



# Density-related effect of red deer browsing on palatable and unpalatable tree species and forest regeneration dynamics

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## ABSTRACT

Large herbivores play a key role in terrestrial ecosystems, and their populations alter the plant composition in many ecosystems. One example is deer, whose populations in the Northern Hemisphere have increased over the last decades. This has resulted in increased browsing pressure on saplings and, as a consequence, has hampered forest regeneration in some areas. Such herbivore-induced changes in the regeneration of forest stands have changed their composition and biodiversity. Although there is an established link between the deer population density and the level of damage caused by browsing, the question remains open: What is the effect of increasing deer density over years on the regeneration of palatable and less browsing-resistant tree species? In this study, we investigated the relationships between the regeneration dynamics of five tree species (European beech *Fagus sylvatica*, silver fir *Abies alba*, sycamore *Acer pseudoplatanus*, hornbeam *Carpinus betulus*, and oak *Quercus* spp.) and browsing pressure in two years with low and high red deer (*Cervus elaphus*) density and at similar roe deer (*Capreolus capreolus*) density. We set up experimental plots in Roztocze National Park (central-eastern Poland), a protected area where natural predators of deer are constantly present. In addition to deer density, we analysed parameters that may affect browsing intensity: height of saplings, forage availability (sapling density), sapling diversity and light intensity (canopy openness). We found that increasing red deer density significantly increased browsing on all tree species, with saplings taller than 50 cm being under the strongest pressure. Moreover, higher deer density altered deer forage selection – it increased their selection for unpalatable European beech and decreased for highly preferred sycamore. Additionally, more species-diverse patches and closed canopy attracted deer and increased the probability of browsing on saplings. Contrary to our predictions, sapling density decreased browsing intensity. The study confirms that high ungulate density has significant effects on tree recruitment and may alter tree species composition of the forest stand. We provide clear evidence that deer herbivory plays a crucial role in tree regeneration in top-down processes in natural ecosystems.

## 1. Introduction

The high abundance of large herbivorous mammals has long been perceived as one of the main factors affecting the structure and function of forest ecosystems (Hester et al., 2006; Newman et al., 2014). Effects can occur both directly and indirectly on seedlings and saplings, ground vegetation, animals, and forest management (Côté et al., 2004; Danell et al., 2006; Nuttle et al., 2014). It should be borne in mind that high densities of forest-dwelling browsers, such as deer, can significantly alter both forest regeneration and the diversity, composition and density of herbaceous understorey vegetation. The current high density of deer

is a widespread phenomenon that occurs both in Europe and in North America and is probably caused by a combination of forestry practices, low hunting pressure and extermination of large carnivores, mainly wolves (*Canis lupus*) and lynxes (*Lynx lynx*) (Kuijper, 2011; Wright et al., 2012; Carpio et al., 2021).

This impact is evident primarily through selective browsing on palatable tree species, which in turn affects their survival, growth rate, and thus the rate of woody regeneration (Risenhoover and Maass, 1987; Rooney and Waller, 2003). This interaction also favours plant species that are avoided by herbivores (unpalatable) or are more resistant to grazing (Horsley et al., 2003a; 2003b; Côté et al., 2004). This shows that

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large herbivorous mammals at high numbers can modify forest ecosystems through alternative succession pathways and changes in species sets (Hidding et al., 2013; Kolstad et al., 2018; De Vriendt et al., 2021). Therefore, some ungulate browsers are so-called keystone species that can modify not only forest regeneration but also the biodiversity of forest ecosystems (Waller and Alverson, 1997).

However, this is still an open debate about where the critical threshold of deer density exceeds that where one can observe the strong pressure of these animals on the environment. The question is difficult because the effects of ungulates on forest ecosystems are nonlinearly related to their densities (Hester et al., 2006; Tremblay et al., 2006). Some studies, such as a 10-year enclosure experiment (Horsley et al., 2003a; 2003b) conducted in Pennsylvania, USA, suggested that deer densities higher than 8 ind./km<sup>2</sup> resulted in a significant shift in vegetation compared to lower densities. Based on results from a similar experiment in the boreal forest in Canada, Tremblay et al. (2007) drew similar conclusions, i.e., that for the protection of browsing-sensitive plants, it is recommended to keep deer densities below 15 ind./km<sup>2</sup>. Despite the fact that enclosure experiments with large ungulates and their pressure on vegetation give us a unique opportunity to control deer density and provide necessary replications, this methodology restricts natural animal movement and creates stronger pressure than that in reality. That is why it would be difficult to transfer results from enclosure studies to natural ecosystems. For example, the results of studies conducted in England in open forest ecosystems (Gill and Morgan, 2010) indicated that forest regeneration is most likely inadequate at densities higher than 14 deer km<sup>-2</sup>. However, it is quite difficult to generalize the impact of all deer species together, especially because each species has characteristic patterns of space use, diet and habitat selection (Putman et al., 1989), which influence their impact on vegetation. Moreover, access to an alternative food source, especially in agricultural fields, can significantly affect the levels of damage caused to trees (Moser et al., 2006; Ward et al., 2008).

The distribution of browsing pressure in forest ecosystems is strongly dependent on abiotic and biotic factors. Topography, which influences meteorological parameters, is one of the most important factors that determines the deer distribution and its pressure on forest regeneration (Balazy et al., 2016; Borowski et al., 2019). Additionally, deer avoid forest roads, as they can increase mortality risk from hunters, so the presence of roads greatly alters deer habitat use, foraging behaviour, and browsing pressure in their vicinity, (Mathisen et al., 2018; Borowski et al., 2020). Moreover, stand structure, which affects food availability and security cover, parameters related to ungulate distribution, can also modify the probability of deer browsing (Borkowski, 2004).

In analysing deer foraging behaviour at a spatial scale, we need to consider browsing as an animal decision based on two different selection steps: between and within patches. The most important factor for patch selection (the first step) is plant quality, species richness and predation risk, which means that deer select patches with a high relative abundance of palatable species (Moser et al., 2006; Bee et al., 2009) and/or with higher species richness (Ohse et al., 2017) or with a lower predation pressure (Kuijper et al., 2013). At the fine scale (the second step of deer selection), the browsing risk for a young tree is also connected to plant composition and structure. For instance, tree palatability, height, architecture, density, nutrient content and composition of surrounding vegetation are the major drivers of browsing probability within patches (Alm Bergvall et al., 2006; Churski et al., 2017; Milne-Rostkowska et al., 2020). This means that palatable tree seedlings have a lower risk of being browsed when they grow amongst unpalatable spiny shrubs (Baraza et al., 2006) or any dense shrub (Moser et al., 2006; Jensen et al., 2012).

