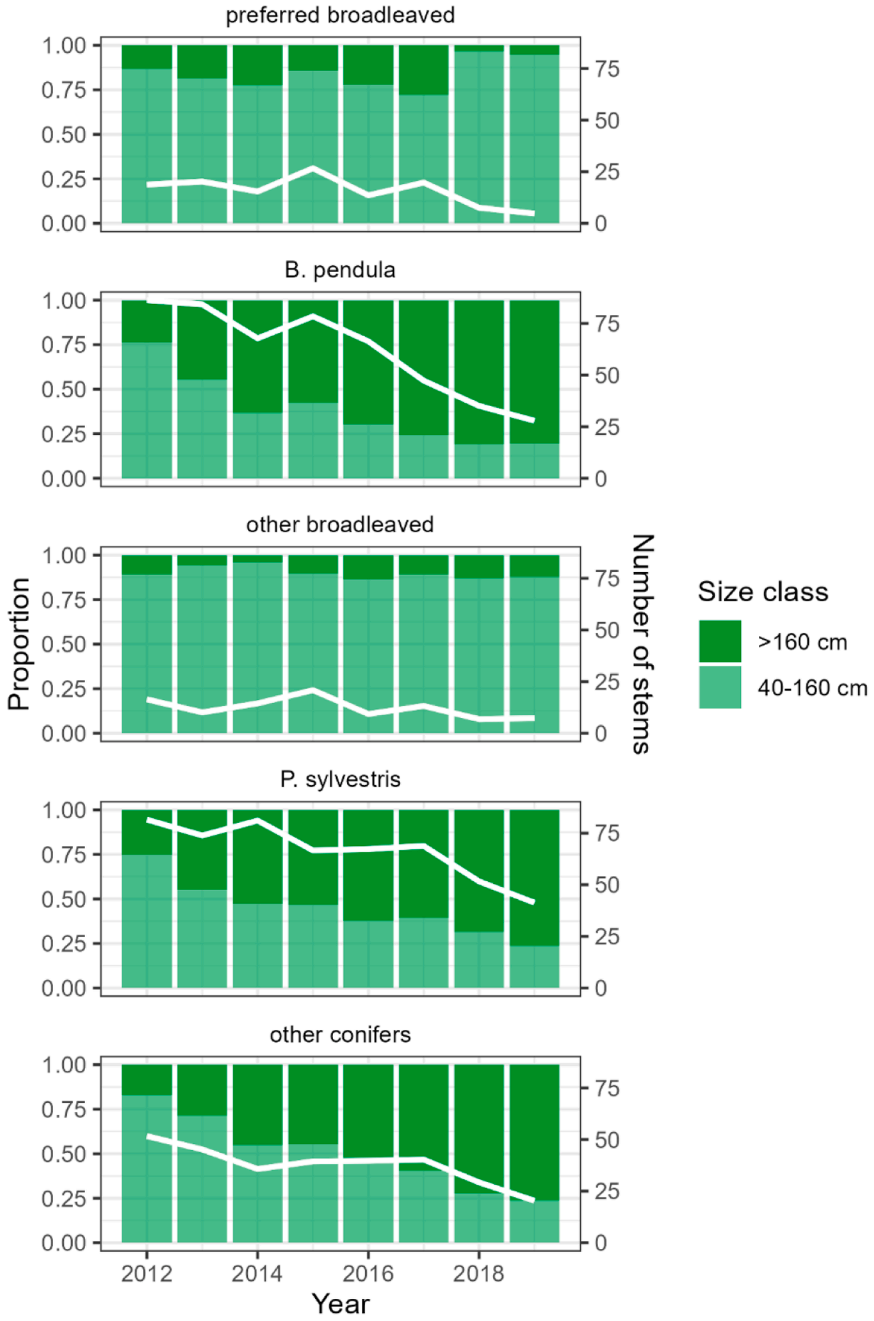

Fig. 3. Shifts in species composition of tree recruitment in De Hoge Veluwe National Park, The Netherlands. Average proportions of individuals in height classes 40–160 cm and > 160 cm (colours), and total number of individuals > 40 cm (lines) in the undisturbed transects established in 2012 (n = 27) for major species and species groups. Preferred broadleaved include *S. aucuparia*, *R. frangula* and *B. pubescens*.

for browsing. With increasing average height an increasing proportion of the terminal shoots gets beyond reach of browsing ungulates and thus will not be scored as browsed. On such a patch plenty of lateral shoots may still be available, so actual browsing may remain high, yet goes unrecorded as only the terminal shoots are assessed. Recording leader shoot removal to assess ungulate browsing would therefore only be appropriate in relatively young patches of regeneration.

