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Fine-scale interventions can reinforce the forest character of the understory vegetation – The effects of different artificial gaps in an oak-dominated forest

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ABSTRACT

Forest biodiversity is threatened by the use of conventional rotation forestry system, while fine-scale interventions of continuous cover forestry, such as gap-cutting, could protect forest habitats and enhance the stand structural heterogeneity. Consequently, their use could maintain biodiversity during the timber production process. It is unclear which gap sizes and shapes can trigger ample natural regeneration while simultaneously maintaining or improving the near-natural character of the understory. The Pilis Gap Experiment examined the five-year effects of four gap types comparing two gap sizes (150 and 300 m^2) and two gap shapes (circular and elongated) on the light and soil moisture conditions and understory vegetation in an oak–hornbeam forest. The investigated understory variables included species richness, total cover, height, shrub cover and cover of five functional groups. Our results indicate an initially increased light in all gap types, but later it decreased in large circular gaps, while remaining more stable in other gap types. Soil moisture increased first, transiently in the circular gaps, and later in the elongated gaps. Species richness temporarily increased in large circular gaps, whereas total cover increased in all gap types. Understory height and shrub cover also increased in large circular gaps. Annual and perennial forb cover remained unchanged in all gap types, although graminoid cover showed transient growth in large elongated gaps. Small gaps had the highest cover of woody seedlings, whereas bramble (*Rubus fruticosus* agg.) cover increased the most in large circular gaps. Species composition exhibited the most significant changes in large circular gaps. From a conservation aspect, all gap types can be considered favorable, as they increase the heterogeneity of the openness and understory vegetation in homogeneous closed stands. Vegetation changes are the most prominent in large circular gaps w spread of bramble here multiple vegetation layers developed. However, the dense cover of bramble and shrubs hinders the effective regeneration of sessile oak (*Quercus petraea*). Smaller gaps slightly increase the heterogeneity of the forest understory and provide ample light and soil moisture to initiate regeneration. In larger gaps, oak regeneration may be supported by applying an elongated shape, mitigating the competition from bramble.

Abbreviations: CCF, continuous cover forestry; CO, uncut control plot; dbRDA, distance-based redundancy analysis; DSF, direct site factor; ISF, indirect site factor; LC, large circular gap; LE, large elongated gap; SC, small circular gap; SE, small elongated gap; VWC, volumetric soil water content.

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1. Introduction

Biodiversity loss represents a significant global risk in the Anthropocene era (World Economic Forum, 2023). In forests, a key contributing factor in this regard is the application of conventional (business-as-usual type) forest management practices (IPBES, 2018). At the same time, there is an increasing social demand for the various ecosystem services of forests including recreation and climate change mitigation, beyond timber production. To uphold forest biodiversity and multifunctionality, European governmental organizations urge transformative management changes (IPBES, 2019; European Commission, 2021). Continuous cover forestry (CCF), proposed as an alternative to conventional rotation forestry systems, presents itself as a viable approach for harmonizing timber production and biodiversity conservation (Mason et al., 2022). The concept behind this forest management system is to mimic the natural fine-scale disturbances present in temperate deciduous forest by creating artificial gaps, while simultaneously maintaining the continuity of the canopy layer at the stand scale (Bengtsson et al., 2000; Diaci, 2006). A growing body of evidence demonstrate that this type of management promotes the preservation of forest biodiversity and ecosystem services (e.g., Elek et al., 2018; Peura et al., 2018; Tomao et al., 2020). Furthermore, Brang et al. (2014) state that this approach can enhance the adaptation of forests to changing climatic conditions. Nevertheless, CCF is competitive with rotation forestry even in timber production (Wobst, 2006; Zingg et al., 2009).

CCF is becoming increasingly popular in Europe (Aszalós et al., 2022). A widely used technique for the natural regeneration within the framework of CCF is gap-cutting, i.e. creating small openings of varying sizes and shapes (typically less than 1000 m^2, Muscolo et al., 2014). However, research has not yet sufficiently explored the impact of various gap-cutting types on forest biodiversity, and the specific technologies involved in these systems are yet to be completely elaborated (Mason et al., 2022). While foresters have already gathered substantial empirical information on these issues (mainly on regeneration, Diaci, 2006), scientific evidence-based data on understory vegetation is still limited (Mason et al., 2022).

The augmented resources within gaps facilitate the initiation of tree regeneration (Schütz et al., 2016). However, the abundance and composition of the herbaceous understory vegetation undergo alterations, as well (Schumann et al., 2003; Tinya et al., 2019). Knowledge of the vegetation responses to gap openings is critical for silvicultural, ecological and conservation perspectives. Several studies showed that, compared to large-scale cutting areas done by rotation forestry, fine-scale gaps do not transform the understory to non-forest vegetation types (Schumann et al., 2003; Tinya et al., 2019; Aszalós et al., 2023), but detailed information regarding the effect of various types of gaps is missing. To achieve successful regeneration of a forest, foresters must identify gap types that favor the desired woody species in their competition with herbs, as noted by Mountford et al. (2006) and Vilhar et al. (2015). The ecological and conservation relevance of the understory is evidenced by the fact that vegetation represents a significant component of biodiversity, and that it affects various other organism groups, not just through trophic interactions, but also by providing habitat for numerous taxa (Gilliam, 2007).

Studying the vegetation development in gaps of oak-hornbeam forests is especially crucial because regenerating the light-demanding oaks (*Quercus spp.*) in small openings is challenging, particularly when shade-tolerant tree species are also present (Mölder et al., 2019). Oak regeneration is problematic across the globe, in both managed and unmanaged forests (Van Couwenberghe et al., 2013; Saniga et al., 2014; Bölöni et al., 2021). Information concerning oak regeneration in gaps and its relationship with the competing understory vegetation is limited and controversial (von Lüpke, 1998; Cowell et al., 2010; Kohler et al., 2020). Additionally, evidence on the primeval character of stand structure, regeneration processes and understory vegetation in oak-dominated forests is scarce, due to prolonged human influence on most stands of this forest type (Parviainen, 2005; Bobiec et al., 2011; Bölöni et al., 2021). Although there are only hypotheses on the drivers, it is likely that oak-dominated forests were more open and had a more heterogeneous structure before the era of rotation forestry systems, as supported by Vera (2000), Hofmeister et al. (2009), and Bobiec et al. (2018). Thus, these forests maintained a more heterogeneous understory layer than the sparse and uniform herb layer found in recent oak-hornbeam forests (Peterken, 1996). Through the fine-scale artificial opening of the canopy, foresters can shift stands towards a more diverse stand structure found in natural forests. Local canopy opening can initiate the diversification of the understory vegetation, which leads to a more complex structure and composition of the herb layer, allowing for suitable habitat conditions for a variety of forest organisms (de Groot et al., 2016; Vild et al., 2024). In addition, oak regeneration can also be initiated in gaps with proper environmental circumstances (Tinya et al., 2020). However, excessive canopy opening may lead to the proliferation of light-flexible competitor species, like bramble (*Rubus fruticosus* agg.), which is a semi-woody, scrambling plant (Balandier et al., 2013). This could impede the natural regeneration (Shields et al., 2007) and hinder the graminoid and forb species, impoverishing the community due to the shading of the understory layer.

The effect of gap establishment on the vegetation depends heavily on gap size and shape, as both have a significant effect on the microclimate conditions (Ritter et al., 2005; Kern et al., 2014; Muscolo et al., 2014). Using the same experiment as in the current study, Horváth et al. (2023) noted that in the first year after the interventions, larger gaps receive greater amounts of relative diffuse light, while gap shape is more influential in determining soil moisture conditions. Gap-cutting increases soil moisture by limiting canopy interception and by reducing transpiration with the loss of tree individuals (Muscolo et al., 2014; Vilhar et al., 2015). Circular gaps have less root penetration towards the gap center compared to elongated gaps of the same size, resulting in lower water uptake and increased soil water content in circular gaps (Horváth et al., 2023).

The objective of this research was to examine the response of the understory vegetation to the creation of gaps with different sizes and shapes in a sessile oak–hornbeam forest in Central Hungary over a five-year period. We performed an experimental study using a full factorial design, including two gap sizes and two gap shapes. We also assessed the impact of different gap types on the light and soil moisture conditions and their effect on the understory response.

Our specific questions were:

1. How do light and soil moisture conditions vary across gaps of various sizes and shapes in comparison to a closed control stand in the first five years after intervention?

2. How do the different gap types impact the species richness, total cover and height of the understory as compared to the uncut stand? How do different gap-cuttings change the cover of the shrub layer?

3. What is the difference in the cover of functional groups (annual forbs, perennial forbs, graminoids, woody regeneration and bramble as an independent functional group) among different gap types and the uncut stand?

4. How does the species composition of the understory vegetation differ in the various gap types and the control?

5. How do the vegetation responses correlate with the light and soil moisture conditions?

The current study have been carried out in the framework of the Pilis Gap Experiment, a multi-taxa forest ecological study initiated in 2018 to examine the impact of various gap types on forest site conditions, biodiversity, and regeneration (https://piliskiserlet.ecolres.hu/en). Horváth et al. (2023) already explored the initial microclimatic responses of gap-cuttings, while Samu et al. (2023) described the changes in spider communities following the interventions.

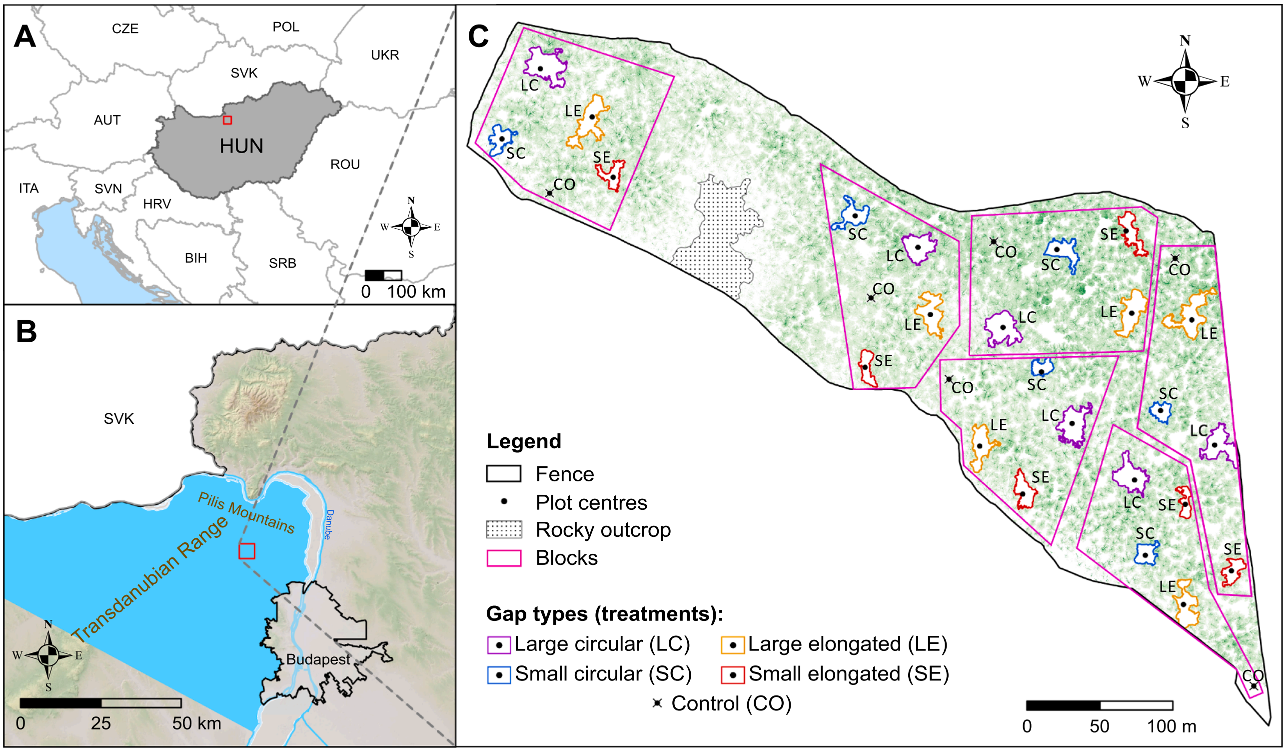

Fig. 1. Location of the experimental area in Hungary (a), situated in the Pilis Mountains, Transdanubian Range (b) and the map of the study area (c). Five treatments have been conducted in six replications (blocks). The large gaps have an area of approximately 300 m^2, while the small gaps have an area of approximately 150 m^2. The green shading represents the canopy projections of the trees based on LiDAR measurements.

