

Research article

Exclusion of wild ungulates is not the Holy Grail: the stronger effect of forestry treatments than exclosures on natural forest regeneration

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ABSTRACT

In managed, oak-dominated forests, reducing canopy cover through forestry interventions is essential for the successful regeneration of light-demanding species; however, browsing by ungulates can hinder this process.

Using an experimental setup in a Central European oak-hornbeam stand, the individual growth rates of oaks (*Quercus petraea* and *Q. cerris*), hornbeam (*Carpinus betulus*), manna ash (*Fraxinus ornus*) and shrubs (with *Acer campestre*, *Crataegus monogyna*, and *Cornus sanguinea* being the most abundant) were compared in plots representing different forestry treatments (rotation forestry: clear-cutting, retention group and preparation cutting, continuous cover forestry: gap-cutting) over seven years. Browsing effects were tested using paired seedlings selected from inside and outside exclosures within each forestry treatment plot.

We found that forestry interventions had a stronger effect on shoot length and estimated leaf area than browsing for oak, hornbeam and manna ash, while the importance of both factors was similar for shrubs. Sapling shoot length increment and browsing intensity were highest in clear-cuts and gaps. Oak and ash showed lower growth rates than hornbeam or shrubs, especially in exclusion plots. Annual growth patterns decreased over time, indicating that interspecific competition became very high in exclosures.

Oak regeneration in gaps and large regeneration areas was similar, but controlling shade-tolerant species is essential. Ungulate exclusion may initially promote regeneration success; however, interspecific competition drives regeneration after a few growing seasons. Reducing overabundant ungulate populations is crucial, but low to medium ungulate densities can reduce interspecific competition without overbrowsing.

1. Introduction

Browsing wild ungulate populations have reportedly increased across the northern temperate forests in recent decades (Gill, 1990; Pellerin et al., 2010), substantially influencing woodland ecosystems. These ecosystem engineer mammals are often considered keystone species in woodland habitats (Allombert et al., 2005; Augustine and McNaughton, 1998; Ramirez et al., 2019; Smit and Putman, 2010). They impact multiple above- and below-ground trophic levels (Gill, 1990; Rooney and Waller, 2003), and their activity through several feedback loops shapes productivity, nutrient cycling, species composition, and forest structure (Côté, 2014; Hobbs, 1996; Mitchell, 2005; Stephan et al., 2017).

The increasing abundance of these species (Carpio et al., 2021) has often led to shifts in their top-down control on tree regeneration (Perea

and Gil, 2014; Post et al., 1997; Valente et al., 2020). This imbalance in plant-herbivore relationship stems from several synergistic drivers. Key contributing factors include land-use changes that expand suitable habitat while leading to fragmented forests and reducing carrying capacity in many temperate regions in Europe; reduced winter mortality due to climate change and supplementary feeding, the absence of top predators; and a decline in hunter numbers, coupled with a shift toward recreational hunting (Carpio et al., 2021; Felton et al., 2017; Holzer et al., 2024; Kuijper, 2011; Massei et al., 2015; Weisberg and Bugmann, 2003).

Numerous studies have reported negative effects of ungulates on forest regeneration, structure, and functioning (Ramirez et al., 2018). Furthermore, a large body of evidence has further implicated ungulate browsing as a leading cause of suppressed – or even failed – natural regeneration and reduced growth rates in commercially important tree

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species, with long-term consequences for forest productivity and resilience (e.g., Côté et al., 2004; Harmer and Gill, 2000; Komonen et al., 2020; Zoltán et al., 2024). In Central European forests, roe deer (*Capreolus capreolus* L.) and red deer (*Cervus elaphus* L.) are the most abundant ungulate species (Linnell et al., 2020), and their impacts are particularly relevant to forest regeneration.

From the 19th century onward, rotation forestry became the dominant system in Europe, based on planting-cultivating-harvesting cycles similar to that used for agricultural crops. This led to even-aged stands with low number of tree species and structural heterogeneity (Aszalós et al., 2022; Chevaux et al., 2022; Diaci, 2006), which were typically managed under clear-cutting, shelterwood or coppice selection forestry systems. Under the rotation forestry framework, protecting natural regeneration from large herbivores has become essential, with ungulate exclusion being the most widely applied technique (Barrere et al., 2021; Csányi and Lehoczki, 2010; Löf et al., 2021). Although this method appears to be effective at high ungulate densities (Edenius and Ericsson, 2007), it tends to concentrate browsing pressure on adjacent areas (Newman et al., 2014; Schäfer et al., 2019). Within exclusions, vegetation homogenization is also commonly observed (Newman et al., 2014). In contrast, freely browsed woodlands with relatively low herbivore pressure typically exhibit greater spatial heterogeneity and tree species richness (Hegland et al., 2013; Hester et al., 2000; Kuijper et al., 2010; Schall et al., 2020).

As an alternative approach to rotation forestry, continuous cover forestry (CCF) system has attracted increasing interest in recent decades. CCF avoids large regeneration areas, with regeneration occurring in small patches beneath canopy gaps, which mimics the fine-scale natural disturbance regime of European temperate forests (Aszalós et al., 2022; Bauhus et al., 2009; Pommerening and Murphy, 2004; Spiecker, 2003). Compared to rotation forestry system, CCF maintains greater horizontal and vertical heterogeneity in stand structure, thereby enhancing forest resilience (Messier et al., 2013; Stokes and Kerr, 2009). Additionally, these small regeneration patches provide forage for ungulates (Kuijper et al., 2009). Despite its ecological advantages (Aszalós et al., 2022; Jensen et al., 2012), CCF is often less preferred in practice than conventional systems due to the more complex planning requirements and the challenges in regenerating light-demanding tree species such as European oaks, particularly *Quercus petraea* (Matt.) Liebl., *Q. robur* L. and *Q. cerris* L. (Harmer and Gill, 2000; Mason et al., 2021; Stokes and Kerr, 2009). Although promising case studies have emerged in recent years (Barrere et al., 2021; Modrow et al., 2020; Tinya et al., 2020, 2025), the management of oak-dominated forests under the framework of CCF remains a subject of ongoing debate.

Sessile oak (*Q. petraea*) is of paramount importance in Central European silviculture due to its high economic value and ecological significance (Löf et al., 2016; Nicolescu et al., 2025; Tinya et al., 2021). As reviewed by Kohler et al. (2020), the key factors influencing the survival and growth of sessile oak recruits include light availability, interspecific competition, browsing, and initial seedling density. The first evident step toward successful oak regeneration is manipulating incoming radiation (Barrere et al., 2021; Kohler et al., 2020; Modrow et al., 2020; VanderMolen and Webster, 2021). However, increased irradiance – particularly in larger canopy openings – can favour fast-growing, shade- and browsing-tolerant understory species over sessile oak, thereby providing a pronounced advantage to these competitor species (Modrow et al., 2020; Tinya et al., 2020; von Lüpke, 1998). In forest stands, where sessile oak is the focal tree species for forest management, the most abundant admixed tree species are typically the shade-tolerant and faster-growing *Carpinus betulus* L. and *Fagus sylvatica* L. (Barrere et al., 2024; Tinya et al., 2025). As neighbouring vegetation overtops the focal species, reduced light levels suppress the growth of oak recruits. Therefore, tending interventions are necessary to support successful oak regeneration (Kohler et al., 2020; Tinya et al., 2025). According to Jensen et al. (2020), interspecific competition *per se* most strongly affects the survival of oak saplings, whereas browsing has a greater impact

on their growth. Because the presence of competing vegetation can reduce browsing rates on target species by diverting herbivory, retaining neighbouring vegetation has been proposed a potential strategy to mitigate browsing-induced height reduction (Felton et al., 2022; Jensen et al., 2020). These competition-facilitation dynamics were examined in depth by Barrere et al. (2024), who emphasized that maintaining or even promoting more palatable alternative forage may enhance oak regeneration, but only under high browsing pressure and when the alternative species have growth rates comparable to those of the focal species (such as sessile oak).

While previous studies have investigated the roles of incoming light, competition, and browsing in oak regeneration, comparatively little field-based evidence exists on how silvicultural systems interact with browsing pressure over time, particularly in multi-species regeneration contexts. Addressing this gap is crucial for refining management strategies under both rotation forestry and continuous cover forestry frameworks, especially given the ecological and economic importance of sessile oak in Central European silviculture.

To fill this knowledge gap, we experimentally compares the effects of different forestry treatments and ungulate browsing on the natural regeneration dynamics of multiple woody species. We monitored the annual growth of saplings and shrubs with and without exposure to ungulate browsing (i.e., excluded or non-excluded individuals) for six consecutive years (2014–2020). The implemented treatments represent rotation forestry system (clear-cutting, retention tree groups within clear-cuts, and preparation cutting) as well as continuous cover forestry system (gap-cutting), with mature, even-aged managed stands without intervention serving as controls. Using this experimental setup, we addressed two main research questions:

- (1) What is the browsing intensity across different forestry treatments?
- (2) How do forestry and exclusion treatments affect the survival, growth and leaf area of regenerating oak, hornbeam, ash, and shrub species, and how do these effects change over time following the interventions?

2. Material & methods

2.1. Study site

The study site is located in the Pilis Mountains, northern Hungary (47°40' N, 18°54' E) on moderate northeast-facing slopes (7.0–10.6°) at 370–470 m above sea level (Fig. 1a). The mean annual temperature ranges from 9.0 to 9.5 °C (16–17 °C in the growing season), and the annual precipitation is 600–650 mm (Dövényi, 2010). The bedrock is a mixture of limestone and sandstone, partly covered with loess. Soil depth varies along a slight topographic gradient, being deeper in the lower parts and shallower at higher elevations. Predominant soil types include brown forest soils and rendzinas near the ridge, with the topsoil (0–20 cm) slightly acidic (pH 4.6 ± 0.2). Despite variations in soil depth, the upper soil layers showed no substantial differences in soil chemical properties that would significantly affect woody vegetation (Kovács et al., 2018).

The experiment was established in 2014 within a homogeneous, two-layered, 80-year-old deciduous forest (Natura 2000 code: 91G0; Council Directive 92/43/EEC, 1992), which had been managed under the scheme of uniform shelterwood system (rotation forestry system) with regular thinnings. Due to its management history, the stand was even-aged, with a relatively uniform vertical and horizontal structure at the onset of the experiment. The upper canopy layer was dominated by sessile oak (*Quercus petraea* (Matt.) Liebl.), while hornbeam (*Carpinus betulus* L.) formed the sub-canopy layer. The relative proportions of admixed tree species were low, with individuals of *Quercus cerris* L., *Fagus sylvatica* L., *Fraxinus ornus* L., *Acer campestre* L., *Sorbus torminalis* (L.) Crantz, and *Prunus avium* L. being rare. Before the implementation of the treatments, the shrub layer was sparse, primarily consisting of the

