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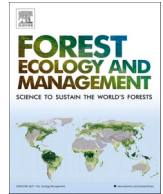
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Impediments affect deer foraging decisions and sapling performance

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ABSTRACT

Impediments, such as tree logs, can prevent access to saplings for deer, and can increase perceived predation risk by blocking view and escape possibilities for deer in areas with large carnivores. Therefore, impediments can influence deer foraging decisions and the trade-off between safety and food of different quality indirectly influencing tree regeneration. The aim of our study was to test how the presence of an impediment affects deer foraging behavior and tree sapling performance of eight species that differ in preference by deer. We planted saplings without, nearby and inside impediments and followed their fate for three consecutive years in Białowieża forest, Poland. We constructed 1 m high impediments of 5 × 5 m that would still allow deer to enter the impediment and forage from the saplings planted inside. However, we never recorded deer inside the impediments. Near the impediments deer visitation rate and cumulative visitation time was reduced. As a result, browsing intensity of all tree species was lower nearby and especially inside the impediment. Deer did not select different tree species without, near or inside the impediment. Due to the overall lower browsing intensity, tree saplings increased in height near the impediment and heights increased significantly within the impediment. The palatable, but browsing intolerant, *Acer platanoides* benefited most from the impediment as this species was highly selected and heavily browsed without an impediment. Followed by the palatable, but more browse tolerant *Tilia cordata* and *Pyrus pyrastrer*. In comparison, the presence of an impediment had a smaller effect on the less preferred *Alnus glutinosa*, *Picea abies* and *Pinus sylvestris* which survived well without an impediment. Our study showed that impediments modified deer behavior as they visited these plots less frequently and thereby indirectly reduced the browsing impact on the preferred tree species. Therefore, the potential for successful recruitment of preferred tree species is higher near an impediment, and especially when surrounded by impediment structures. In the long-term, the presence of natural impediments like tree logs allows browsing intolerant tree species to escape browsing, ultimately leading to a more diverse forest composition.

1. Introduction

Dead wood is an important factor enhancing forest biodiversity in general (Paillet et al., 2009), including effects on vegetation. Herbaceous plants and tree saplings often grow on tree logs (Fukasawa and Ando, 2018; Orman et al., 2016) and tree logs also can act as protective structures against ungulate browsers and facilitate tree regeneration (Heinemann and Kitzberger 2006, Smit et al., 2012, van Ginkel et al., 2013, 2018, Kuijper et al., 2013), thereby influencing forest tree species composition in the long term.

Considering ungulate-plant interactions, downed wood can facilitate

tree regeneration in two ways. Firstly, dead wood can form a physical barrier that reduces or completely prevents ungulates access to tree saplings, thereby reducing the browsing pressure and increasing successful sapling establishment (de Chantal and Granström, 2007; Smit et al., 2015; Winnie, 2012). Secondly, in areas where large carnivores are present, downed tree logs can act as a risk factor as they block view and escape possibilities. As a result, tree logs are avoided, or deer allocate more time to vigilance at the cost of reduced foraging time when in the vicinity of logs (Halofsky and Ripple, 2008; Kuijper et al., 2015). The lower visitation rate and foraging time near tree logs results in a reduced browsing pressure, allowing saplings to grow taller and escape above the

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herbivore browsing line of 200 cm (Kuijper et al., 2013; Ripple and Beschta, 2003; Smit et al., 2012; van Ginkel et al., 2018). Hence, by increasing the foraging costs, tree logs can directly (via physical protection) and indirectly (via protection resulting from increased perceived risk) create ‘windows of opportunity’ for successful tree regeneration (Beschta et al., 2018; Kuijper et al., 2013; Ripple and Beschta, 2006; van Ginkel et al., 2018; Winnie, 2014). However, the relative importance of both mechanisms for tree recruitment is currently debated (Beschta et al., 2014; Winnie, 2014, 2012).

According to the foraging theory, the costs of foraging for deer near an impediment depend on the trade-off between food acquisition and risk avoidance (Brown and Kotler, 2004; Lima and Dill, 1990; Mangel and Clark, 1986; McArthur et al., 2014). Ungulates generally move from risky, high quality foraging sites towards safe low quality habitats in response to increased predation risk, which can result in a change in diet composition (Barnier et al., 2014; Creel et al., 2009; Hernández and Laundré, 2005; Valeix et al., 2009), with potential consequences for fitness (Barnier et al., 2014; Christianson and Creel, 2010). This shift towards low-quality habitats could be compensated for by consuming more or being more selective by choosing higher quality plants. In old-growth forests with downed wood and natural gap dynamics, most food patches are heterogeneous in terms of tree species (Bobiec et al., 2000; Churski et al., 2017), which differ in nutritional value and hence preference for ungulate herbivores (Augustine and McNaughton, 1998). As such, the choice between food and safety of deer near tree logs is likely influenced by the tree species present. At more risky sites, herbivores are found to quit foraging sooner (Iribarren and Kotler, 2012) unless higher quantity or better quality food is available that could compensate for the higher foraging costs (Bonnot et al., 2017; Kotler and Blaustein, 1995; Nersesian et al., 2011; Stears and Shrader, 2015). Thus, if the food quantity or quality more than compensates for the costs, herbivores may accept a higher risk of predation (Bonnot et al., 2017; Brown and Kotler, 2004; Nersesian et al., 2011). However, these experimental results were derived from homogenous food patches (with one type of food source), and it is unclear how increased risk will affect the natural foraging decisions of an ungulate in heterogeneous food patches.

The aim of our study is to investigate how impediments influence deer foraging behavior (i.e. visitation rate, foraging time and preference towards different tree species) and link this to tree sapling browsing intensity and performance. We designed an experiment with eight tree species that differ in preference by deer, and manipulated risk for deer by erecting an artificial impediment that acted either as a visual or as a visual and physical barrier. We planted saplings inside, nearby and without an impediment. Camera traps were used to record deer visitation rate and behavior. We assume that the impediment will be perceived as risky and therefore we hypothesize that the number of deer visits will decrease near and especially inside impediments. When deer are present we expect increased vigilance levels, decreased foraging time and more selective browsing on high-quality trees to compensate for the lost foraging time. We hypothesize that the change in deer behavior near impediments will lead to reduced sapling browsing, taller saplings and a higher survival. As a result, we expect the less preferred species to perform better than the preferred species.