4.3. Feeding preference

We found that ungulates strongly preferred broadleaved species over conifers (Fig. 2), and that this indeed created a negative feedback mechanism that reinforced the dominance of conifers and effectively blocked shifts of the tree species community towards the deciduous-dominated state desired by managers (Fig. 4; Fig. 5). This dichotomy in preference between conifers and broadleaved species is not a general phenomenon, however, as certain conifers may be preferred as well, like *Abies alba* in Central Europe or *Tsuga* canadensis in Midwestern United States (Rooney and Waller, 2003; Motta, 1996) in which case over-browsing may even promote broadleaved species rather than conifers (Stromayer and Warren, 1997; Augustine and McNaughton, 1998).

Ungulate browsing preference is linked to the relative food quality of the plant species involved, which may vary with site conditions. Light availability has slight effects on the nutritional and forage quality of plants, generally being higher in shaded versus open habitats (Hartley et al., 1997; Molvar et al., 1993; Ford et al., 1994; Baraza et al., 2010). In our study, however, preferences hardly varied over the years or soil fertility classes (See supplementary material Figure S4, Figure S5).

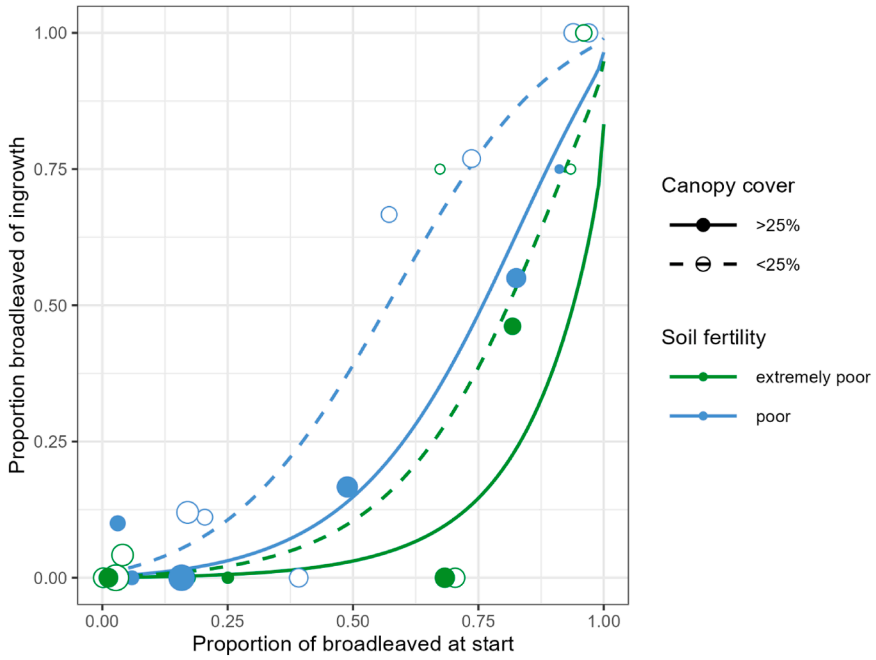

Fig. 4. The relation between composition of the tree regeneration (individuals > 40 cm in height, average over three years) in transects established in 2012, and the percentage of broadleaved tree species in the cohort > 5 cm dbh in 2024 in De Hoge Veluwe National Park, The Netherlands. Soil fertility classes (See supplementary material Fig. S2) were grouped into categories extremely poor (class 1) and poor (classes 2 and 3).