Taking into account the published results of studies and experiments on deer pressure in forest ecosystems, we found that increasing deer density could greatly affect the regeneration of palatable tree species (Tremblay et al., 2006; Gill and Morgan, 2010; Nuttle et al., 2014). The results of a long-term study conducted in a natural lowland European

forest indicated that the total recruitment of all tree species was negatively correlated with the total ungulate density and red deer density (Kuijper et al., 2010). Contrary to other studies, however, tree species responses to herbivory varied greatly and were related to the selection of herbivores; more preferred forage species (hornbeam, *Carpinus betulus*) were positively related to herbivory density, whereas the less preferred species were negatively related to the same factor. This means that tree recruitment of preferred and browsing-tolerant species could be higher with increasing herbivore pressure. According to unexpected results from the study conducted by Kuijper et al. (2010) and the lack of similar long-term European studies focused on deer density and forest regeneration, we present 10-year data on forest regeneration with a fourfold increase in red deer (*Cervus elaphus*) density. Therefore, here, we examine how the increasing red deer density at constant roe deer (*Capreolus capreolus*) density affects forest regeneration. We were especially interested in measuring the level of deer browsing pressure on palatable and unpalatable tree species at low and moderate red deer densities in natural ecosystems. Specifically, we sought to answer the following research questions:

- 1) Does increasing red deer density affect tree species selection?
- 2) Does deer density increase tree browsing in species-rich plots, as predicted by optimal foraging theory and the nutrient balance hypothesis?
- 3) Do forage quantity (the number of seedlings) and security cover on plots influence the extent of tree browsing?

## 2. Materials and methods

### 2.1. Study area

Roztocze National Park (RNP) is located in the central-eastern part of Poland (50°60' N, 23°03' E) (Fig. 1) and covers an area of 84,83 km<sup>2</sup>. Forests are the main and dominant type of ecosystem (95.5%) with different types of protection levels. The majority of the National Park remains under the active protection zone at 72.41 km<sup>2</sup> (85%), while the strictly protected zone and landscape protection zone cover 10.29 km<sup>2</sup> (12.1%) and 2.12 km<sup>2</sup> (2.5%), respectively. Most of the forest communities in RNP (ca. 70%) are natural, dominating European beech (*Fagus sylvatica*), silver fir (*Abies alba*) and hornbeam woodland communities. However, one-third of RNP is occupied by secondary forest communities, with Scots pine (*Pinus sylvestris*) dominating (Tittenbrun, 2013).

The area is highlands with elevations varying from 223 to 364 m a.s.l. The climate is considered a transition zone between the maritime (Atlantic) and continental climates (Szafer and Zarzycki, 1977), with warm, dry summers and frosty winters. During the study period (2007 –

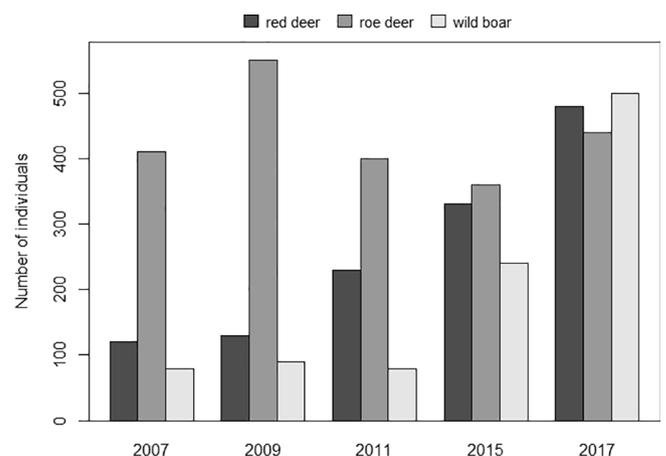


Fig. 1. Numbers of the three sympatric ungulate species in Roztocze National Park: red deer, roe deer and wild boar, as well as their natural predators: wolves and lynx in the years 2007 – 2017, based on data from drive counts.

2017), the mean annual air temperature was 7.9 °C, with the coldest month in January (average -2.7 °C) and the warmest month in July (average 19 °C). The mean annual precipitation amounts to 736 mm, and the growing season usually lasts 216 days (<http://roztoczanski.pl/>). Snow cover persists for two and a half months. The diversity of the species composition of stands and their structure are the result of both natural processes and many years of human influence in these areas.

Four major forest types are found within the RNP (with dominant trees in parentheses): coniferous forest (*Pinus sylvestris*), mixed coniferous forest (*Pinus sylvestris*, *Picea abies*, *Abies alba* and *Quercus robur*), mixed deciduous forest (*Abies alba*, *Fagus sylvatica* and *Carpinus betulus*), and deciduous forest (*Fagus sylvatica*, *Quercus robur*, *Carpinus betulus* and *Acer platanoides*).

In the RNP, there are populations of natural large predators such as wolf and lynx as well as free-ranging populations of red deer, roe deer and wild boar (*Sus scrofa*). The deer population density in the RNP is monitored by drive counting (Borkowski et al., 2011), and it was observed that within a decade (2007–2017), the number and composition of the deer populations changed greatly. While the red deer population density increased fourfold – from 1.4 to 5.6 ind./km<sup>2</sup>, the roe deer population density was stable and amounted to 4.8 ind./km<sup>2</sup> (Fig. 1). In total, deer density increased from 6.2 ind./km<sup>2</sup> in 2007 to 10.4 ind./km<sup>2</sup> in 2017.

