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Effects of opening winter enclosures on red deer movement and local browsing pressure: An experimental assessment

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ABSTRACT

Winter enclosures are an important wildlife management tool in mountainous regions of Central Europe. They are implemented to reduce browsing pressure and bark peeling caused by red deer (*Cervus elaphus*) during winter by lowering their numbers in the surrounding landscape. However, the enclosures require high levels of maintenance and increase local animal densities, which could potentially enhance the spread of diseases and parasites. Therefore, it is of great interest to evaluate the effectiveness of winter enclosures in restricting red deer movement and minimizing browsing damage. Thus, this study employs an experimental approach to analyse the impact of winter enclosure management on these two parameters in the Bohemian Forest Ecosystem. Three treatments were implemented: (1) four winter enclosures kept closed (regular management), (2) four winter enclosures opened earlier (opened earlier), and (3) two winter enclosures left open all winter (open fences).The median winter home range of red deer increased sixfold under the open fences treatment compared to the previous year, though the home ranges still did not extend beyond the borders of the protected area. At the same time, browsing probabilities for all tree species decreased in the vicinity of the enclosures in the open fences treatment. No change in browsing probability was observed around the enclosures opened earlier compared to the previous year. These results suggest that the main factor contributing to changes in browsing pressure caused by the experimental treatments was that red deer overwintering outside the open fences enclosures gained access to supplementary feeding in winter, consequently reducing their browsing activities in the vicinity of these enclosures. Therefore, winter enclosures may not always outperform unfenced feeding stations as a management tool to reduce browsing pressure.

1. Introduction

Forests play an essential ecological and economic role, by functioning as carbon sinks and maintaining biodiversity, while providing carbon-neutral building materials and renewable energy (Bonan, 2008; Moroni, 2013; Paillet et al., 2010). However, in areas with high ungulate populations, browsing can hinder natural forest regeneration and, to a greater extent, the success of artificial tree plantations for forestry (Barančeková et al., 2007; Côté et al., 2004). Selective browsing pressure often disproportionately affects climate change-tolerant plant species and may hamper silvicultural goals (Champagne et al., 2021; Putman, 1996). Therefore, wildlife management faces the challenge of

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balancing the conservation of healthy wild ungulate populations with the potential for natural regeneration and the success of planting of target tree species.

In addition to reducing overall population density through hunting (Hothorn and Müller, 2010) and its strategic use to deter animals from certain areas (Cromsigt et al., 2013), non-lethal strategies are also used to mitigate browsing pressure.

In Europe, this is most often achieved by using fences to restrict ungulate access to areas where forests should regenerate (Hardalau et al., 2024). However, their procurement and maintenance are costly (Redick and Jacobs, 2020). Another commonly applied approach is to improve the availability of alternative forage sources to reduce browsing pressure on palatable tree species in managed forests (Ara et al., 2022; Felton et al., 2022; Loosen et al., 2021; Meronk and Long, 2025). Supplementary winter feeding is a commonly implemented, but controversial, management tool (Milner et al., 2014). While maintaining deer densities and improving their body condition have been cited as reasons for supplementary feeding, its main purpose is the reduction of damage to forestry and agriculture (Peek et al., 2002; Putman and Staines, 2004). Presumably even more effective tools in this regard are winter enclosures, which are used for the management of red deer (*Cervus elaphus*) in Bavaria, Austria and the Czech Republic. They combine supplementary feeding with fencing to restrict animal movement during the season when forest regeneration is most at risk of damage. In autumn, animals are lured into these enclosures by supplementary feeding and bait. The gates are closed in winter and reopened in spring, once the vegetation green-up has started (Apollonio et al., 2010; Belotti et al., 2014; Henrich et al., 2021; Silovský et al., 2024).

The red deer is the most widespread deer species in Europe after the roe deer (*Capreolus capreolus*) (Burbaitė and Csányi, 2012; Linnell et al., 2020). It is classified as an intermediate feeder, with a diet that relies on grazing in summer, but mostly on browsing during winter (Krojerová-Prokešová et al., 2010; Spitzer et al., 2020). Compared to roe deer, the daily energy intake of red deer is five and a half to seven times higher during the winter months (Arnold et al., 2015; König et al., 2023). Moreover, red deer feed by bark stripping (Verheyden et al., 2006), making them a primary problem species for forestry. They may maintain the same home range year-round in some areas, but migratory movements are common in regions with high seasonal variability, especially in the mountains (Bischof et al., 2012; Mysterud et al., 2011; Peters et al., 2017; Rivrud et al., 2016).

Winter enclosures are employed in mountain ranges such as the eastern Alps and the Bohemian Forest Ecosystem, which cannot support year-round high red deer densities (Putman and Staines, 2004; Wotschikowsky et al., 2010). Their goal is to prevent the migration of the red deer population to lower altitudes in winter, thereby avoiding conflicts with forestry, agriculture and infrastructure development in the valleys (Gerner et al., 2012; Putman and Moore, 2002). Although they are assumed to be more effective than open feeding stations in this regard, winter enclosures are not without controversy as a management tool. The high density of animals inside the enclosures can facilitate the spread of infectious diseases and parasites, such as bovine tuberculosis and the giant liver fluke (*Fascioloides magna*) (Dorn-In et al., 2020; Eggert et al., 2013; Kasny et al., 2012; Menke et al., 2019) and lead to elevated nutrient concentrations in plants (Trepel et al., 2025). Furthermore, enclosed red deer populations are often considered semi-domestic, as the influence of natural selection is limited (Hayward and Kerley, 2009; Mysterud, 2010). They are therefore at odds with the goals of protected areas such as national parks, which, in accordance with the International Union for Conservation of Nature (IUCN) guidelines for protected area management categories (Dudley, 2008), have the overarching aim to reduce human impacts on ecosystems, including all wild animal populations (van Beeck Calkoen *et al.*, 2020). Finally, maintaining winter enclosures is also more costly than other deer management strategies, such as open feeding stations.