2. Material and methods

2.1. Białowieża forest

Białowieża forest (52°45'N, 23°50'E), is a temperate lowland forest on the border of Poland (580 km²) and Belarus (800 km²). The Polish part of the forest consists of Białowieża National Park (100 km²), with a hands-off policy, and State Forests (480 km²). We performed our experiment in the State Forest where logging and seasonal hunting is allowed and which is freely accessible for hikers and cyclists and only accessible by car with a permit.

The forest has a continental climate with mean annual precipitation

of 641 mm, and a mean annual temperature of 6.8 °C. The forest consists of a mosaic of multi-aged and multi-species forest stands and is dominated by a mixture of European hornbeam (*Carpinus betulus*), small-leaved lime (*Tilia cordata*), Norway maple (*Acer platanoides*), oak (*Quercus robur*), black alder (*Alnus glutinosa*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) in different compositions. The small river valleys and floodplain forests are dominated by black alder, whereas the rest of the forest is a mixture of the above mentioned tree species occurring in different ratios. In the entire Białowieża forest, but especially in Białowieża National Park, there is a substantial amount of dead wood covering the forest floor (Bobiec, 2002). This dead wood can be in the form of single trees as well as several trees that have fallen over each other.

The natural ungulate assemblage of red deer (*Cervus elaphus*, 4.7 individuals km⁻²), roe deer (*Capreolus capreolus*, 0.8 ind. km⁻²), European bison (*Bison bonansus*, 0.8 ind. km⁻²), moose (*Alces alces*, 0.06 ind. km⁻²) and wild boar (*Sus scrofa*, 3.2 ind. km⁻²; Kuijper et al., 2014) co-occurs with the natural predators wolf (*Canis lupus*, 2–3 ind. per 100 km²) and lynx (*Lynx lynx*, 1–3 ind. per 100 km²; Schmidt et al., 2009). In Białowieża forest, red deer are the most dominant browsers as they are the most abundant, both in numbers and total biomass, and have the highest percentage of woody species in their diet (Gębczyńska, 1980; Gębczyńska and Krasieńska, 1972). Roe deer and European bison also browse woody species, but to a lesser extent (Gębczyńska, 1980; Gębczyńska and Krasieńska, 1972), and moose occurs in such low densities that it is expected to have a minor influence on sapling performance. Of all browser species, red deer is assumed to play the dominant role in reducing tree recruitment (Kuijper et al., 2010b). The wolf mainly preys upon red deer, followed by roe deer and wild boar (Jędrzejewski et al., 2002, 2000). Roe deer is the main food source for lynx, whereas European Bison and moose are hardly preyed upon (Jędrzejewski et al., 2002, 2000).

2.2. Sapling planting experiment

Saplings of eight species were planted on 14 sites in the Białowieża State Forests district of the managed part of the Polish forest. We actively searched for forest gaps to plant saplings, since sapling survival is higher inside canopy gaps (Churski et al., 2017; Kuijper et al., 2010a). The sites were located in small mowed meadows within the forest as well as natural occurring forest gaps. The average distance between our sites is 8.2 ± 0.4 km (±SE, range: 1–15.2 km).

In April 2015, we planted on each site 128 saplings in a split-plot design. Sixty-four saplings were planted on a plot with an impediment and the other 64 saplings were planted on a control plot without an impediment, at a minimum distance of 50 m (Fig. 1).

On the impediment plot saplings were planted in an ‘inner’ and an ‘outer’-square (see Fig. 1), meaning that 32 saplings were planted at 0.5 m on the outside of the barrier (from here on: near impediment) and 32 saplings were planted at 0.5 m from the barrier inside the impediment (from here on: inside impediment). The saplings planted inside the impediment are therefore surrounded by impediments. On the control plot the two squares of planted saplings were not separated by an impediment (from here on: without impediment), which allowed us to control for the position of the trees as a potential confounding factor. We erected a barrier of 1 m high in a square of 5 m by 5 m tightly wrapped in black ‘canvas’. This barrier blocks the view and creates a physical impediment with comparable dimensions as large tree logs. Kuijper et al. (2015) showed that large tree logs are perceived by red deer as risky in areas where wolves are present. With our impediments, we aimed to create similar fear effects in a standardized way to enhance the perceived risk by deer. As the impediment is only 1 m high, deer could jump over and forage inside. However, once inside, the view of the deer, is blocked on all sides in combination with more physical barriers. As a result, escaping a carnivore attack is expected to become more difficult. Therefore, we expect deer will perceive foraging inside the impediment

