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Canopy gaps are less susceptible to disturbance-related and invasive herbs than clear-cuts: Temporal changes in the understorey after experimental silvicultural treatments

Réka Aszalós [a,*], Bence Kovács [a,b], Flóra Tinya [a], Csaba Németh [a,c], Csenge Veronika Horváth [a,d], Péter Ódor [a,c,e]

[a] *Centre for Ecological Research, Institute of Ecology and Botany, Alkotmány u. 2-4, H-2163 Vácrátót, Hungary*
[b] *Eötvös Loránd University, Department of Plant Systematics, Ecology and Theoretical Biology, Pázmány Péter stny. 1/C, H-1117 Budapest, Hungary*
[c] *National Laboratory for Health Security, Centre for Ecological Research, Karolina út 29, H-1113 Budapest, Hungary*
[d] *Doctoral School of Biology, Institute of Biology, ELTE Eötvös Loránd University, Pázmány Péter stny. 1/C, H-1117 Budapest, Hungary*
[e] *University of Sopron, Forestry Faculty, Institute of Environmental Protection and Nature Conservation, Bajcsy-Zsilinszky u. 4, H-9400 Sopron, Hungary*

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ABSTRACT

Forest management has a major impact on the understorey vegetation, with the intensity and type of the applied silvicultural treatments driving variable vegetation responses. We compared understorey variables across different experimental silvicultural treatments in a temperate oak-hornbeam forest in Central Hungary. Five treatment types were used in six replicates representing rotation and selection silvicultural systems: control (C), clear-cutting (CC), gap-cutting (G), preparation cutting (P), and retention tree group (R). The response of several understorey variables was investigated to the treatments in the first six years after their implementation in 2014.

We assessed how understorey variables change in response to different forestry treatments, how these responses vary with time, and how game exclusion affects them. We then evaluated how well the treatments can preserve the forest character of the vegetation.

We found a large temporal variability in the understorey variables over the study period. In all cases, the interventions led to an initial increase in species richness, followed by a decline later, where the regeneration layer started to close. The regeneration layer grew most intensively in G and CC. At the end of the study, R had the highest average species number, comprising a heterogeneous group of perennial forb species. The interventions all resulted in a rapid increase in total herb layer cover, mainly in favour of graminoid and perennial species. The extent of cover increase depended primarily on the amount of additional light received (CC > G > P > R > C). Turnover and beta diversity values also decreased in a similar order. The effect of game exclusion was especially pronounced in the case of the CC and G, where game browsing significantly slowed the regeneration outside the fences. The most significant changes in almost all variables were in the CC. It had the highest number of indicator species, many of them annual, disturbance-related, and invasive. G preserved the forest character of the vegetation better and proved to be less susceptible to the mass appearance of disturbance-related and invasive herbaceous species.

Increasing the share of continuous cover forestry methods is crucial to preserve the forest herb layer. Rotation forestry with large cutting areas is not recommended or should be kept at low landscape rates, as these areas are highly exposed to disturbance-related and invasive species. Leaving retention tree groups can be key to the survival of numerous forest plant species.

Nomenclature: Király (2009).

1. Introduction

Forest ecosystems provide habitat to a significant part of Europe's

* Corresponding author.
E-mail address: aszalos.reka@ecolres.hu (R. Aszalós).

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biodiversity, including species of high conservation value (Lindenmayer et al., 2006, Muys et al., 2022). Since the proportion of primary and old-growth forests in Europe is very low (Sabatini et al., 2018), conservational, recreational, and economic purposes are generally integrated into forest management (Kraus and Krumm, 2013). Hence, understanding the effect of silvicultural systems on different forest-dwelling taxa is a requisite scientific task, which is essential for developing sustainable forest management methods (Durak, 2012, Tinya et al., 2021, Burrascano et al., 2021).