Despite these drawbacks, attempts to replace winter enclosures with open feeding stations often face strong opposition of stakeholders and may ultimately fail. This was evident in the Bavarian Forest National Park, where forest owners and hunters successfully opposed the exploration of such alternatives by raising concerns about increased browsing and bark-peeling damage in neighboring privately owned forests, despite a lack of scientific evidence (Gerner et al., 2012; Ludwig et al., 2012). The presumed advantages of winter enclosures over open feeding stations in terms of reducing browsing pressure and preventing forest damage in private forests near protected areas have never been systematically tested, so their effectiveness remains unclear.

To fill this knowledge gap, we conducted an experiment designed to analyze the effect of different winter enclosure treatments in the Bohemian Forest Ecosystem on the behavior of red deer and consequently the browsing pressure, which is a rare opportunity in ungulate-forest systems. Our treatments were designed to investigate converting these winter enclosures into open feeding stations and to advance the enclosures' spring opening by one month. This latter treatment is relevant for reducing the risk of transmission of pathogens and parasites, such as the giant liver fluke, which increases with rising temperatures in spring (Erhardova-Kotrla, 1971). We hypothesized that opening the winter enclosures entirely would only lead to a moderate increase in the winter home range sizes of red deer, as deer reduce their movement rates in order to conserve energy in cold and snowy conditions (Pépin et al., 2009). Consequently, we expected browsing pressure on woody regeneration in their immediate vicinity to increase compared to the previous winter, when the deer were confined to the enclosures. An earlier opening of the winter enclosures was assumed to strongly impact red deer movement, as the animals follow the vegetation growth (Rivrud et al., 2016). By contrast, browsing pressure in the vicinity of the enclosures should not be significantly affected, given the shorter period during which the enclosure gates are open, the increased home range size, and the availability of herbaceous plants as alternative food sources, all of which limit the impact on tree regeneration.

2. Materials and methods

2.1. Study area

The study area is located in the Bohemian Forest Ecosystem and contains Central Europe's largest strictly protected forest area, consisting of the Bavarian Forest National Park (BFNP, 240 km^2) in Germany and the Šumava National Park (SNP, 685 km^2) in Czech Republic. Furthermore, it includes the neighbouring State Forest of Neureichenau (SFNR 152 km^2).

The elevational gradient ranges from 570 to 1453 m above sea level, with average annual temperatures between 2°C and 5°C. The yearly precipitation varies between 830 mm and 2280 mm, with a significant contribution from snowfall at higher altitudes (Heurich et al., 2010). Norway spruce (*Picea abies*) is the dominant tree species in all three administrative subareas (BFNP, SNP, SFNR), followed by European beech (*Fagus sylvatica*) and silver fir (*Abies alba*) (van der Knaap et al., 2020). The predominance of spruce has led to large bark beetle (*Ips typographus*) outbreaks since the 1990s (König et al., 2023). Together with the consequences of large storms and subsequent management decisions (i.e., removing bark beetle infested trees and spruce deadwood versus non-intervention), those events have shaped the landscape and therefore the red deer distribution (Oeser et al., 2021; Tourani et al., 2023).

Red deer densities vary between the three administrative subareas. They are lowest in the SFNR and highest in the SNP (Tourani et al., 2023). Grey wolf (*Canis lupus*) and Eurasian lynx (*Lynx lynx*) are present in the study area as natural predators of red deer. While the well-established lynx population has only a minor impact on the red deer population as roe deer are the main prey item by far, the re-establishment of wolves in the area since 2015 might have the potential to influence the abundance and distribution of red deer in the ecosystem (Heurich et al., 2012; Hulva et al., 2024; Palmero et al., 2021; Wölfl et al., 2001).

2.2. Wildlife management

Management goals differ throughout the study area. As national parks, the BFNP and the SNP aim to protect biodiversity and the natural processes underlying it, while minimizing the negative impact of wildlife on private land in the vicinity of the parks (Janík, 2020). In the SFNR, management goals revolve around the sustainable use of a state-owned production forest. With regard to wildlife management, all three administrations share a common interest in maintaining a healthy population of native wildlife species, while enabling the natural regeneration of native vegetation (Janík, 2020). Hunting is the primary tool for controlling the red deer populations in all administrative subareas. The hunting season for red deer is closed by law in late winter and spring (01.02.–31.05. in Bavaria, 16.01.–31.07. in the Czech Republic); beyond that further legal sex- and age specific restrictions for hunting are in place. The other abundant deer species in the study area, roe deer, has not been hunted in the BFNP since 2012 (van Beeck Calkoen et al., 2019) and is hunted in low numbers and small areas in the SNP (Janík, 2020). Both national parks have established large, connected non-hunting zones for all wildlife species (Fig. 1). These zones make up 75 % (181.6 km^2) of the BFNP and > 10 % (70.8 km^2 ha) of the SNP. In the SFNR, wildlife management is practised across its territory, with minor exceptions.

On the German side, the red deer population is limited to a designated so-called 'red deer area'of 603.8 km^2 (Heurich and Neufanger, 2005; Möst et al., 2015), including the BFNP and SFNR. Every red deer in a hunting district outside of this area must be shot, according to the Bavarian hunting law.

Sixteen winter enclosures, ranging in size from 5 to 60 ha, have been established in the study area (4 in the BFNP, 2 in the SFNR, and 10 in the SNP). Red deer are initially attracted with high-quality feed (grass silage and hay) in autumn or early winter. The gates of the enclosures are closed between October and December, confining the animals until mid-April or the beginning of May, depending on the greening in spring. In the BFNP, pre-enclosures are used to trap stragglers, which then enter the main enclosure or are culled (Heurich et al., 2011). This is also true for the only winter enclosure that is surrounded by, but therefore not part of, a non-hunting zone, Neuhüttenwiese. All animals overwintering in winter enclosures are consequently exposed to hunting pressure. During the hunting period 2021/22, 192 red deer (85 %) were killed from high seats across the management zone of the BFNP and 36 (15 %) were killed within the pre-enclosures. In the SNP, the use of pre-enclosures for the culling of captured animals is illegal under Czech hunting law (Janík, 2020). Instead, to accommodate stragglers, small one-way gates are used to allow as many individuals as possible to enter the enclosures. The SFNR also does not use their enclosures for hunting. Consequently, annual harvests in the SNP and the SFNR are conducted