2. Methods

2.1. Study area

The Pilis Gap Experiment is situated on the hill Hosszú-hegy (Pilis Mountains, Transdanubian Range, Hungary 47°40′ N, 18°54′ E; Fig. 1(a, b)), on moderate northeast-facing slopes (18.2° ± 14.9°) at 390–460 m altitude. The area has a humid continental climate, with mean annual temperature of 9.0–9.5 °C and mean annual precipitation of 650 mm (Dövényi, 2010). The bedrock of the experimental area comprises sandstone with loess intermingled with limestone (Dövényi, 2010). The most common soil types are Luvisols (predominantly brown forest soils with clay illuviation) and Rendzic Leptosol. The soil has a slightly acidic pH of 4.6 ± 0.2 and its depth varies between 70 and 150 cm across a gentle topographic gradient (Horváth et al., 2023). The study area is located in a Hungarian oak–hornbeam forest (Natura 2000 code: 91G0, Council, 1992) that was previously managed by shelterwood forestry system. The most recent intervention was a thinning in 2010. As a result of this management type, the stand was even-aged (90 years old) and exhibited uniform structure and species composition prior to the experimental treatments. The upper canopy layer was dominated by sessile oak (*Quercus petraea*), with *Carpinus betulus* forming a secondary canopy layer (Horváth et al., 2023). Admixing species present included *Quercus cerris*, *Fraxinus ornus* and *Sorbus torminalis*. The shrub layer was scarce, and largely comprised of *Carpinus betulus* and *Fraxinus ornus* patches with some admixing shrub species (such as *Cornus sanguinea*, *C. mas*, *Crataegus monogyna* and *Ligustrum vulgare*). Following the thinning in 2010, a dense understory layer has emerged with both general and mesic forest species, of which *Carex pilosa*, *Melica uniflora* and *Galium schultesii* were the most prevalent.

2.2. Experimental design

Five treatment types were implemented in a randomized complete block design across six blocks as replicates, resulting in a total of 30 plots (Fig. 1(c)) as the following:

(1) large circular gaps (LC): diameter: 20 m, area: approx. 300 m^2 (equivalent to a 1:1 gap diameter to canopy height ratio);

(2) small circular gaps (SC): diameter: 14 m, area: approx. 150 m^2 (equivalent to a 0.6 diameter to height ratio);

(3) large elongated gaps (LE): 10 m × 30 m rectangles, area: approx. 300 m^2;

(4) small elongated gaps (SE): 7 m × 21 m rectangles, area: approx. 150 m^2;

(5) uncut control (CO).

Gaps were established in February 2019, using the expanded gap concept (Runkle, 1982). The orientation of elongated gaps was north-south. Detailed description of the gaps can be found in Horváth et al. (2023), photos of the plots are on Figure A.1. The entire 9.7-hectare experimental area was fenced against ungulates.

2.3. Data collection

The understory sampling followed a Before-After-Control-Impact design. The first survey took place in 2018 (before the interventions), and was later repeated every year until 2023, during April and June. Understory vegetation was sampled in the center of each plot using a 2 m × 2 m quadrat. Our assumption was that with gap centers we can represent that part of the gaps which shows the strongest difference from the closed forests. Moreover, as the gaps were all relatively small in size, the gap centers were expected to reflect the effects caused by gap closure (i.e. growth of the surrounding tree canopies), too. Percentage cover for all herbaceous vascular plant species and woody species less than 0.5 m in height was estimated visually. Most of the species were recorded in June, while in April, we recorded species that can be detected optimally in spring. Some species, occurring both in spring and summer, were sampled on both occasions, and for each species, we chose the higher cover values for analysis. Understory height for each quadrat was

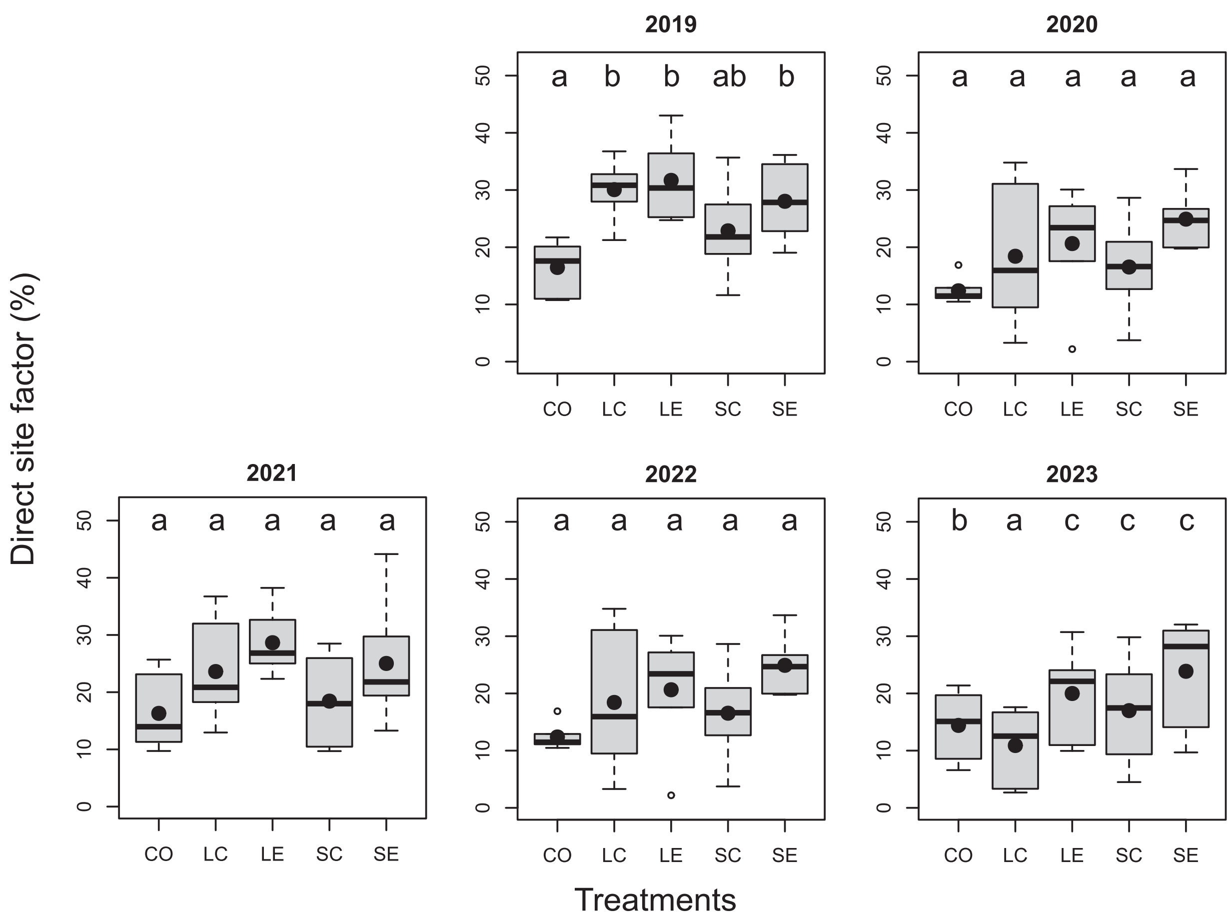

Fig. 2. Boxplots of the relative direct light (DSF) in the different treatments for the studied years. Interventions were carried out in winter 2018–2019. CO = uncut control, LC = large circular, LE = large elongated, SC = small circular, SE = small elongated gaps. Black dots represent the mean values. Different letters indicate significant differences at $P < 0.05$ level.

described by a visual estimate which captured the characteristic height of the whole understory layer within the plot on a 10 cm resolution scale. The total cover of the shrub layer (woody species above 50 cm height but below 5 cm diameter at breast height) was also registered in each quadrat by visual estimations. The nomenclature of plants follows Király (2009).

In 2018, relative diffuse light (diffuse non-interceptance, which is the percentage of diffuse light coming through the canopy) was estimated by LAI-2000 Plant Canopy Analyzer (LI-COR Inc., Lincoln, USA). We conducted measurements in the center of each plot at a height of 1.3 meters above ground level. Measurements were taken in July and in order to prevent direct light reaching the sensor, always at dusk. A 270° view restrictor masked the segment of the sky containing the sun and the operator (LI-COR Inc. 1992). Above-canopy reference measurements were taken in a nearby open field. Since 2019, hemispherical photographs were used to estimate light in the gap centers at a height of 1.3 m using a KODAK PIXPRO SP360 camera. To reduce any bias caused by capturing the sun-disk or the reflectance of direct sunlight on the leaves, all photographs were taken at dusk. The WinSCANOPY 2019 software (Regent Instruments Inc., Québec, Canada) was used to calculate diffuse and direct components of the incoming radiation (indirect and direct site factor, ISF and DSF respectively; %) relative to above-canopy light. The analysis period for the radiation calculation was between 01 May and 30 September. To ensure comparability of light data collected by different instruments during the pre- and post-treatment periods, parallel measurements were conducted in 2020 using the Plant Canopy Analyzer and hemispherical photography. The diffuse non-interceptance values measured by the Plant Canopy Analyzer were calibrated and converted by regression to the ISF values obtained from the hemispherical photographs.

Soil moisture was measured in 2018 by a FieldScout TDR 350 probe equipped with 7.5 cm steel rods (Spectrum Technologies Inc., Aurora, USA). Two measurement campaigns were carried out in the vegetation season, one in June and one in August. Four measurements were taken at the midpoints of the sides of the vegetation quadrat for each plot. The volumetric soil water content (VWC; m^3/m^3) of each plot was then expressed as the average of the values of the four measurements. From 2019, soil moisture (VWC) data were continuously collected from the upper 14 cm soil layer by TMS-4 loggers with 15-min logging intervals (TOMST s.r.o., Praha, CZ, Wild et al., 2019).

2.4. Data analysis

Linear mixed-effects models were built at the plot level, to explore (a) the effect of silvicultural treatments on the measured light (ISF, DSF) and soil moisture (VWC) variables and (b) the effect of treatments on understory variables, for each year separately, from 2018 to 2023 (Zuur et al., 2009). The relationship between light and soil moisture levels and understory variables was also analyzed using linear mixed-effects models (c). This analysis was conducted solely for the fifth year following the gap creation (2023) due to the assumption that there would be minimal discrepancy between the results of the different years but the longer-time responses are more robust.