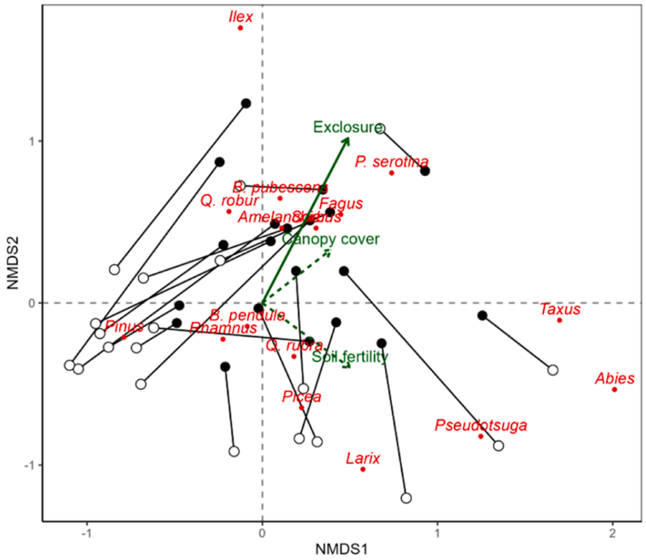

Fig. 5. Impacts of ungulate exclusion on the species composition of tree recruitment in De Hoge Veluwe National Park, The Netherlands. The nonmetric multidimensional scaling (NMDS) ordination plot shows tree species composition differences among exclosure-control plots pairs and environmental parameters. Stress = 0.197. Exclosure plots are shown as filled circles, control plots as open circles. Lines connect exclosure-control pairs. Individual species (heights > 50 cm) are indicated by dots. The environmental factor 'Exclosure' ($p < 0.001$) was significantly correlated to the ordination (See supplementary material Table S6 for model output). Neither canopy cover class ('covered') nor soil fertility class were significantly correlated to the ordination and their directions indicated by dotted lines.

Likewise, Boulanger et al. (2009) found no systematic differences in selectivity patterns of red and roe deer over time or with different ungulate densities, which made them suggest that preference by browsing ungulates might be considered as a relevant plant trait in analysing tree community dynamics.

4.4. Apparent competition between tree species

We found evidence for apparent competition among tree species. Selective browsing caused preferred species – all broadleaved species – to decrease in absolute height relative to plots inaccessible to ungulates. This was also the case for the avoided *P. sylvestris* (See supplementary material Figure S7). Yet, in regeneration patches accessible to ungulates the relative heights of broadleaved species were consistently lower as compared to the coniferous species (Fig. 6; See supplementary material Figure S8), suggesting a clear competitive advantage of the latter. When protected against browsing, the relative heights of broadleaved species increased significantly, while the relative heights of the most abundant conifer, *P. sylvestris*, significantly decreased (Table 1). The competitive advantage of conifers is therefore not caused by inherently higher growth rates, but rather mediated by the influence of ungulates on preferred broadleaved species. This is in line with other studies measuring the effects of ungulate browsing on the competitive positions of tree species in forest regeneration (Ammer, 1996; D'Aprile et al., 2020; Nopp-Mayr et al., 2020). Strong effects of ungulate browsing on height growth have been demonstrated in many other studies, while species differences in seedling densities due to browsing are generally less pronounced (Candaele et al., 2023; Nopp-Mayr et al., 2020; Bödeker et al., 2023). The loss of leader shoots due to browsing only leads to direct mortality after repeated browsing over several years (Eiberle and Nigg, 1987; Clasen et al., 2015), so the contribution of browsing in the dominance of conifers in the regenerating community is more due to ensuing height differences rather than reduction of the number of broadleaved individuals.