## 2.2. Study design and measurements

Browsing surveys were conducted in RNP in 2007 and 2017 as a part of forest monitoring. During each of these surveys, 315 permanent plots regularly distributed in a 500 × 500 m grid were sampled (Supplementary Fig. S1). In this study, we monitored natural regeneration based on the above systematically arranged plots. In spring and early summer (April – June), around each of the 315 study plot centres, two concentric circular subplots were established: P1 = 100 m<sup>2</sup> (5.64 m radius) and P2 = 400 m<sup>2</sup> (11.28 m radius). The assessment and measurements of the natural regeneration of trees were performed in subplot P1. In this subplot, the number of young saplings in two height classes, i.e., ≤ 0.50 and 0.51–1.50 m, was noted for each tree species present. To analyse the impact of deer on woody vegetation, the browsing of terminal shoots of saplings was recorded. Only the presence of fresh browsing indicating deer pressure from the last winter – early spring seasons was measured. Based on a larger subplot (P2), the number of trees with diameters at breast height (DBH) > 7 cm and their DBH were recorded.

## 2.3. Statistical analyses

We evaluated deer browsing intensity by modelling the proportion of trees browsed in a generalized additive model (GAM, Hastie and Tibshirani, 1990) using the *mgcv* library (Wood, 2011) in R (R Core Team, 2020). This framework allowed for simultaneously accounting for spatial autocorrelation and random effects in the data in a binomial model. The response variable was the proportion of trees browsed. We assumed a logit link for the response. The survey year (2007 and 2017) as a substitute for red deer density (low and high), sapling species, sapling height class (≤ 0.5 m and from over 0.5 to 1.5 m), sapling density (all species, log-transformed), sapling species diversity (Simpson's diversity index), and stand basal area (SBA) were used as predictor variables. For the purpose of this analysis, tree species that were present in less than 1/3 of locations (both years) were pooled as "other". Therefore, we distinguished the following species: beech, fir, sycamore, hornbeam and oak. SBA served as a proxy for forest canopy openness and is defined here as the area occupied by the cross-section of tree trunks and stems at breast height. We also included interactions of survey year and species with the remaining predictors to assess the potential species-specific modulating effects of these variables on between-year and species differences. All these effects were set up as parametric terms. We accounted

for nonindependence of the data within plots by including random effects of the plot (as a random-effect smooth term in GAM). To accommodate spatial autocorrelation, we added a Gaussian process smooth term of the plot coordinates. The residual spatial autocorrelation in the model was evaluated with Moran's I test over distances from 0 to 4000 m (using package *spdep*, Bivand et al., 2013). We examined the data points for outliers using Cook's distance, and following that we decreased the weight of 10 extremely influential observations to 0.25. Because of a large sample size, we did not perform model simplification and base our inference on the full model. We tested for the species-specific effect of the survey year and its interaction with other explanatory variables by performing multiple likelihood-ratio tests of the full model with restricted models that excluded the effect of survey year for each tree species. We used predictor effect plots to assess the role of each predictor. The plots were created using the *effects* package (Fox and Weisberg, 2019).

To assess deer feeding selectivity for tree species, we used Jacob's D selectivity index (Jacobs 1974) following the formula  $D = (r - p) / (r + p - 2rp)$ , where  $r$  is the proportion of each tree in the sample of browsed trees and  $p$  is the proportion of each species in the entire sample.  $D$  varies from -1, the least selected, to 1, strong selection, with 0 indicating no selection. We calculated the selectivity indices separately for each year, for all plots pooled, and for each plot separately to assess the variability of browsing selectivity. We compared the distribution of the indices for each tree species between years using the Kolmogorov-Smirnov test.

For proportions and the D index, we present the mean, SD, and median values weighted by the number of trees in the plot, which was done to reduce the influence of extreme values caused by very low tree numbers.

## 3. Results

In total, 30 202 and 25 982 individual trees in regeneration phase were counted in the plots in 2007 and 2017, respectively (Supplementary Table S1).

On average, in 2007, there were 101.7 (±165.7 SD) trees in a plot and 86.9 (±134.3 SD) trees in 2017, ranging from 1 to 1600 trees in 2007 and from 1 to 852 trees in 2017 (see Supplementary Fig. S2). The most widely occurring species was beech (264 plots), followed by silver fir (198), sycamore (159), hornbeam (159), and oak (118). The remaining species, including ash (*Fraxinus excelsior*), maple (*Acer platanoides*), pine, lime (*Tilia cordata*), and elm (*Ulmus* sp.) were present in 272 of the plots. The number of tree species in a plot ranged from 1 to 9 (mean 4.5 ± 1.84 SD).

### 3.1. Deer pressure

The average proportion of trees browsed (PTB) in a plot was 22.0 ± 22.0% SD in 2007 (year with low red deer density) and 33.6 ± 28.1% SD in 2017 (year with high red deer density). The overall mean PTB was the highest for sycamore and hornbeam (48 ± 37% SD and 46 ± 37% SD, respectively) and the lowest for beech (15.1 ± 26% SD) (Supplementary Table S2).

The model for PTB explained 69.5% of the deviance, and confirmed the overall significant increase in PTB between the two survey years for all tree species (p-values ≤ 0.005; Supplementary Table S3 and Fig. 2) and in both height classes (p-values ≤ 0.006; Supplementary Table S4 and Fig. 3). Interactions with other explanatory variables did not change this general pattern over most of their range. The model showed that tree species had the largest effect on PTB, followed by the survey year and sapling height class (Table 1). Of the habitat-related variables, Simpson's diversity index had the greatest influence on PTB (Table 1).

For most species, PTB increased with tree height (p-values ≤ 0.0004, Supplementary Table S3 and Fig. 3). The exception were fir and beech in the year with low red deer density (2007), where the PTB was lower in