For 2018, only relative diffuse light data were available, while for the years 2019–2023, both relative direct and diffuse light were analyzed, in separate models. Among the soil moisture variables, we used the mean values of the daily means for the vegetation period (from 01 May to 30 September) in the case of every year. The year 2018 was an exception,

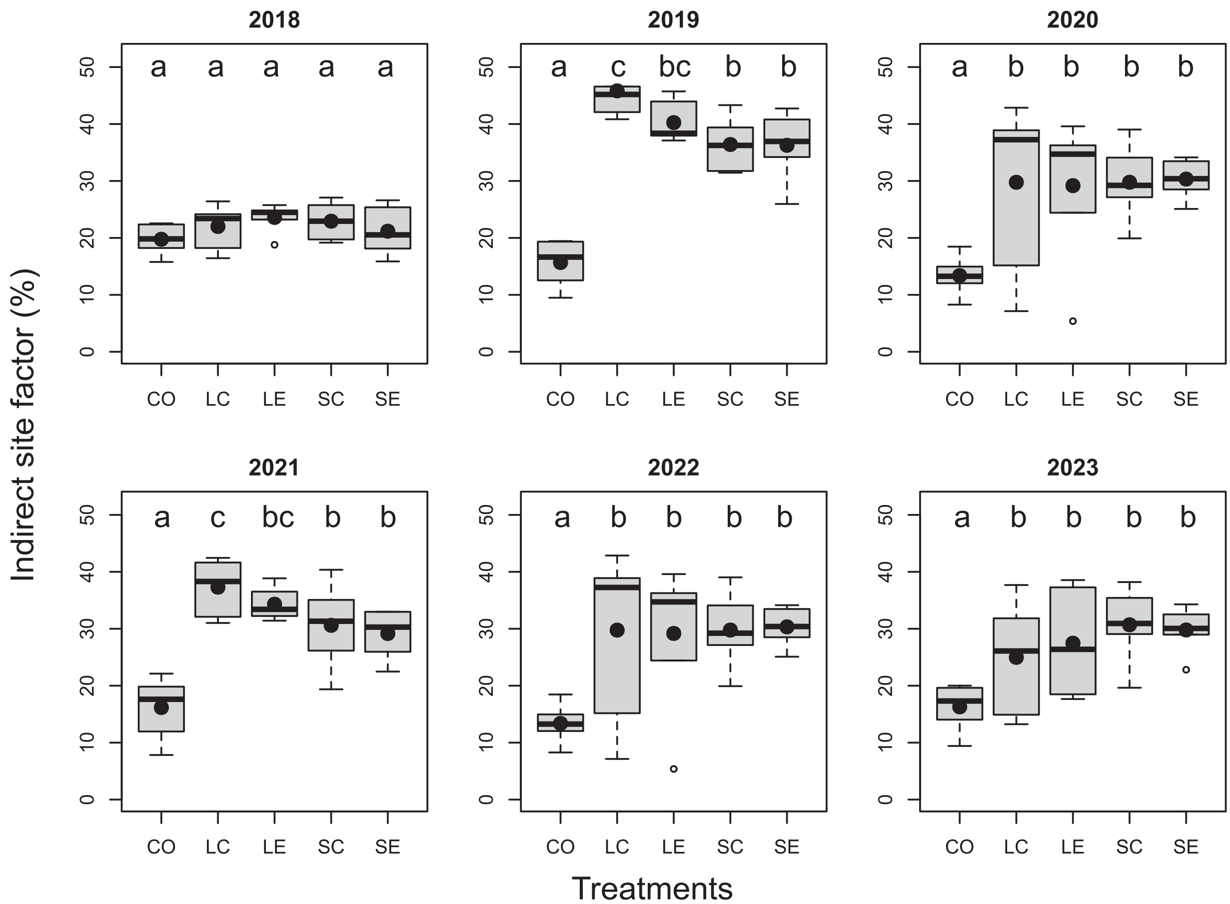

Fig. 3. Boxplots of the relative diffuse light (ISF) in the different treatments for the studied years. Interventions were carried out in winter 2018–2019. CO = uncut control, LC = large circular, LE = large elongated, SC = small circular, SE = small elongated gaps. Black dots represent the mean values. Different letters indicate significant differences at P < 0.05 level.

for this year only two data per plot were available (June, August), originated from the instantaneous measurements with the TDR.

The vegetation variables examined were species richness, total understory cover, mean understory height, cover of the shrub layer and cover of functional groups. Species richness was calculated as the number of vascular plant species in each quadrat for each year. Total understory cover was obtained by summarizing the cover of each species for each quadrat, for each year. For shrub cover, the relationship with light was not analyzed, because light values measured at 1.3 m height did not represent well the amount of light received by the shrub layer (which was higher than 1.3 m in several cases). Species were classified into functional groups such as annual forbs, perennial forbs (including fern species), graminoids (species of the families *Poaceae*, *Cyperaceae,* and *Juncaceae*) and woody regeneration based on the Raunkiaer's plant life-forms (Király, 2009); and the total cover of these groups was calculated as the sum of the cover of the species in the group. Bramble (*Rubus fruticosus* agg.) was considered and analyzed as a fifth, individual functional group, due to its distinctive growth characteristics and its special effect on the understory vegetation and oak regeneration (Kohler et al., 2020; Laurent et al., 2017).

Fixed effects were the treatments (a and b) or the environmental (light and soil moisture) variables (c). Block was used as a random factor. In the case of treatment – soil moisture models, month-level mean values of the daily means were used as soil moisture data (i.e. five data per year: May, June, July, August, September), and month was used as a second random factor. For 2018, the instantaneous values measured in June and August (i.e. two data per year) were used. To meet the normality requirement for the residual distributions, ln- or square root transformation was applied to several understory variables. If the treatment effect was significant (P < 0.05), multiple comparisons were performed with user-defined contrasts to find the significantly different treatment types (Bretz et al., 2010).

Relationships between treatments, environmental variables (light

Table 1
Mixed-effects models for the studied light and soil moisture variables. Fixed effect: treatment type, random factor: block (and month in the soil water content models).

Year	Model parameters	Environmental variables		
		DSF	ISF	VWC
2018	F-value	NA	1.541	0.519
	p	NA	0.229	0.722
	R^2_{pseudo}	NA	0.316	0.837
2019	F-value	**5.283**	**37.201**	**8.798**
	p	**0.005**	**< .0001**	**< .0001**
	R^2_{pseudo}	**0.429**	**0.839**	0.390
2020	F-value	1.958	**3.832**	**8.780**
	p	0.140	**0.018**	**< .0001**
	R^2_{pseudo}	0.25652	**0.370**	**0.251**
2021	F-value	2.828	**22.517**	**2.732**
	p	0.052	**< .0001**	**0.032**
	R^2_{pseudo}	0.40889	**0.783**	**0.679**
2022	F-value	1.958	**3.832**	2.340
	p	0.140	**0.018**	0.059
	R^2_{pseudo}	0.25652	0.370	0.596
2023	F-value	**4.134**	**4.670**	2.894
	p	**0.013**	**0.008**	0.025
	R^2_{pseudo}	**0.575**	**0.471**	0.541

DSF = direct site factor, ISF = indirect site factor, VWC = volumetric soil water content. Values in boldface indicate significant treatment effects.

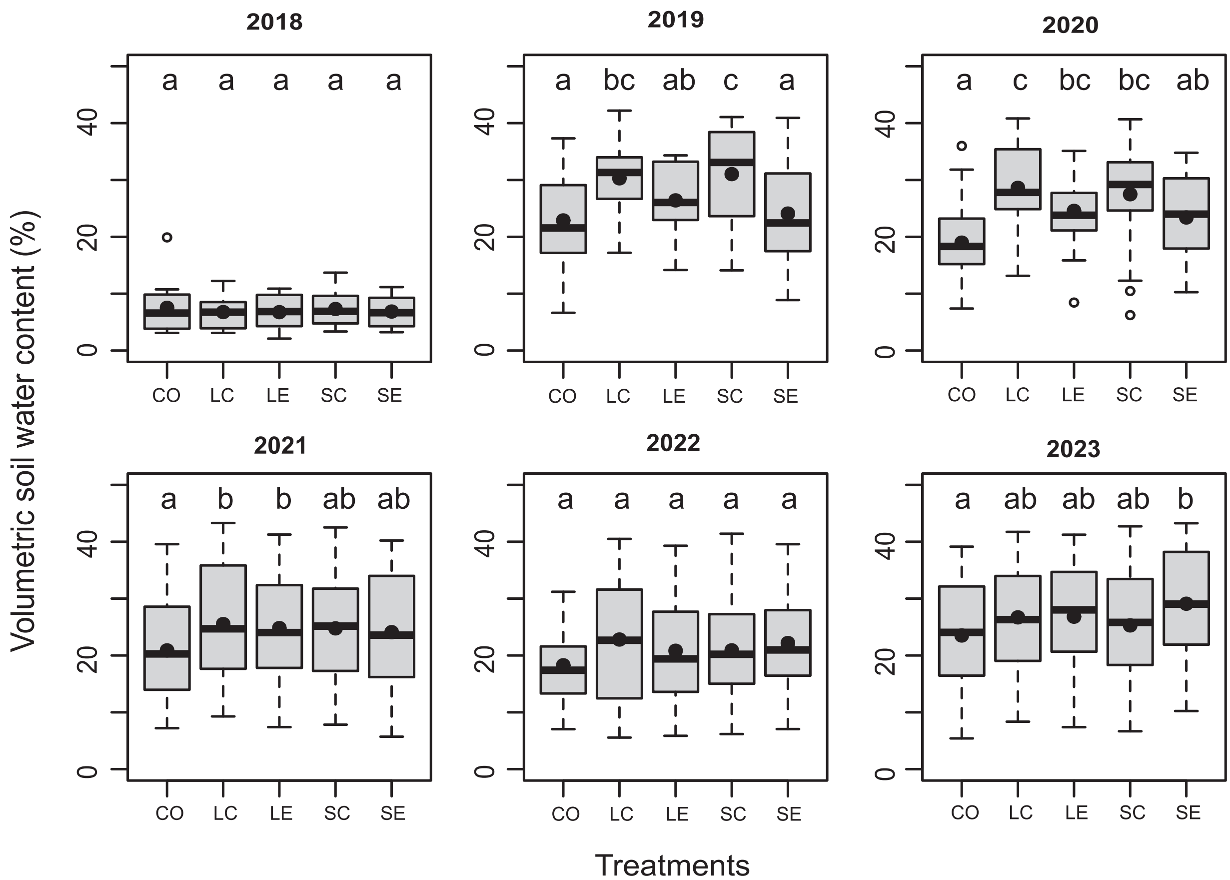

Fig. 4. Boxplots of the volumetric soil water content (VWC, %) in the different treatments for the studied years. Interventions were carried out in winter 2018–2019. CO = uncut control, LC = large circular, LE = large elongated, SC = small circular, SE = small elongated gaps. Black dots represent the mean values. Different letters indicate significant differences at $P < 0.05$ level. Soil moisture in 2018 and in the subsequent years was measured on different ways, therefore the absolute values between 2018 and the following years are not comparable.

and soil moisture) and understory species composition were assessed by distance-based redundancy analysis (dbRDA) using Bray-Curtis dissimilarity and the ln-transformed species cover data (Legendre and Legendre, 2012). Plot-level mean ISF and DSF and vegetation season mean VWC were used as canonical variables (in separate models), and block was used as covariable. On the dbRDA plots, treatments were indicated by convex hulls.

All analyses were performed with R version 4.2.2 (R Development Core Team, 2022). Mixed models were conducted using the R package "nlme" (Pinheiro et al., 2022) and multiple comparisons were performed with the "glht" function of the "multcomp" package (Hothorn et al., 2023). Determination coefficients of the mixed models were calculated using the "MuMIn" package (Bartoń, 2022). The "vegan" package was used for the dbRDA (Oksanen et al., 2022).