Competition for light is a dominant mechanism in direct species interactions in young regeneration patches, with species locked in an arms race to gain height or pre-empt radiation by their leaf display (Craine and Dybzinski, 2013). Rapid height increment greatly determines success and survival of species in young multi-species communities, especially for light demanding species (Dekker et al., 2009). Most species in our study are relatively light demanding (Niinemets and Valladares,

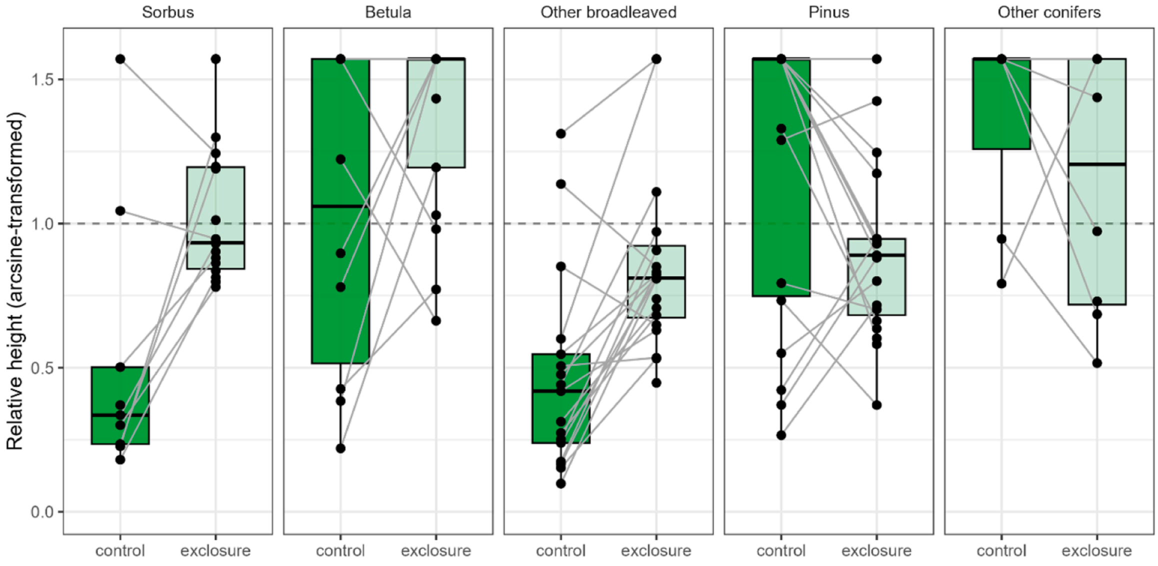

Fig. 6. Box plots of the average relative heights of tree species (groups) in exclosure and control plots in 2022 in De Hoge Veluwe National Park, The Netherlands. Lines connect the exclosure plots and associated control plots. Relative heights were calculated as the ratio between the 95th percentile of heights in a plot and the maximum 95th percentile of heights of the species (group) in the plot. The species (group) with the maximum height has a relative height of 1. Data were arcsine transformed prior to analysis.

Table 1
Output of the linear mixed models estimating the effect of plot type (exclosure or control) as fixed factor, and with site as random factor, on the arcsine transformed relative heights by species and species groups in the exclosure-control plots in 2022.

Species(group)		Estimate	t-value	p
Sorbus aucuparia	Intercept	0.533	4.764	< 0.001
	Exclosure	0.497	3.819	0.001
Betula pendula	Intercept	1.029	7.852	< 0.001
	Exclosure	0.344	2.176	0.045
Other broadleaved	Intercept	0.472	5.760	< 0.001
	Exclosure	0.406	4.901	< 0.001
Pinus sylvestris	Intercept	1.181	12.217	< 0.001
	Exclosure	-0.281	-2.517	0.022
Other conifers	Intercept	1.363	8.872	< 0.001
	Exclosure	-0.231	-1.170	0.283

2006) so survival very much depends on attaining a favourable canopy position in an early developmental stage of the regenerating community.

The only broadleaved species escaping this competitive exclusion was *B. pendula.* It was relatively avoided by ungulates (Fig. 2), which may be due to its high abundance in the community: Ohse et al. (2017) showed that browsing on *F. sylvatica* was reduced when growing in plots with a high density of *F. sylvatica* or when species diversity was high. *B. pendula* is among the species with the fastest juvenile height growth (Ovenden et al., 2024). In a Swedish study, Bergqvist et al. (2009) showed that *B. pendula* was able to quickly gain height and escape browsing within three years after establishment when unprotected from ungulates. In the current study, almost all ingrowth into the 5 cm dbh cohort in the transects (Fig. 4) was represented by *B. pendula*, so even though heights of *B. pendula* were reduced when exposed to browsing (Fig. 6; See supplementary material Figure S7), the high abundance and fast growth still enabled individual trees to grow above maximum browsing height and establish in the canopy (See supplementary material Figure S7).