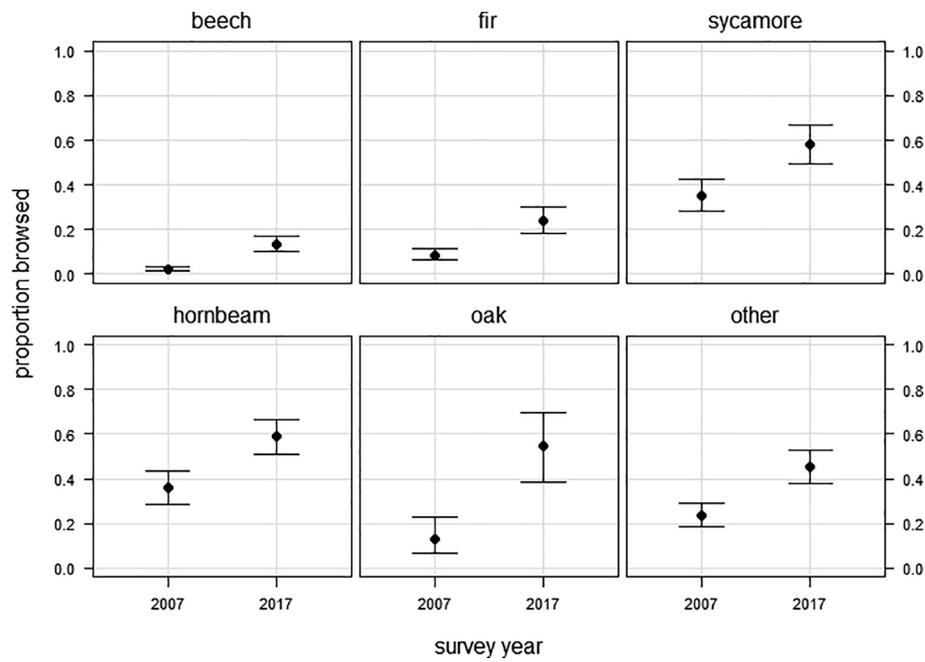


Fig. 2. Average predictions of the final model for the proportion of trees browsed (PTB) by deer in Roztocze National Park in relation to survey year (2007, low and 2017, high red deer density). Bullets and whiskers show mean fitted values with 95% confidence intervals. The fitted values are weighted averages over all other groups. All remaining continuous predictors were set to their mean values.

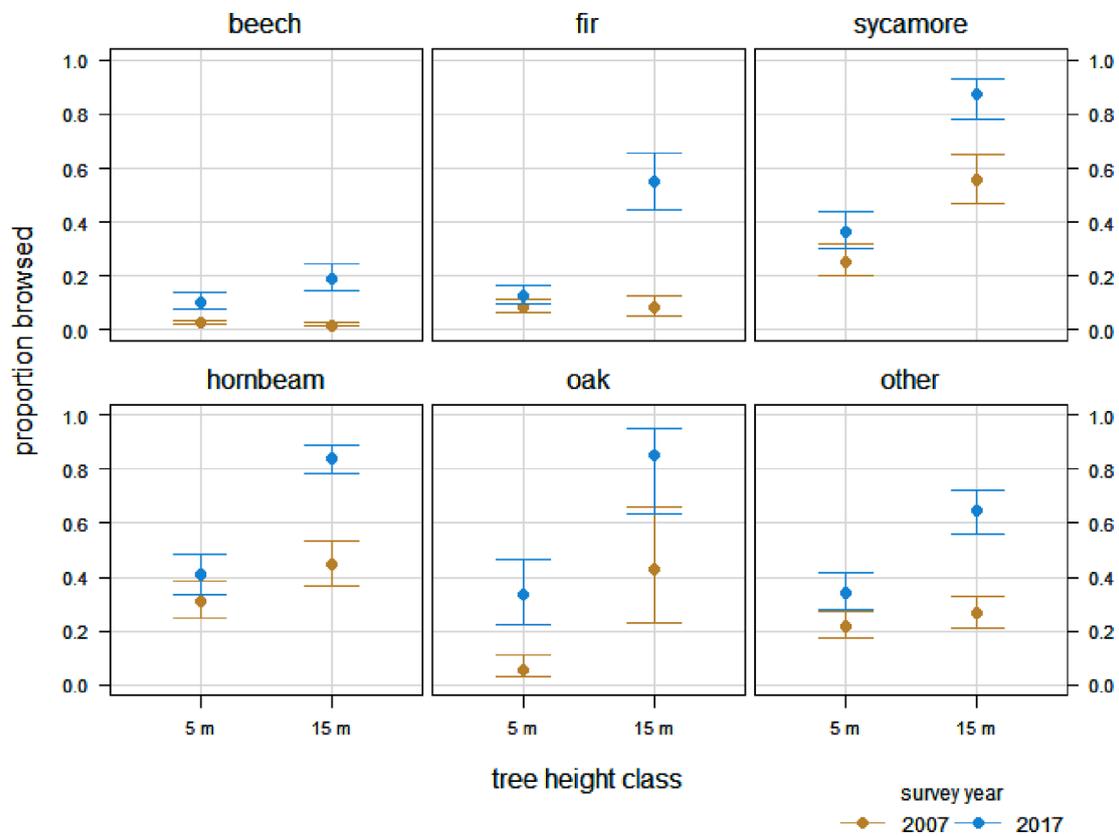


Fig. 3. Average predictions of the final model for the proportion of trees browsed (PTB) by deer in Roztocze National Park in relation to tree height class ( $\leq 50$  cm and  $> 50$  cm) and survey year. For details, see the description to Fig. 2.

taller saplings (Fig. 3), however for fir this decrease was non-significant (Supplementary Table S3). The diversity of tree species in a plot, expressed as the Simpson diversity index (SDI), exerted a different effect on PTB in the two survey years and in a species-specific manner (Fig. 4).

The overall effect of SDI was significant in all species except oak ( $p$ -values  $\leq 0.002$ ; Supplementary Table S5), and the change in the effect strength between survey years was detected for all species except oak and fir ( $p$ -values  $\leq 0.02$ ; Supplementary Table S4). In 2007, the PTB

**Table 1**

ANOVA (type 2) table of the model for the proportion of trees browsed. As explanatory variables, the model included tree species, survey year, sapling species diversity (Simpson’s diversity index, SDI), stand basal area (SBA), sapling height (with two groups: ≤ 0.50 m and (0.5–1.50] m), sapling density (log-transformed, denoted log(sapling density)), as well as their three-way interactions. In all cases, Wald tests yielded  $p \ll 0.0001$ , except for one (marked with ‘a’) with  $p = 0.0006$ . The ‘relative effect’ is an increase in residual deviance after removal of a term (and its higher-order terms, which corresponds to the type 2 ANOVA), given as a percentage of the highest value.