Forest management has an impact on all groups of forest-dwelling organisms (Paillet et al., 2010, Chaudhary et al., 2016, Elek et al., 2018, Muys et al., 2022) and alterations in its type or intensity induce significant changes in forest communities, e.g., in the understorey vegetation (Halpern et al., 2005, Kelemen et al., 2012, Duguid and Ashton, 2013, Klynge et al., 2020, Kirby et al., 2022). The composition and density of the canopy control light availability and affect microclimate and soil conditions (Craig and MacDonald, 2009, Von Arx et al., 2013, Kermavnar et al., 2019, Kermavnar et al., 2020, Hukić et al., 2021). In managed temperate forests, species richness and cover of the understorey often increase greatly with the increase in available light (Moore and Vankat, 1986, Goldblum, 1997, Gálhidy et al., 2006, Dormann et al., 2020) as a result of different forestry treatments (Collins and Pickett, 1987, Tinya et al., 2019, Beese et al., 2022). In most cases, after an initial increase, the cover of the understorey starts to decrease with canopy redevelopment after a few years (Moore and Vankat, 1996, Klynge et al., 2020, Beese et al., 2022). Changes over time after management interventions can be highly variable regarding species number, cover, and composition (Kirby et al., 2022). Hence, studies based on well-designed permanent-plot observations and experiments are essential in assessing long-term vegetation development (Bakker et al., 1996, Bakker et al., 2002, Tinya et al., 2023).

The strength and direction of responses depend primarily on the intensity of the human disturbance. Timber-oriented intensive forest management practices homogenize forest stands and landscapes (Puettmann et al., 2009), often leading to the decline of many elements of biodiversity (Hobson and Schieck, 1999, Brunet et al., 2010, Drapeau et al., 2016, Savilaakso et a. 2021). After the final cut, rotation forestry methods create a smaller or larger (1–10 ha) area without canopy cover, locally eliminating its microclimatic buffering capacity (Chen et al., 1999, Keenan and Kimmins, 1993). The main purpose for creating these felling areas is to promotie tree regeneration, wether natural or artificial. However, the strongly altered environmental conditions can trigger significant responses in the understorey (Small and McCarthy, 2002, Duguid and Ashton, 2013). An important criticism of such management is precisely that it radically alters the forest microclimate, simplifies forest structure, and therefore strongly impacts forest biota, including the understorey vegetation (Godefroid et al., 2006, Chaudhary et al., 2016, Tinya et al., 2019). Initial successional stages after intensive management interventions can maximize species richness, generally due to an increase in the proportion of annual, light-demanding, and often exotic species (Battles et al., 2001, Macdonald and Fenniak, 2007, Kirby, 2015, Kermavnar et al., 2018, Tinya et al., 2019). Selection systems (continuous cover forestry), with the creation of relatively small gaps in the canopy, preserve the forest climate better than large cuttings of rotation systems (Kovács et al., 2020). Therefore, understorey responses in gaps are expected to be less pronounced (Falk et al., 2008), and the proportion of forest species to be higher (Battles et al., 2001) than in clearcuts. A review by Savilaakso et al., (2021) highlights that uneven-aged forests created by selection systems host more forest-dependent species than even-aged forests of rotation silvicultural systems. On the other hand, intense regeneration cutting or clear-cutting can have a negative effect on shade-tolerant forest species (Brunet et al., 2010).

Besides intervention type, intensity, and the time elapsed since the interventions, the herbivory of wild ungulates also plays an essential role in determining the structure and composition of forest vegetation (Putman, 1996, Côté et al., 2004, Boulanger et al., 2015, Chevaux et al., 2022). In a significant part of Europe, the impact of grazing and browsing is often so severe that it conflicts with economic and conservation purposes (Putman, 1996, Côté et al., 2004, Bernes et al., 2018, Ramirez et al., 2018). One of the most relevant effects is the hindering or complete prevention of forest regeneration (Côté et al., 2004, Palmer et al., 2004, Ramirez et al., 2018). Herbivory of wild ungulates, especially deer, can greatly reduce shrub cover and abundance of forest forb species, while substantially increasing the abundance of graminoids and exotic species (Frerker et al., 2014, Jensen et al., 2012). Comparative studies on the herbivory-understorey relation, forest regeneration, and forest functions are often based on exclusion studies (e.g., Barrere et al., 2021, Jensen et al., 2012, Royo and Carson, 2022).