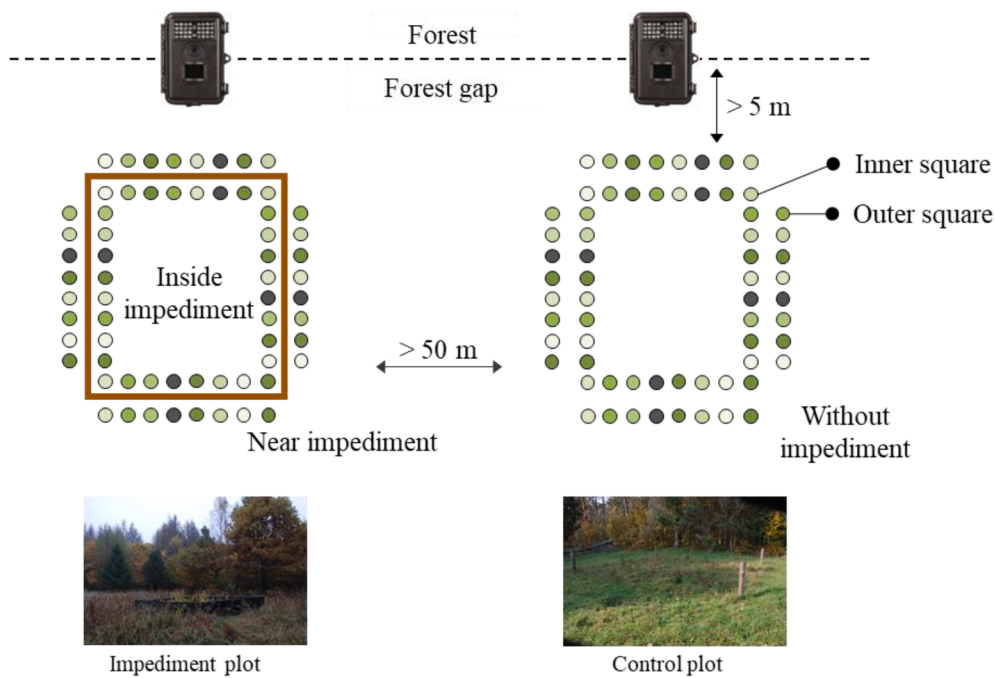


Fig. 1. Schematic design of the planting experiment replicated on 14 sites in Białowieża forest, Poland. On each site a total of 128 saplings were planted. We planted 64 saplings on an impediment plot where a barrier of 1 m high was erected in a plot of 5 m by 5 m. The aim of the impediment was to increase perceived risk, as it blocks the view and escape possibilities for deer. Thirty-two saplings were planted both inside the impediment, and near the impediment at a distance of 0.5 m. As a control, we planted 64 saplings in an identical array without an impediment. We used naturally occurring tree species that were preferred forage species for red deer (*Acer platanoides*, *Pyrus pyrastrer*, *Carpinus betulus*, *Tilia cordata* and *Quercus robur*) and less preferred tree species (*Picea abies*, *Pinus sylvestris* and *Alnus glutinosa*). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

as more risky than near the impediment. Previous studies have also suggested that more impediments (i.e. tree logs) in the surroundings promotes sapling performance, via increased risk effects (Kuijper et al., 2013). On the control plot we did not manipulate the perceived risk for deer as the saplings were planted without an impediment. The control plot was marked with four wooden poles on each corner.

We randomized sapling order to diminish possible neighbor effects, as the probability of being browsed can be affected by the palatability of the neighboring sapling species (Skarpe and Hester, 2008). On each site, the control plot was an exact copy of the impediment plot in terms of sapling species order, with the absence of the impediment as the only difference. We chose to plant eight tree species that occur naturally in the Białowieża forest, and differ in preference by the browsing herbivores. Norway maple (*Acer platanoides*), wild pear (*Pyrus pyrastrer*), small-leaved lime (*Tilia cordata*), pedunculate oak (*Quercus robur*) and hornbeam (*Carpinus betulus*) are highly preferred species, whereas Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and black alder (*Alnus glutinosa*) are not preferred by the browsers (Churski et al., 2017; Kuijper et al., 2010b).

2.3. Deer foraging behavior

To estimate how the impediment affects deer behavior we placed camera traps (Bushnell Trophy Cam HD 2013, or Ecotone SGN-5220) at a height of circa one meter attached to a tree on each impediment and control plot. The camera trap started recording one-minute videos when triggered by movement detected by a Passive Infrared motion sensor. The recording time-interval was set to one second, meaning that the camera would immediately start recording another video when the animals were still present at the plot. The experimental plots were in the center of the detection zone of the cameras. We recorded all deer within view of the cameras (i.e. both on the plot and in the vicinity of the plot) to quantify deer visitation rate and behavior. Cameras were placed in the field in six different camera trapping sessions divided over the seasons to get a representative view of deer foraging behavior during the entire year: 28 April – 8 July 2015, 11 November 2015 – 2 February 2016, 17 May – 29 June 2016, 23 January – 28 March 2017, 8 May – 26 June 2017 and 12 March – 4 April 2018. This resulted in a total of 6296 trapping days.

All recorded red deer or roe deer, the most abundant browsers, and most susceptible to predation (Jędrzejewski et al., 2002), were analyzed for foraging and vigilance behavior when present for longer than 4 s on the plots, following the protocol of Kuijper et al. (2014). Deer recorded on consecutive videos within a five minute interval were combined and analyzed as one visit (Kuijper et al., 2014). During each visit, the behavior of every recorded individual was scored, including each individual in a group of deer. By doing so we get an estimate of the overall foraging pressure as this affects sapling performance. A deer was classified as vigilant when standing still with his head held parallel to the body, staring or looking around without chewing (Kuijper et al., 2014). A deer was classified as foraging when it was grazing from grasses, forbs, or browsing from woody species (Kuijper et al., 2014). Behaviors like walking, running, sniffing and a leftover group were also classified, but not used for further analysis.

2.4. Sapling measurements

To estimate the effect of the impediment on deer foraging behavior we measured the sapling browsing intensity. As measurement for browsing we counted how much of the ten highest woody twigs were browsed (following Kuijper et al., 2013). To estimate the impact of deer foraging on tree regeneration we measured sapling survival and sapling height increment. Sapling height, diameter and browsing intensity were measured at the start (April) and the end (October) of each growing season for three consecutive years, starting in April 2015. Height (in cm) was measured as the highest woody part of the sapling. Sapling diameter was measured to the nearest millimeter with a caliper at the base of the sapling.

2.5. Statistical analysis

2.5.1. Deer behavior

We recorded a total of 713 red deer visits and 352 roe deer visits. Visitation rate of red deer and roe deer was calculated as the total number of visits within the view of the camera divided by the total number of camera trapping days, for both the plots with and without impediment from April 2015 until April 2018. The effect of the impediments on visitation rate of both deer species was analyzed with a linear

mixed effect model from the ‘nlme-package’ (Pinheiro et al., 2018), with the single terms Plot (two levels: with impediment and without impediment) and Species (two levels: red deer and roe deer) and their interaction. The random intercept of Plot was nested in Site. With the Holm posthoc-test we tested per deer species for pairwise differences between the plots with and without the impediment.