3. Results

3.1. Changes in light and soil moisture conditions in the different treatments

Immediately after the interventions, both relative diffuse and direct light were higher in all gap types than in the closed stand (Table B.1). In this first year, the highest amount of light was found in the large gaps, however, difference was significant only in the case of relative diffuse light, between the large circular and the small gaps (Figs. 2, 3, Table 1). Over the years, the amount of light started to decrease. The strongest decline was observable in the case of the relative direct light in large circular gaps, where it decreased below its values in the control for the fifth year after the interventions. In the other gap types, DSF was significantly higher than in the closed stand in the fifth year. The relative diffuse light showed the strongest decrease in the large gaps, while in the small ones it stabilized around 30 % for the first five years. Therefore, the significant difference in the relative diffuse light between the small and large gaps disappeared for the fourth year, however, it remained higher in all gap types than in the control even in year 5.

Soil moisture became significantly higher than in the control in the circular gaps immediately after the interventions, and in the large elongated gaps in the second year after the gap creations. In subsequent years, the soil moisture in these gap types gradually decreased to the level of the control. Soil moisture in the small elongated gaps increased above the level of the control in the fifth year – by this time only this gap type was significantly wetter than the control (Table B.2, Fig. 4, Table 1).

3.2. Understory vegetation in the different treatments

3.2.1. Descriptive results

During the six years of the survey, we found a total of 74 vascular plant species, including 11 annual forbs, 41 perennial forbs (including one fern), 11 graminoid species, and seedlings of 10 woody species (7 tree and 3 shrub species) and bramble (Table B.3). Mean species richness per quadrat ranged from 9 to 15, while total understory cover averaged around 100 % in the controls, and in some gaps it could even exceed 200 % due to the multi-layered vegetation developed (Table B.4). The average height of the understory was around 40–50 cm in the controls and in the gap plots before the cutting and increased to a maximum of 120–140 cm in some gaps. Shrub cover was below 4 % before the gap-creations and increased to a maximum of 80–95 % in some gaps

Table 2
Mixed-effects models for the studied understory variables. Fixed effect: treatment type, random factor: block.

Year	Model parameters	General understory variables				Cover of the functional groups				
		Species richness	Total cover	Under-story height	Shrub cover	Annual forbs	Perennial forbs	Graminoids	Woody regene-ration	*Rubus fruticosus* agg.
2018	F-value	0.239	1.011	0.901	1.619	1.258	0.884	0.468	0.509	0.174
	p	0.913	0.425	0.482	0.209	0.319	0.491	0.758	0.730	0.949
	R^2_{pseudo}	0.032	0.327	0.100	0.183	0.333	0.264	0.608	0.191	0.023
	Transf.			ln				ln	ln	ln
2019	F-value	1.279	1.790	0.722	1.097	2.203	1.658	0.651	0.690	0.064
	p	0.311	0.171	0.587	0.385	0.105	0.199	0.633	0.608	0.992
	R^2_{pseudo}	0.213	0.440	0.376	0.131	0.471	0.499	0.680	0.326	0.009
	Transf.			ln				ln	ln	ln
2020	F-value	**4.616**	**4.193**	0.299	1.469	3.219	0.464	2.246	**5.037**	0.987
	p	**0.008**	**0.013**	0.875	0.249	0.034	0.762	0.100	**0.006**	0.437
	R^2_{pseudo}	**0.410**	**0.394**	0.388	0.206	0.381	0.474	0.476	**0.685**	0.120
	Transf.			ln				sqrt		
2021	F-value	2.303	**7.840**	0.560	1.282	**3.019**	2.200	**4.216**	**6.669**	**4.000**
	p	0.094	**0.001**	0.694	0.310	**0.042**	0.106	**0.012**	**0.001**	**0.015**
	R^2_{pseudo}	0.241	**0.557**	0.129	0.176	**0.407**	0.488	**0.680**	**0.534**	**0.356**
	Transf.			ln				ln		
2022	F-value	1.394	**5.103**	0.658	1.350	1.298	2.035	**4.100**	**7.534**	**5.777**
	p	0.272	**0.005**	0.628	0.286	0.304	0.128	**0.014**	**0.001**	**0.003**
	R^2_{pseudo}	0.163	**0.471**	0.160	0.381	0.247	0.508	**0.581**	0.558	0.482
	Transf.			ln				sqrt		
2023	F-value	1.487	**4.733**	0.716	0.641	1.734	**3.866**	**3.779**	**3.648**	**6.855**
	p	0.244	**0.008**	0.591	0.639	0.182	**0.017**	**0.019**	**0.022**	**0.001**
	R^2_{pseudo}	0.170	**0.473**	0.257	0.207	0.264	**0.587**	**0.609**	**0.379**	**0.525**
	Transf.			ln				ln	ln	

Transf.: In several cases, an ln or square root transformation was applied.

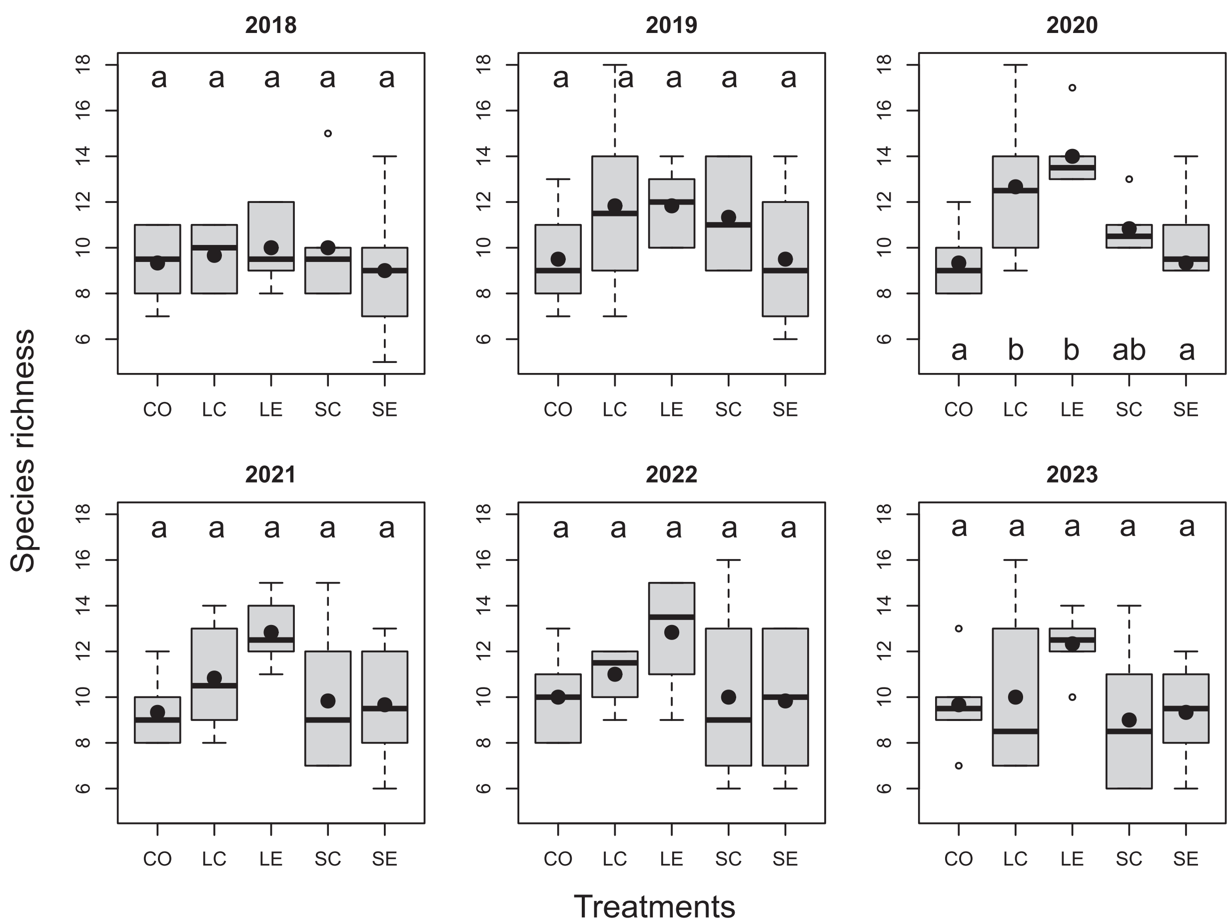

Fig. 5. Boxplots of the species richness in the different treatments for the studied years. Interventions were carried out in winter 2018–2019. CO = uncut control, LC = large circular, LE = large elongated, SC = small circular, SE = small elongated gaps. Black dots represent the mean values. Different letters indicate significant differences at P < 0.05 level.

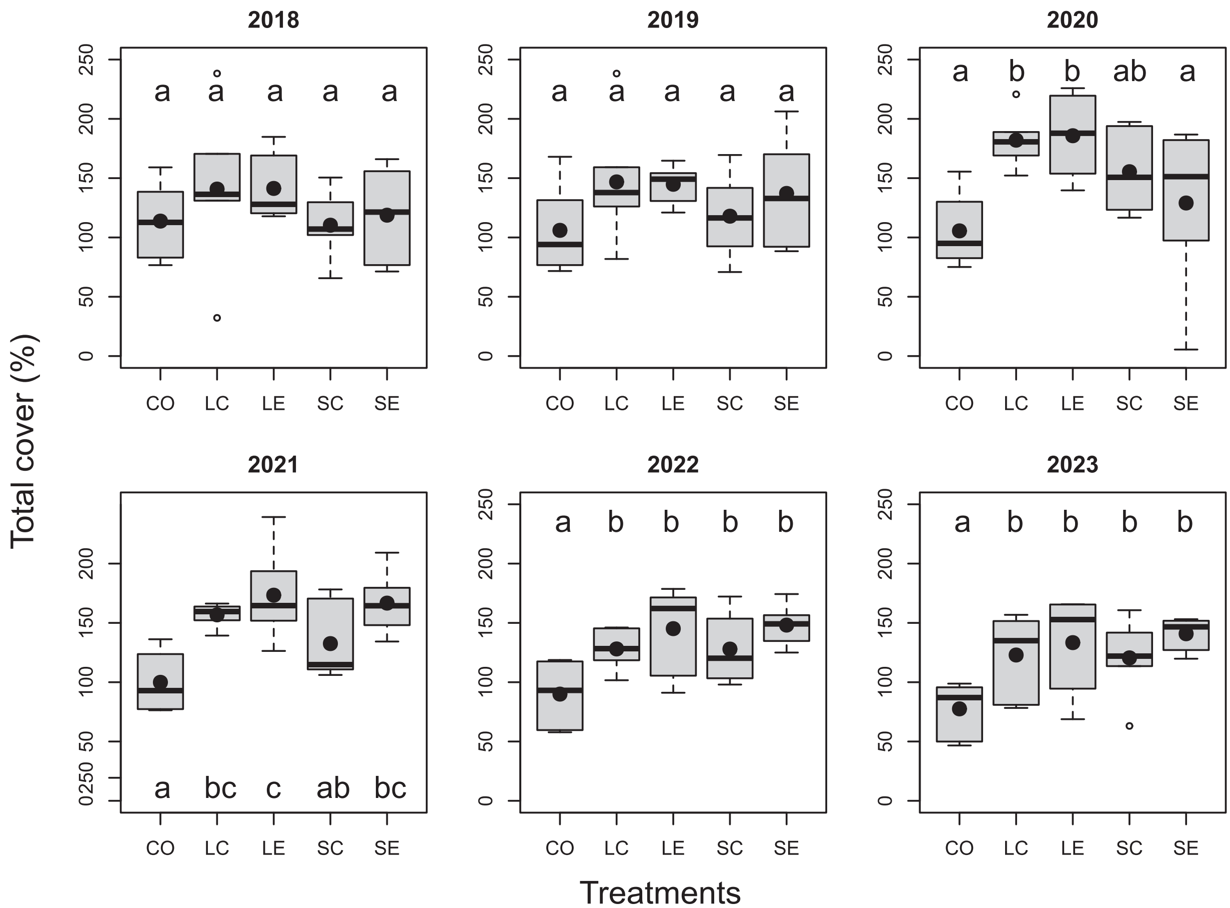

Fig. 6. Boxplots of the total cover in the different treatments for the studied years. Interventions were carried out in winter 2018–2019. CO = uncut control, LC = large circular, LE = large elongated, SC = small circular, SE = small elongated gaps. Black dots represent the mean values. Different letters indicate significant differences at $P < 0.05$ level.