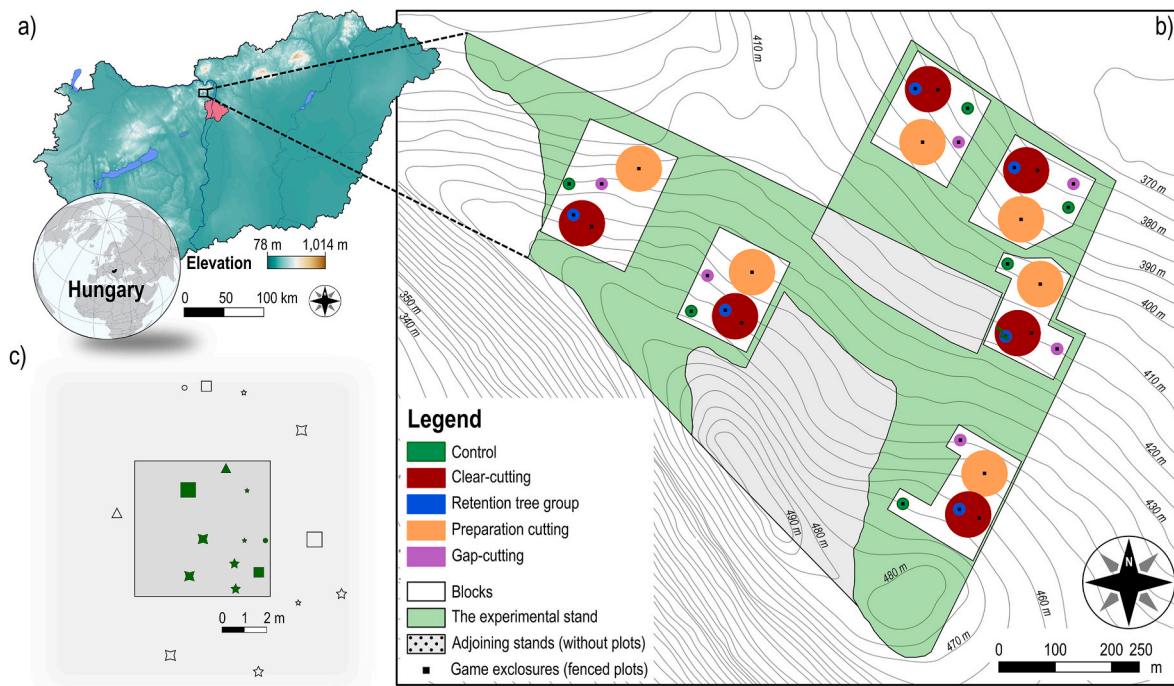


Fig. 1. The location of the Pilis Forestry Systems Experiment (47°40' N, 18°54' E) in Hungary (a); the experimental design of the five treatments within six blocks as replicates in the study site (b); and the graphical representation of a sampling plot with a 6 m × 6 m deer-exclusion in the central zone (c). Graphical representation of the sapling pairs. Saplings of different woody species are coded with different shapes; the sizes of the elementary shapes refer to the height classes, individuals inside and outside the exclusion are green and white, respectively.

natural regeneration of tree species and a few shrub-like species, including *Crataegus monogyna* Jacq., *Cornus mas* L., *Cornus sanguinea* L., *Ligustrum vulgare* L. and *Euonymus verrucosus* Scop. The understory layer was composed of generalist and mesic forest species, dominated by *Carex pilosa* Scop., *Melica uniflora* Retz., *Cardamine bulbifera* L., *Galium odoratum* (L.) Scop., and *Galium schultesii* Vest. Herb layer cover was 40% before the treatments (2014).

The stand is characterized by the presence of wild boar (*Sus scrofa* L.), red deer (*Cervus elaphus* L.), and roe deer (*Capreolus capreolus* L.). The annual hunting bags of these wild ungulate species remained relatively constant from 2014 to 2020, with a slight decline over the six-year period (Table S1 in Appendix I.). Average densities of red deer and roe deer during the study period were 1.5 and 1.6 individuals per km², respectively, which are lower than typical densities reported in woodlands of other submontane regions of Hungary (Fig. S1) and Central Europe. For example, average red deer densities in the German and Czech regions of Bohemia are 2.5 and 3.5 ind./km², respectively (Tourani et al., 2023), while in Slovenia, population densities range from 0.1 to 20 ind./km² (Stergar and Jerina, 2017). Roe deer densities vary widely across Europe, ranging from 4.5 to 73.5 individuals per km² (Flajšman et al., 2018), with submontane regions of southwestern Poland reporting values of 0.4–1.4 ind./km² (Kopij, 2023).

2.2. Experimental design

This study is part of the Pilis Forestry Systems Experiment (<https://piliskiserlet.ecolres.hu/en>), established in 2014 to investigate the effects of different forestry interventions on forest site conditions (microclimate and soil), biodiversity across multiple taxa, and natural regeneration. The present experiment comprises 30 plots arranged in six blocks with five treatments, following a before-after control-impact (BACI) design (Christie et al., 2019); therefore, all measurements were conducted using consistent methodology in the pre-treatment year (2014), prior to the implementation of the forestry treatments (Tables 2 and Figure S2, Appendix I.). In a complete block arrangement (Fig. 1b),

six blocks were used as replicates, each containing four treatment types and one control. Three of the treatments belong to the rotation forestry system. These treatments were (1) clear-cutting (CC): a circular clear-felled area (diameter: 80 m) where all tree individuals were removed; (2) preparation cutting (P): a circular, evenly distributed partial cutting area (diameter: 80 m), where 30% of the canopy trees were removed (those have a diameter at breast height ≥ 5 cm and/or height ≥ 2 m), based on the total basal area, and all sub-canopy individuals including tall shrubs were also cut; and (3) retention tree group (R): within each clear-cut, a circular area (diameter: 20 m) without intervention, a group of 8–12 tree individuals and the shrub layer were untouched. The fourth treatment type, representing CCF is (4) gap-cutting (G), where all tree individuals were removed within a 20 m diameter circle (that corresponds to one-tree-length in diameter). In addition, (5) control (C) plots without intervention were established in each block. All treatments were applied in the winter of 2014/2015.

To study the effects of browsing, a 6 m × 6 m exclusion was established in the centre of each study plot against wild ungulates using 1.6 m high wire fencing. As several tree individuals exceeded the original fence height by 2017 (the third year of the experiment), the fences were raised to 3 m. To further protect the saplings from hares (*Lepus europaeus* Pallas) inside the enclosures, an additional denser wire mesh was installed near the ground (up to 0.5 m).

In order to distinguish the effects of browsing and forestry treatments on regeneration, naturally regenerated saplings were studied in paired comparisons of fenced (i.e., large mammals excluded) and unfenced (i.e., exposed to browsing) individuals (Fig. 1c). Naturally regenerated rather than planted saplings were used to avoid planting-related stress and to maximize early survival (Pemán et al., 2017). Pairs were selected and marked before the implementation of the silvicultural interventions (in 2014), with individuals matching by species, height, browsing history, and overall shape (i.e., either both browsed or both unbrowsed, with similar browsing-induced morphology). The unfenced pair member was chosen within a search radius of 10 m from the fenced individual, minimizing distances between paired individuals while maximizing sample

size per plot. As a result, the study design is not balanced with equal sample sizes across species. A detailed description of the shape and browsing assessment is provided in [Appendix II](#).

In total, 180 pairs were monitored. Sample sizes do not reflect the relative proportions of natural woody regeneration of the studied stands. Not all available oak and hornbeam individuals were selected; thus, admixed tree species became overrepresented in our sample. This approach enabled comparisons in regeneration differences among four species groups: oaks (*Quercus petraea* and *Q. cerris*), hornbeam, manna ash (*Fraxinus ornus*) and shrubs (*Crataegus monogyna*, *Cornus sanguinea*, *Rosa canina*, *Euonymus verrucosus*, *Acer campestre*, *Prunus avium*, *Sorbus torminalis*). The two oak species were combined due to the low abundance of *Q. cerris*, and woody species with shrubby character were similarly grouped for the same reason.

2.3. Data collection and analysis

The development of uniquely labelled saplings was monitored from 2014 to 2020. Browsing incidence was recorded as clear evidence of ungulate browsing (i.e., missing terminal buds) on the main shoots of the selected individuals ([Appendix II](#)). Six growth-related variables were measured annually, including sapling height, terminal shoot length, and green biomass. To identify key independent variables, principal component analysis (PCA) was applied to the six-year changes in these metrics separately for each species group. PCA identified shoot length and leaf area growth rates as the most relevant and uncorrelated variables. Detailed results of the ordination are provided in [Appendix III](#).

Shoot length was defined as the longest distance between the ground and the top of the straightened terminal shoot (either primary or secondary). Measurements were taken with 0.5 cm accuracy. Leaf area was estimated by multiplying the surface area of an average-sized leaf by the total number of leaves per individual. Only leaves with more than 50 % intact area were taken into account, and individual leaf area was approximated as an ellipse. While this variable is not suitable for interspecific comparisons ([Fotelli et al., 2000](#); [Kohen et al., 1993](#)), it can indicate the intraspecific effects of ungulate exclusion on photosynthetic surface area, an indicator of annual growth potential, with a reasonable degree of accuracy. Measurements were taken each autumn before leaf shedding (September–October).

All statistical analyses were performed in the R statistical environment (R version 4.0.5; [R Core Team, 2022](#)). First, annual browsing ratios were analysed using a generalised linear mixed-effects model (GLMM) included forestry treatment (F) with five categories (C, R, P, CC, G), exclusion treatment (E) with two levels (excluded and not excluded), sampling year (Y) as a factor with six levels (2015, 2016, 2017, 2018, 2019, and 2020) and their paired interaction terms as fixed effects ([Zuur et al., 2009](#)). Block/pair was included as random effect. Second, to examine treatment-related differences in survival, the six-year survival rates of the four species groups were explored separately using binomial GLMMs with logit link-function. Fixed effects included F, E and their interaction term (F:E). Block/pair was treated as a nested random factor ([Appendix IV](#)). These models were implemented using the 'lme4' package ([Bates et al., 2015](#)).

We then assessed the treatment effects on the growth rates of individuals monitored. Growth was expressed as (1) overall increment between 2014 and 2020 (i.e., six-year change); and (2) annual changes between consecutive years. Given the substantial range in leaf area (0.78–112,718 cm²), a logarithmic transformation (log₁₀) was applied prior to analysis. All analyses were performed separately for each species group due to differences in shoot morphology, ecological demands and growth rates. First, we constructed mixed-effects models, where fixed effects were F, E and their interaction (F:E), and block/pair was used as a nested random factor. Depending on the residual error structure, either linear mixed-effects models (LMMs; Gaussian error) or GLMMs (Gamma error, log link-function) were used ([Zuur et al., 2009](#)). Second, we analysed annual changes in terminal shoot length, the most

influential growth-related variable identified. Here, the fixed effects were F, E, Y, and their two-way interactions. Initial sapling height was included as a covariate, and block/pair as a nested random effect. For all species, random intercept models with Gaussian error structure were used ([Zuur et al., 2009](#)). In addition to the full models, individual LMMs ('sub-models') were constructed for each year to evaluate annual shoot growth responses (referred to as length) within each species group. These models included only F, E, and F:E as fixed effects.

For all models, variance homogeneity and residual distribution were checked using the 'DHARMA' package ([Hartig, 2021](#)). Model fits were evaluated by likelihood ratio tests and by calculating the conditional and marginal coefficient of determination (R_c^2 and R_m^2 , respectively) obtained with the 'MuMIn' package ([Bartoń, 2020](#)). The explanatory power of fixed effects was tested by analysis of deviance (χ^2 and p values; [Zuur et al., 2009](#)), and their effects were determined by likelihood-ratio-based Wald's χ^2 tests by 'car' package ([Fox and Weisberg, 2019](#)). Contrasts were then examined with Tukey's multiple comparisons procedure ($\alpha = 0.05$) for all pairwise comparisons by estimated marginal means based on the constructed mixed-effects models using the 'emmeans' package ([Lenth, 2021](#)).

3. Results

Altogether 180 sapling pairs (58 oaks, 33 hornbeam, 48 manna ash, and 44 shrubs) were involved in the analyses ([Table S3](#)). Across the study period, approximately 60% of the selected individuals outside the enclosures showed signs of browsing ([Tables S4 and S5](#)). The browsing ratio of non-excluded individuals was highest in clear-cuts and gaps during the first three post-treatment years, intermediate in control plots and preparation cuts, and lowest in retention tree groups ([Fig. 2](#)). From 2018 onward, no significant differences were observed among the forestry treatments. Overall, shrubs and hornbeam were the most intensively browsed species groups ([Fig. 2](#)).