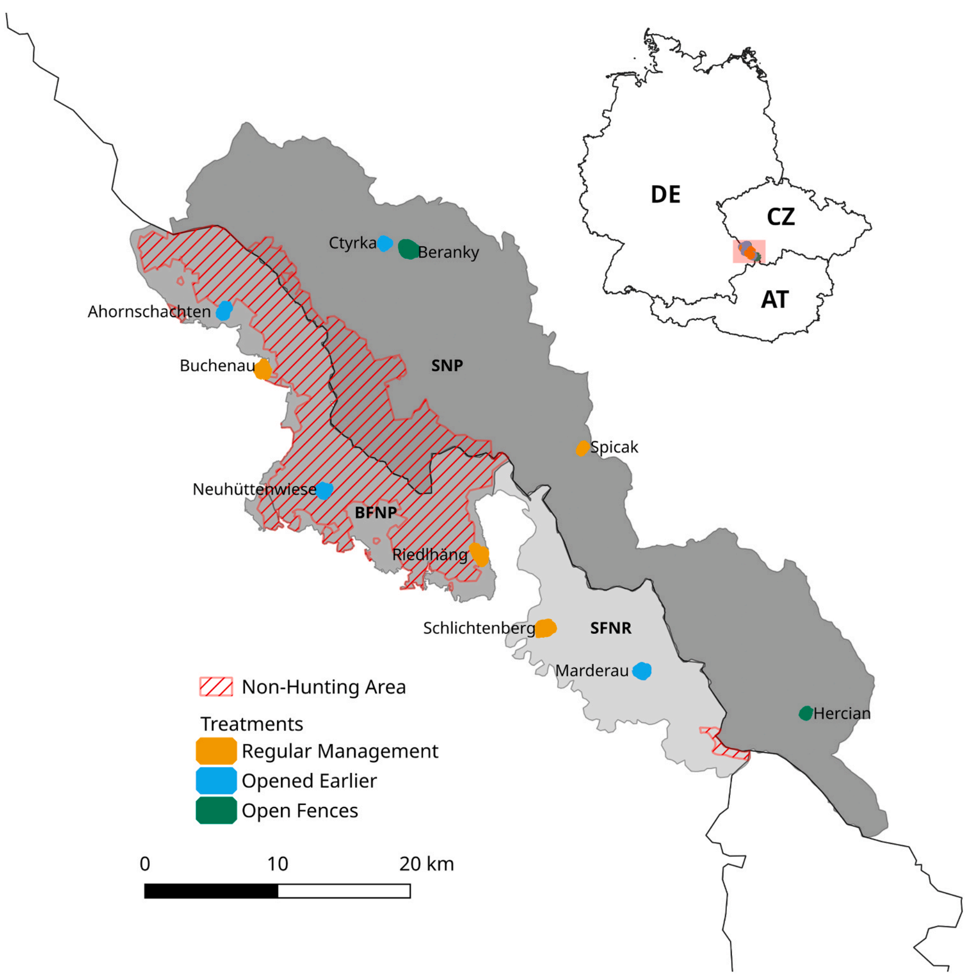

Fig. 1. Overview of the study area and the winter enclosures that were included in the study. The study area is located in the Bohemian Forest, along the Czech-German border, and consists of three administrative sub-areas: State Forest of Neureichenau (SFNR, Germany), Šumava National Park (SNP, Czech Republic) and Bavarian Forest National Park (BFNP, Germany). Three types of winter enclosure treatments were established: regular management(orange), opened earlier (blue), and open fences (green). The non-hunting area is hatched in red.

by individual hunts from high seats, by stalking, or in drive hunts in autumn.

2.3. Study design

Ten winter enclosures in the Bohemian Forest Ecosystem were included in the experiment and subjected to three treatments (Table 1): (1) Two enclosures in the SNP were managed as open fences enclosures, with the gates being left open throughout winter and spring, while maintaining feeding inside the enclosure, (2) four enclosures, two in the BFNP and one each in the SFNR and the SNP, were opened in spring roughly one month before the average opening date of the previous five years for the respective enclosure, while feeding was conducted as usual and (3) another four enclosures, two in the BFNP and one each in the SFNR and SNP, were operated as usual. Entirely suspending supplementary feeding in winter was not tested since it could have negatively impacted animal welfare.

Of the overall 16 enclosures within the study area, six could not be included in the study due to their proximity to other enclosures, making it impossible to discern the impacts of the treatments. They operated as usual during the study period. The open fence treatments were restricted to two enclosures on the Czech side as it was legally difficult to establish this treatment on the German side (BFNP, SFNR), because the risk of red deer migrating to lower elevations outside the ‘red deer area’ in winter had to be kept minimal. The selected enclosures were distributed over the whole study area (Fig. 1).

2.4. GPS telemetry

GPS Plus collars (Vectronic Aerospace, Berlin, Germany) were used to track 84 red deer, recording a position once per hour (Table 1). Animals were collared in 2019–2021 and collars remained attached for a maximum of two years before automatically dropping off near the end of their battery lifespan. Among the collared individuals, 37 were monitored across both the winter 2020/21 and 2021/22. Most individuals ($n = 45$) were captured in catching corrals, allowing handling without immobilization. In enclosures not equipped with catching corrals, animals ($n = 39$) were immobilized using a “Hellabrunn mixture” consisting of 400 mg of ketamine (100 mg/ml) and 500 mg of xylazine (Xylased) (Kreeger and Arnemo, 2018). Animal handling and marking was approved by the Ethics Committees of the Government of Upper Bavaria (permit number: ROB-55.2–2532.Vet_02–21–132) and of the Ministry of the Environment of the Czech Republic (MZP/2019/630/361).

The space use of individual red deer in the winter and spring before and during winter enclosure treatment implementation was compared based on the hourly positional data. The data were processed with the amt R package (Signer et al., 2019) and filtered using the Eurodeer filter criteria (Bjørneraas et al., 2010; Urbano and Cagnacci, 2014). Data on step length, speed and direction (angle) between successive positions of a given individual were extracted. A data point was removed if all of the following criteria were fulfilled: speed > 15,000 m/h, step length > 5 km and a turning angle between 170° and 190°. Additionally, 26 outlier GPS positions were removed after visual inspection.