Like across much of Europe, rotation forestry is predominant in Hungary (91%), with the clear-cutting system more prevalent in the lowlands and shelterwood system in the hilly and mountainous areas (Hungarian National Land Centre, 2021, Aszalós et al., 2022). The share of selection systems is only 1.5% but is growing steadily. Oak-dominated forests are managed typically by rotation forestry in Hungary: by uniform shelterwood systems or clear-cutting systems (Aszalós et al., 2022); however, selection systems are applied in an increasing number of areas of forestry companies.

The relationship between silvicultural practices and the understorey of temperate forests has been the subject of many earlier studies (Godefroid et al., 2005b, Halpern et al., 2005, Duguid and Ashton, 2013, Kutnar et al., 2015, de Groot et al., 2016, Kermavnar et al., 2018, Kirby et al., 2022, Beese et al., 2022). However, only few studies have investigated the relationship between forest management and understorey vegetation in European oak-dominated habitats (Brunet et al., 1996, Götmark et al., 2005). Moreover, investigating the effect of several different management methods on the understorey in the same experiment is very rare (Zenner et al., 2006, Halpern et al., 2005).

This study investigates the differences in understorey variables by comparing silvicultural treatment types in a temperate oak-hornbeam forest stand in Central Hungary. We were curious about the response of understorey vegetation to specific management interventions representing rotation forestry and selection forestry methods in the framework of a field experiment. Our questions were:

1. How do individual understorey variables (species richness, total cover, beta diversity, regeneration density, and turnover) change in response to different forestry treatments?
2. What are the responses of different functional groups (annual forbs, perennial forbs, graminoids, and tree seedlings) and functionally important individual species (plant species with the highest overall cover and disturbance-related species) to the treatments?
3. Which plant species are associated with the different treatments as indicator species?
4. How do the responses mentioned above vary with time?
5. Which treatments preserve the forest character of the vegetation (the number of light-demanding and disturbance-related species remains low after treatments)?
6. How do game exclusion fences modify the responses of the understorey in different treatments?

The research is part of the Pilis Forestry Systems Experiment, a multi-taxon forest ecological study framework launched in 2014 to investigate the effect of different forestry treatments on forest site conditions, biodiversity, and regeneration (https://piliskiserlet.ecolres.hu/en). This initiative aims to contribute scientifically to the underpinning of sustainable forest management in Hungary that mitigates some effects of climate change and slows biodiversity loss. The experiment explored the effects of various forestry treatments on microclimate and other site conditions (Kovács et al., 2018, Kovács et al., 2020), on several zoological taxa (Boros et al., 2019, Samu et al., 2021, Elek et al., 2022), on the development of understorey vegetation and woody regeneration at short-term (Tinya et al., 2019, Tinya et al., 2020), and on multi-taxa biodiversity (Elek et al., 2018).

2. Materials and methods

2.1. Study area

The study area is located in the Pilis Mountains (47°40′N, 18°54′E), the north-eastern ridge of the Transdanubian Range, Hungary (Fig. 1a). Elevations range from 370 to 470 m a.s.l., the average annual mean temperature is 9.0–9.5 °C, and the mean annual precipitation is 600–650 mm (Dövényi, 2010). The bedrock is limestone and sandstone with loess; the most common soil type is lessivage brown forest soil (luvisol), which is slightly acidic (pH of the top 20 cm layer between 4.2 and 5.3, Kovács et al., 2018). The experiment was conducted in a 40-hectare, 80-year-old, managed sessile oak–hornbeam forest stand (Natura 2000 code: 91G0, European Commission, 1992). Before the experiment, the stand was managed by shelterwood silvicultural system, resulting in an even-aged, structurally homogeneous stand. The canopy layer is dominated by sessile oak (*Quercus petraea*), having a 28 cm mean diameter at breast height and a 21-meter mean tree height. Subordinate species of the canopy layer are Turkey oak (*Quercus cerris*), beech (*Fagus sylvatica*), and wild cherry (*Prunus avium*). Hornbeam (*Carpinus betulus*) forms a ~11 m high secondary canopy layer with manna ash (*Fraxinus ornus*) as an admixing species. The shrub layer is scarce. The understorey cover was 50% on average before the interventions, dominated by *Carex pilosa* and *Melica uniflora*.