Survival was largely unaffected by exclusion treatments for most species. However, for oaks, enclosures significantly improved survival, especially in forestry treatments that opened the upper canopy, such as clear-cuts, gaps, and preparation cuts ([Fig. 3](#), [Fig. S8](#) and [Table S6](#)).

Models were developed for each measured growth-related variable ([Appendix V](#)); however, only the six-year changes in shoot length and leaf area are reported here ([Table 1](#), [Fig. 4](#)). In general, shoot length was more sensitive to the fixed factors than leaf area, as indicated by higher conditional pseudo- R^2 values (0.658–0.784 and 0.376–0.564, respectively). Regarding the six-year increments, the mixed effects models showed that forestry treatments (F) had a stronger effect on growth for all species than exclusion (E), except for shrubs, where forestry and exclusion treatments were similarly important variables ([Table 1](#)). Among species, oaks and ash had slower growth than hornbeam and shrubs ([Fig. 4](#)). The effect of forestry treatments was significant in all cases, with the greatest growth in clear-cuts and gaps, moderate in preparation cuts, and lowest in controls and retention tree groups ([Fig. 4](#)).

The two most open environments (gaps and clear-cuts) showed the strongest exclusion effect ([Fig. 4](#), [Table 1](#)). Specifically, significant exclusion effects over six years were found for oaks in clear-cuts and gaps; for manna ash in gaps; and for shrubs in clear-cuts, gaps, and retention tree groups. Shrubs exhibited the largest treatment response, with marked differences in shoot length and leaf area (e.g., in clear-cuts, shoot length increased by 351.9 cm inside vs. 46.7 cm outside the fences; leaf area: 11,997 cm² vs. 5,521 cm²).

To analyse annual patterns, we focused on shoot length ([Table 2](#), [Fig. 5](#)). The exclusion effect on the annual growth was strongest in clear-cutting and gap-cutting treatments, particularly early in the regeneration process. Forestry treatment and year had much larger effects on oak, hornbeam, and ash ($\chi^2 = 30$ –130) than exclusion ($\chi^2 = 10$ –11), whereas for shrubs, exclusion had comparable importance to forestry treatment ($\chi^2 = 55$ and 71, respectively).

Species-specific responses varied over time ([Fig. 5](#), [Table S8](#)). Oaks

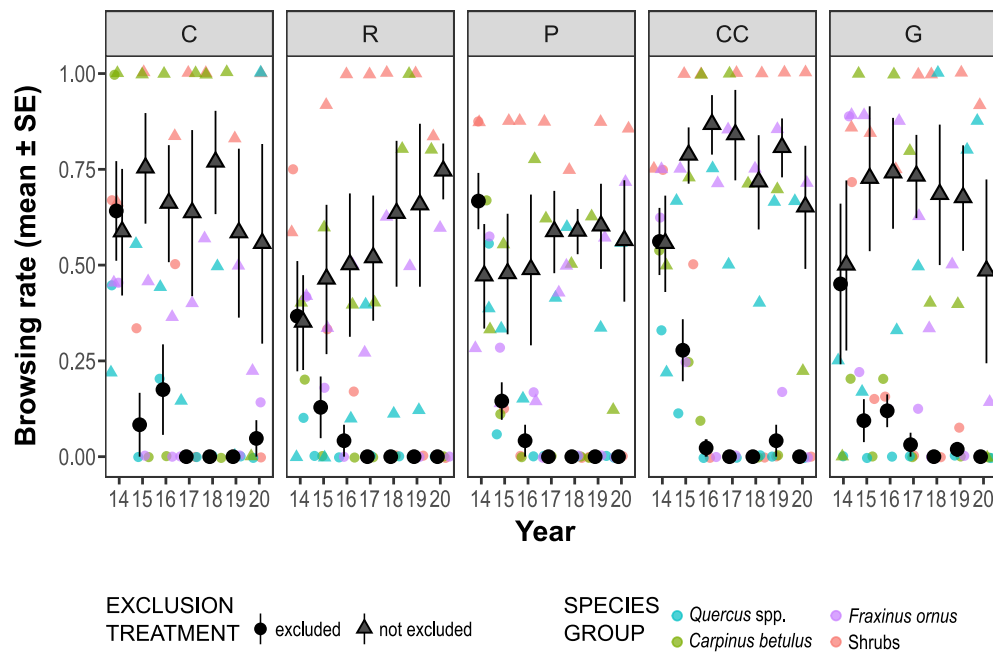


Fig. 2. Annual browsing rates across forestry treatments, shown separately for individuals inside (dots) and outside (triangles) the deer exclosures. In addition to overall annual means $\pm$ standard error (SE), species group-specific averages are indicated using coloured symbols. Forestry treatments are coded as follows: C – closed control, R – retention tree group, P – preparation cutting, CC – clear-cutting, and G – gap-cutting.

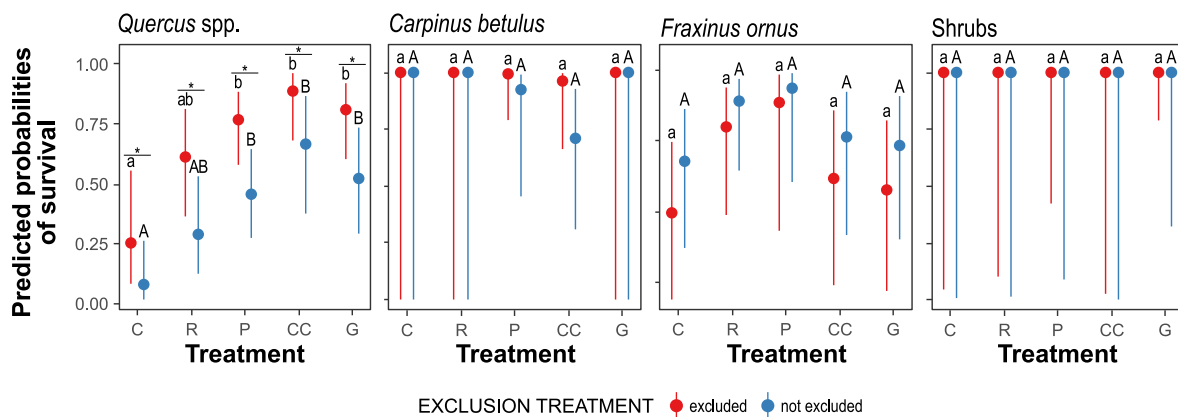


Fig. 3. Predicted survival rates in response to forestry and exclusion treatments. Forestry treatments are coded as follows: C – closed control, R – retention tree group, P – preparation cutting, G – gap-cutting, and CC – clear-cutting. Significant differences between treatment types are indicated by different letters: lowercase letters for excluded individuals and capital letters for not excluded individuals. Asterisks denote significant exclusion effects. Tukey-type multiple comparisons were used to assess statistical differences ($\alpha = 0.05$).

Table 1

Model parameters of overall (six-year) changes of length and leaf area. General and generalised linear mixed effects models (LMM and GLMM, respectively) were built separately for each species group. Forestry treatments (T), ungulate exclusion treatment (E) and their interaction were used as fixed effects. The explanatory power of the tested variables was evaluated by Wald's II-type analysis of deviance (Chi^2 and p values are listed). For the models, the goodness-of-fit measures (Chi^2 and p), as well as the conditional (R_m^2) and marginal (R_c^2) coefficient of determinations, are presented.

Variable	Species group	Model type	Model				Forestry treatment (F)		Exclusion treatment (E)		Interaction (F:E)	
			Chi^2	p	R_m^2	R_c^2	Chi^2	p	Chi^2	p	Chi^2	p
Shoot length	<i>Quercus</i>	LMM	66.63	<0.001	0.623	0.632	96.83	<0.001	8.95	0.002	7.34	0.062
	<i>Carpinus</i>	LMM	50.36	<0.001	0.565	0.766	69.74	<0.001	4.83	0.028	4.65	0.325
	<i>Fraxinus</i>	LMM	69.94	<0.001	0.617	0.823	76.76	<0.001	13.33	<0.001	18.42	0.001
	Shrubs	GLMM	73.73	<0.001	0.609	0.811	35.46	<0.001	53.79	<0.001	10.86	0.199
Leaf area	<i>Quercus</i>	LMM	46.72	<0.001	0.490	0.497	57.51	<0.001	0.59	0.439	2.64	0.451
	<i>Carpinus</i>	LMM	31.42	0.0002	0.402	0.821	27.05	<0.001	3.29	0.069	5.79	0.215
	<i>Fraxinus</i>	LMM	59.26	<0.001	0.553	0.553	84.67	<0.001	4.76	0.029	3.55	0.471
	Shrubs	LMM	39.41	<0.001	0.355	0.428	17.14	0.002	19.92	<0.001	7.84	0.096

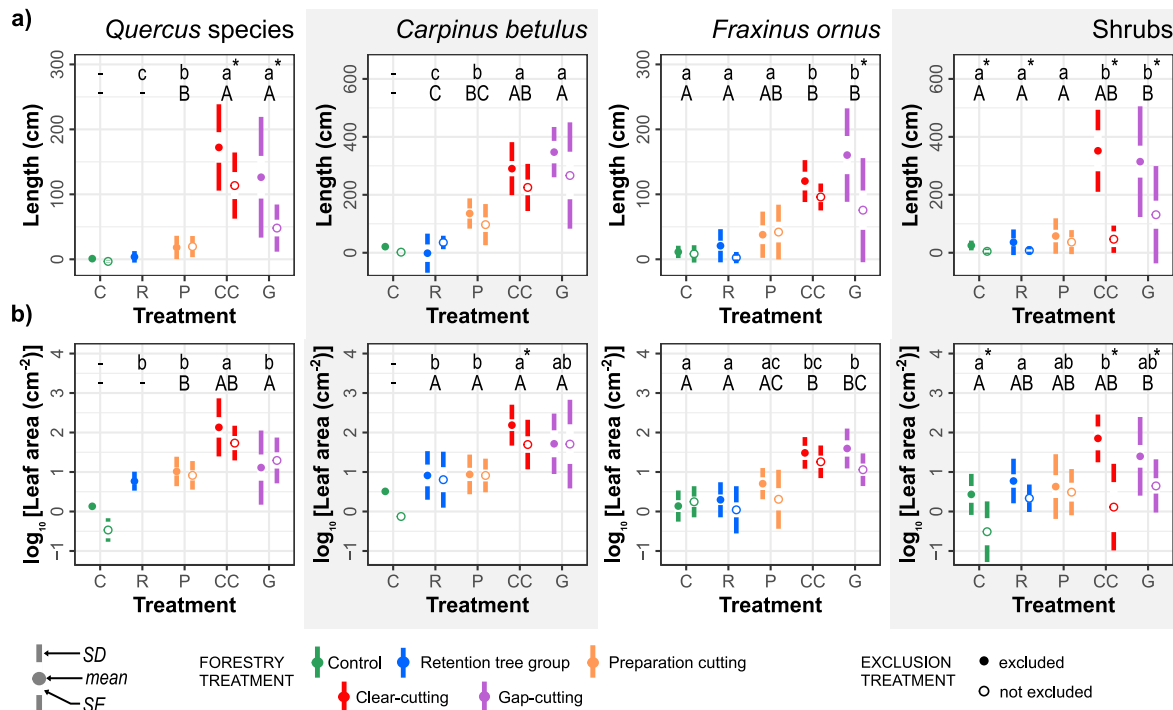


Fig. 4. Overall six-year changes in (a) terminal shoot length and (b) leaf area across different forestry treatments and exclusion levels. Forestry treatments include control (C), retention tree group (R), preparation cutting (P), clear-cutting (CC) and gap-cutting (G). Excluded individuals are coded as solid circles; non-excluded as empty circles. Circles indicate group means; the white space around the circles represents the standard error of the mean (SE), and vertical lines denote standard deviations (SD). Significant differences among forestry treatments (based on Tukey-type multiple comparisons, $\alpha = 0.05$) are indicated by different letters, lower case for excluded individuals and upper case for non-excluded individuals. Asterisks denote significant differences between excluded and non-excluded individuals within the same forestry treatment.

grew slowly in the initial years but responded positively to exclusion in clear-cuts and gaps until year five. By 2020, this pattern weakened or even reversed, with unexcluded saplings slightly outperforming excluded ones in some cases. Hornbeam showed consistently strong growth, particularly in gaps, with exclusion effects diminishing after year four. Manna ash had a slower start but accelerated from year three onward, especially in clear-cuts and gaps, with limited but detectable exclusion effects in specific years (e.g., 2019). Shrubs were the most responsive group overall: their growth was strongly influenced by both forestry and exclusion treatments from the first year onward, with consistently higher annual growth in fenced plots despite high variability.