For the home range analysis, we focused on the period when all the enclosures were closed simultaneously during the winter of 2021/22 (winter period: January 21st to April 3rd) and the time when most of the opened earlier enclosures were opened earlier than in the previous year (spring period: April 4th to 28th). Home ranges were calculated monthly and for these two seasonal time frames using autocorrelated kernel density estimation (AKDE) and an isopleth level of 0.95. This method is considered to be most suitable for data with high spatio-temporal autocorrelation (Fleming et al., 2015), which is inherent to positional data with an hourly resolution. As the home range sizes were not normally distributed, Kruskal-Wallis tests were used to compare them before and during treatment implementation for each treatment type

Table 1
Overview of the winter enclosures and treatments in the three administrative units of the Bohemian Forest: State Forest of Neureichenau (SFNR), Germany, Šumava National Park (SNP), Czech Republic and Bavarian Forest National Park (BFNP), Germany. Distance from the national park (NP) borders is given in negative values for enclosures inside the parks. The number of red deer refers to the counted individuals inside the winter enclosure in the respective winter. The number of collared red deer is given in parentheses.

Treatment in winter 2021/2022	Administrative subarea	Enclosure name	Distance from NP border (m)	Size (ha)	Closed period in winter 2020/21 (from–to)	Closed period in winter 2021/22 (from–to)	Number of red deer 2020/2021	Number of red deer 2021/2022
Opened earlier	BFNP	Ahornschachten	-496	29	21.11.2020–30.04.2021	23.11.2021–14.04.2022	44 (3)	37 (3)
Opened earlier	BFNP	Neuhüttenwiese	-2522	35	30.10.2020–07.05.2021	29.11.2021–05.04.2022	121 (9)	118 (4)
Opened earlier	SFNR	Marderau	2541	38	12.02.2021–28.04.2021	22.11.2021–04.04.2022	165 (5)	172 (8)
Opened earlier	SNP	Ctyrka	-2646	16	11.01.2021–11.04.2021	20.01.2022–05.04.2022	84 (5)	81(5)
Open fences	SNP	Beranky	-2875	61	05.01.2021–22.04.2021		123. (4)	*(4)
Open fences	SNP	Hercian	-3199	11	18.01.2021–04.04.2021		41(4)	*(4)
Regular management	BFNP	Buchenau	-0	45	30.10.2020–06.05.2021	22.10.2021–13.05.2022	71 (5)	81 (18)
Regular management	BFNP	Riedlhäng	-170	48	30.01.2021–12.04.2021	23.11.2021–19.04.2022	72 (6)	51 (13)
Regular management	SFNR	Schlichtenberg	3933	57	03.02.2021–05.05.2021	12.12.2021–09.05.2022	70 (5)	75 (6)
Regular management	SNP	Spicak	-464	8	07.01.2021–04.05.2021	12.01.2021–02.05.2022	71 (4)	62 (6)

* The number of red deer in the open fences enclosures was not estimated.

(open fences, opened earlier, regular management) and time frame (winter, spring).

2.5. Browsing inventory

Two browsing inventories were conducted between April and May in 2021 and 2022, adapting the methodology described in Bödecker et al. (2021). Inventory plots were established at the center of 25 randomly selected 250 × 250 m grid cells within a 1-km buffer around each winter enclosure. The closest regeneration area from each inventory plot was used for the survey. The regeneration areas had to fulfill the following criteria: (1) a regeneration density of ≥ 1300 trees per hectare (ha) with a height between 20 cm and 2 m and (2) the longest straight line crossing the regeneration area being between 50 m and 100 m long. The latter requirement originated from the need to place a transect of least 40 m, with a minimum distance of 5 m to the edges of the regeneration area at each end. Predetermined randomly chosen replacement inventory plots were used if no suitable regeneration area could be located