We were interested in the overall foraging pressure, and therefore

$$\text{Overall browsing intensity} = \frac{\text{browsed twigs } t1 + \text{browsed twigs } t2 + \dots + \text{browsed twigs } t6}{\text{total twigs } t1 + \text{total twigs } t2 + \dots + \text{total twigs } t6}$$

summed the time each individual deer spent on each plot and divided this by the number of days the camera was operating, to get the cumulative visitation time, foraging time and the time vigilant per deer species per recording day. For this analysis, camera trap data from April 2015 until June 2017 were used. The cumulative visitation time was analyzed using a similar model structure as we used for the visitation rate model. We calculated the proportion of time foraging by dividing the cumulative foraging time by the cumulative visitation time per plot for both red deer and roe deer. Proportion of time deer spent on vigilance was calculated the same way. We analyzed the proportion of time spent foraging and vigilant with a generalized linear model with a binomial error structure (Bates et al., 2015) and similar fixed effects as for the visitation rate. Due to overfitting of the model we could not include random effects for the analysis of time spent on foraging and vigilance. With the Holm posthoc-test we tested per deer species for pairwise differences between the plots with and without the impediment.

2.5.2. Sapling measurements

We had to exclude *C. betulus* from the analysis, because ca. 70% of the saplings died during the first year (weak planting material for this species). Therefore we decided to execute the statistical analysis with the seven remaining tree species.

Following Kuijper et al. (2010b), we calculated the Jacobs selectivity index $D = (r - p) / (r + p - 2rp)$ (Jacobs, 1974) to see which of the planted tree species are preferred by the ungulate browsers. Where r = proportion of each sapling species in the total of browsed trees, and p = proportion of each sapling species in the entire sample. The index varies between -1 least preferred, to 1 most preferred species, as a result of browsing by all ungulate species combined.

At the start of the experiment the mean sapling height was 35.6 ± 0.4 cm ($\pm$ SE, range 7.5–105 cm), with *P. sylvestris* being the shortest tree species and *T. cordata* the tallest (Appendix A, Fig. A1). As the height of the saplings at the start of the experiment differed between the tree species and we wanted to compare sapling performance over time, we calculated the net sapling height increment as $HI = \text{Height } t_6 - \text{Height } t_0$, where $\text{Height } t_0$ is the sapling height at the start of the experiment in April 2015, and $\text{Height } t_6$ is the sapling height after three years of the experiment in April 2018.

Per tree species we analyzed the sapling height increment with a linear mixed effects model using Plot (two levels: i.e. with and without impediment) and Square (two levels: i.e. ‘inner’ and ‘outer’) and their interaction as fixed effects and Square nested in Plot and Plot nested in Site (Site/Plot/Square) as random intercept to take the experimental design into account. To do a posthoc analysis on the interaction term Plot:Square we used the emmeans-package (Lenth et al., 2019) for pairwise comparisons of the contrasts on the calculated least square means, with the Tukey method to adjust for comparing four groups.

Our measurement of browsing intensity is a snapshot of browsing at that particular moment in time. Browsing during winter time can be more detrimental for evergreens than deciduous species due to seasonal

differences in nutrient allocation patterns (Millard et al., 2001). As we measured browsing intensity at the start and the end of the growing season, and since the severity of browsing depends on the moment the saplings is browsed, we combined these snapshots and calculated an overall browsing intensity:

We used a generalized linear mixed effects model (Bates et al., 2015) with a binomial error distribution to analyze sapling browsing intensity for each tree species separately. The fixed and random effects were similar as described for the net sapling height increment model. As described for the net sapling height increment model, we tested for pairwise comparisons with the emmeans-package. For both the sapling height increment model and the overall browsing intensity model we only included the saplings that survived until April 2018.

Sapling survival was analyzed using a similar model structure as described for the sapling browsing intensity model (i.e. a generalized linear mixed-effects model (Bates et al., 2015) with a binomial error distribution with similar fixed and random effects). We modelled the survival for each tree species separately as a full model did not converge.

3. Results

3.1. Deer behavior (rate and time)

Red deer visited the plots without an impediment 2.1 times more than the plots with an impediment (total nr. of visits: 486 vs 227; $\chi^2(1) = 14.9$, $P = 0.0002$), resulting in 2.6-fold higher cumulative visitation time per day in the absence of impediments ($\chi^2(1) = 31.5$, $P < 0.0001$; Fig. 2). There were no recordings of deer (or any of the other ungulates) inside the impediment to forage from the saplings inside the impediment. Roe deer visitation rate showed a similar, though not significant trend, and was almost a two-fold higher on plots without an impediment (total nr. of visits: 228 vs 124; $\chi^2(1) = 3.3$, $P = 0.071$). The cumulative visitation time of roe deer was also not significantly influenced by the presence of an impediment ($\chi^2(1) = 0.5$, $P = 0.467$).

3.2. Deer behavior (time spent on behaviors)

The proportion of time red deer and roe deer spent on foraging on plots with an impediment did not differ from plots without an impediment (red deer: $\chi^2(1) = 0.1$, $P = 0.750$; roe deer $\chi^2(1) = 1.03$, $P = 0.622$). Both red deer and roe deer did not change vigilance levels near an impediment (red deer: $\chi^2(1) = 0.04$, $P = 0.840$; roe deer: $\chi^2(1) = 0.75$, $P = 0.774$; Fig. 2).

3.3. Jacobs selectivity index and browsing intensity

In general, it seems that the preference for particular tree species by the browsers did not change in the presence of an impediment. Without an impediment *A. glutinosa* and *P. abies* were least selected during the first full year of the experiment, and were just as *P. sylvestris* and *T. cordata* even less selected near or inside the impediment (Fig. 3A). The browsers preferred foraging from *A. platanoides*, *P. pyramidalis* and *Q. robur* in absence of an impediment and when foraging near the impediment. Inside the impediment almost none of the saplings were browsed (19 saplings had browsing marks out of 326 alive saplings) after the first year, and therefore all species were browsed less than expected based on