4. Discussion

Our findings only partially support the widely accepted view that browsing pressure is a major obstacle to adopting alternative silvicultural systems, such as continuous cover forestry and mixed-species stands (Clasen et al., 2015; Ficko et al., 2016; Kern et al., 2017; Mason et al., 2021). In the early regeneration phase (<10 years), forestry treatments *per se* had a stronger influence on tree recruitment than ungulate exclusion, except for shrubs, which responded equally to both factors. This aligns with the moderate to low ungulate densities in the study area (hunting bag data for red deer: 1.1 ind./km²) compared to other submontane regions of Hungary (2.07 [0.98–3.54] ind./km²; see Fig. S1 for details or Zoltán et al., 2024), likely due to the systematic game management strategy of Pilis Parkerdő Ltd.

Browsing pressure on woody recruits temporarily increased in clear-cuts and gaps, likely due to more intensive foraging in canopy openings. Previous studies have shown that browsers not only visit such open areas more frequently but also remain there longer than in adjacent closed stands (Kuijper et al., 2009; Reimoser and Gossow, 1996; Churski et al., 2017). However, differences in browsing pressure among forestry treatments diminished over time as recruits grew taller and the regeneration layer

began to close (by 2019, see also Aszalós et al., 2023). With browsing ratios around 60%, our results suggest that individual plants can still escape browsing and grow successfully, even in the most heavily browsed plots, thereby maintaining regeneration potential across treatments.

Forestry and exclusion treatments did not significantly affect the mortality of naturally regenerated hornbeam, ash, or shrub individuals – contrasting with previous short-term findings on planted saplings (Tinya et al., 2020). In contrast, oaks showed higher survival rates inside exclosures across all forestry treatments, including controls. Oaks were also sensitive to light availability, with survival increasing in more open conditions such as preparation cuts, gaps, and clear-cuts. Similar trends have been reported in other studies. For instance, Murphy et al. (2022) and Leonardsson et al. (2015) found that oak sapling survival was up to three times higher inside fences, likely due to reduced browsing pressure and increased competition with other woody species (see also Jensen et al., 2020), although this effect was absent in seedlings shorter than 20 cm. The positive relationship between canopy openness and oak survival has been widely observed (e.g., Kelly, 2002; Annighöfer et al., 2015; Modrow et al., 2020; Tinya et al., 2020). Furthermore, Churski et al. (2017) highlighted that species with lower architectural plasticity, such as oak, benefit more from exclosures than more plastic species like hornbeam. Supporting our findings, Barrere et al. (2021) emphasized that the interaction between canopy openness and deer exclusion (or other forms of ungulate control) is particularly beneficial for early oak regeneration, noting that the combined effects of light availability and exclosures on forest dynamics are still insufficiently explored.

Growth rates were consistently higher in clear-cuts and gaps than in preparation cuts, retention tree groups, and closed control plots. This pattern likely reflects increased light and soil moisture availability, which have been shown to enhance sapling growth (Barrere et al., 2021; Modrow et al., 2020; Tinya et al., 2020). Although light levels are highest in clear-cuts, artificial gaps can provide similarly favourable environmental conditions for woody regeneration, including oaks, due

Table 2
Annual changes of length. Results of the linear mixed effects models (LMMs) on the yearly length increment by measured species groups. Forestry treatments (T), ungulate exclusion treatment (E), year (Y) and their paired interactions were used as fixed terms, and initial height (I) as covariate. The explanatory power of the tested variables was evaluated by Wald's II-type analysis of deviance (Chi^2 and p values are listed). The models' goodness-of-fit was measured by likelihood-ratio tests based on the conditional (R_c^2) and marginal (R_m^2) coefficient of determination, respectively.

Model	F			E			Y			F:E			F:Y			E:Y			I		
	Chi ²	p	R _m ²	Chi ²	p	R _c ²	Chi ²	p	R _c ²	Chi ²	p	R _c ²	Chi ²	p	R _c ²	Chi ²	p	R _c ²	Chi ²	p	R _c ²
Oaks	239.93	<0.001	0.405	0.439	<0.001	0.18	10.18	0.001	0.001	56.76	<0.001	0.009	97.32	<0.001	0.001	9.17	0.102	0.85	0.356		
Hornbeam	248.18	<0.001	0.515	0.610	<0.001	0.89	10.89	0.001	0.001	149.59	<0.001	0.334	86.27	<0.001	0.001	14.32	0.014	0.93	0.334		
Ash	250.40	<0.001	0.482	0.520	<0.001	10.74	10.74	0.001	0.001	61.76	<0.001	0.005	108.76	<0.001	0.001	11.26	0.047	34.09	<0.001		
Shrubs	245.41	<0.001	0.444	0.595	<0.001	71.13	71.13	<0.001	<0.001	23.63	<0.001	<0.001	65.72	<0.001	<0.001	4.76	0.447	10.05	0.002		

to elevated soil moisture, lower diurnal temperature variability and buffered vapour pressure deficit (Kovács et al., 2020; Lendzion and Leuschner, 2009; Meeussen et al., 2022; Modrow et al., 2020; von Arx et al., 2013). Our results on shoot length and leaf area increments suggest that gap-cutting offers a regeneration potential comparable to clear-cuts, as no significant differences were found in growth-related variables between these treatments (except for the leaf area increment of oaks within exclosures). These results are also in line with previous findings reporting that survival and height growth of planted oak, hornbeam, and common ash (*Fraxinus excelsior* L.) saplings were highest in gaps and clear-cuts five years post-treatment (Tinya et al., 2020).

Species differed markedly in their regeneration responses, reflecting variation in growth strategies, palatability, and competition tolerance. Oaks (*Quercus petraea* and *Q. cerris*) showed slow initial growth, peaking in gaps and clear-cuts. As palatable species preferred by ungulates (Boulanger et al., 2009; Gaudry et al., 2022; Ohse et al., 2017), their highest annual growth occurred within fenced plots – consistent with previous studies (e.g., Barrere et al., 2021; Candaele et al., 2023; Thomas-Van Gundy et al., 2014). However, their performance declined over time due to overtopping by hornbeam, a faster-growing, shade-tolerant competitor and dominant species of the subcanopy layer in oak-hornbeam forests. While fencing enhanced oak growth initially, this benefit diminished as interspecific competition intensified, which is consistent with the findings of Leonardsson et al. (2015) and Modrow et al. (2020). In some cases, oaks outside fences could perform better due to reduced competition and possible dilution effects caused by co-occurring, more palatable neighbouring species (Barrere et al., 2024; Jensen et al., 2020). Hornbeam, in contrast, showed immediate and vigorous growth, especially in gaps, and remained highly competitive. From the fourth year onward, hornbeam suppressed oaks in both gaps and clear-cuts (as also reported by Tinya et al., 2020), which is a common outcome in mixed oak stands (e.g., Dietz et al., 2022; Kuijper et al., 2010). However, non-excluded hornbeam individuals grew more from 2019 onward, likely due to intensified intraspecific competition within exclosures. Shade-tolerant species such as hornbeam are generally less vulnerable to browsing, and their morphological plasticity enhances their competitive ability (Rossell et al., 2007). Hornbeam can regenerate even under substantial browsing pressure by producing lateral shoots and developing a 'cage-like' architecture (Churski et al., 2017). Despite being frequently browsed, hornbeam still attained greater overall height than most European tree species under high ungulate densities (Kuijper et al., 2010). Manna ash, similar to oaks, regenerated slowly and showed improved growth within fences despite the enhanced interspecific competition (see also Nopp-Mayr et al., 2020). As a documented shade-tolerant species, ash performs best under moderate light and low water stress (Helluy et al., 2021), which aligns with our finding of the highest regeneration rates occurring in gaps. *Fraxinus* species are highly palatable and vulnerable to browsing, often suffering height reductions from repeated herbivory due to their limited compensatory growth (Kupferschmid and Bugmann, 2008). Consequently, their regeneration success is closely linked to local ungulate density (Kuijper et al., 2010; Ohse et al., 2017). Shrubs responded most strongly to the exclusion treatment, showing pronounced differences in both shoot length and leaf area. Despite their architectural flexibility, they are frequently browsed (see Fig. 2) and can therefore decline substantially in abundance and diversity (Boulanger et al., 2009; Hedwall et al., 2018; Pellerin et al., 2010). Traits like dense wood and shrubby growth may further increase their palatability (Boulanger et al., 2009).

The interaction between silvicultural treatments and ungulate exclusion had a strong influence on the regeneration outcomes. Fencing had the greatest effect in open treatments, especially clear-cuts and gaps, where higher light availability supports vigorous sapling growth but also increases visibility and attractiveness to herbivores (Barrere et al., 2021; Kuijper et al., 2009; Reimoser and Gossow, 1996). Consequently, the benefits of ungulate exclusion were amplified under these conditions, particularly for highly palatable but less browsing-tolerant species like