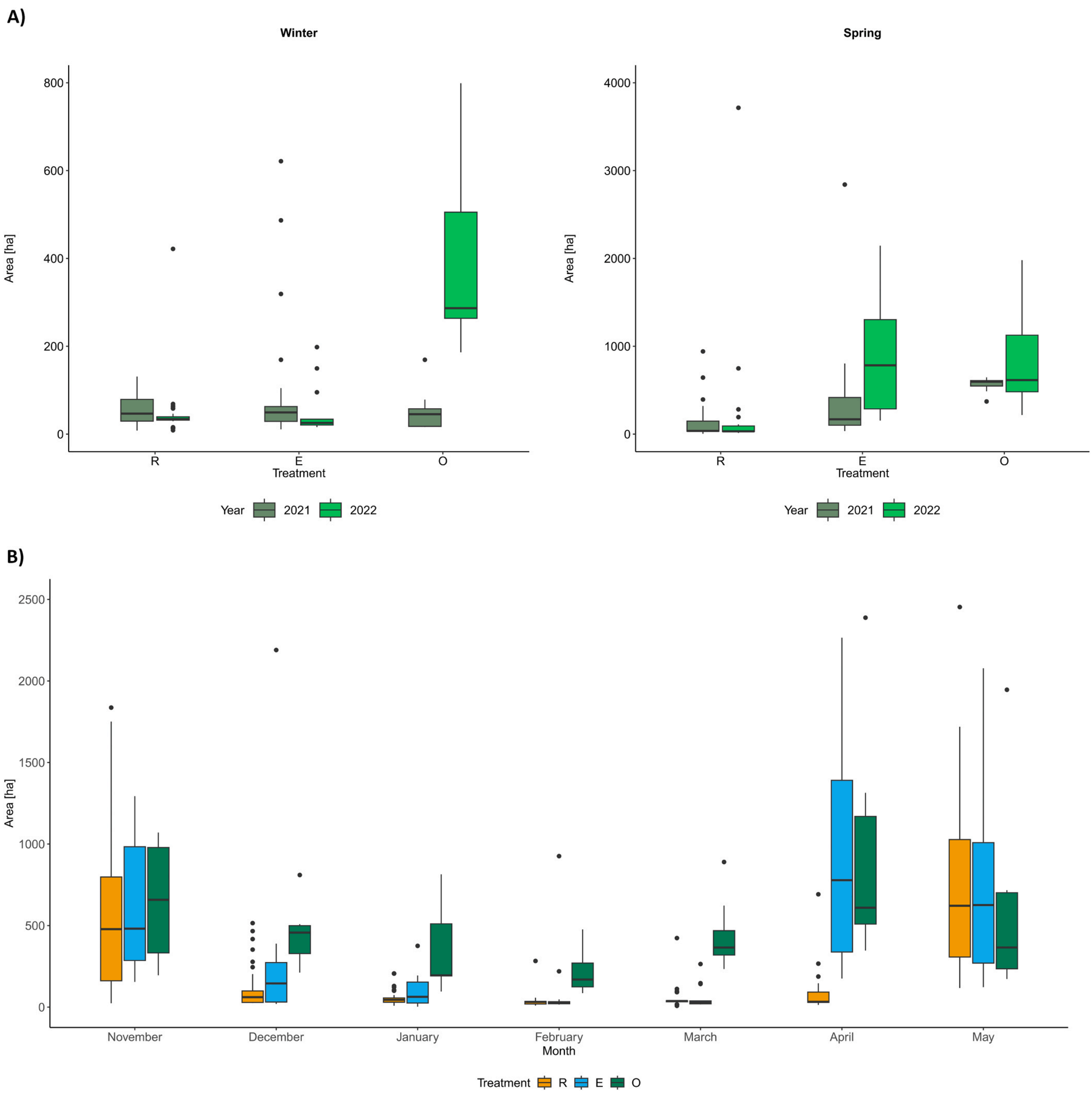

Fig. 2. (A) Seasonal home range sizes (ha) of GPS-collared red deer (n = 81) in the year before the implementation of the treatments (2021) and during the year of the treatments (2022): **R** regular management, **E** opened earlier, **O** open fences. Winter home ranges are estimated for the period from 21.01. to 04.04. when all R and E enclosures were closed in 2022 and spring home ranges are estimated for the period 04.04.–28.04. when most of the E enclosures were open in 2022. In four instances (two in the winter enclosures Ctyrka and Marderau respectively), the winter home ranges unexpectedly extended beyond the enclosures, as the animals managed to exploit holes in the fences. (B) Monthly development of home range sizes (ha) of GPS-collared red deer in the winter 2021/22 (n = 79). From the 446 monthly home ranges, 12 outliers with home range sizes > 2500 ha were omitted from the plot (min = 2571.7 ha; max = 5559.6 ha): 7 in treatment R, 4 in treatment E, and 1 in treatment O. The plot is not meant for within month comparison between treatments due to different enclosure sizes.

within a distance of 125 m around a selected inventory plot.

Upon identification of a suitable regeneration area, a transect through the area was established, featuring five sampling points marked with poles. The first pole was placed at the beginning of the transect, the fifth at its end, with the remaining three poles evenly spaced between them (sampling points #2, #3 & #4).

At each sampling point, the 15 closest trees that matched the above requirements were surveyed. In addition, to increase the number of samples for rare tree species, the five closest trees of these species within a radius of 5 m were recorded at sampling points #2 and #4. Tree species were considered rare if they accounted for < 5 % of the total regeneration in the study area. Consequently, all locally occurring tree species apart from Norway spruce and European beech were considered rare. The height, species, and leading shoot browsing status of each tree were recorded. A browsed leading shoot was defined by damage caused by cervid browsing (thus excluding abiotic damage such as snow, browsing by other mammals, or insect damage). The leading shoot was not considered browsed if an undamaged replacement shoot was present.

To document ungulate browsing pressure, 250 separate inventory plots, 25 per enclosure, were surveyed. Consequently, the opened earlier and regular management treatments were monitored with 100 inventory plots each, while the open fences treatment was monitored with 50 inventory plots.

The browsing probability (BP) was computed using a generalized logistic mixed-effect regression model, with the year of the inventory as a fixed effect with a fixed intercept and the inventory plot ID as a random intercept (following Bödeker et al., 2021). The 2021 inventory served as the baseline before treatment implementation and the 2022 inventory was used to assess the impact of the treatments.

To test whether the change in BP between 2021 and 2022 was significant, 95 % confidence intervals were calculated for the difference in logits. As this required a linear hypothesis, the predictor of the difference in logits was set to zero, i.e., H_0 was defined as no change between years.

Both the BP and the change in BP between years were modeled for each of the four most common tree species in each treatment, resulting in four models per treatment. In addition, four models were also computed for each of the two enclosures that had been converted to open fences (Beranky and Hercian) and for each of the regularly managed enclosures. We selected the four most common tree species for analysis: Norway spruce, European beech, silver fir, and common rowan (*Sorbus aucuparia*). However, in the analysis of the open fences treatment, the low sample size (n < 20) of silver fir necessitated its replacement by the next most common tree species, sycamore maple (*Acer pseudoplatanus*). We did not compare browsing pressure between