4.5. *Effects on the tree species community*

The exclosure study showed that browsing had a strong effect on the course of succession, shifting the composition of tree recruitment towards conifers. While the plots accessible to ungulates showed a large variation in species composition, yet invariably with a dominance of conifers (mainly *P. sylvestris*), exclusion of ungulates resulted in a convergence of the vegetation with a high abundance of broadleaved species (Fig. 5). Such shifts in species composition have been reported in many studies investigating ungulate effects, along with a reduction in tree species diversity and richness when exposed to browsing (e.g., Gill and Beardall, 2001; Ramirez et al., 2019; Kuiters and Slim, 2002). Shifts in species composition depend on the local species pool and the browsing pressure and preferences of the local ungulate populations (DiTommaso et al., 2014; Ramirez et al., 2019; Stromayer and Warren, 1997). Our study was too short to determine whether alternate stable states might be induced by ungulate browsing (cf. Schmitz and Sinclair, 1997; Stromayer and Warren, 1997), but under the current browsing pressure in the study area ungulates clearly facilitate the maintenance of a conifer-dominated canopy.

Under shaded conditions, ungulate browsing may also lead to “apparent shade intolerance”, when preferred shade tolerant species are strongly reduced in height in favour of species avoided by ungulates (Modrý et al., 2004; Schulze et al., 2014). Sparse tree regeneration under a forest canopy then prompts managers to create canopy gaps to facilitate the establishment of a mixed tree regeneration, not realizing that browsing rather than shade limits seedling establishment and sapling growth. This may, in fact, only intensify the problem, as large canopy openings attract ungulates and thus locally increases browsing pressure (Hardalau et al., 2024; Kuijper et al., 2009; Schulze et al., 2014; Reimoser and Gossow, 1996; Latham et al., 1997) leading to a subsequent loss of preferred species and ultimately the reestablishment of a tree canopy dominated by non-preferred species, in this case mostly conifers.

4.6. *Limitations*

The habitat use of the ungulate populations in this study was restricted to the enclosed area of De Hoge Veluwe National Park with an ungulate density that is considered relatively high (Fig. 1). This limits the spatial range of habitat selection potential, so it may be assumed that the present population exploits all possible habitats in the Park, leading to a low differentiation in habitat use for browsing. Furthermore, it is likely that the lack of effects related to the spatial scale of browsing is a result of the relatively small range in variation of certain environmental variables, combined with a relatively high ungulate density. Soil fertility ranges from extremely poor drift sands with very low nutrient availability (especially low in P, Ca, Mg, K) and water holding capacity, to dry inceptisols with only slightly better nutrient availability and water holding capacity. All soils are strongly acidified with pH-values below 3.5 (Abdullah et al., 2024). These adverse soil conditions are likely to affect species composition in conjunction with browsing. However, the NMDS (Fig. 5) revealed no significant effect of soil fertility class on species composition, probably due to the relatively low variation between soils present. Variation in crown cover was higher, but when canopy cover was high this was mostly dominated by *P. sylvestris*, a species with translucent canopies that limit light attenuation (Ellenberg, 1996). As we selected transects based on the presence of regeneration vulnerable to leader shoot browsing with sufficient density, we did not directly control for specific environmental factors and their interactions that could have an effect on the tree species composition. Further studies could reveal relevant interactions between probability of establishment, species performance and browsing, mediated by environmental factors.