(Table B.5).

Annual forbs were scarce and only the local spread of some species (mostly the invasive *Impatiens parviflora*) in some quadrats resulted in higher cover values. Perennial forbs were more abundant, with *Galium schultesii* dominating the gaps (Table B.3 and B.6). Among the graminoids, *Carex pilosa* and *Melica uniflora* formed a matrix of the understory vegetation, both in the closed stand and in the gaps. Sessile oak (*Quercus petraea*) seedlings established in large numbers in 2019, driving the process of the woody regeneration. The other woody species were much less abundant (Table B.3 and B.7). The initially low cover of *Rubus fruticosus* agg. multiplied over the years in several gaps, and in some quadrats, it covered more than 95 % in the fifth year after the interventions (Table B.3 and B.8).

3.2.2. *The effect of treatments on the measured general understory variables*

Species richness did not respond immediately to the gap-cuttings, just in the second year after the interventions, when it became significantly higher in the large gaps than in the closed forest. However, this increase proved to be temporary, and from the third year, the number of species fell back to the level of the control plots (Table 2, Fig. 5).

Similar to species richness, total understory cover increased in the large gaps, in the second year after the intervention. However, here the differences from the control remained significant over the years, and the cover in the small gaps also increased to the level of the large gaps by year 4. Since then, the understory cover in all gap types has been significantly higher than in the closed stand (Table 2, Fig. 6).

The height of the understory in the large circular gaps became significantly higher than in the control in the second year after the interventions and stabilized at this level. In the third year, a temporal increase was also observed in the small circular gaps, but then here the height decreased. In the elongated gaps, the understory height never differed significantly from the closed stand (Table 2, Fig. 7).

Shrub cover responded to the treatments only from the third year. Compared to the control, shrub cover first increased significantly in the large circular gaps, and then, in year 4, also in the large elongated gaps. Shrub cover in small gaps was never significantly higher than in the closed stand, but a slight increase was observed in the small circular gap (Table 2, Fig. 8).

3.2.3. *The effect of treatments on the cover of the functional groups*

Below, we describe the response of the five investigated functional groups to the treatments in the studied years.

Annual forbs were very scarce and showed no significant response to the cuttings (Table 2). Only certain species occasionally spread in particular plots, but this phenomenon was independent of treatment type.

Perennial forbs also did not show any significant response to the treatments (Table 2). There was a slight, non-significant increase in the large circular gaps in the first years after gap-cutting, but by the fifth year, this had fallen back to the level of the control plots.

Graminoid cover was significantly higher in the large elongated gaps than in the control in the second and third years after the interventions (Table 2, Fig. 9). A significant difference from the closed stand was also observed in the small circular gaps in the second year and in the small elongated gaps in the third year. By the fourth year, however, graminoid abundance had withdrawn to control level in each gap type.

In the first few years after the interventions, the cover of the woody

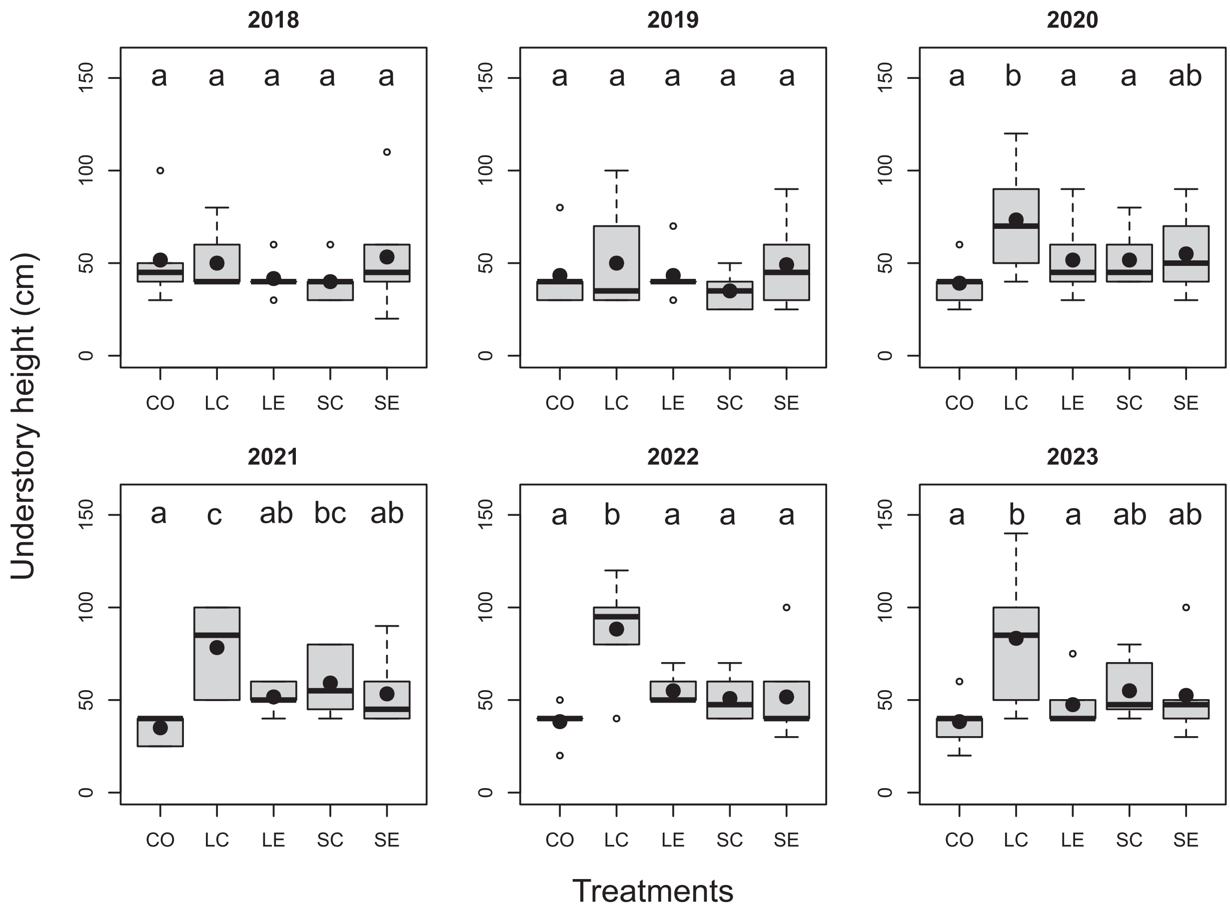

Fig. 7. Boxplots of the understory height in the different treatments for the studied years. Interventions were carried out in winter 2018–2019. CO = uncut control, LC = large circular, LE = large elongated, SC = small circular, SE = small elongated gaps. Black dots represent the mean values. Different letters indicate significant differences at $P < 0.05$ level.

regeneration (dominated by *Quercus petraea* seedlings) increased in all plots, even in the controls (Table 2, Fig. 10). However, by 2023, the cover in the closed stand decreased to the original level. Even in the large gaps (especially in the large circular gaps) there was a slight decrease, while in the small gaps, the woody cover remained high, significantly higher than in the closed stand.

Bramble cover became significantly higher in the large circular gaps than in the control in the third year after gap creations and remained significant in the following years, as well. Its abundance in the other gap types was intermediate (Table 2, Fig. 11).

3.2.4. Relationship between the environmental (light and soil moisture) and understory variables

In the fifth year after the interventions, none of the vegetation variables showed a significant relationship with the soil moisture (Table C.1). The total understory cover and the cover of graminoids and woody species showed a significant positive relationship with the relative diffuse light (Table 3, Fig. 12). Total and graminoid cover also correlated significantly with direct light, while woody species did not (Table C.2, Figure C.1). The other investigated understory variables did not show any correlation with the measured light values.

3.2.5. Species composition in the different treatments

Based on the dbRDA analysis, soil moisture had a significant effect on species composition only before the interventions (2018), while it was not significant in any year after the gaps were created (Table D.1). Therefore, we only present the ordination plots using light as an explanatory variable. Based on the models using the relative diffuse light, the species composition of the different treatments was similar before the interventions (Fig. 13, Table D.2). After the gap creations, the hulls of the treatments started to separate from each other. This separation was maximal in the third year (2021): the large circular gaps and the control plots separated completely from each other and from the other gap types, while the hulls of the small gaps and the large elongated gaps overlapped, between the hulls of the control and the large circular gaps. The separation was only partly along the first axis (light) and partly along the second axis. In the fourth year, the hulls began to converge. However, the large circular gaps and the control plots still did not overlap, even in the fifth year. The response to the direct light was similar, but along the direct light, a stronger convergence was observable between the large circular gaps and controls for the fifth year (Table D.3, Figure D.1).

4. Discussion

Based on our results, gap-cutting with 150 and 300 m^2 gaps does not lead to drastic changes in the understory of oak-hornbeam forests: the vegetation essentially preserves its forest character. However, when different aspects of the vegetation are examined in detail, complex responses can be explored, which are largely dependent on the gap type (size and shape). Changes can only partly be explained by alterations in light, other factors may also play an important role. We could not prove significant relationship between soil moisture and vegetation, although the pattern of several understory variables across the different gap types followed the coupled availability of light and soil moisture. In our earlier study from the same area, investigating the effects of various treatments of rotation and continuous cover forestry systems on understory vegetation, we could statistically capture the effect of soil moisture on the