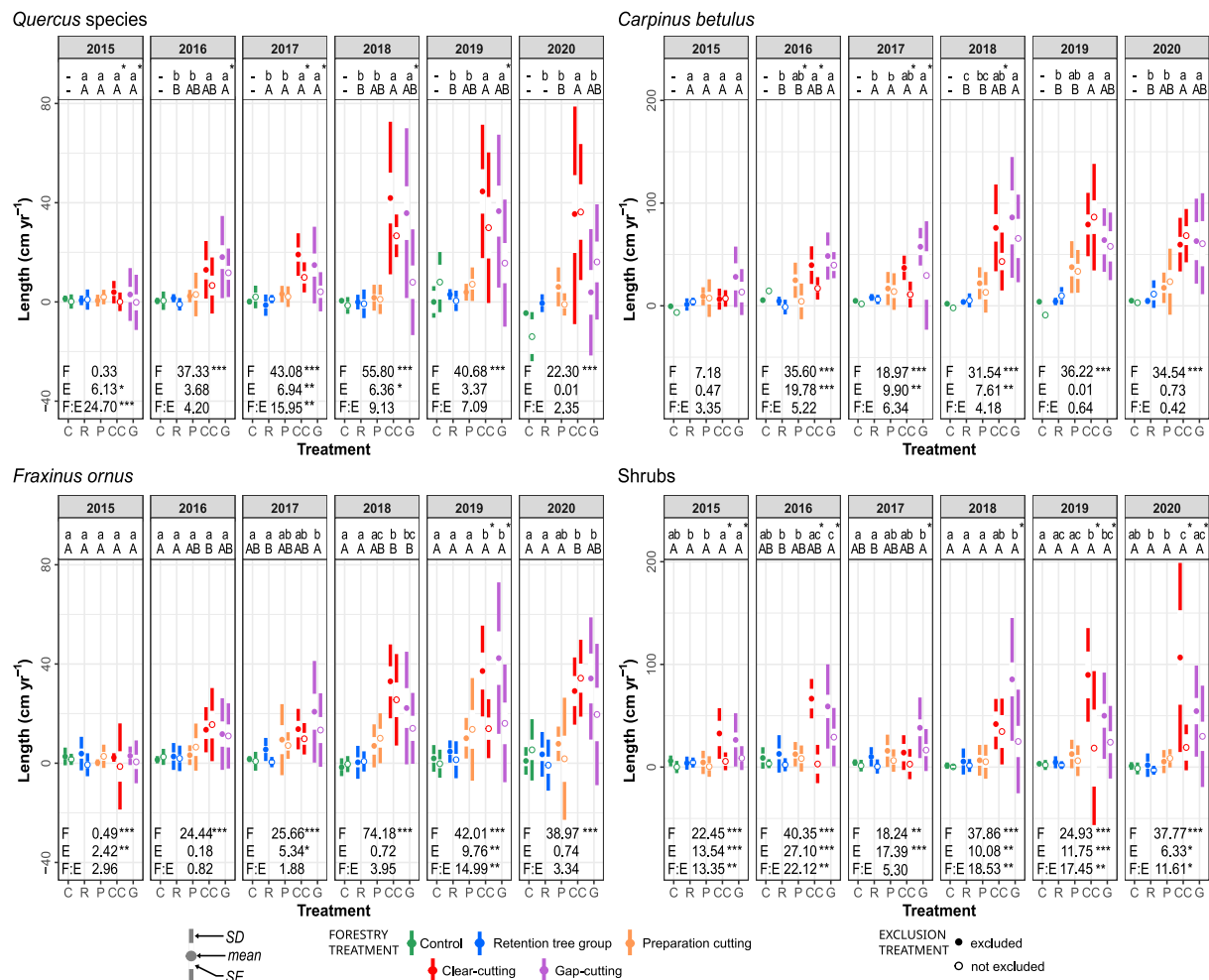


Fig. 5. The effects of forestry (T) and exclusion (E) treatments and their interaction (T:E) on annual terminal shoot growth across six consecutive post-treatment years. Forestry treatments include control (C), retention tree group (R), preparation cutting (P), clear-cutting (CC) and gap-cutting (G). Excluded individuals are represented by solid circles; non-excluded as empty circles. Circles indicate group means; the white space around the circles represents the standard error of the mean (SE), and vertical lines denote standard deviations (SD). Significant differences among forestry treatments (based on Tukey-type multiple comparisons, $\alpha = 0.05$) are indicated by different letters, lower case for excluded individuals and upper case for non-excluded individuals. Asterisks denote significant differences between excluded and non-excluded individuals within the same forestry treatment. Wald's type-II test results (with Chi²- and p-values) are shown at the bottom of each facet (**p < 0.01, *p < 0.05).

oak and ash. The pronounced growth differences in shrubs between fenced and unfenced plots within clear-cuts suggest a dilution effect driven by increased plant density and diversity (Holík et al., 2021; Boulanger et al., 2009). These findings highlight that while treatments creating more open stands with enhanced resource availability, successful regeneration depends on managing both browsing and competition. An integrated approach, combining selective fencing, targeted competition control, and mixtures of species with varying palatability appears to be the most promising for supporting regeneration under close-to-nature forestry systems (Candaele et al., 2023; Modrow et al., 2020; VanderMolen and Webster, 2021).

The effects of browsing and treatments on regeneration also changed over time. Initially, regeneration was fastest in clear-cuts and gaps due to higher light availability (Kovács et al., 2020; Tinya et al., 2020), particularly within enclosures where browsing did not limit shoot growth. However, from the fifth post-treatment year onward, intensified competition within enclosures began to slow regeneration. While some dominant individuals, mainly hornbeam, continued to grow, many suppressed saplings, including oak and manna ash, showed reduced growth (Barrere et al., 2024; Holzer et al., 2024). This strong competition was less evident in unfenced plots. Our results, consistent with

previous studies (Modrow et al., 2020; Tinya et al., 2020; von Lüpke, 1998), confirm that ungulate exclusion alone does not guarantee successful oak regeneration; managing shade-tolerant competitors remains essential. Notably, shrub regeneration was consistently higher in fenced plots and showed no time-related variation, suggesting that the growth of this species group is very sensitive to browsing (Boulanger et al., 2009; Jensen et al., 2012). Another important aspect of the temporal dynamics is that sapling growth tends to be near-exponential with age, reducing browsing risk as individuals exceed typical ungulates reach (ca. 2 m; Walters et al., 2020). Early in the experiment, hornbeam height growth was greater within enclosures, but later growth rates converged, likely reflecting reduced browsing pressure as saplings escaped herbivory. Similarly, oak growth outside enclosures continued to increase over time, possibly nearing or surpassing browsing height thresholds. These trends align with findings that browsing effects tend to decrease as succession progresses and saplings outgrow herbivore reach, while competition becomes increasingly influential (Cacciatori et al., 2025; Harmer, 2001; Jensen and Löf, 2017). Incorporating sapling height and browsing risk into management decisions – such as informing optimal timing for fence removal – could support more effective regeneration success in both rotation and continuous-cover forestry contexts.

5. Management implications

Forests managed under continuous cover forestry system are often face challenges in regenerating light-demanding, slow-growing species with limited competitive ability such as sessile oak (Barrere et al., 2021, 2024; Kern et al., 2017; Tinya et al., 2020, 2025). When oaks are target species, as in many Central European oak-dominated forests, management requires careful planning in terms of propagule availability or initial sapling density, gap size, and control of competing vegetation (Kohler et al., 2020; Modrow et al., 2020). Assuming constant ungulate density, large canopy openings are expected to provide optimal light levels but also increase browsing frequency on oak saplings, which can severely hinder regeneration (Barrere et al., 2021; Bergquist et al., 2003; Blossey et al., 2019; Knapp et al., 2019; Ligot et al., 2013). In contrast, small gaps may reduce browsing pressure but intensify competition with shade-tolerant, fast-growing woody species – another significant barrier to successful oak regeneration (Annighöfer et al., 2015; Barrere et al., 2021; Hannah, 1987; Ligot et al., 2013).

Conventional practice advocates that successful oak regeneration depends on clear-cuts or large gaps, fencing to exclude browsing ungulates, and intensive control of competing vegetation. Our results challenge this view, demonstrating that oak saplings can attain comparable growth rates in moderately sized gaps (diameter-to-tree-height ratio of one) as in clear-cuts, even without fencing or systematic competitor removal. This finding highlights a promising pathway for implementing close-to-nature silviculture with lower intervention intensities. Moreover, unlike clear-cutting or terminal cutting of the shelterwood system, CCF imposes no rigid requirements regarding timing, minimal sapling abundance, or target height for oak regeneration. Instead, it focuses on achieving desired timber quality and maintaining oak at defined relative proportions, thereby providing greater flexibility in adapting regeneration strategies to site-specific conditions (Aszalós et al., 2022; Pommerening and Murphy, 2004).

During the early regeneration stages, oaks grew more successfully inside exclosures across treatments. However, over time, shade-tolerant competitors such as hornbeam intensified and curtailed oak growth, despite browsing exclusion. This suggests that long-term success depends less on fencing alone and more on active, targeted tending, such as breaking the apical shoots of competitive species or gradually enlarging canopy gaps (Kuehne et al., 2020; Mölder et al., 2019). Although not tested directly, natural barriers such as logging residues, coarse woody debris, or thorny shrubs may also reduce browsing pressure by physically limiting ungulate access. This could be a particularly relevant strategy in forests with low to moderate ungulate densities (Hagge et al., 2019; Schwegmann et al., 2023; Smit et al., 2012). These insights support a shift toward adaptive, cost-effective, and site-specific forest regeneration strategies rather than rigid reliance on fencing.

Although our study provides only indirect evidence (e.g., Fig. 2), it underscores the potential role of a well-developed shrub layer in diluting browsing pressure on focal tree species in mesic, oak-dominated forests. Shrubs, being more palatable alternative forage, have been reported to attract herbivores and divert browsing pressure from oak recruits (Jensen et al., 2012; Kuijper et al., 2010; Ohse et al., 2017). Therefore, increasing the abundance and diversity of shrub and admixed tree species both within canopy openings and in the adjacent forest matrix may be beneficial, which is in line with the 'dynamic foodscape' approach (Bödeker et al., 2023; Royo et al., 2017). This would support a shift from shrub removal toward the strategic maintenance or enhancement of the shrub layer, as it functions both as ecological buffers and important habitats supporting forest biodiversity (Donnelly and Yu, 2021; Stiegel et al., 2020; Tinya et al., 2021). The added structural complexity further improves habitat complexity and forest resilience (Messier et al., 2013).

Beyond diverging forage availability, reducing population densities of browsers through culling is of crucial importance (Barrere et al., 2024; Bödeker et al., 2023; Carpio et al., 2021; Kuijper et al., 2010; Modrow et al., 2020). At moderate or low browsing pressure, ungulates

can even facilitate oak regeneration by suppressing competing vegetation. However, such aims are only achievable if ungulate densities are kept at lower levels, which requires coordinated actions and cooperation between forestry and wildlife management sectors (Champagne et al., 2021; Linnell et al., 2020).

In summary, our findings demonstrate that oak regeneration is feasible under continuous cover forestry without resorting to high-intensity interventions but only if browsing pressure is controlled and structural complexity is enhanced. These insights support the transition toward more sustainable and ecologically informed forest management across Central Europe.

6. Conclusions

Using an open-field experimental setup, we demonstrated that oaks can regenerate successfully both in conventional clear-cuts and under the framework of continuous cover forestry, particularly within artificial gaps. Our results indicate that ungulate exclusion is not the ultimate tool for supporting regeneration processes due to the strong interspecific competition between the target tree species and the fast-growing and browse-tolerant admixed species. This study highlights the potential role of shrubs as natural herbivore attractants that can protect oak saplings by diverting browsing pressure. Maintaining lower ungulate densities may therefore provide more favourable conditions for forest regeneration than the complete fencing of regeneration areas. Collectively, these findings underline that integrating wildlife management, structural complexity, and adaptive silvicultural practices can effectively promote oak regeneration under close-to-nature forestry systems.

CRedit authorship contribution statement

Lilla E. Szabó: Writing – original draft, Visualization, Investigation, Conceptualization. **Péter Ódor:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Bence Tóth:** Writing – review & editing, Investigation, Conceptualization. **Péter Csépanyi:** Writing – review & editing. **Bence Kovács:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2025.127831>.

Data availability

Data attached as Supplementary Table.