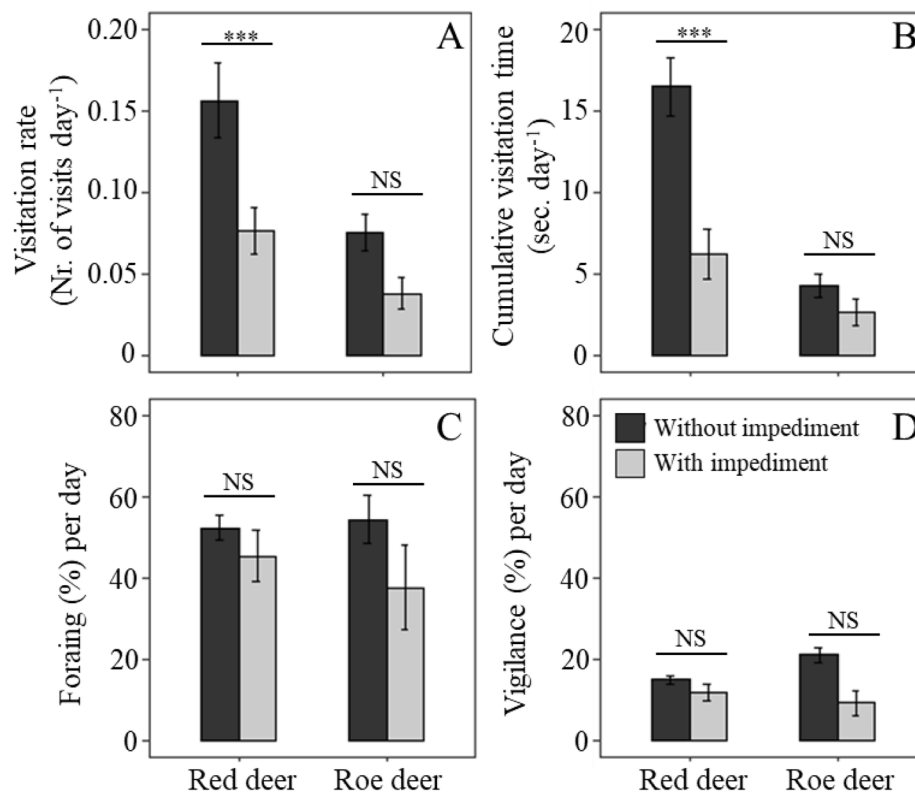


Fig. 2. Visitation rate and behavior of red deer and roe deer without and nearby the impediment. As we have no records of deer jumping inside the impediment we did not show this in these graphs. Visitation rate (A) and absolute visitation time (B) was for both red deer and roe deer significantly higher without an impediment. Deer foraged (C) more without an impediment, but were also more vigilant (D) without an impediment, compared to nearby an impediment.

availability, hence the negative values for the Jacobs selectivity index.

As expected, we found that for all tree species the overall browsing intensity of the saplings planted on the inner and outer square depends on the presence of an impediment (interaction between presence/absence treatment and position of trees on inner or outer square; p -values range from $p < 0.0001$ to $p = 0.004$; Fig. 3B). Indeed, posthoc tests showed that without an impediment overall sapling browsing intensity does not differ between the outer and inner square for all tree species, whereas on plots with an impediment saplings were significantly less browsed in the inner square compared to the outer (Appendix A, Table A1). All species had the highest browsing intensity on the plots without an impediment (Fig. 3B). Saplings near the impediment were less browsed compared to saplings without an impediment, but the reduction is only significant for *A. platanoides* (−22%), *P. sylvestris* (−26%) and *P. pyraeaster* (−10%; Appendix A, Table A1). Growing nearby an impediment affects browsing intensity only to a small extent for *A. glutinosa* (−7%), *P. abies* (−5%) and *T. cordata* (−7%; Fig. 3B; Appendix A, Table A1). Browsing intensity for all tree species was significantly lower when growing inside the impediment compared to growing nearby or without an impediment (Appendix A, Table A1).

3.4. Sapling survival and height increment

After three consecutive years, 929 of the 1568 (59.2%) planted saplings survived. Without an impediment the survival rate was 41% and 43% respectively for the inner and outer square (inner square: 183/448, and outer square 191/448). Near the impediment there was a comparable survival rate of 40% (179/448), but in contrast inside the impediment the sapling survival increased to 68% (304/448). For all tree species sapling survival without an impediment was similar for the inner and outer square, and also comparable to the saplings planted near the impediment (Appendix A, Table A2). Sapling survival for *A. platanoides*,

P. abies, *P. sylvestris*, *T. cordata* and *Q. robur* was significantly higher inside the impediment, whereas survival of the other tree species inside the impediment was not affected (Fig. 4, Appendix A, Table A2). Overall, survival of *A. glutinosa* was relatively low and did not increase near or inside the impediment. In contrast, the survival of *P. pyraeaster* was relatively high in absence of an impediment and also did not further increase when planted near or inside the impediment (Fig. 4).

As for survival, sapling height increment without an impediment was not significantly different for the inner and outer square of saplings (Appendix A, Table A3, Fig. 4). The saplings of all tree species near the impediment increased in height more compared to the saplings without an impediment, though this increase was only significant for *P. abies* (Appendix A, Table A3). Nevertheless, *T. cordata* and *P. pyraeaster* seem to profit the most with, on average, a 4.7-fold and 3.1-fold increase in height near the impediment. The saplings inside the impediment were hardly browsed and grew significantly taller than the saplings near and without the impediment (Appendix A, Table A3). The saplings that profited most from growing inside the impediment were *A. platanoides* (7.9-fold increase) and *T. cordata* (6.4-fold increase), followed by *P. pyraeaster*, *Q. robur* and *P. sylvestris* (all three ~4.5-fold increase), as they increased most in height compared to their conspecifics growing without an impediment (Fig. 5).