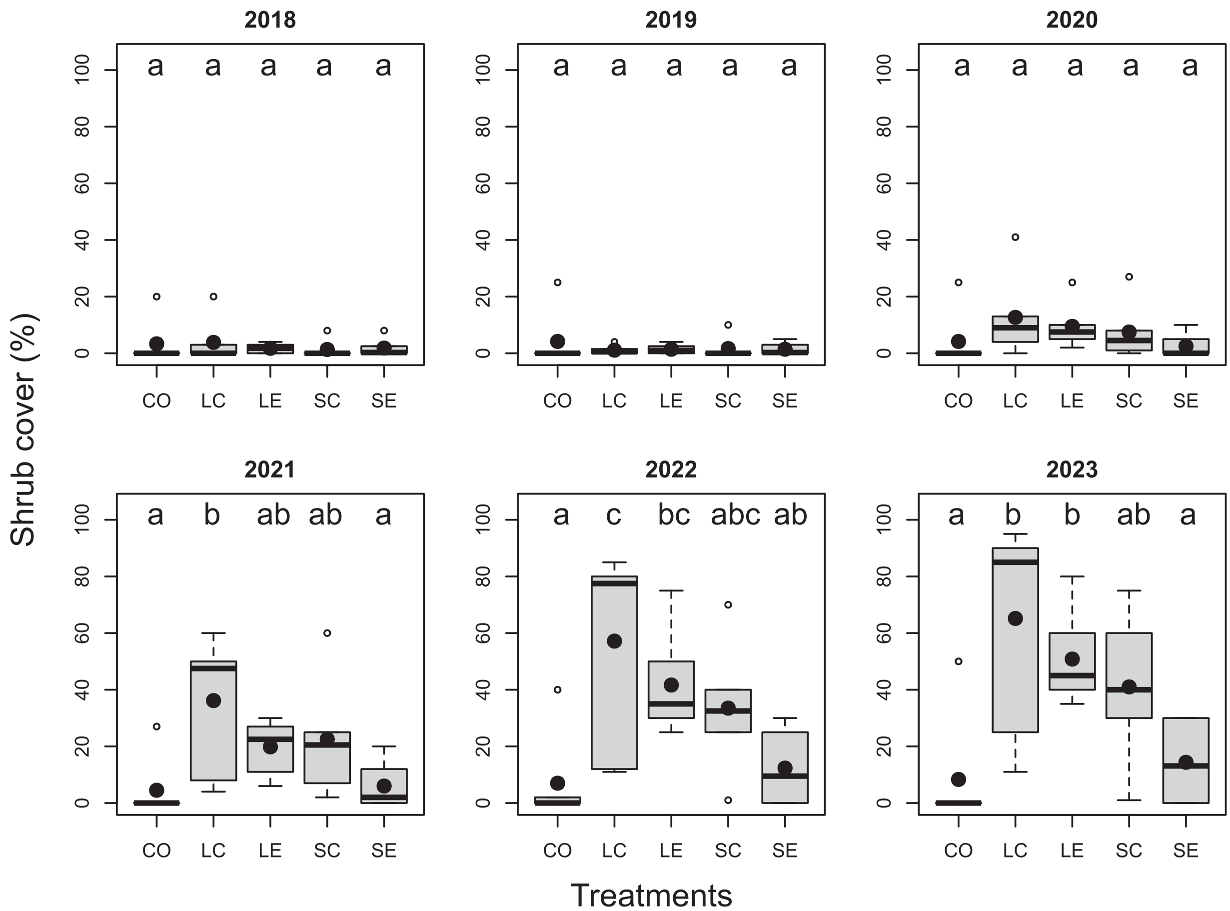

Fig. 8. Boxplots of the shrub cover in the different treatments for the studied years. Interventions were carried out in winter 2018–2019. CO = uncut control, LC = large circular, LE = large elongated, SC = small circular, SE = small elongated gaps. Black dots represent the mean values. Different letters indicate significant differences at $P < 0.05$ level.

understory of gaps (Tinya et al., 2019). Therefore, we assume that it may contribute to the pattern of understory across the gap types even in the current study, but its detection requires further investigation. In the following we discuss the environmental conditions and the understory of the different treatment types.

4.1. Closed forest

The closed forest that served as control, exhibited a sparse understory, yet it was not completely nudum due to the encroachment of graminoids (predominantly *Carex pilosa* and *Melica uniflora*) following a thinning ten years before. Oak mast years result in a temporary increase in seedling cover, but the seedlings disappear after a few years, as the closed stand does not provide sufficient light for the further development of the seedlings after the nutrient reserves of the acorns have been depleted (von Lüpke, 1998).

4.2. General considerations for all gap types

The opening of the canopy layer results in an immediate increase in relative direct and diffuse light within the gaps, as shown also by the detailed microclimate study of Horváth et al. (2023) within the same experiment. They demonstrated that, in the case of the investigated relatively small gap sizes, the abiotic conditions of differently shaped and sized gaps differ both at gap edges and in the gap centers. Gap-type specific differences in the microclimate conditions in the center of the gaps were also demonstrated by Brown (1993) in tropical rainforests and by Prévost and Raymond (2012) in boreal forests.

After a transient increase in species richness within specific gap types, this phenomenon disappears by the third year after the interventions. This finding aligns with the results of previous studies by Burton et al. (2014) and Sabo et al. (2019), who found that changes in species richness after gap-cutting are temporary in northern hardwood forests. The increase in understory cover in gaps proved to be more stable. By the fifth year after the interventions, total cover remained high in all gap types and was strongly related to the amount of light. Several other studies have also demonstrated that the increased light following canopy opening leads to the encroachment of understory vegetation (Sabo et al., 2019; Aszalós et al., 2023).

In our study, the annual forbs were not related to either treatment, light or soil moisture and occurred in very low abundance. This contradicts the results of Aszalós et al. (2023), who, studying gaps similar to our large ones in the same area, found an initial significant increase (albeit temporary). Presumably, the bare soil surface required for the establishment of annuals was missing in our study area, because more competitive graminoid species were already present in the whole stand.

Similarly, the perennial forbs were not influenced either by the treatments, or light or soil moisture conditions. There were no perennials that could sufficiently compete with bramble and woody species; thus they could not achieve a considerable cover in any gap types studied. Even the most abundant perennial forb, *Galium schultesii* is a weak competitor due to its gracile structure.

While the total cover was similar and the abundance of forb species did not differ across gap types, the ordination plots revealed that different species contributed to the total cover in different gap types. The compositional differences between the gap types are observed primarily along the light gradient. These differences are most pronounced in the third year, after which the gap types begin to overlap and approach the

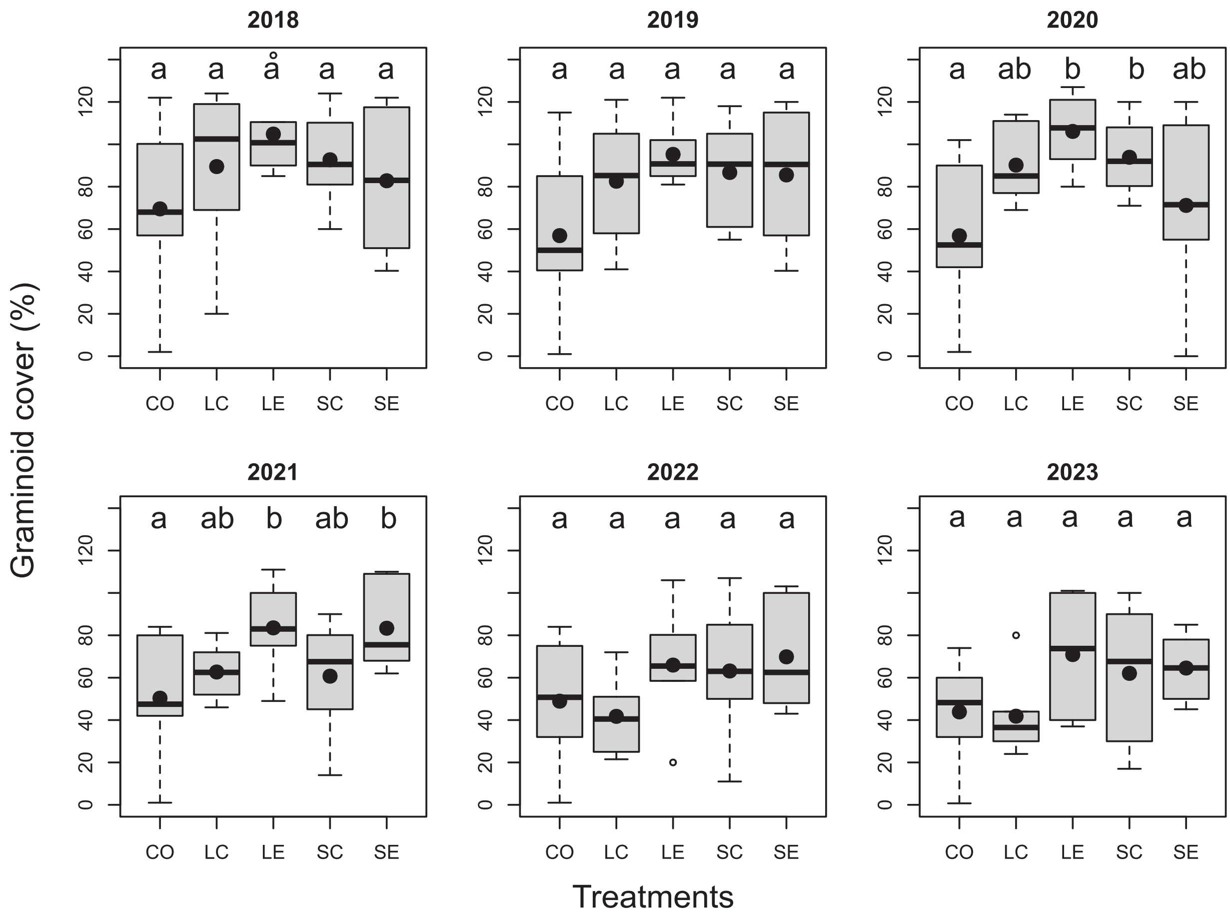

Fig. 9. Boxplots of the graminoid cover in the different treatments for the studied years. Interventions were carried out in winter 2018–2019. CO = uncut control, LC = large circular, LE = large elongated, SC = small circular, SE = small elongated gaps. Black dots represent the mean values. Different letters indicate significant differences at P < 0.05 level.

control. However, it should be noted that these compositional changes are less pronounced than those caused by more intensive harvesting practices, such as clear-cutting (Kermavnar et al., 2019; Tinya et al., 2019; Aszalós et al., 2023). The resilience of the understory species composition to fine-scale gap-cutting was suggested already by Schumann et al. (2003), who studied an oak-pine stand in the USA.

4.3. Large circular gaps

The most significant abiotic and vegetation changes in the first five years following gap creation occur in large circular gaps. The initial high level of relative direct and diffuse light experienced here is in accordance with previous findings (e.g., Gálhidy et al., 2006; Abd Latif and Blackburn, 2010; Vilhar et al., 2015). Soil moisture also immediately increases in circular gaps. These abiotic conditions could be responsible for the rapid increase in species richness and understory cover observed in the large gaps, already in the second year. The study of Burton et al. (2014) supports that species richness increases more markedly in larger gaps, a finding that is also consistent with the results of Gálhidy et al. (2006) regarding understory cover.

However, for the third year, some strong competitor herbaceous and woody species have become dominant in this gap type. The highest cover of bramble was observed in large circular gaps, which is in agreement with the findings of Govaert et al. (2021). Bramble is a light-flexible species (Mountford et al., 2006; Shields et al., 2007) that can spread at bright places, but is also able to tolerate deep shade (Balandier et al., 2013). Although bramble cover in the fifth year after the interventions was not related to either light or soil moisture, it is assumed that its preference for large circular gaps may be explained by the initial coupled availability of light and soil moisture in this gap type. Another explanation for the lack of a significant relationship with light may be the fact that in some cases, bramble outgrew the height of the light measurements, leading to low light levels at the measurement height and below, but high light availability for bramble itself. The high bramble abundance also leads to a significant increase in the height of the understory in the large circular gaps.

The well-developed shrub layer that has been established in this gap type was not dominated by sessile oak, which is the dominant species of the overstory, but rather by *Carpinus betulus* and other competitive species, e.g., *Cornus sanguinea*. The spread of bramble, *Carpinus* and *Cornus* results in a significant alteration of the vegetation structure, leading to the formation of a multi-layered vegetation, and a notable reduction in direct light intensity below the control level. A reduction in soil moisture was also observed after a few years, which can also be explained by the developed dense vegetation: it might intercept rainfall and transpire a considerable amount of water from the soil. A similar phenomenon was documented by Sabo et al. (2023) in a North American gap-cutting experiment, where they found that the increase in light and soil moisture is transient in large gaps.

The expansion of the mentioned competitive species and the reduction in irradiance may have contributed to the decline in species richness observed from the third year onwards. Sabo et al. (2019) also found in northern hardwood forests that the developed sapling layer suppresses the herb layer after a few years. Shading by bramble and the shrub layer can also explain the decline in woody regeneration (predominantly oak seedlings) in the understory layer of this gap type. This is supported by the fact that, based on the results presented here, woody regeneration cover in the fifth year is significantly correlated with light intensity.