References

- Allombert, S., Gaston, A.J., Martin, J.-L., 2005. A natural experiment on the impact of overabundant deer on songbird populations. *Biol. Conserv.* 126, 1–13. <https://doi.org/10.1016/j.biocon.2005.04.001>.
- Annighöfer, P., Beckschäfer, P., Vor, T., Ammer, C., 2015. Regeneration patterns of European Oak Species (*Quercus petraea* (Matt.) Liebl., *Quercus robur* L.) in dependence of environment and neighborhood. *PLoS One* 10, e0134935. <https://doi.org/10.1371/journal.pone.0134935>.
- Aszalós, R., Kovács, B., Tinya, F., Németh, C., Horváth, C.V., Ódor, P., 2023. Canopy gaps are less susceptible to disturbance-related and invasive herbs than clear-cuts: temporal changes in the understorey after experimental silvicultural treatments. *For. Ecol. Manag.* 549, 121438. <https://doi.org/10.1016/j.foreco.2023.121438>.
- Aszalós, R., Thom, D., Aakala, T., Angelstam, P., Brümelis, G., Gálhidy, L., Gratzner, G., Hlásny, T., Katzensteiner, K., Kovács, B., Knoke, T., Larrieu, L., Motta, R., Müller, J., Ódor, P., Rozenberger, D., Paillet, Y., Pitar, D., Standovář, T., Svoboda, M., Szwagrzyk, J., Toscani, P., Keeton, W.S., 2022. Natural disturbance regimes as a guide for sustainable forest management in Europe. *Ecol. Appl.* 32. <https://doi.org/10.1002/eap.2596>.
- Augustine, D.J., McNaughton, S.J., 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *J. Wildl. Manag.* 62, 1165–1183. <https://doi.org/10.2307/3801981>.
- Barrere, J., Ligot, G., Boulanger, V., Collet, C., Courbaud, B., De Coligny, F., Mårell, A., Saïd, S., Balandier, P., 2024. Oak regeneration facing deer browsing: can competition between saplings offset the diversion effect? A simulation experiment. *Ecol. Model.* 489, 110608. <https://doi.org/10.1016/j.ecolmodel.2023.110608>.
- Barrere, J., Petersson, L.K., Boulanger, V., Collet, C., Felton, A.M., Löf, M., Saïd, S., 2021. Canopy openness and exclusion of wild ungulates act synergistically to improve oak natural regeneration. *For. Ecol. Manag.* 487, 118976. <https://doi.org/10.1016/j.foreco.2021.118976>.
- Bartoň, K., 2020. MuMIn: multi-model inference. R package version. <https://doi.org/10.32614/CRAN.package.MuMIn>, 1.43.17.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Software* 67. <https://doi.org/10.18637/jss.v067.i01>.
- Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. *For. Ecol. Manag.* 258, 525–537. <https://doi.org/10.1016/j.foreco.2009.01.053>.
- Bergquist, J., Örlander, G., Nilsson, U., 2003. Interactions among forestry regeneration treatments, plant vigour and browsing damage by deer. *N. For.* 25, 25–40. <https://doi.org/10.1023/A:1022378908827>.
- Blossey, B., Curtis, P., Boulanger, J., Dávalos, A., 2019. Red oak seedlings as indicators of deer browse pressure: gauging the outcome of different white-tailed deer management approaches. *Ecol. Evol.* 9, 13085–13103. <https://doi.org/10.1002/ece3.5729>.
- Bödeker, K., Jordan-Fragstein, C., Vor, T., Ammer, C., Knoke, T., 2023. Abrupt height growth setbacks show overbrowsing of tree saplings, which can be reduced by raising deer harvest. *Sci. Rep.* 13, 12021. <https://doi.org/10.1038/s41598-023-38951-8>.
- Boulanger, V., Baltzinger, C., Saïd, S., Ballon, P., Picard, J.-F., Dupouey, J.-L., 2009. Ranking temperate woody species along a gradient of browsing by deer. *For. Ecol. Manag.* 258, 1397–1406. <https://doi.org/10.1016/j.foreco.2009.06.055>.
- Cacciatori, C., Gazda, A., Bodziarczyk, J., Foremnik, K., Madalcho, A.B., Maciejewski, Z., Pielech, R., Tomsik, A., Zięba, A., Zwijacz-Kozica, T., Szwagrzyk, J., 2025. Deer browsing increases stem slenderness and crown irregularity and modifies the effects of light gradients on architecture of forest tree saplings. *Ecol. Evol.* 15, e70837. <https://doi.org/10.1002/ece3.70837>.
- Candaele, R., Ligot, G., Licoppe, A., Lievens, J., Fichet, V., Jonard, M., André, F., Lejeune, P., 2023. Interspecific growth reductions caused by wild ungulates on tree seedlings and their implications for temperate quercus-fagus forests. *Forests* 14, 1330. <https://doi.org/10.3390/f14071330>.
- Carpio, A.J., Apollonio, M., Acevedo, P., 2021. Wild ungulate overabundance in Europe: Contexts, causes, monitoring and management recommendations. *Mamm. Rev.* 51, 95–108. <https://doi.org/10.1111/mam.12221>.
- Champagne, E., Raymond, P., Royo, A.A., Speed, J.D.M., Tremblay, J.-P., Côté, S.D., 2021. A review of ungulate impacts on the success of climate-adapted forest management strategies. *Curr. Forestry Reports* 7, 305–320. <https://doi.org/10.1007/s40725-021-00148-5>.
- Chevaux, L., Mårell, A., Baltzinger, C., Boulanger, V., Cadet, S., Chevalier, R., Debaive, N., Dumas, Y., Gosselin, M., Gosselin, F., Rocquencourt, A., Paillet, Y., 2022. Effects of stand structure and ungulates on understory vegetation in managed and unmanaged forests. *Ecol. Appl.* 32, e2531. <https://doi.org/10.1002/eap.2531>.
- Christie, A.P., Amano, T., Martin, P.A., Shackelford, G.E., Simmons, B.I., Sutherland, W. J., 2019. Simple study designs in ecology produce inaccurate estimates of biodiversity responses. *J. Appl. Ecol.* 56, 2742–2754. <https://doi.org/10.1111/1365-2664.13499>.
- Churski, M., Bubnicki, J.W., Jędrzejewska, B., Kuijper, D.P.J., Croomsigt, J.P.G.M., 2017. Brown world forests: increased ungulate browsing keeps temperate trees in recruitment bottlenecks in resource hotspots. *New Phytol.* 214, 158–168. <https://doi.org/10.1111/nph.14345>.
- Clasen, C., Heurich, M., Glaesener, L., Kennel, E., Knoke, T., 2015. What factors affect the survival of tree saplings under browsing, and how can a loss of admixed tree species be forecast? *Ecol. Model.* 305, 1–9. <https://doi.org/10.1016/j.ecolmodel.2015.03.002>.
- Côté, S., 2014. Ecological impacts of deer overabundance on temperate and boreal forests. *Annu. Rev. Ecol. Evol. Systemat.* 35, 114–147. <https://doi.org/10.1146/annurev.ecolsys.35.021103.105725>.
- Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics* 35, 113–147. <https://doi.org/10.1146/annurev.ecolsys.35.021103.105725>.
- Council Directive 92/43/EEC, 1992. Council Directive 92/43/EEC of 21 May 1992 on the Conservation of Natural Habitats and of Wild Fauna and Flora.
- Csányi, S., Lehoczi, R., 2010. Ungulates and their management in Hungary. In: Apollonio, M., Andersen, R., Putman, R. (Eds.), *European Ungulates and their Management in the 21st Century*. Cambridge University Press, Cambridge, pp. 291–318.
- Diaci, J., 2006. Nature-based forestry in Central Europe: alternatives to industrial forestry and strict preservation. In: *Studia Forestalia Slovenica*. Biotechnical Faculty, University of Ljubljana, Ljubljana.
- Dietz, L., Gégout, J.-C., Dupouey, J.-L., Lacombe, E., Laurent, L., Collet, C., 2022. Beech and hornbeam dominate oak 20 years after the creation of storm-induced gaps. *For. Ecol. Manag.* 503, 119758. <https://doi.org/10.1016/j.foreco.2021.119758>.
- Donnelly, A., Yu, R., 2021. Temperate deciduous shrub phenology: the overlooked forest layer. *Int. J. Biometeorol.* 65, 343–355. <https://doi.org/10.1007/s00484-019-01743-9>.
- Dövényi, Z. (Ed.), 2010. Magyarország Kistájainak Katasztora [Inventory of Microregions in Hungary], second ed. MTA Földrajztudományi Kutatóintézet, Budapest.
- Edenius, L., Ericsson, G., 2007. Aspen demographics in relation to spatial context and ungulate browsing: implications for conservation and forest management. *Biol. Conserv.* 135, 293–301. <https://doi.org/10.1016/j.biocon.2006.10.052>.
- Felton, A.M., Felton, A., Croomsigt, J.P.G.M., Edenius, L., Malmsten, J., Wam, H.K., 2017. Interactions between ungulates, forests, and supplementary feeding: the role of nutritional balancing in determining outcomes. *Mammal Research* 62, 1–7. <https://doi.org/10.1007/s13364-016-0301-1>.
- Felton, A.M., Hedwall, P.-O., Felton, A., Widemo, F., Wallgren, M., Holmström, E., Löfmark, E., Malmsten, J., Karine Wam, H., 2022. Forage availability, supplementary feed and ungulate density: associations with ungulate damage in pine production forests. *For. Ecol. Manag.* 513, 120187. <https://doi.org/10.1016/j.foreco.2022.120187>.
- Ficko, A., Roessiger, J., Bončina, A., 2016. Can the use of continuous cover forestry alone maintain silver fir (*Abies alba* Mill.) in central European mountain forests? *Forestry* 89, 412–421. <https://doi.org/10.1093/forestry/cpw013>.
- Flajsman, K., Borowik, T., Pokorný, B., Jędrzejewska, B., 2018. Effects of population density and female body mass on litter size in European roe deer at a continental scale. *Mammalian Research* 63, 91–98. <https://doi.org/10.1007/s13364-017-0348-7>.
- Fotelli, M.N., Radoglou, K.M., Constantinidou, H.-I.A., 2000. Water stress responses of seedlings of four Mediterranean oak species. *Tree Physiol.* 20, 1065–1075. <https://doi.org/10.1093/treephys/20.16.1065>.
- Fox, J., Weisberg, S., 2019. *An R Companion to Applied Regression*, third ed. SAGE, Los Angeles London New Delhi Singapore Washington, DC Melbourne.
- Gaudry, W., Gaillard, J.-M., Saïd, S., Mårell, A., Baltzinger, C., Rocquencourt, A., Bonenfant, C., 2022. Population density and plant availability interplay to shape browsing intensity by roe deer in a deciduous forest. *For. Ecol. Manag.* 515, 120153. <https://doi.org/10.1016/j.foreco.2022.120153>.
- Gill, R., 1990. Monitoring the Status of European and North American Cervids : [Final Report for UNEP GEMS Project ST 4101-84-02 (PP 2551)], GEMS Information Series. UNEP.
- Hagge, J., Müller, J., Bässler, C., Biebl, S.S., Brandl, R., Drexler, M., Gruppe, A., Hotes, S., Hothorn, T., Langhammer, P., Stark, H., Wirtz, R., Zimmerer, V., Myerud, A., 2019. Deadwood retention in forests lowers short-term browsing pressure on silver fir saplings by overabundant deer. *For. Ecol. Manag.* 451, 117531. <https://doi.org/10.1016/j.foreco.2019.117531>.
- Hannah, P.R., 1987. Regeneration methods for oaks. *N. J. Appl. For.* 4, 97–101. <https://doi.org/10.1093/njaf/4.2.97>.
- Harmer, R., Gill, R., 2000. Natural regeneration in Broadleaved woodlands: deer browsing and the establishment of advance regeneration. *Forestry Commission Information Note* 35.
- Harmer, R., 2001. The effect of plant competition and simulated summer browsing by deer on tree regeneration. *J. Appl. Ecol.* 38, 1094–1103. <https://doi.org/10.1046/j.1365-2664.2001.00664.x>.
- Hartig, F., 2021. DHARMA: residual diagnostics for hierarchical (Multi-Level/mixed) regression models. R package version 0.4.4. <https://doi.org/10.32614/CRAN.package.DHARMA>.
- Hedwall, P., Churski, M., Jędrzejewska, B., Miścicki, S., Kuijper, D.P.J., 2018. Functional composition of temperate forest trees under chronic ungulate herbivory. *J. Veg. Sci.* 29, 179–188. <https://doi.org/10.1111/jvs.12623>.
- Hegland, S.J., Lilleeng, M.S., Moe, S.R., 2013. Old-growth forest floor richness increases with red deer herbivory intensity. *For. Ecol. Manag.* 310, 267–274.
- Helluy, M., Gavinet, J., Prévosto, B., Fernandez, C., 2021. Influence of light, water stress and shrub cover on sapling survival and height growth: the case of *A. unedo*, *F. ornus* and *S. domestica* under Mediterranean climate. *Eur. J. Forest Res.* 140, 635–647. <https://doi.org/10.1007/s10342-021-01356-1>.
- Hester, A.J., Edenius, L., Buttenschön, R.M., Kuiter, A.T., 2000. Interactions between forests and herbivores: the role of controlled grazing experiments. *Forestry* 73, 381–391. <https://doi.org/10.1093/forestry/73.4.381>.
- Hobbs, N.T., 1996. Modification of ecosystems by ungulates. *J. Wildl. Manag.* 60, 695–713. <https://doi.org/10.2307/3802368>.
- Hofik, J., Janík, D., Hort, L., Adam, D., 2021. Neighbourhood effects modify deer herbivory on tree seedlings. *Eur. J. Forest Res.* 140, 403–417. <https://doi.org/10.1007/s10342-020-01339-8>.