2.2. Experimental design

The silvicultural treatments were implemented in a randomized complete block design between December 2014 and January 2015, using five treatments in six blocks as replicates (Fig. 1b).

The treatments were the following:

1. Control (C): closed canopy stand without any treatment;
2. Clear-cutting (CC): a 0.5 ha circular clear-felled area of 80 m diameter, surrounded by a closed canopy stand;
3. Gap-cutting (G): an artificial circular gap in the closed stand (20 m diameter, corresponding to the height of one canopy tree);
4. Preparation cutting (P): 30% of the total basal area of the dominant tree layer and the whole secondary tree layer was removed in a spatially uniform way in a circle of 80 m diameter;
5. Retention tree group (R): a circular group of trees (20 m diameter, 8–12 dominant individuals, with an undisturbed subcanopy layer) was retained in each clear-cutting area.

Clear-cutting, preparation cutting, and retention tree groups represent characteristic interventions of rotation forestry systems. The creation of gaps is the most widely used intervention action in selection forestry systems; therefore, gap-cutting represents continuous cover forestry.

The intensity of the treatments, expressed in canopy openness after the interventions in the middle of the treatments, is decreasing in CC (97.5 %), G (55.2 %), P (29.8 %), R (18.1 %), and C (6.5%) order (Tinya et al., 2019, Kovács et al., 2020). In this sense, canopy openness and thus average values of photosynthetically active radiation (PAR) were the highest in clear-cuttings, intermediate in gaps, and lower in preparation cuts and retention tree groups (Kovács et al., 2018, Kovács et al., 2020).

2.3. Data collection and the studied understorey variables

Altogether, 30 plots were studied in six blocks of the five treatments. We surveyed the vascular plants of the understorey in 2 m × 2 m sized quadrats in each plot inside and outside of a 6 m × 6 m fenced exclosure that kept out large-bodied herbivores (red deer, roe deer, mouflon, wild boar, hare, Fig. 1c). The exclosures were located in the middle of the treatments. Hence, each of the 30 plots had one quadrat inside (‘fenced quadrat’) and one outside (‘unfenced quadrat’) of the exclosure, for a total sample size of 60 quadrats. The fenced quadrats were always located in the north-east corner within the exclosures. At the beginning