Model parameter	df	$\chi^2$	Relative effect (%)
tree species	47.2	6896	100.0
survey year	26.8	2418	35.1
SDI	11.0	715	10.4
sapling height	11.0	1017	14.7
SBA	12.5	232	3.4
log(sapling density)	11.6	221	3.2
tree species × survey year	25.0	622	9.0
tree species × SDI	10.2	415	6.0
tree species × sapling height	10.2	320	4.6
tree species × SBA	9.6	169	2.4
tree species × log(sapling density)	9.1	212	3.1
survey year × SDI	6.2	463	6.7
survey year × sapling height	5.6	304	4.4
survey year × SBA	6.1	66	1.0
survey year × log(sapling density)	5.9	70	1.0
tree species × survey year × SDI	5.4	380	5.5
tree species × survey year × sapling height <sup>a</sup>	4.9	22	0.3
tree species × survey year × SBA	5.0	44	0.6
tree species × survey year × log(sapling density)	4.9	65	0.9

increased with SDI in fir, sycamore and the “other” group, decreased in beech, otherwise it had little effect. In 2017, however, the effect of species diversity on PTB became more positive (i.e., stronger increase) in beech and hornbeam, weaker (in sycamore), or shifted to negative (in

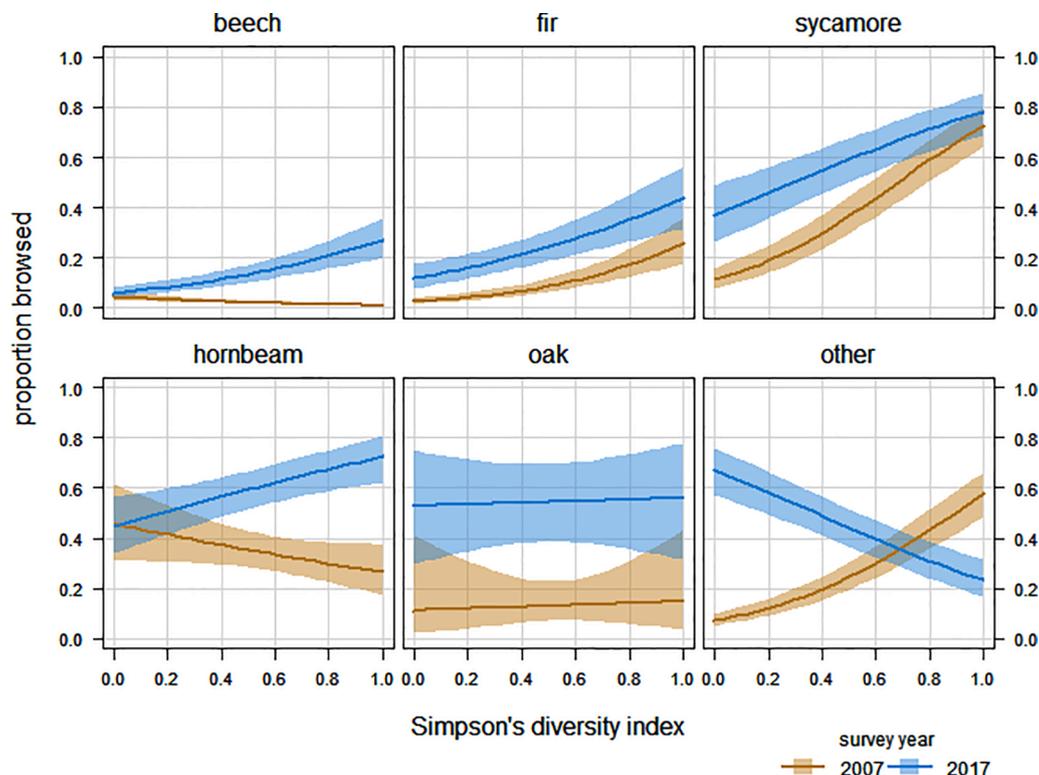
the “other” species) (Fig. 4; Supplementary Table S4).

The modifying effect of the stand basal area (SBA) also differed between the survey years and between species (Supplementary Table S3). Generally, the effect of SBA in 2007 was small and in 2017 it became stronger and shifted towards positive (Fig. 5). Significant effect of SBA was found for all species (p-values ≤ 0.0025) but hornbeam and the “other” group (Supplementary Table S5). The change in the effect of SBA between survey years was detected for all species (p-values ≤ 0.009) except for sycamore and hornbeam. In sycamore, PTB increased with SBA in both years. In fir PTB decreased with SBA in 2007, and in the remaining species it did not change (Supplementary Table S3). In 2017, SBA had a positive effect on PTB for sycamore, beech, oak and hornbeam (Supplementary Table S3; Fig. 5).

The density of saplings was also affecting the PTB (Fig. 6, Supplementary Table S3). In general, PTB decreased with sapling density, although in sycamore and hornbeam much less significant effect was detected (p-values = 0.03; Supplementary Table S5). In 2007, PTB decreased with sapling density in beech, fir, sycamore and oak (Supplementary Table S3). For sycamore and oak, there was a significant positive shift of an effect of seedling density in 2017 compared to 2007 (p-values ≤ 0.006; Supplementary Table S5); whereas for the “other” species, there was a significant increase in the strength of the seedling density effect (p-value = 0.007; Supplementary Table S5).

**3.2. Deer selectivity for tree species**

The selectivity index indicated that the most selected tree species were hornbeam and sycamore, the least selected were beech and fir, while there was almost no selection for oak (D close to 0; Supplementary Table S1). The overall global selection did not differ markedly between the survey years. The plotwise D indices may be more indicative with respect to the local tree distribution, and the mean D showed larger between-year differences for the negatively selected species (Fig. 7). The comparison of the distributions of per-plot D-indices showed that only



**Fig. 4.** Average predictions of the final model for the proportion of trees browsed (PTB) by deer in Roztocze National Park in relation to tree species diversity expressed as Simpson’s Diversity Index, and survey year. For details, see the description to Fig. 2.