- Holzer, D., Bödeker, K., Rammer, W., Knoke, T., 2024. Evaluating dynamic tree-species-shifting and height development caused by ungulate browsing in forest regeneration using a process-based modeling approach. *Ecol. Model.* 493, 110741. <https://doi.org/10.1016/j.ecolmodel.2024.110741>.
- Jensen, A., Petersson, L., Felton, A., Löf, M., Persson, M., 2020. What happens to oak growth and survival when there is both competition and browsing? *bioRxiv*. <https://doi.org/10.1101/2020.03.09.983437>, 2020.03.09.983437.
- Jensen, A.M., Götmark, F., Löf, M., 2012. Shrubs protect oak seedlings against ungulate browsing in temperate broadleaved forests of conservation interest: a field experiment. *For. Ecol. Manag.* 266, 187–193. <https://doi.org/10.1016/j.foreco.2011.11.022>.
- Jensen, A.M., Löf, M., 2017. Effects of interspecific competition from surrounding vegetation on mortality, growth and stem development in young oaks (*Quercus robur*). *For. Ecol. Manag.* 392, 176–183. <https://doi.org/10.1016/j.foreco.2017.03.009>.
- Kelly, D., 2002. The regeneration of *Quercus petraea* (sessile oak) in southwest Ireland: a 25-year experimental study. *For. Ecol. Manag.* 166 (1–3), 207–226. [https://doi.org/10.1016/S0378-1127\(01\)00670-3](https://doi.org/10.1016/S0378-1127(01)00670-3).
- Kern, C.C., Burton, J.I., Raymond, P., D'Amato, A.W., Keeton, W.S., Royo, A.A., Walters, M.B., Webster, C.R., Willis, J.L., 2017. Challenges facing gap-based silviculture and possible solutions for mesic northern forests in North America. *Forestry* 90, 4–17. <https://doi.org/10.1093/forestry/cpw024>.
- Knapp, S.P., Webster, C.R., Kern, C.C., 2019. The composition and height of saplings capturing silvicultural gaps at two long-term experiments in managed Northern Hardwood forests. *Forests* 10, 855.
- Kohen, A.E., Venet, L., Mousseau, M., 1993. Growth and photosynthesis of two deciduous forest species at elevated carbon dioxide. *Funct. Ecol.* 7, 480. <https://doi.org/10.2307/2390035>.
- Kohler, M., Pyttel, P., Kuehne, C., Modrow, T., Bauhus, J., 2020. On the knowns and unknowns of natural regeneration of silviculturally managed sessile oak (*Quercus petraea* (Matt.) Liebl.) forests—a literature review. *Ann. For. Sci.* 77, 101. <https://doi.org/10.1007/s13595-020-00998-2>.
- Komonen, A., Paananen, E., Elo, M., Valkonen, S., 2020. Browsing hinders the regeneration of broadleaved trees in uneven-aged forest management in southern Finland. *Scand. J. For. Res.* 35, 134–138. <https://doi.org/10.1080/02827581.2020.1761443>.
- Kopij, G., 2023. Spatial and temporal variation in population densities of the roe deer *Capreolus capreolus* and the red deer *Cervus elaphus* in SW Poland. *J. Agric. For.* 69. <https://doi.org/10.17707/AgricFor.69.1.12>.
- Kovács, B., Tinya, F., Guba, E., Németh, C., Sass, V., Bidló, A., Ódor, P., 2018. The short-term effects of experimental forestry treatments on site conditions in an oak–hornbeam forest. *Forests* 9, 406. <https://doi.org/10.3390/f9070406>.
- Kovács, B., Tinya, F., Németh, C., Ódor, P., 2020. Unfolding the effects of different forestry treatments on microclimate in oak forests: results of a 4-yr experiment. *Ecol. Appl.* 30. <https://doi.org/10.1002/eap.2043>.
- Kuehne, C., Pyttel, P., Modrow, T., Kohnle, U., Bauhus, J., 2020. Seedling development and regeneration success after 10 years following group selection harvesting in a sessile oak (*Quercus petraea* [Mattuschka] Liebl.) stand. *Ann. For. Sci.* 77, 71. <https://doi.org/10.1007/s13595-020-00972-y>.
- Kuijper, D.P.J., 2011. Lack of natural control mechanisms increases wildlife–forestry conflict in managed temperate European forest systems. *Eur. J. For. Res.* 130, 895–909. <https://doi.org/10.1007/s10342-011-0523-3>.
- Kuijper, D.P.J., Croomsigt, J.P.G.M., Churski, M., Adam, B., Jędrzejewska, B., Jędrzejewski, W., 2009. Do ungulates preferentially feed in forest gaps in European temperate forest? *For. Ecol. Manag.* 258, 1528–1535. <https://doi.org/10.1016/j.foreco.2009.07.010>.
- Kuijper, D.P.J., Jędrzejewska, B., Brzezicki, B., Churski, M., Jędrzejewski, W., Żybura, H., 2010. Fluctuating ungulate density shapes tree recruitment in natural stands of the Białowieża Primeval Forest, Poland: fluctuating ungulate density shapes tree recruitment. *J. Veg. Sci.* 21, 1082–1098. <https://doi.org/10.1111/j.1654-1103.2010.01217.x>.
- Kupferschmid, A.D., Bugmann, H., 2008. Ungulate browsing in winter reduces the growth of *Fraxinus* and *Acer* saplings in subsequent unbrowsed years. *Plant Ecol.* 198, 121–134. <https://doi.org/10.1007/s11258-007-9390-x>.
- Lendzion, J., Leuschner, C., 2009. Temperate forest herbs are adapted to high air humidity — evidence from climate chamber and humidity manipulation experiments in the field. *Can. J. For. Res.* 39, 2332–2342. <https://doi.org/10.1139/X09-143>.
- Lenth, R.V., 2021. emmeans: estimated marginal means, aka least-squares means. R package version 1.6.3. <https://doi.org/10.32614/CRAN.package.emmeans>.
- Leonardsson, J., Löf, M., Götmark, F., 2015. Exlosures can favour natural regeneration of oak after conservation-oriented thinning in mixed forests in Sweden: a 10-year study. *For. Ecol. Manag.* 354, 1–9. <https://doi.org/10.1016/j.foreco.2015.07.004>.
- Ligot, G., Balandier, P., Fayolle, A., Lejeune, P., Claessens, H., 2013. Height competition between *Quercus petraea* and *Fagus sylvatica* natural regeneration in mixed and uneven-aged stands. *For. Ecol. Manag.* 304, 391–398. <https://doi.org/10.1016/j.foreco.2013.05.050>.
- Linnell, J.D.C., Cretois, B., Nilsen, E.B., Rolandsen, C.M., Solberg, E.J., Veiberg, V., Kaczensky, P., Van Moorter, B., Panzacchi, M., Rauset, G.R., Kaltenborn, B., 2020. The challenges and opportunities of coexisting with wild ungulates in the human-dominated landscapes of Europe's Anthropocene. *Biol. Conserv.* 244, 108500. <https://doi.org/10.1016/j.biocon.2020.108500>.
- Löf, M., Barrere, J., Engman, M., Petersson, L.K., Villalobos, A., 2021. The influence of fencing on seedling establishment during reforestation of oak stands: a comparison of artificial and natural regeneration techniques including costs. *Eur. J. For. Res.* 140, 807–817. <https://doi.org/10.1007/s10342-021-01369-w>.
- Löf, M., Brunet, J., Filyushkina, A., Lindblad, M., Skovsgaard, J.P., Felton, A., 2016. Management of oak forests: striking a balance between timber production, biodiversity and cultural services. *International Journal of Biodiversity Science, Ecosystem Services & Management* 12, 59–73. <https://doi.org/10.1080/2151-3732.2015.1120780>.
- Mason, W.L., Diaci, J., Carvalho, J., Valkonen, S., 2021. Continuous cover forestry in Europe: usage and the knowledge gaps and challenges to wider adoption. *Forestry* 95, 1–12. <https://doi.org/10.1093/forestry/cpab038>.
- Massei, G., Kindberg, J., Licoppe, A., Gacić, D., Šprem, N., Kamler, J., Baubet, E., Hohmann, U., Monaco, A., Ozoliņš, J., Cellina, S., Podgórski, T., Fonseca, C., Markov, N., Pokorný, B., Rosell, C., Náhlik, A., 2015. Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. *Pest Manag. Sci.* 71, 492–500. <https://doi.org/10.1002/ps.3965>.
- Meeussen, C., De Pauw, K., Sanczuk, P., Brunet, J., Cousins, S.A.O., Gasperini, C., Hedwall, P.-O., Iacopetti, G., Lenoir, J., Plue, J., Selvi, F., Spicher, F., Uria Diez, J., Verheyen, K., Vangansbeke, P., De Frenne, P., 2022. Initial oak regeneration responses to experimental warming along microclimatic and macroclimatic gradients. *Plant Biol.* 24, 745–757. <https://doi.org/10.1111/plb.13412>.
- Messier, C.C., Puettmann, K.J., Coates, K.D. (Eds.), 2013. *Managing Forests as Complex Adaptive Systems: Building Resilience to the Challenge of Global Change*, first ed. The Earthscan Forest Library. Earthscan from. Routledge, Abingdon.
- Mitchell, F.J.G., 2005. How open were European primeval forests? Hypothesis testing using palaeoecological data. *J. Ecol.* 93, 168–177. <https://doi.org/10.1111/j.1365-2745.2004.00964.x>.
- Modrow, T., Kuehne, C., Saha, S., Bauhus, J., Pyttel, P.L., 2020. Photosynthetic performance, height growth, and dominance of naturally regenerated sessile oak (*Quercus petraea* [Mattuschka] Liebl.) seedlings in small-scale canopy openings of varying sizes. *Eur. J. For. Res.* 139, 41–52. <https://doi.org/10.1007/s10342-019-01238-7>.
- Mölder, A., Sennhenn-Reulen, H., Fischer, C., Rumpf, H., Schönfelder, E., Stockmann, J., Nagel, R.-V., 2019. Success factors for high-quality oak forests? Hypothesis testing using palaeoecological data. *J. Ecol.* 93, 168–177. <https://doi.org/10.1111/j.1365-2745.2004.00964.x>.
- Murphy, T.R., Hanley, M.E., Ellis, J.S., Lunt, P.H., 2022. Optimizing opportunities for oak woodland expansion into upland pastures. *Ecological Solutions and Evidence* 3, e12126. <https://doi.org/10.1002/2688-8319.12126>.
- Newman, M., Mitchell, F.J.G., Kelly, D.L., 2014. Exclusion of large herbivores: long-term changes within the plant community. *For. Ecol. Manag.* 321, 136–144. <https://doi.org/10.1016/j.foreco.2013.09.010>.
- Niculescu, V.-N., Vor, T., Brus, R., Dodan, M., Perić, S., Podrázský, V., Andrašev, S., Tsavkov, E., Ayan, S., Yücedağ, C., Trajkov, P., Kolevska, D.D., Buzatu-Goanță, C., Păstor, M., Macejovský, V., Modránský, J., Kliz, M., Gil, W., Lavnyy, V., Madsen, P., La Porta, N., Bartlett, D., 2025. Management of sessile oak (*Quercus petraea* (Matt.) Liebl.), a major forest species in Europe. *J. For. Res.* 36, 78. <https://doi.org/10.1007/s11676-025-01868-1>.
- Nopp-Mayr, U., Reimoser, S., Reimoser, F., Sachser, F., Obermair, L., Gratzner, G., 2020. Analyzing long-term impacts of ungulate herbivory on forest-recruitment dynamics at community and species level contrasting tree densities versus maximum heights. *Sci. Rep.* 10, 20274. <https://doi.org/10.1038/s41598-020-76843-3>.
- Ohse, B., Seele, C., Holzwarth, F., Wirth, C., 2017. Different facets of tree sapling diversity influence browsing intensity by deer dependent on spatial scale. *Ecol. Evol.* 7, 6779–6789. <https://doi.org/10.1002/ece3.3217>.
- Pellerin, M., Said, S., Richard, E., Hamann, J.-L., Dubois-Coli, C., Hum, P., 2010. Impact of deer on temperate forest vegetation and woody debris as protection of forest regeneration against browsing. *For. Ecol. Manag.* 260, 429–437. <https://doi.org/10.1016/j.foreco.2010.04.031>.
- Pemán, J., Chirino, E., Espelta, J.M., Jacobs, D.F., Martín-Gómez, P., Navarro-Cerrillo, R., Oliet, J.A., Vilagrosa, A., Villar-Salvador, P., Gil-Pelegrín, E., 2017. Physiological keys for natural and artificial regeneration of oaks. In: Gil-Pelegrín, E., Peguero-Pina, J.J., Sancho-Knapik, D. (Eds.), *Oaks Physiological Ecology. Exploring the Functional Diversity of Genus Quercus L., Tree Physiology*. Springer, Cham, Cham, pp. 453–511. https://doi.org/10.1007/978-3-319-69099-5_14.
- Perea, R., Gil, L., 2014. Tree regeneration under high levels of wild ungulates: the use of chemically vs. physically-defended shrubs. *For. Ecol. Manag.* 312, 47–54. <https://doi.org/10.1016/j.foreco.2013.10.022>.
- Pommerening, A., Murphy, S.T., 2004. A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. *Forestry* 77, 27–44. <https://doi.org/10.1093/forestry/77.1.27>.
- Post, E., Nils Chr, S., Langvatn, R., Fromentin, J.-M., 1997. *Global climate change and phenotypic variation among Red Deer cohorts*. *Proceedings: Biological Sciences* 264, 1317–1324.
- R Core Team, 2022. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Ramirez, J.L., Jansen, P.A., den Ouden, J., Goudzwaard, L., Poorter, L., 2019. Long-term effects of wild ungulates on the structure, composition and succession of temperate forests. *For. Ecol. Manag.* 432, 478–488. <https://doi.org/10.1016/j.foreco.2018.09.049>.
- Ramirez, J.L., Jansen, P.A., Poorter, L., 2018. Effects of wild ungulates on the regeneration, structure and functioning of temperate forests: a semi-quantitative review. *For. Ecol. Manag.* 424, 406–419. <https://doi.org/10.1016/j.foreco.2018.05.016>.
- Reimoser, F., Gossow, H., 1996. Impact of ungulates on forest vegetation and its dependence on the silvicultural system. *For. Ecol. Manag.* 88, 107–119. [https://doi.org/10.1016/S0378-1127\(96\)03816-9](https://doi.org/10.1016/S0378-1127(96)03816-9).