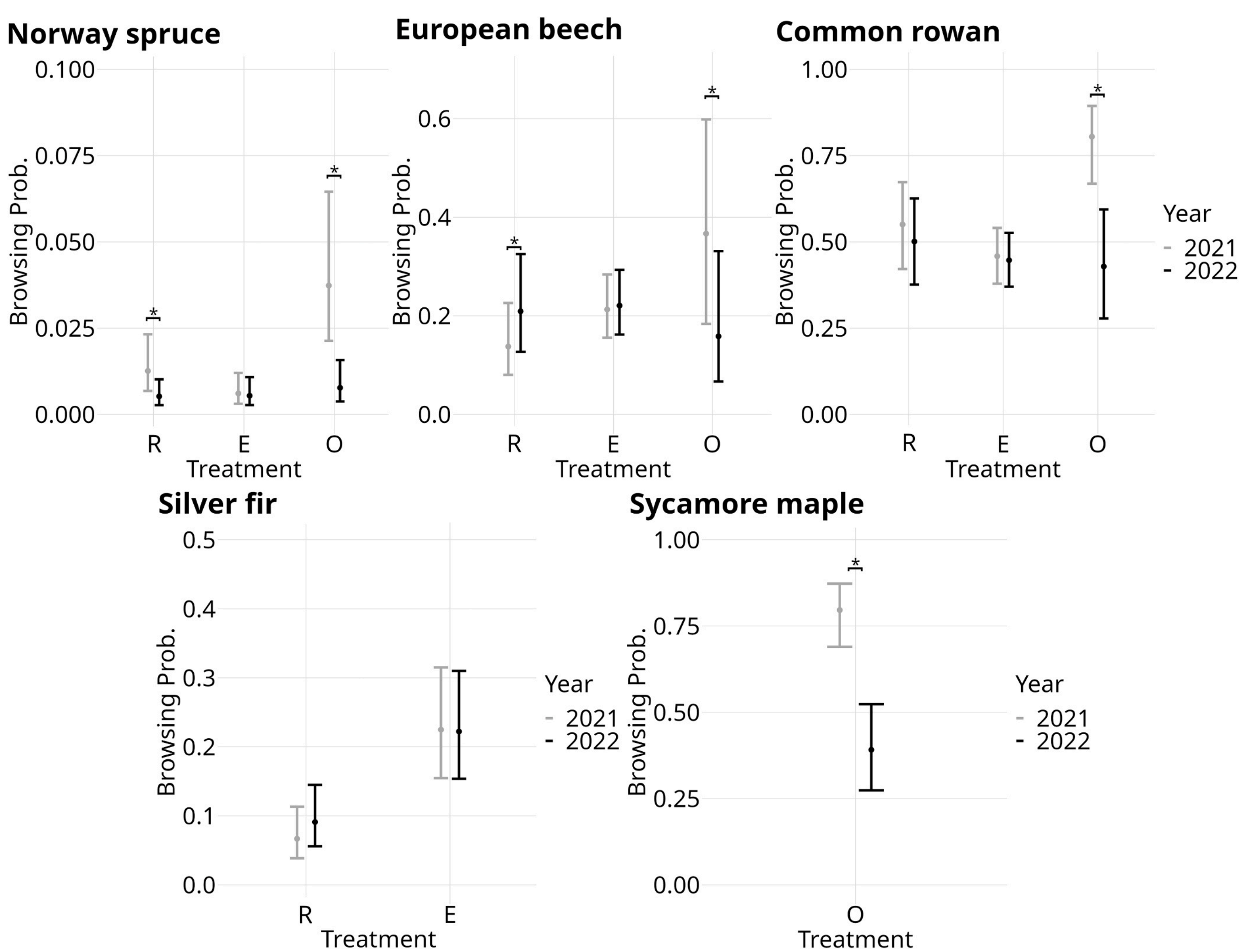

Fig. 3. Browsing probabilities for tree species around the winter enclosures as predicted by a generalized linear mixed regression. (Left to right: spruce (Picea abies), beech (Fagus sylvatica) and rowan (Sorbus aucoparia)) before (2021, gray) and during (2022, black) implementation of the treatments: regular management (R), opened earlier (E) and open fences (O). Significant changes between years are marked with *. The values displayed in the figure and the model evaluation metrics are provided in Table S6.

Table 2
Summary statistics for the logarithmic change in the browsing probability (BP) between the year before the treatments and the treatment year (2021–2022) calculated using a generalized logistic regression. The logarithmic coefficient and standard error (in parentheses) are displayed for each treatment. Positive values indicate an increase, and negative values a decrease in BP.

	European beech	Silver fir	Norway spruce	Common rowan	Sycamore maple
Open fences	–1.12 *** (0.24)		–1.61 *** (0.25)	–1.7 *** (0.21)	–1.81 *** (0.21)
Opened earlier	0.05 (0.1)	–0.01 (0.19)	–0.12 (0.19)	–0.05 (0.13)	
Regular management	0.50 *** (0.12)	0.34 (0.21)	–0.89 *** (0.17)	–0.2 (0.18)	

*** $p < 0.001$, * $p < 0.05$

treatments within the same year.

For each model, residuals were checked using the DHARMa R package (Hartig and Lohse, 2022). All analyses were conducted in R 4.3.2 (R Core Team, 2021).

3. Results

3.1. Red deer movement

Red deer in the open fences treatment expanded their seasonal home ranges significantly in the treatment winter (min = 186, max = 799) vs. the previous winter (min = 16, max = 169) (χ^2== 11.29, df = 1, p = 0.0008, n = 8 in 2021/ 8 in 2022) (Fig. 2).The median winter home range size increased by 6.3 times from 45 ha to 287 ha. Despite the increase in home range size, none of the home ranges extended beyond the borders of the national parks in winter. The median overlap of the winter home ranges with the enclosures and the 1-km buffers around them was 82.78 % (min:3.23 %, max=100 %). The monthly home ranges sizes show a minimum in February, but there was little variation between December and March (Fig. 2).

In spring, there was no significant difference in the size of the seasonal home ranges between the treatment year and the year pre-treatment for the open fences treatment (χ^2== 0.18, df = 1, p = 0.67, n = 8 in 2021/ 8 in 2022), but the increase in size was significant for the enclosures opened earlier (χ^2= 11.16, df = 1, p = 0.0008, n = 22 in 2021/ 16 in 2022). Five spring home ranges from the deer in the open fences treatment and 13 from the deer in the opened earlier treatment extended beyond the borders of the national parks (Median and minimum overlap with the area of the national parks: 100 % & 97.80 % for open fences, 84.15 % & 7.78 % for opened earlier).The median overlap of the spring home ranges with the 1-km buffers around the winter enclosures was 34.48 % (min: 0.47 %, max: 99.34 %) for the open fences treatment and 36.49 % (min: 14.33 %, max: 86.86 %) for the opened earlier treatment.

3.2. Browsing

Regeneration areas near the open fences enclosures had significantly lower browsing probabilities during the treatment year (2022) than during the previous year (2021) for all considered tree species (Norway spruce, European beech, sycamore maple, and common rowan; Fig. 3, Table 2).

There was no evidence of a change in browsing probability for any of the evaluated tree species in the vicinity of the opened earlier enclosures (Norway spruce, European beech, and common rowan). In the surroundings of the regularly managed enclosures, there were also no changes for silver fir and common rowan, whereas the BP was lower for Norway spruce and higher for European beech during the treatment year than during the previous year. However, these deltas were by ~14 % smaller for European beech and by ~3 % smaller for Norway spruce than those observed for the same tree species around the open fences enclosures (Fig. 3, Table2).