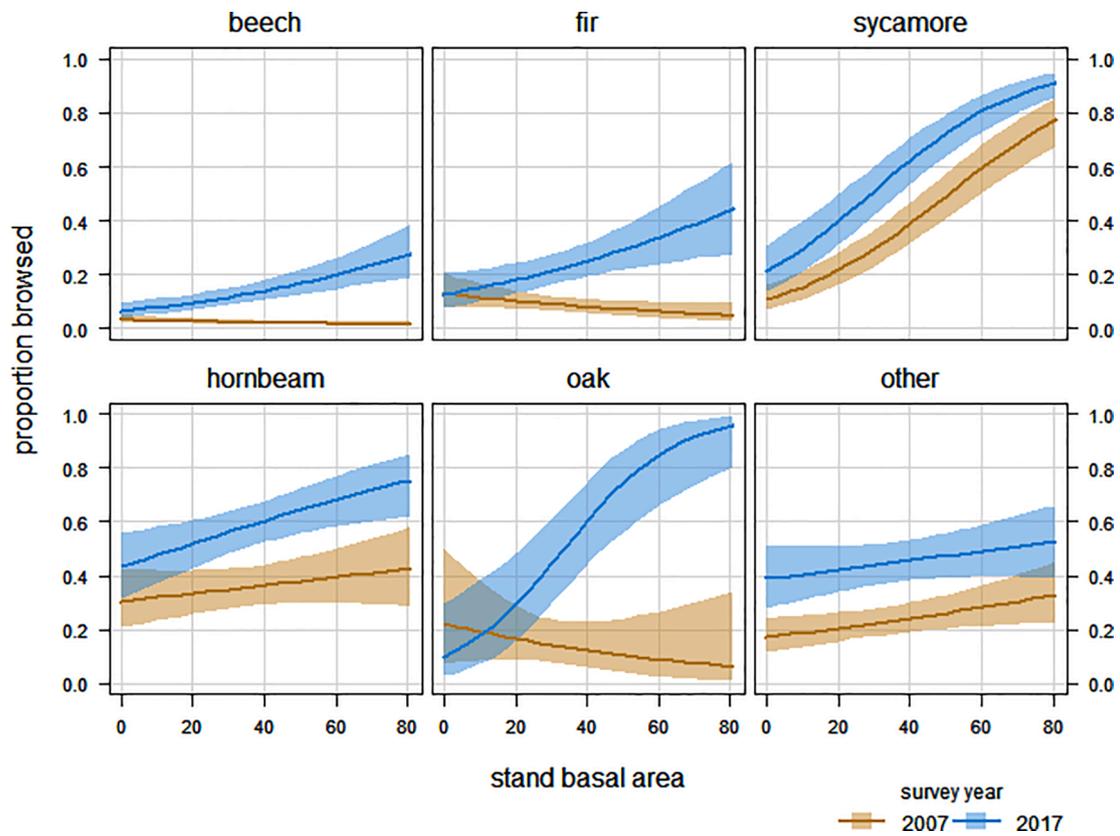


Fig. 5. Average predictions of the final model for the proportion of trees browsed (PTB) by deer in Roztocze National Park in relation to canopy openness expressed as Stand Basal Area (SBA), and survey year. For details, see the description to Fig. 2.

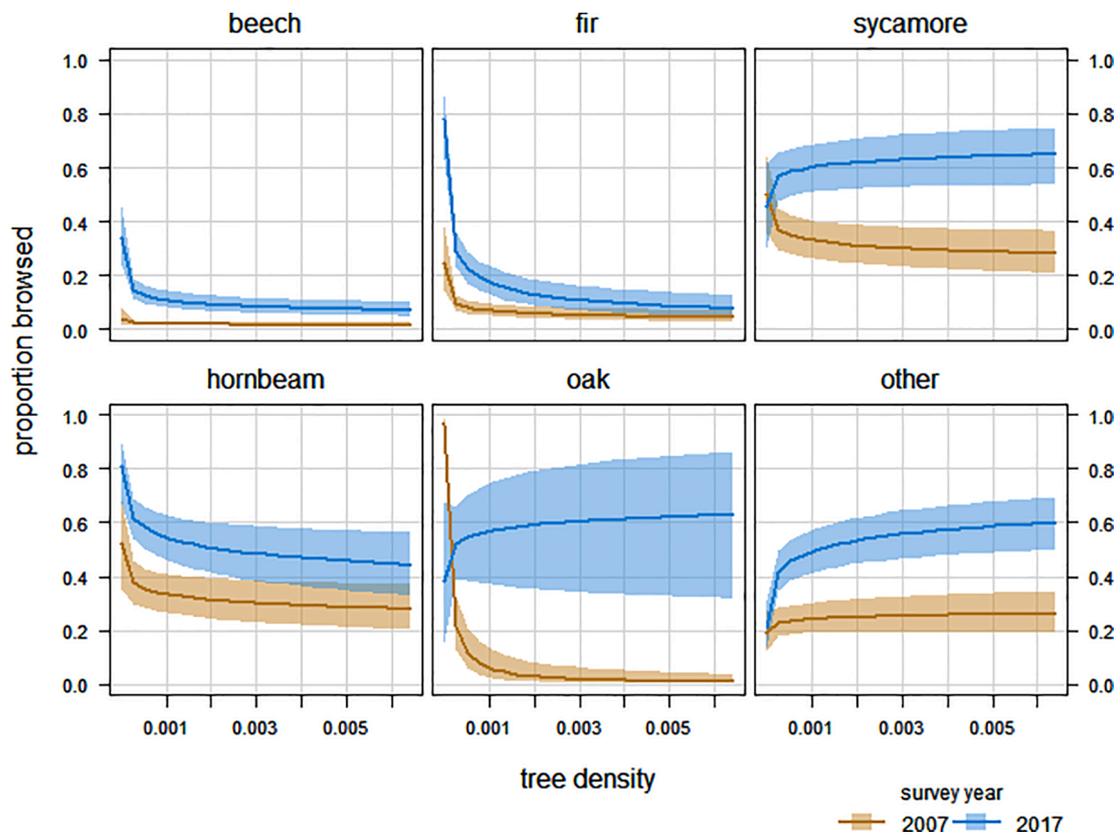


Fig. 6. Average predictions of the final model for the proportion of trees browsed (PTB) by deer in Roztocze National Park in relation to seedling density in a plot, and survey year. For details, see the description to Fig. 2.

the selection for beech and sycamore changed significantly between the survey years: the mean selection for beech increased, whereas that for sycamore decreased (Supplementary Table S1).