- Rooney, T.P., Waller, D.M., 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *For. Ecol. Manag.* 181, 165–176. [https://doi.org/10.1016/S0378-1127\(03\)00130-0](https://doi.org/10.1016/S0378-1127(03)00130-0).
- Rossell, C.R., Patch, S., Susan, S., 2007. Effects of deer browsing on native and non-native vegetation in a mixed oak-beech forest on the Atlantic coastal plain. *Northeast. Nat.* 14, 61–72.
- Royo, A.A., Kramer, D.W., Miller, K.V., Nibbelink, N.P., Stout, S.L., 2017. Spatio-temporal variation in foodscapes modifies deer browsing impact on vegetation. *Landsc. Ecol.* 32, 2281–2295. <https://doi.org/10.1007/s10980-017-0568-x>.
- Schäfer, D., Prati, D., Schall, P., Ammer, C., Fischer, M., 2019. Exclusion of large herbivores affects understorey shrub vegetation more than herb vegetation across 147 forest sites in three German regions. *PLoS One* 14, e0218741. <https://doi.org/10.1371/journal.pone.0218741>.
- Schall, P., Heinrichs, S., Ammer, C., Ayasse, M., Boch, S., Buscot, F., Fischer, M., Goldmann, K., Overmann, J., Schulze, E.-D., Sikorski, J., Weisser, W.W., Wubet, T., Gossner, M.M., 2020. Can multi-taxa diversity in European beech forest landscapes be increased by combining different management systems? *J. Appl. Ecol.* 57, 1363–1375. <https://doi.org/10.1111/1365-2664.13635>.
- Schwegmann, S., Mörsdorf, M., Bhardwaj, M., Storch, I., 2023. Effects of understory characteristics on browsing patterns of roe deer in central European mountain forests. *Ecol. Evol.* 13, e10431. <https://doi.org/10.1002/ece3.10431>.
- Smit, C., Kuijper, D.P.J., Prentice, D., Wassen, M.J., Croomsigt, J.P.G.M., 2012. Coarse woody debris facilitates oak recruitment in Białowieża Primeval Forest, Poland. *For. Ecol. Manag.* 284, 133–141. <https://doi.org/10.1016/j.foreco.2012.07.052>.
- Smit, C., Putman, R., 2010. Large Herbivores as “Environmental Engineers.” Cambridge University Press, Cambridge, pp. 260–283.
- Spiecker, H., 2003. Silvicultural management in maintaining biodiversity and resistance of forests in Europe—Temperate zone. *J. Environ. Manag.* 67, 55–65. [https://doi.org/10.1016/S0301-4797\(02\)00188-3](https://doi.org/10.1016/S0301-4797(02)00188-3).
- Stephan, J.G., Pourazari, F., Tattersdill, K., Kobayashi, T., Nishizawa, K., De Long, J.R., 2017. Long-term deer enclosure alters soil properties, plant traits, understory plant community and insect herbivory, but not the functional relationships among them. *Oecologia* 184, 685–699. <https://doi.org/10.1007/s00442-017-3895-3>.
- Stergar, M., Jerina, K., 2017. Wildlife and forest management measures significantly impact red deer population density. *Šumarski list* 141, 149–150. <https://doi.org/10.31298/sl.141.3-4>.
- Stiegel, S., Korfthage, A., Mantilla-Contreras, J., 2020. Does the shrub layer act as an intermediary? Effects on abundance of insects and abundances of particular insect orders caught flying in the canopies of deciduous forests in Central Germany. *Eur. J. Entomol.* 117, 409–419. <https://doi.org/10.14411/eje.2020.045>.
- Stokes, V., Kerr, G., 2009. The Evidence Supporting the Use of CCF in Adapting Scotland's Forests to the Risks of Climate Change. Forest Research, Farnham, UK, p. 53. <https://www.forestresearch.gov.uk/>. (Accessed 28 February 2025).
- Thomas-Van Gundy, M., Rentch, J., Adams, M.B., Carson, W., 2014. Reversing legacy effects in the understory of an oak-dominated forest. *Can. J. For. Res.* 44, 350–364. <https://doi.org/10.1139/cjfr-2013-0375>.
- Tinya, F., Csépanyi, P., Horváth, C.V., Kovács, B., Németh, C., Ódor, P., 2025. Fine-scale interventions can reinforce the forest character of the understory vegetation – the effects of different artificial gaps in an oak-dominated forest. *For. Ecol. Manag.* 578, 122471. <https://doi.org/10.1016/j.foreco.2024.122471>.
- Tinya, F., Kovács, B., Aszalós, R., Tóth, B., Csépanyi, P., Németh, C., Ódor, P., 2020. Initial regeneration success of tree species after different forestry treatments in a sessile oak-hornbeam forest. *For. Ecol. Manag.* 459, 117810. <https://doi.org/10.1016/j.foreco.2019.117810>.
- Tinya, F., Kovács, B., Bidló, A., Dima, B., Kutszegi, G., Lakatos, F., Mag, Z., Márialigeti, S., Nascimbene, J., Samu, F., Siller, I., Szél, G., Ódor, P., 2021. Environmental drivers of forest biodiversity in temperate mixed forests – a multi-taxon approach. *Sci. Total Environ.* 795, 148720. <https://doi.org/10.1016/j.scitotenv.2021.148720>.
- Tourani, M., Franke, F., Heurich, M., Henrich, M., Peterka, T., Ebert, C., Oeser, J., Edelhoft, H., Milleret, C., Dupont, P., Bischof, R., Peters, W., 2023. Spatial variation in red deer density in a transboundary forest ecosystem. *Sci. Rep.* 13, 4561. <https://doi.org/10.1038/s41598-023-31283-7>.
- Valente, A.M., Acevedo, P., Figueiredo, A.M., Fonseca, C., Torres, R.T., 2020. Overabundant wild ungulate populations in Europe: management with consideration of socio-ecological consequences. *Mamm. Rev.* 50, 353–366. <https://doi.org/10.1111/mam.12202>.
- VanderMolen, M.S., Webster, C.R., 2021. Influence of deer herbivory on regeneration dynamics and gap capture in experimental gaps, 18 years post-harvest. *For. Ecol. Manag.* 501, 119675. <https://doi.org/10.1016/j.foreco.2021.119675>.
- von Arx, G., Graf Pannatier, E., Thimonier, A., Rebetez, M., 2013. Microclimate in forests with varying leaf area index and soil moisture: potential implications for seedling establishment in a changing climate. *J. Ecol.* 101, 1201–1213. <https://doi.org/10.1111/1365-2745.12121>.
- von Lüpke, B., 1998. Silvicultural methods of oak regeneration with special respect to shade tolerant mixed species. *For. Ecol. Manag.* 106, 19–26. [https://doi.org/10.1016/S0378-1127\(97\)00235-1](https://doi.org/10.1016/S0378-1127(97)00235-1).
- Walters, M.B., Farinosi, E.J., Willis, J.L., 2020. Deer browsing and shrub competition set sapling recruitment height and interact with light to shape recruitment niches for temperate forest tree species. *For. Ecol. Manag.* 467, 118134. <https://doi.org/10.1016/j.foreco.2020.118134>.
- Weisberg, P.J., Bugmann, H., 2003. Forest dynamics and ungulate herbivory: from leaf to landscape. *For. Ecol. Manag.* 181, 1–12. [https://doi.org/10.1016/S0378-1127\(03\)00123-3](https://doi.org/10.1016/S0378-1127(03)00123-3).
- Zoltán, L., Szmorad, F., Standovár, T., 2024. Heavy ungulate pressure behind the disappearance of regeneration in Hungarian forests. *Forests* 15, 54. <https://doi.org/10.3390/f15010054>.
- Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology with R*, Statistics for Biology and Health. Springer, New York, NY.