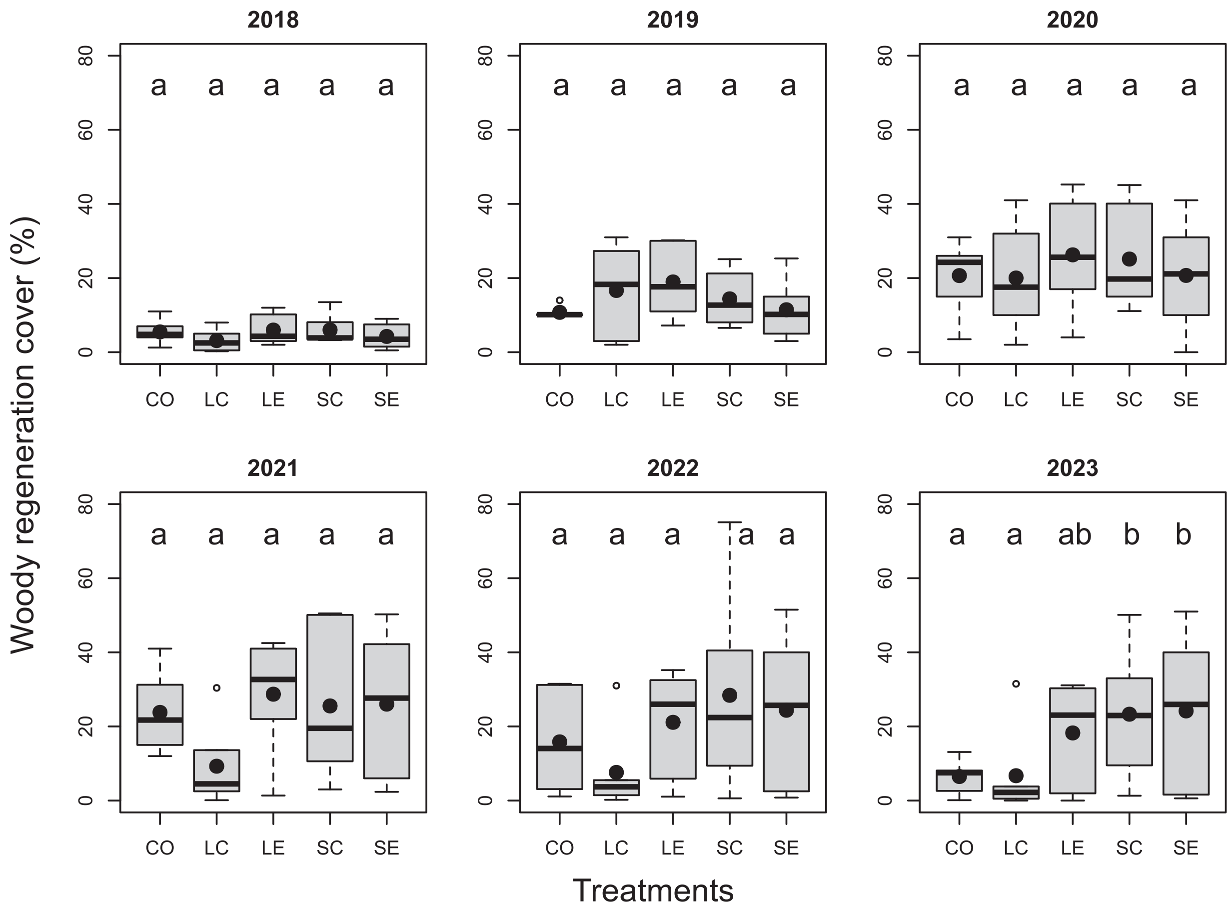

Fig. 10. Boxplots of the cover of the woody regeneration in the different treatments for the studied years. Interventions were carried out in winter 2018–2019. CO = uncut control, LC = large circular, LE = large elongated, SC = small circular, SE = small elongated gaps. Black dots represent the mean values. Different letters indicate significant differences at P < 0.05 level.

Diaci et al. (2008) and Ligot et al. (2013) also found that oaks exhibit enhanced growth under high levels of direct sunlight. Widen et al. (2018) found that regeneration success is determined by the initial regeneration abundance, rather than the *Rubus* cover. However, in their studied stand, the *Rubus* species was *R. idaeus* which species is less prone to climbing than bramble (*Rubus fruticosus agg*). In addition, initial seedling abundance was not a limiting factor in our study, as it was high in each plot due to the mast year. The outlined compositional changes in the understory of the large circular gaps are also reflected in the ordination, which shows that species composition differs the most in this gap type compared to the closed stand.

4.4. Large elongated gaps

In the large elongated gaps, where a substantial initial increase in direct light was observed, coupled with only an intermediate increase in soil moisture, vegetation changes were intermediate. The shrub layer and bramble cover are moderate here, therefore the amount of light does not decrease here as rapidly as in the large circular gaps. Species richness and the total understory cover react similarly as in the large circular gaps, but the composition is distinct, and the differences to the closed stand are smaller than in the large circular gaps. For the second year after the interventions, the cover of the graminoid species, especially *Carex pilosa,* increases in this gap type. In northern hardwood stands, Shields et al. (2007) also found that graminoids became more abundant in larger gaps. Among our gap types, large elongated gaps may be the most favorable for graminoids on the one hand due to the increased diffuse light, as the relationship between graminoids and diffuse light intensity was significantly positive. On the other hand, the lower cover of strong competitors compared to the large circular gaps may also play a role. The same conditions can favor the development of woody regeneration (composed mainly of oak). However, the graminoid cover seems to be less stable, decreasing after a few years, which can be explained by the slight decrease in direct irradiance, as graminoids are also related to this light component.

4.5. Small circular gaps

The small circular gaps receive less additional light than the large gaps, but in the absence of dense shrub layer and a high bramble cover, this light surplus remains more stable over the years. In the early years, a considerable amount of additional soil moisture occurs, but its recovery to the level of the closed stand can be observed more quickly than in the large gaps. Several studies have also found that the increase in soil moisture after gap-cutting is transient and disappears first in the smaller gaps (Ritter et al., 2005; Sabo et al., 2023). The increased light allows the vegetation cover to increase, but its composition changes only slightly compared to the closed stand, without any species becoming dominant. This allows sessile oak regeneration to be more successful than in the large gaps.

4.6. Small elongated gaps

The small elongated gaps are only slightly brighter than the closed stand. The amount of diffuse light is almost the same as in the small circular gaps, but the direct light is slightly higher in the small elongated gaps than in the small circular ones in the first year after the gap creation. In the northern hemisphere, most of the direct light comes from the

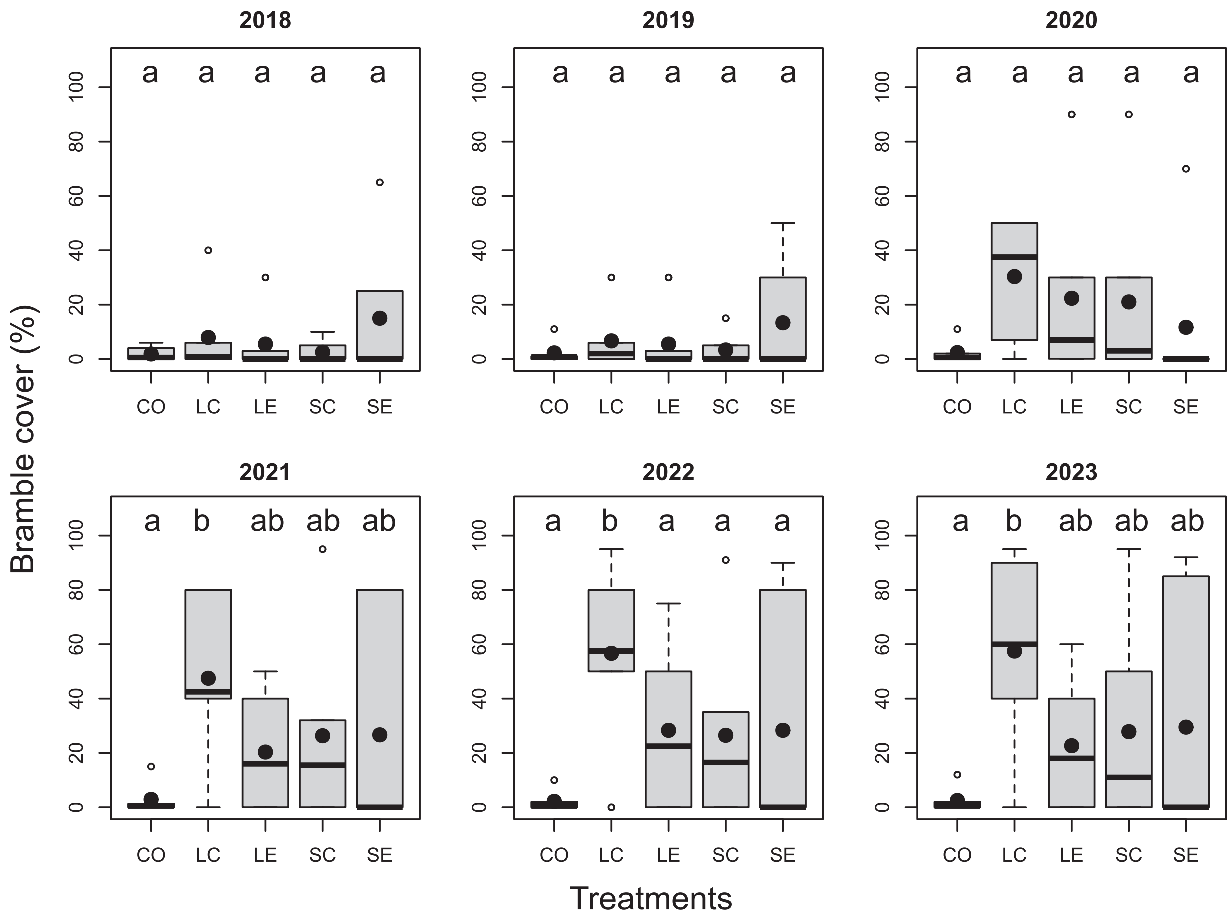

Fig. 11. Boxplots of the bramble cover in the different treatments for the studied years. Interventions were carried out in winter 2018–2019. CO = uncut control, LC = large circular, LE = large elongated, SC = small circular, SE = small elongated gaps. Black dots represent the mean values. Different letters indicate significant differences at P < 0.05 level.

Table 3
Mixed-effects models for the relationship between relative diffuse light (ISF) and understory variables in the fifth year after the interventions (2023). Random factor: block.

Model parameters	Species richness	Total cover	Understory height	Annual forb cover	Perennial forb cover	Graminoid cover	Cover of the woody regeneration	Cover of *Rubus fruticosus* agg.
F-value	1.437	**11.187**	1.591	3.661	2.591	**5.651**	**4.551**	1.731
p	0.243	**0.003**	0.220	0.068	0.121	**0.026**	**0.044**	0.201
R^2_{pseudo}	0.047	**0.451**	0.130	0.218	0.177	**0.188**	**0.423**	0.461
Transf.			ln	ln				ln

Transf.: in several cases, an ln transformation was applied to the dependent variable. Values in boldface indicate significant relationships.

south, thus its amount in the center of the gaps depends mainly on the distance of the gap center from the southern edge of the gap (Diaci et al., 2008). For the same area, this distance, and therefore the amount of direct light entering the center of an elongated gap, is greater than that of a circular gap. Soil moisture in the early years is the lowest here among the gap types.