The changes in browsing probabilities differed between the two open fences enclosures. Following the overall trend of the treatment, the BP at Beranky decreased during the treatment year for the four most common tree species (Norway spruce, European beech, sycamore maple, and common rowan) in comparison to the previous year (Figure S1 & Table S4). At Hercian, the browsing probability for birch increased, but it did not change significantly for common rowan and it decreased for spruce and beech (Figure S2 & Table S5).

4. Discussion

Our study revealed that opening the winter enclosures in the Bohemian Forest Ecosystem enabled deer to expand their home ranges by a factor of six during winter. Nevertheless, browsing pressure in the vicinity of the enclosures decreased for all tree species compared to the previous winter with regular enclosure management. In contrast, we found no consistent trends in browsing probability for enclosures that were operated regularly or opened earlier during the treatment year.

4.1. Effects of changed winter enclosure management on red deer movement

Red deer densities in the study area fluctuate seasonally under natural conditions (Henrich et al., 2022). In summer, most animals gather on the mountain ridges along the border, migrating to the valleys, where the winter enclosures are located, when snow accumulates and forage becomes sparse at higher elevations (Rivrud et al., 2016). Migration into private forests is not desired and even legally prohibited on the German side by the extent of the ‘red deer area’ to prevent damage. Therefore, supplementary feeding has to be provided to keep the animals in the area during winter, which is legally required, under the Bavarian hunting law, during periods of forage scarcity.

As expected, winter home ranges of red deer in the open fences treatment increased compared to the previous winter when they were confined to the enclosures. The maximum observed home range size was slightly larger than twice that of alpine red deer (336 ha), whose winter home ranges are strongly linked to supplementary feeding sites (Duscher et al., 2009). This indicates that the effects of the open fences treatment were comparable to those of conventional supplementary feeding. Compared to the Alps with steeper, more rugged terrain and higher snow cover, the difference in winter home range sizes of red deer at an open feeding station can be at least partly explained by lower required energy expenditures to travel a certain distance. Nevertheless, the winter home ranges of red deer subject to the open fences treatment very rarely extended beyond the borders of the national parks. While 80 % of the landowners previously agreed that damages in economically managed forests are an obstacle to allowing red deer to roam freely (Gerner et al., 2012), this concern appears unjustified based on our results. However, the two enclosures that were left open in our study are located relatively far from the borders of the national parks (Table 1) and the outcome may be different when opening enclosures located closer to the edges of the protected area or if feeding stations are located outside of the national parks that may act as attraction points. The development of monthly home ranges confirms the results of Pépin et al. (2009), who found the minimum of red deer moving activity in February.

The observed increase in home range size of free-ranging red deer in spring aligns well with the concept of green wave surfing (Rivrud et al., 2016). It is linked to vegetation greening and will thus vary from year to year depending on environmental conditions. The winter enclosure Hercian was already opened early in 2021 (Table 1), explaining the non-significant difference between the treatment and pre-treatment year home ranges for the open fence enclosures.

4.2. Effects of changed winter enclosure management on browsing

Contrary to our initial hypothesis, browsing pressure did not increase in the vicinity of the winter enclosures when red deer, which would otherwise be confined to the enclosures, expanded their home ranges in winter, allowing them to browse over a larger area. Instead, we observed a decrease in browsing pressure, presumably due to animals overwintering outside the enclosures. Recent results from systematic camera trapping studies (Henrich et al., 2025; Henrich et al., 2022) showed that a considerable proportion of the red deer population stays outside the winter enclosures in the BFNP, with winter population densities of 1.2 (95 % confidence interval = 0.8–1.9) animals/km^2 in 2018/19 and 1.01 (95 % confidence interval = 0.6–1.6) animals/km^2 in 2019/20. Unpublished data analyzed with the same methods as in the previously mentioned publications show red deer winter densities of 0.45 (95 % confidence interval = 0.2–1.0) animals/km^2 in the SFNR and 1.79 (95 % confidence interval = 0.9–3.7) animals/km^2 in the SNP in 2018/19. However, it is difficult to translate these numbers into the proportion of the red deer population staying outside of the enclosures in winter, not only because of the considerable width of the confidence intervals, but also because camera traps being covered by snow can introduce systematic bias. The working camera traps are no longer distributed randomly with regard to habitat features in the study area such as elevation and forest density, which makes it difficult to relate the density estimate to a specific area. On the other hand, manual counts of red deer by wildlife managers outside the enclosures are opportunistic and unstandardized, but allow at least for conclusions on temporal developments given that they were conducted consistently over time. In the BFNP, the proportion of red deer counted outside vs. inside the enclosures ranged from 10 % to 47 % over 20 years from 2002 to 2021. However, some strong increases, e.g. between 2013 and 2014, suggest methodological changes (Table S6).

The spatial aggregation of red deer in winter is significantly influenced by the location of the winter enclosures, as relative densities decrease with the distance to an enclosure (Trepel et al., 2025). This pattern can be explained by the fact that red deer are attracted to the enclosures by the provided feed, but remain outside when the gates are closed. This means that, under regular management, they lose access to supplementary feeding for most of the winter and increase browsing in the vicinity of the enclosures (Möst et al., 2015). The open fences treatment restored their access, reducing their need to browse in order to fulfil their nutritional requirements. Within our study area, this effect seems to have outweighed the browsing by animals previously confined to the enclosures, resulting in the observed reduction in browsing pressure. However, this outcome will vary with the proportion of red deer overwintering outside vs. inside the winter enclosures. This proportion could be increased in two ways: artificial feeding and baiting outside the winter enclosures should be stopped across the whole region (at least within a radius of 1.6 km, based on the maximum winter home range size in the open fences treatment) to attract the animals effectively to the feeding station. Hunting pressure in the vicinity of the enclosures could also be increased to remove individuals overwintering outside the winter enclosures from the population. Furthermore, the risk of being hunted ("hunting for fear"; Cromsigt et al., 2013) may drive deer into the enclosures, where hunting is not allowed. However, the proportion of the deer population that can overwinter in the enclosures may be limited by their capacity and a high population density could prevent lower-status animals from accessing sufficient supplementary feed (Ceacero et al., 2012).