After three years, 29 saplings were taller than 150 cm (Appendix A, Fig. A2), a height at which saplings can be considered to be relatively safe from browsing (Kuijper et al. 2013). Six out of these 29 saplings were growing near the impediment, and were dominated by *A. glutinosa* (five compared to one *T. cordata*), while the remaining 23 saplings were growing inside the impediment. Inside the impediment, 11 saplings of *A. glutinosa* were >150 cm, followed by *A. platanoides* (9x), *T. cordata* (3x), *P. pyraeaster* (2x) and *Q. robur* (1x). Trees > 200 cm are completely safe from browsing as their leading shoot cannot be browsed they have escaped the browsing line (Renaud et al., 2003). In our experiment seven

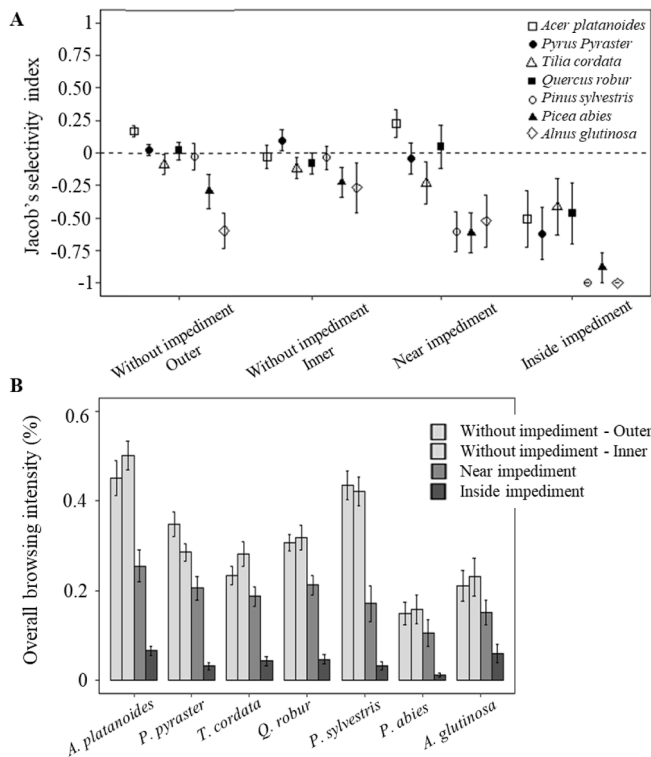


Fig. 3. Jacobs selectivity index (A) and overall browsing intensity (B) for the four treatments. Jacobs index was calculated after the first full year of the experiment, and varies between -1 least selected, to 1 most selected species, as a result of browsing by all ungulate species combined. The overall browsing intensity is a combination of browsing measured multiple times over three years of experiment. Deer do not change tree species preferability in response to an impediment, but reduce their overall browsing intensity. Without an impediment *A. glutinosa* and *P. abies* were least selected. Of the saplings planted near the impediment *A. glutinosa*, *P. abies*, *P. sylvestris* and *T. cordata* were least selected, and *A. platanoides* was most selected. The saplings inside the impediment were hardly browsed, and are therefore all negatively selected.

saplings grew beyond the browsing line of 200 cm, and all escapees were *A. glutinosa* of which five were growing inside the impediment and two near the impediment (Appendix A, Fig. A2).

4. Discussion

Impediments have been shown to increase deer vigilance levels (Halofsky and Ripple, 2008; Kuijper et al., 2015) leading to a reduction in tree sapling browsing intensity (Kuijper et al., 2013; Smit et al., 2012; van Ginkel et al., 2018), which positively influences successful tree recruitment (Ripple and Beschta, 2006; Smit et al., 2012; Winnie, 2012; Kuijper et al., 2015; van Ginkel et al., 2018). In this experimental study

we aimed to investigate these different successive effects simultaneously. We found that the presence of an impediment reduced deer visitation rate and cumulative visitation time, resulting in a lower overall sapling browsing intensity, leading to a positive influence on tree performance. Deer did not seem to change their preference for different tree species in the presence or absence of an impediment. The overall reduction in browsing intensity made preferred tree species (*A. platanoides*, *T. cordata* and *P. pyraeaster*) profit more from the protective effects of growing nearby or inside impediments than less preferred tree species (*A. glutinosa*, *P. abies* and *P. sylvestris*).

4.1. Impediment effect on deer behavior and foraging decisions

Impediments have been shown to be avoided by deer, and if deer visit impediments their vigilance levels increase at the cost of foraging (Halofsky and Ripple, 2008; Kuijper et al., 2015). In compliance, deer visited our plots with an impediment less and we did not have footage of deer daring to jump inside the impediment. Moreover, we found the trend that both red deer and roe deer tended to forage less near an impediment. Our results are in line with the trade-off between food acquisition and risk avoidance (Lima and Dill, 1990). Conceivably, deer perceived our impediment plots as risky and therefore avoided the impediment and foraged less. Opposite from expected, we did not find that in the presence of an impediment deer would become more

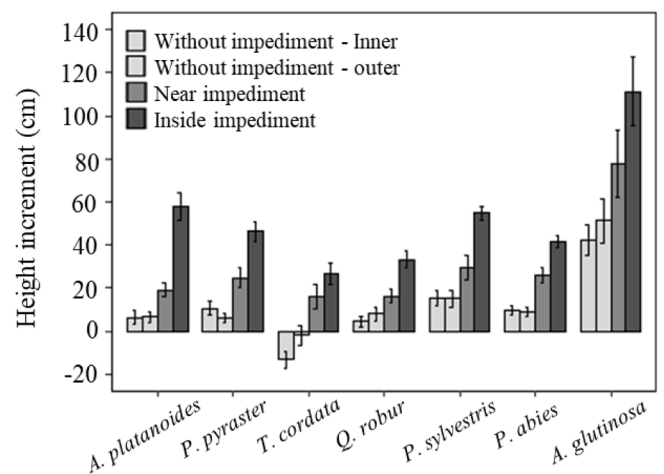


Fig. 5. Sapling height increment (cm; Mean $\pm$ SE) per tree species for each treatment after three years. Without an impediment the sapling height increment of the saplings from the inner circle did not differ from the saplings of the outer circle. For the saplings planted near the impediment there was a tendency for larger increment (compared to saplings without impediment), but this was only significant for *P. abies*. The saplings inside the impediment increased most in height compared to the saplings without or nearby the impediment, and this increment was significantly more for all species, except for *A. glutinosa*.