#### 4. Discussion

We have presented results confirming that an increase in the red deer population can considerably increase browsing pressure on both small and large saplings of a range of tree species. The overall tree browsing increased by 12% in years of high deer density compared to those of low deer density. Our finding is in line with the results of many previous studies, where it has been shown that ungulate density per se is the most important factor determining browsing pressure (e.g., Tremblay et al., 2007; Ward et al., 2008). However, we must keep in mind that the picture of browsing pressure observed in the year of high deer densities (2017) reflects not only deer densities in that particular year and their effects on woody vegetation, but also increasing deer densities in previous years and their effects on forage availability.

The increase in browsing pressure from deer varied depending on the height of the saplings, with the highest pressure exerted on seedlings taller than 50 cm. Other studies also noted that taller seedlings are more vulnerable to top-down processes, such as deer pressure (Tremblay et al., 2007; Kuijper et al., 2010; Szwagrzyk et al., 2020). Interestingly, we observed higher browsing pressure on taller seedlings of almost all available tree species in years with both low and high red deer density. There were two exceptions, however – browsing on beech and fir in a year when low deer density was similarly low. Presumably, the least preferred of these tree species was browsed occasionally in 2007, but as the deer density increased, the animals started browsing on taller seedlings of all available tree species, including the previously avoided ones. Van Beeck Calkoen et al. (2019) have shown, using eDNA to identify species-specific tree browsing, that the majority of browsing on

tall saplings (> 0.5 m) was caused by red deer, whereas on small ones ( $\leq$  0.5 m), it was caused by roe deer. A clear relationship between red deer density and browsing on tall seedlings was also observed in the Białowieża Forest under similar red deer density (Kuijper et al., 2010). Contrary to the results of Kuijper et al. (2010), in our study system (Roztocze National Park), top-down processes affected saplings regardless of the height class. The most likely explanation is that in our study, the population density of roe deer, a species foraging on shorter seedlings (van Beeck Calkoen et al., 2019), was twice as high as that in Białowieża.

One of the main questions closely related to the processes of increasing deer density is how it has changed the browsing intensity on woody vegetation of the forest floor, especially on palatable tree species. Our results indicate that the fourfold increase in red deer density increased browsing pressure on palatable tree species (hornbeam and sycamore) from 20% to 40%. In the year with high red deer density, over 80% hornbeam and sycamore saplings taller than 50 cm were browsed. Additionally, we observed increased browsing pressure on two tree species considered nonpreferred: European beech and silver fir. This indicates that deer densities of approximately 10 ind./km<sup>2</sup>, which we found in our study, in mixed European lowland forests heavily affect woody vegetation by exerting strong selection pressure on palatable tree species (Augustine and McNaughton, 1998) and their regeneration ability (Kuijper et al., 2010).

In our study, deer exhibited a clear selection for certain tree species. The most selected were sycamore and hornbeam, oak was consumed according to availability, and European beech and silver fir were the least selected (Supplementary Table S1). This selection is in line with other previous studies (Boulanger et al., 2009; Kuijper et al., 2010; Ohse et al., 2017;), with one exception, the silver fir, which is usually considered a tree preferred by deer (van Beeck Calkoen et al., 2019; Klopčič et al., 2010). However, Szwagrzyk et al. (2020) also observed

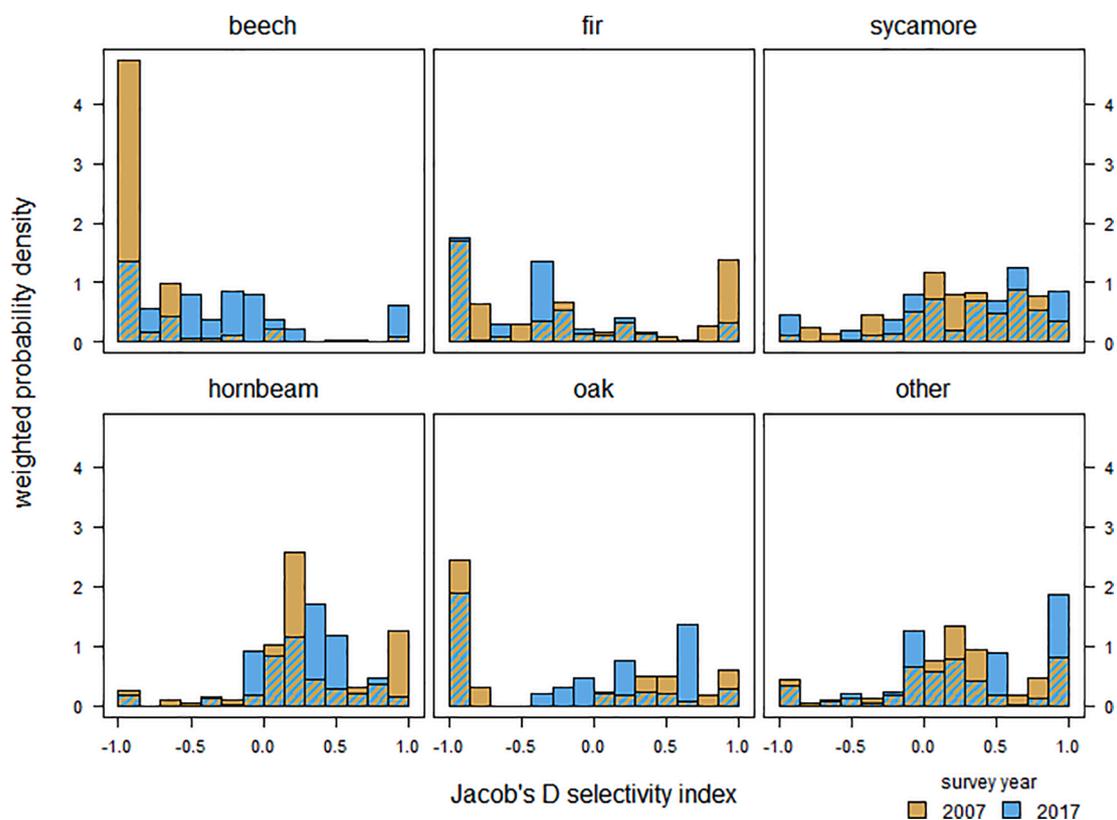


Fig. 7. Deer feeding selectivity for different tree species in the study area. The histograms show the distribution of Jacob's D selectivity indices calculated for each study plot and for each of the two years of the study, weighted by the number of trees in the plot to reduce the influence of extreme values caused by very low tree numbers. Dashed areas represent overlapping histogram bars.

avoidance of silver fir by deer in Tatra National Park. The observed results can be explained by a higher availability of more preferred species, such as hornbeam and sycamore. Additionally, silver fir is an occasional deer food that is browsed mostly in winter due to a shortage of food (Häsler and Senn, 2012).