Probably due to the moderate amount of both light and soil moisture in the initial years, none of the strong competitor species (bramble, *Carpinus betulus* or *Cornus sanguinea*) encroaches here. This allows the light conditions to remain stable for several years, and the decrease in soil moisture experienced in the other gap types is not observed here, either. The species composition of the small elongated gaps remains the most similar to that of the control stand, and in the fifth year, they overlap again on the ordination plot. The stable abiotic conditions and the absence of the dense bramble and shrub layer provide good conditions for oak seedlings. Therefore, the main change in this gap type is the slow, slight increase in vegetation cover, primarily driven by the increase in seedling (predominantly oak seedling) cover. Our finding that oak seedlings develop best in those treatments (small gaps) that simultaneously had additional light and low competition levels are consistent with the comprehensive analysis of Annighöfer et al. (2015), who found a complex effect of light and competing vegetation on oak regeneration. The fact that the benefits of large gaps with high irradiance are reduced by the developed herb layer, which can outcompete woody regeneration, is also confirmed by other studies (e.g., Shields et al., 2007; Kohler et al., 2020; Xu et al., 2023).

5. Conclusions and implications for conservation and management

Gaps of 300 m^2 or less do not alter the forest microclimate and understory vegetation substantially. Compared to larger-scale cuttings, they preserve the forest character of the species composition, regardless of the gap size and shape. At the same time, all studied gap types

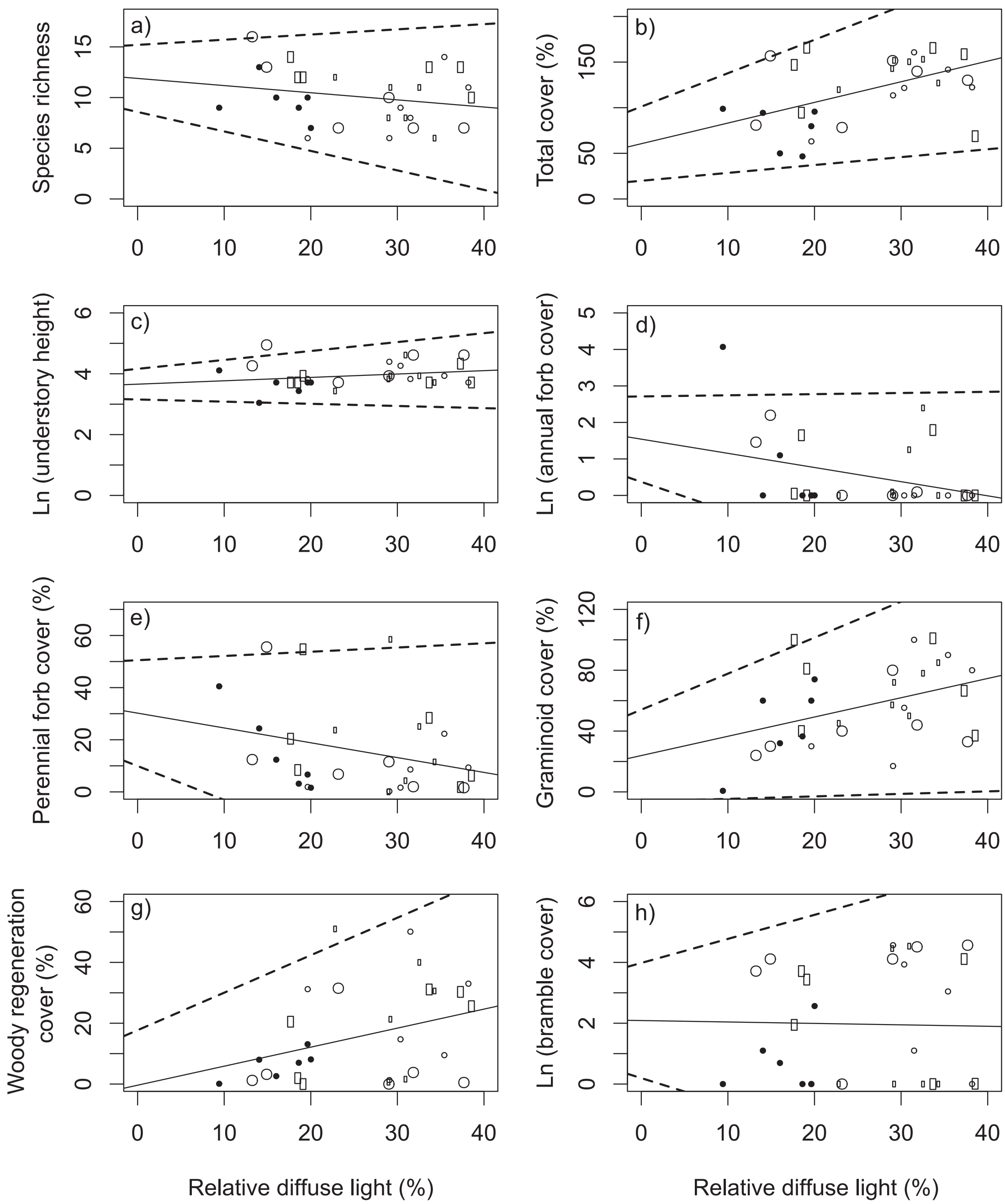

Fig. 12. Scatter plot of the understory variables as a function of the relative diffuse light (ISF) in the fifth year after the interventions (2023). (a) species richness, (b) total cover (%),(c) ln transformed understory height, (d) ln transformed annual forb cover, (e) perennial forb cover (%),(f) graminoid cover (%), (g) cover of the woody regeneration (%), and (h) ln transformed bramble (*Rubus fruticosus agg.*) cover. Shape of the points indicates the gap type: large rectangle: large elongated gap; small rectangle: small elongated gap; large circle: large circular gap; small circle: small circular gap. Regression lines of the applied mixed models are fitted (solid lines) with a 95 % confidence interval (dashed lines).

increase the originally low understory cover, and the large circular gap also increases the height of the understory and result in the development of a dense shrub layer. The increased heterogeneity of the openness, understory vegetation and shrub layer resulting from these gaps of 300 m^2 or smaller may be beneficial from a conservation perspective. This makes the forest structure more similar to the complex, multi-layered, and also horizontally heterogeneous structure of old-growth forests. The resulting more diverse abiotic conditions and microhabitats may also allow for an increase in biodiversity compared to homogeneous closed forests.

From the silvicultural perspective, small gaps proved to be the best-performing, as even their low light surplus seems to be sufficient for the initial stages of oak regeneration, while keeping the amount of light low enough to prevent the rapid encroachment of competitors. Although the direct effect of soil moisture on vegetation could not be detected, it is hypothesized that in large circular gaps, the high levels of both light and soil moisture tilt the competition towards the semi-woody scrambling bramble and the more competitive woody species, such as *Carpinus betulus* or *Cornus sanguinea*, inhibiting the oak regeneration.

The limitation of our study is that we only investigated the center of

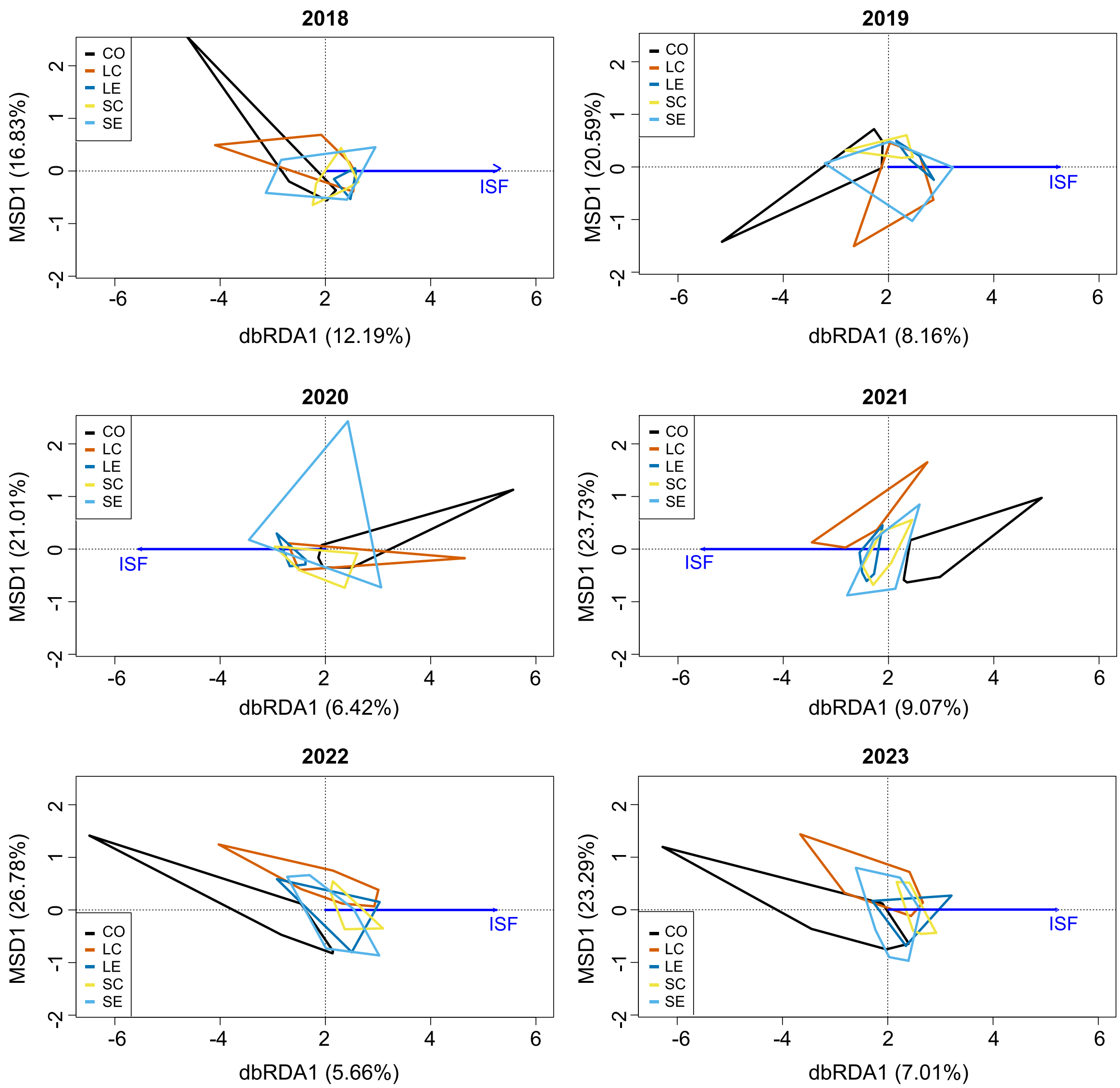

Fig. 13. dbRDA plots of the understory in the different treatments for the studied years (2018–2023), using relative diffuse light (ISF) as an explanatory variable (represented by the arrow). Interventions were carried out in winter 2018–2019. CO = uncut control, LC = large circular, LE = large elongated, SC = small circular, SE = small elongated gaps. Explained variances (%) of the axes are given.

the gaps, while site conditions show strong spatial variability within the gaps (Ritter et al., 2005; Horváth et al., 2023). Further studies are planned to evaluate the regeneration success at various microsites within the gaps.

It should also be noted that we only analyzed the five-year response to gap-creation. Oak becomes especially light-demanding after several years, when its root system becomes strong enough to utilize the extra amount of light (von Lüpke, 1998; Tinya et al., 2020). Therefore, it is possible that an extension of small gaps may be needed later to maintain the sufficient light conditions for oak regeneration – we plan to investigate this issue in the forthcoming years. However, if it is not possible to gradually increase the light available for oak regeneration and large gaps are created in one step, applying an elongated gap shape can successfully moderate the spread of bramble and other competitors.

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CRediT authorship contribution statement

Péter Csépányi: Writing – review & editing, Conceptualization. **Flora Tinya:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Csaba Németh:** Writing – review & editing, Investigation, Formal analysis. **Bence Kovács:** Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Péter Ódor:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Csenge Veronika Horváth:** Writing – review & editing, Investigation.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122471.

Data availability

Research data are available at the Mendeley Data repository: https://doi.org/10.17632/j52xddrrms.1

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