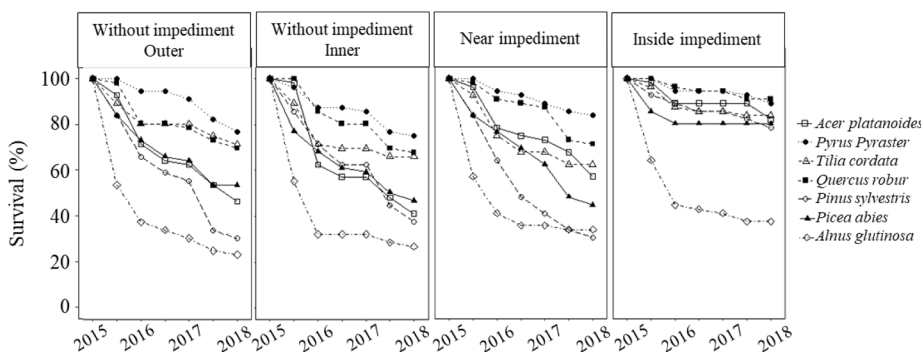


Fig. 4. Sapling survival rate for the four treatments per species over time. After three years of the experiment the saplings of *A. platanoides*, *P. abies*, *P. sylvestris*, and *Q. robur* had a significantly higher survival inside the impediment compared to the saplings of these species growing nearby or without an impediment. *A. glutinosa*, the most soil moisture dependent species and thus most susceptible to heat waves and drought periods among the planted species (Tyler et al., 2021), had a relatively low survival on all treatments. Its sharp decline during the first year, is probably explained by the drought and the high temperatures during the planting season. *P. pyraeaster* generally had a high survival rate which was not affected by the presence of an impediment.

selective to compensate for the higher costs. We found that, based on the Jacobs selectivity index, the deer preferred *A. platanooides*, *P. pyrastrer* and *T. cordata* and hardly selected the less palatable *P. abies*, *P. sylvestris* and *A. glutinosa* both at plots without an impediment and near an impediment. Overall, our impediments reduced deer visitation rate and foraging time, but did surprisingly not change the deer preference.

4.2. Impediment effect on sapling performance

Even though deer preference was not altered by the impediments, the response of the saplings to the reduced visitation rate and foraging time on the impediment plot is tree species specific. As we did not find any difference in sapling performance between the saplings planted on the inner and outer square in absence of an impediment, we from now on group them and refer to them in the discussion as saplings without impediment.

Especially *A. platanooides*, *P. sylvestris* and *P. abies* seem to profit from the impediments, though the mechanism underlying the increased survival is likely different between the deciduous and evergreen species. Our study showed that nearby and without an impediment, *A. platanooides* was most selected by the deer, resulting in a high browsing intensity and only a small height increase in three years' time. Inside impediments, *A. platanooides* increased in survival and almost an 8-fold in height, resulting in a high potential for saplings to outgrow the browsing line of 200 cm in the long term. The reduction in browsing likely explains the better survival for *A. platanooides* inside the impediment, since frequent browsing is known to reduce the survival rate (Gill and Fuller 2007, Smit et al. 2012, Churski et al. 2017). Despite the negative selection of the two evergreens, *P. sylvestris* and *P. abies* were browsed mainly during winter time (personal observation). As these conifers are not browse tolerant (Churski et al., 2017; Skarpe and Hester, 2008; Vandenbergh et al., 2009) the browsing, albeit less intensive, probably reduced the sapling survival in our experiment.

Without an impediment preferred species that are more browse tolerant can still have high survival. *P. pyrastrer* and *Q. robur* were, just like *A. platanooides*, assumed to be preferred species. However, based on our Jacob's selectivity index, both species were not positively or negatively selected by deer and had an average browsing intensity. In contrast to *A. platanooides*, *P. pyrastrer* and *Q. robur* are much more browsing tolerant which likely explains why their sapling survival was to only a small extent influenced by the impediment. Yet, the saplings grew taller inside the impediment, probably due to the lower browsing intensity. Previous studies performed in the Białowieża forest also found that *Q. robur* saplings grow taller near impediment structures (Bobiec et al., 2011; Smit et al., 2012; van Ginkel et al., 2013). The tannin-containing *A. glutinosa* was negatively selected by the browsers and was hardly browsed upon, which explains the lack of influence of the impediment on *A. glutinosa* survival. During our study, we observed a sharp drop in survival in the first year, which is probably due to suffering from an extreme drought period in the year of planting (personal observation). The saplings that survived the first year performed well, and showed the biggest height increase of all species. Only saplings of *A. glutinosa* managed to escape the browsing line of 200 cm during the three years of the experiment. Concluding, it was not the difference in preference, but the overall reduction in browsing intensity that made trees perform better near and inside the impediments. In that way, the more browse intolerant and preferred species (*A. platanooides*, *T. cordata* and *P. pyrastrer*) did relatively better and profited the most.

4.3. Risk-induced sapling protection by impediments?

By simultaneously manipulating and observing deer behavior, we could link the presumed risk-effects of impediments directly to sapling performance. Ford and Goheen (2015) advocated the approach of manipulating and observing different trophic levels as a necessity to quantify cascading effects, which could resolve the ongoing debate

about risk-induced trophic cascades (Beschta et al., 2014; Beschta and Ripple, 2013; Kauffman et al., 2013, 2010; Winnie, 2014, 2012). We observed a lower deer visitation rate, lower cumulative visitation time, a trend of reduced foraging time and a lower browsing intensity on tree saplings nearby and inside the impediment. These observations indicate that deer perceive foraging near the impediment as risky, leading to improved sapling performance (in line with Halofsky and Ripple, 2008; Kuijper et al., 2015; van Ginkel et al., 2018). It is clear from our data that deer avoided the impediments, but whether this avoidance was purely risk-driven is debatable. If it is risk-driven we would expect deer to allocate more time to vigilance near the impediment and less time to foraging, to reduce predation risk as was found by Kuijper et al. (2015). Contrary to predicted, we observed a trend of decreased vigilance for deer on the impediment plots, but in line with the risk-driven hypothesis, we did observe a trend of less foraging. Our camera data showed that deer walked more on plots with than without impediment (Appendix A, Fig. A3). Though the trend of decreased vigilance near impediments seems to contradict the risk-driven hypothesis, risk could still be the driving force behind our observed patterns. Whether deer take the risk to forage on perceived risky sites not only depends on the quality of the food available, but also on the individual's physiological state and personality (McArthur et al., 2014; Mella et al., 2015; Winnie and Creel, 2007). Bold individuals or individuals with a poor body condition may take more risk to acquire qualitatively good food (Mella et al., 2015; Winnie and Creel, 2007). It is possible that only the bolder deer or deer in poor condition approached and foraged near our impediments, which may explain why we did not observe higher, but even lower vigilance levels near the impediments. If so, impediment avoidance is risk-driven by filtering out the risk-sensitive shy deer in good condition from the risk-insensitive bold deer in poorer condition. Our hypothesis needs further testing in future experiments as the influence of personality and body condition in combination with the ecology of fear concept on foraging decisions is hardly studied (see Brown and Kotler, 2004). An alternative mechanism underlying the avoidance of our impediments could be convenience: why walk towards an obstacle blocking the route, when there is also food in the surroundings? With our experimental design (i.e. two plots within a gap, one with an impediment and one without), it is more convenient to forage on a plot without an impediment as it allows deer to roam around more freely. If convenience is the driving mechanism, the impediment offers some sort of physical protection by just being there even though the access to the saplings is not blocked. Despite our efforts to collect data of both deer behavior as well as sapling performance, we still cannot completely disentangle the physical and risk-induced effects of impediments on deer behavior, and whether the underlying mechanism of avoidance is risk-driven or a matter of convenience remains debatable.