While access by free-roaming red deer to supplementary feeding stations is a plausible explanation for the reduced browsing damage at the open fences enclosures, additional studies using GPS-collared deer overwintering outside the enclosures or an appropriate camera trapping design would be needed to confirm this hypothesis.

As expected, we detected no changes in browsing pressure for any tree species around the enclosures that were opened one month earlier than usual. This may be partly explained by the deer already being able to take advantage of the vegetation green-up and gaining access to alternative high-quality food sources other than the shoots of trees (Rivrud et al., 2016), as the consumption of coniferous trees indeed decreases in spring (Krojerová-Prokešová et al., 2010).

In addition, the spatial extent of the browsing survey might have prevented the detection of significant effects on browsing by the earlier opening of the winter enclosures. Our movement data of GPS-collared red deer showed that the browsing inventory sites were appropriately positioned to assess the effects of the treatments on winter browsing, since the median overlap of the 1-km buffer around the winter enclosures and the winter home ranges of the red deer from the open fences enclosures was 83 %. It is therefore unlikely that we missed a measurable increase in browsing pressure outside the inventory areas during winter for the open fences treatment. In the spring period however, the median overlap of the red deer home ranges with the area, in which the browsing inventory was conducted, decreased to 35–37 % for the opened earlier and open fences treatments. Consequently, browsing in spring might have been distributed over an area more than three times larger than the extent of the browsing inventory. Therefore, it can be assumed that the distribution of red deer has diluted browsing pressure across the study area, thereby preventing a measurable effect of treatment on browsing within the inventory area. Consequently the possibility that an earlier opening of the winter enclosures increased browsing pressure across the whole study area outside the enclosures cannot be excluded.

4.3. General impacts on browsing pressure

Beside the open fences treatment, we also observed significant changes in browsing probability at the regularly managed winter enclosures. While many factors can affect browsing pressure, the population density of red deer is the most important. The number of red deer per winter enclosure did not change strongly between the two winters of our study (Table 1). Small changes in the number of animals in the enclosures might be explained by differences in reproduction, hunting pressure, or predation on the animals of the respective enclosures during the period when they are roaming freely. They may be visible in the browsing survey results: The increase in browsing pressure for European beech at the regularly managed enclosures can be attributed to the surroundings of the winter enclosure Buchenau (Figure S3), where the number of animals in the enclosure increased by 14 %. Similarly, the decrease in browsing pressure for Norway spruce is supported by the survey results from the winter enclosure Spicak (Figure S6), where red deer counts decreased by 13 %. Potentially, the number of animals in the surroundings of these enclosures might have increased at the same rate, or even more strongly, explaining the trends in browsing pressure. Local winter enclosure management can also have a substantial impact, as the number of red deer increased by 29 % in the winter enclosure Riedlhäng. Still, browsing did not differ significantly for Norway spruce and decreased only slightly for European beech (Figure S4). An important factor might be when and how often the enclosure's gates are opened to let in stragglers.

We were not able to account for roe deer browsing. Genetic analyses have shown that in our study area red deer and roe deer are responsible for an approximately equal share of the browsing, when they occur at similar densities (van Beeck Calkoen et al., 2019). However, approximately 50 % of the roe deer population is migratory and leaves the study area during late winter and early spring (Cagnacci et al., 2011). The remaining roe deer have been observed entering winter enclosures only in a few instances, as they primarily overwinter outside. Their presence was therefore not expected to be strongly affected by the treatments, nor was roe deer browsing likely to have influenced the observed changes in browsing pressure.

Anthropogenic factors, such as the distance to the next winter enclosure and hiking trail, as well as to the hunting zone, are important predictors of browsing pressure in our study area (Möst et al., 2015). They can be considered constant between the two years of the study, analogous to forest composition and structure.

In contrast, climate and weather-related variables such as temperature and precipitation can be seen as confounding factors for the comparison between years. The number of days with snow cover in January and February was similar between our treatment year and the previous year, but the former began with harsher conditions and ended with a quicker rise in temperatures in spring (Table S7). However, these differences in climatic influences are likely to have affected browsing in the vicinity of all winter enclosures similarly. Differences in the temporal trends between treatments can therefore not be attributed to them.

5. Conclusions

Winter enclosures are a regular wildlife management tool employed to reduce browsing pressure on surrounding forests in Central Europe (Silovský et al., 2024). While evidence for the use of similar tools is globally scarce, such enclosures could be considered a management option for other browser species exhibiting seasonal movements or a higher propensity to browse during specific seasons. They are presumed to be more effective than unfenced supplementary feeding sites, as they better control the distribution of animals and their access to surrounding areas during critical times for browsing damage.

Under the current situation in the study area however, with many red deer overwintering in the vicinity instead of inside the winter enclosures, open feeding seems more effective than enclosures in reducing browsing pressure. Additional advantages include lower maintenance efforts and a reduced risk of pathogen transmission without the artificially high animal densities in fenced areas. If the majority of the red deer population overwinters inside, winter enclosures may still be more effective than open feeding in minimizing browsing pressure. In this scenario, the opened earlier treatment can at least minimize the risk of pathogen transmission when temperatures start to rise in spring, which is the most critical period for disease and parasite spread.

However, under climate change scenarios, winters are expected to become milder. This means that winter enclosures may become less attractive to red deer for overwintering, and they may lose their effectiveness in reducing browsing pressure, even in areas where they currently still work. We therefore recommend a regular evaluation of the intended effects of winter enclosures and supplementary feeding to avoid ineffective and costly wildlife management practices.

CRediT authorship contribution statement

Marco Heurich: Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Nikolaus Haas:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis. **Wibke Peters:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Tomáš Peterka:** Writing – review & editing, Project administration, Data curation, Conceptualization. **Marc Velling:** Writing – review & editing, Supervision, Project administration, Methodology, Data curation. **Maik Henrich:** Writing – review & editing, Supervision, Conceptualization. **Pavla Jůnková Vymyslická:** Writing – review & editing, Project administration, Data curation. **Wiebke Neumann:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Jaroslav Červenka:** Writing – review & editing, Resources, Conceptualization. **Frederik Franke:** Writing – review & editing, Project administration, Data curation, Conceptualization.

Declaration of Competing Interest

The authors have no conflict of interest to declare.

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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.2025.123379.

Data availability

Data will be made available on request.

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