Interestingly, increasing red deer density changed the selection pattern for two tree species: European beech became more selected, and sycamore became less selected. A possible explanation is that the rise in the numbers of red deer resulted in an increase in browsing pressure at a landscape scale, where beech is the dominant species. Moreover, red deer are intermediate feeders whose diet also contains a high proportion of high-fibre food items, such as grasses (Barančková et al., 2010; Krojerová-Prokešová et al., 2010), contrary to roe deer, which are typical concentrate browsers and more selective towards particular tree species.

Apart from deer density, some environmental factors can also affect the browsing intensity (Carter and Fredericksen, 2007; Mårell et al., 2018; Petersson et al., 2020). For example, food diversity – the richness of sapling species in a particular food patch – can affect browsing probability. This can be driven mainly by palatable deer tree species, which attract deer to patches with higher sapling species richness (Ohse et al., 2017). In our study, browsing pressure in the context of the seedling diversity index (SDI) was affected by deer density (year of the study) and tree species. In the year with low red deer density (2007), higher SDI increased the probability of browsing on fir, sycamore and “other” tree species. However, in the year with high red deer density, higher SDI increased the browsing pressure on beech, hornbeam, sycamore and fir, decreasing the browsing pressure on “other” species and did not have any impact on oak. In our opinion, the observed pattern of deer foraging behaviour indicated that under high browsing pressure (high red deer number), a higher SDI attracts deer to particular patches with nonpreferred tree species such as European beech or balsam fir. This, in turn, results in higher browsing on unpalatable tree species. This result is in contrast to the results obtained by Ohse et al. (2017) in central Germany, where browsing proportions of individual species were lower when growing within a species-rich patch. In our study, as in a study conducted by Vehviläinen and Koricheva (2006) in Finland on moose and deer, browsing tended to increase with increasing SDI, as predicted by the associational susceptibility hypothesis (Brown and Ewel, 1987; White and Whitham, 2000). According to the optimal foraging theory (Stephens and Krebs, 1986) browsing herbivores, to maximize their instantaneous rate of intake, should spend longer and consume more resources (saplings in this case) in areas of high forage quality. Therefore, in our study area, where European beech is a dominating species, patches with a high SDI indicate the containment of the preferred plant species and should be perceived as high quality by deer. Hence, browsing pressure by deer on low-preferred tree species growing in the species-rich plots is as strong as on high-preferred tree species.

In the less common tree species (pine, ash, maple, linden, and elm), which we have analysed together, in the year of high red deer density the proportion of saplings browsed was lower when they grew within a species-rich patch. However, the opposite was observed in the year with low red deer density. In the studied area, seedlings of palatable tree species from the “other” group grow in species-rich plots with a higher proportion of unpalatable beech (Z. Borowski, unpublished data). When browsing pressure from red deer increased (year 2017), palatable tree seedlings in this group of species would benefit from diverse neighbourhoods through browsing pressure diluted over individuals of other tree species.

Contrary to our predictions, higher availability of winter food to deer in a particular patch, calculated as the number of available tree saplings, decreased the level of browsing pressure in years with either low or high red deer density. Only for oak and sycamore in the year with high deer density did we observe an opposite trend that higher food availability increased the browsing probability of these species. According to

foraging theories (Spalinger and Hobbs, 1992; Stephens and Krebs, 1986), a high number of saplings should increase the browsing probability in a patch. In our study, however, we did not observe such a relationship. It is possible that in our study system, the number of seedlings in each particular patch was much higher than the minimum threshold predictions based on foraging theories.

The results of previous studies (Staines and Welch, 1984; Kuijper et al., 2009; Möst et al., 2015) indicated that some environmental variables, such as canopy openness (forest gaps), increased the visit rate by ungulates – especially red deer – and promoted browsing probability. Open forest stands are characterized by low crown closure, allowing light to reach the saplings and thus increasing nutrient availability (Ritter and Vesterdal, 2006). We assume that this improves forage availability for ungulates by enhanced regeneration of trees, which makes saplings more attractive to deer and increases browsing probabilities. The results of our study show that in years with low red deer density (except for sycamore), we observed a similar trend, with increased light intensity (inverse of SBA) increasing the probability of deer browsing.

After 10 years, over which deer density increased, an opposite pattern was observed: the proportion of browsed stems was inversely related to the proxy of light intensity (stand basal area) for all tree species (except less common species which we analysed as one group). A similar relationship was found in our experiment conducted in the same area (Borowski et al., 2020) – the probability of oak browsing increased with decreasing visibility, without any relationship to habitat use based on pellet group counts. The most intuitive explanation is that efficient deer foraging occurs during daylight hours when security plant cover is important as a buffer against wolves (Creel et al. 2005, Gervasi et al. 2013) and humans (Mathisen et al., 2018). A possible cause is that in the 10-year period from 2007 to 2017, tourist activity, which increased greatly in Roztocze National Park, affected deer foraging behaviour.

## 5. Conclusions

An increase in the red deer population exerted high browsing pressure on tree regeneration, which was strongly concentrated for saplings taller than 50 cm from all available tree species. Moreover, the increased population changed deer forage selection, i.e., increased the selection for unpalatable European beech and decreased that of highly preferred sycamore. High species diversity of saplings in a patch increased the probability of browsing of the majority of species, except for sycamore and oak. This resulted in an increase in the occurrence of palatable species with increasing species diversity. Similarly, canopy openness plays an important role in deer foraging behaviour during years with high deer densities – plots with lower light availability (with closed canopies) attracted deer and increased the probability of browsing on saplings. Contrary to our expectations, deer browsing in the year with high population density was not related to sapling availability in a patch. The results of this study strongly suggest that increased red deer population density leads to altered browsing patterns in the landscape, which may also have a long-term impact on future forest development.

## 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. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119442>.

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