We do not have recordings of deer entering our impediments to forage from the saplings planted inside, though physically it is possible for deer to jump over a barrier of 1 m (Barasona et al., 2013). This indicates that deer find it either too risky inside these impediments and/or that the food present inside is not worth the effort, leading to taller saplings and a higher survival. At the start of the experiment the saplings were on average 35.6 cm, which is lower than the impediment height of 1 m. As we have no observations of deer inside the impediment, we argue that at the start the saplings were out of reach and thus physically protected against browsing. In line, several studies found that saplings grow taller when surrounded by downed wood (Kuijper et al., 2013; Ripple and Larsen, 2001; Smit et al., 2012; Winnie, 2012). However, we noticed that when the saplings grew taller than the impediment, the saplings inside had some browsing marks. We have a few videos of deer recorded foraging from the saplings inside the impediment without entering the impediment. This suggests that at an early stage, the saplings inside the impediment were mainly physically protected against browsing, but when they grow taller induced risk becomes probably more important to protect saplings against browsing.

4.4. Impediments make the forest composition more diverse

Our experiment ran for three years, which is short when talking about long-term effects, but we found some clear patterns that match with previous studies (Churski et al., 2017; Kuijper et al., 2010b). Our findings show that the less palatable *P. abies*, *P. sylvestris* and *A. glutinosa* are the least selected by the browsing community, and therefore have the highest potential in the absence of impediments. However, in contrast with saplings inside impediments, none of the saplings managed to escape the browse trap in absence of an impediment during three years of study (Appendix A, Fig. A2). Therefore long-term experimental studies are necessary, since simulations showed it should take *P. abies* almost 30 years to grow beyond the browsing line in the presence of ungulates (Churski et al., 2017). In the future forest composition of Białowieża, *C. betulus* is also expected to play a dominant role as it is a browse tolerant species (Churski et al., 2017; Kuijper et al., 2010b), but unfortunately we cannot confirm that with our study as we had to exclude *C. betulus* from the analysis.

Overall, the preferred and less browsing tolerant species (*A. platanoides*, *T. cordata* and *P. pyrastrer*) profit from an impediment with increased survival and by growing taller which increases the chances to reach the canopy. The saplings of *T. cordata* and *P. pyrastrer* already profit from an impediment nearby by growing taller, but profit most from being surrounded by impediment structures just as *A. platanoides*, causing several saplings to reach a height of >150 cm within three years (Appendix A, Fig. A2). Our results correspond to two studies that suggested *A. platanoides* and *T. cordata* can escape the browsing line within several years when browsing pressure is reduced, for example when ungulate populations crash, but do not have a chance when browsers occur in high densities (Churski et al., 2017; Kuijper et al., 2010b). Our result has important implications for the forest composition in the long term. Without the protection of an impediment only the less preferred and browse tolerant trees will recruit (such as *A. glutinosa* at wet places or *C. betulus* Kuijper et al., 2010b; Churski et al., 2017), but the lower browsing intensity near impediments gives highly preferred and less browsing tolerant species (such as *A. platanoides*, *T. cordata*, *P. pyrastrer* and *Q. robur*) a higher chance for successful regeneration, and therefore impediments enhance the tree community diversity.

Dead wood should meet certain criteria to improve sapling performance. Firstly, tree logs should be high and long enough to act as a visual and escape impediment for the main browser in this system, red deer (Kuijper et al., 2013; van Ginkel et al., 2018). Our study showed that an impediment of 5 m long and 1 m high already had a positive effect on saplings. Secondly, the wood should decay slowly to be present for multiple years to function as a persistent sapling refuge from browsing ungulates. When saplings grow beyond the impediment they were sometimes browsed (personal observation), illustrating that impediments mainly provide temporal protection during the first stages of sapling development. Within Białowieża National Park, such natural impediments are present in the form of hardwood oak (*Q. robur*) tree logs, and spruces (*P. abies*) that died from spruce bark beetle (*Ips typographus*) outbreaks. However the amount of dead wood is strongly reduced due to regular forestry activities in the managed part of Białowieża forest (Bobiec, 2002), similar to most managed forests. For forestry management in areas aiming at a more natural forest development, we recommend in line with Smit et al. (2012) to allow large dimensions of dead wood covering the forest floor to enhance natural regeneration and promote diversity in forest composition.

CRediT authorship contribution statement

Hermine Annette Lisa Ginkel: Conceptualization, Methodology, Investigation, Formal analysis, Data curation, Visualization, Writing - original draft, Project administration, Funding acquisition. **Marcin Churski:** Conceptualization, Methodology, Resources, Writing - review

& editing. **Dries Pieter Jan Kuijper:** Conceptualization, Methodology, Resources, Writing - review & editing, Funding acquisition, Supervision. **Christian Smit:** Conceptualization, Methodology, Resources, Writing - review & editing, Funding acquisition, Supervision.

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 data

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