We determined browsing preference by calculating electivity based on the removal of terminal shoots in early autumn. The general assumption here is that electivity is related to forage quality, which varies over the seasons (Moser et al., 2006; Hanley and Barnard, 2014; Dumont et al., 2005). The total impact of browsing extends through the winter season. This partly depends on ungulate species: roe deer, as a typical browser, will continue to consume buds and twigs during winter (Moser et al., 2006) while red deer, as an intermediate feeder, will mostly shift to non-woody forage, such as grasses (Dumont et al., 2005; Groot Bruinderink and Hazebroek, 1995). In our study area, conifers constitute a minor part of the yearly diet of the ungulate species present. Mouflon will regularly include conifers in their diet in substantial amounts (Marchand et al., 2013), red deer and roe browse on *P. sylvestris* and other conifers mostly in winter or when alternative food sources are scarce (Groot Bruinderink and Hazebroek, 1995; Cornelis et al., 1999; Zweifel-Schielly et al., 2012; Storms et al., 2008). By assessing browsing incidence on plants in autumn, total relative impact of browsing on the performance of a particular tree species may thus be over- or underestimated in this study.

4.7. Implications for management

Our findings provide empirical evidence for the idea that ungulates block restoration of conifer-dominated forests at the European sand belt into a broadleaved-dominated state (Kuiters and Slim, 2002; Heinze et al., 2011) and instead prolong the existing dominance of coniferous species. However, it would be erroneous to ascribe the lack of regeneration of broadleaved tree species solely to browsing-inflicted damage by ungulates (cf. Senn and Suter, 2003). During the 19th and early 20th centuries, reafforestation of heathlands and drift sands in the European sand belt created a forest landscape dominated by *P. sylvestris* (Koster, 2009) often followed by a second generation of introduced conifers like *Pseudotsuga menziesii*, *Larix kaempferi* and *Picea abies.* Coniferous species thus dominate the seed rain. Broadleaved tree species are less common and mostly represented by *B. pendula*, *Q. robur* and *F. sylvatica* (Schelhaas et al., 2022). Previous land use and high deposition loads of nitrogen and sulphur have caused soil acidification and nutrient leaching, creating impoverished soils that restrict the establishment of more demanding tree species (Skidmore et al., 2024).

Dutch nature policy focusses on a substantial increase of broadleaved tree species by planting or natural regeneration after selectively removing coniferous species. This intends to increase general biodiversity by raising tree species diversity and improving litter quality and soil fertility (Desie et al., 2020), and to increase forest resilience to climate change (Morin et al., 2018; Blondeel et al., 2024). Such conversion would require a substantial decrease in ungulate browsing pressure (Ammer et al., 2010; Hardalau et al., 2024; Champagne et al., 2021; Angst, Kupferschmid, 2023; Candaele et al., 2023). Reduction of ungulates densities by culling would be the most effective measure as it can decrease browsing incidence and thus enhance regeneration success within a few years (Hothorn and Müller, 2010; Bödeker et al., 2023; Rooney et al., 2015), but this meets resistance (Apollonio et al., 2010) and requires an integrated and adaptive approach (Beguin et al., 2016). Fencing against ungulates usually sufficiently reduces browsing pressure, but is expensive and only locally protects regeneration, leaving the larger part of the forest regeneration exposed to ungulates which may disrupt forest ecosystem structure and function into the far future (Nuttle et al., 2011; Ramirez et al., 2021).

The recent comeback of wolf in Western Europe is expected to change ungulate behaviour and exert some control over population densities, potentially reducing browsing pressure, at least on a local scale (Van Beest et al., 2013; Hardalau et al., 2024; Van Ginkel et al., 2019). It is not likely, however, that overall browsing levels will sufficiently decrease in the presence of wolf packs. Predator-prey interactions in anthropogenic landscapes are highly context-dependent (Van Beeck Calkoen et al., 2018; Kuijper et al., 2024), and predation by wolf may not reduce ungulate population densities strongly enough to lower browsing pressure below the threshold that would allow successful regeneration of most broadleaved species (Lippitsch et al., 2024; Brice et al., 2025). Culling of ungulates may remain necessary to enable the urgent restoration of forest landscape in the European Sand Belt.

CRediT authorship contribution statement

Jakob Leidekker: Writing – review & editing, Resources, Data curation. **Annemieke Visser-Winterink:** Writing – review & editing, Supervision. **Leontien Krul:** Writing – review & editing, Supervision, Resources. **Patrick A. Jansen:** Writing – original draft, Visualization, Formal analysis, Conceptualization. **Jan den Ouden:** Writing – original draft, Visualization, Methodology, Investigation, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123558.

Data availability

Data will be made available on request.

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