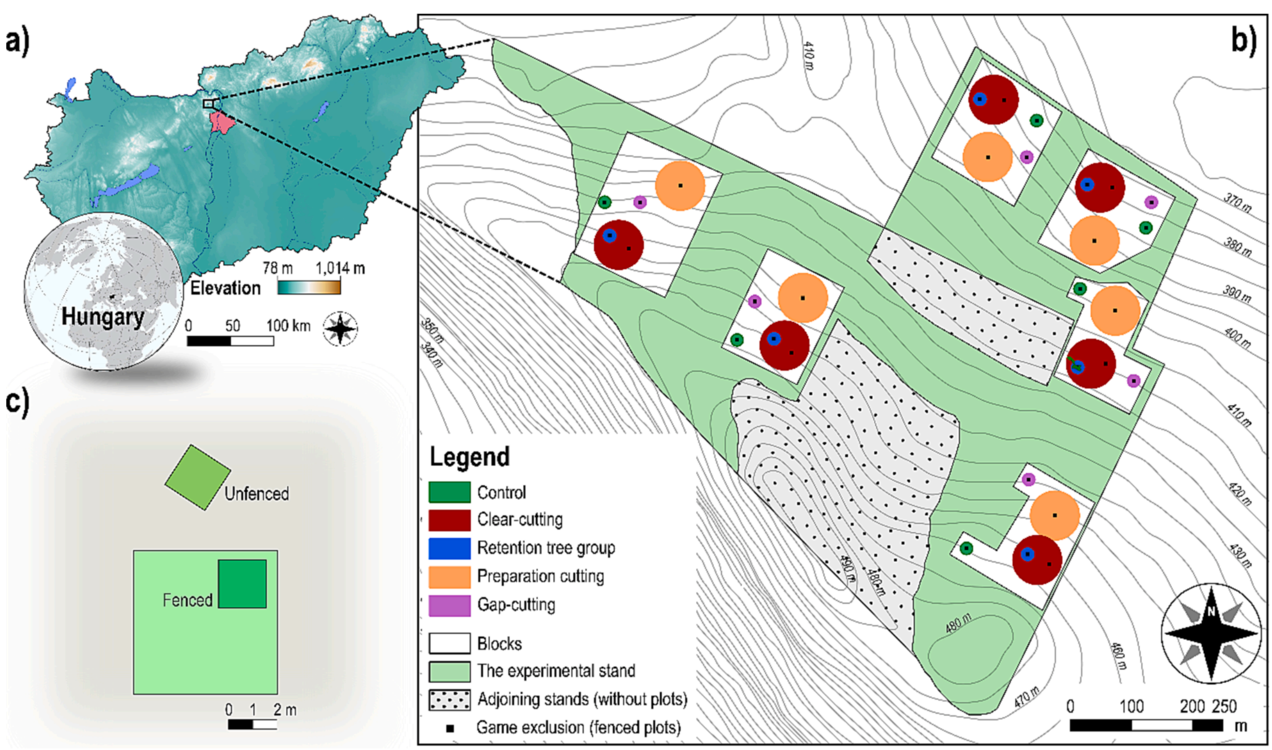

Fig. 1. Overview map of the study area: a) location in Hungary (Pilis Mountains; 47°40′N, 18°54′E), b) the experimental design with five treatment types in six blocks as replicates, and c) an example of the arrangement of 2 m × 2 m permanent quadrats inside and outside of a 6 m × 6 m fenced exclosure that can be found in each plot.

of the survey, for comparability, we designated each unfenced quadrat so that its vegetation resembled that of the fenced quadrat of the given plot. Accordingly, the unfenced quadrats could be located anywhere around the exclosures, but no more than two metres from the fence. Understorey data collection followed the concept of Before-After-Control-Impact (BACI) design. Therefore, the first survey was carried out in 2014 (before the interventions) and then repeated every year until 2020, each spring and summer.

During the survey of the understorey, the herb layer and the regeneration layer were surveyed separately. According to our definition, *herb layer* included individuals of woody species below 50 cm in height ('seedlings') and all herbaceous species. Their cover was estimated in percentage in all the 60 quadrats. With the spring survey, we aimed to document species that characteristically occurred during the spring and whose leaves had retracted by the time of the summer survey (e.g. *Anemone ranunculoides, Cardamine bulbifera, Corydalis solida, Ranunculus ficaria, Senecio vernalis, Symphytum tuberosum*). The *regeneration layer* was defined as individuals of woody species higher than 50 cm in height, whose diameter at breast height is thinner than 5 cm ('saplings'). The number of saplings for each woody species was counted in all 60 quadrats. The nomenclature of the species follows Király (2009).

The understory was analysed on three levels: community, functional groups, and selected plant species. On the community level, we analysed the following variables:

1. Species richness: number of vascular plant species in the herb layer each year.

2. Total cover: sum of the estimated cover of herb layer species. For those species estimated both in spring and summer, we used the higher cover value for the given year.

3. Beta diversity: the mean Euclidean distance (Podani, 2000) between quadrat pairs of the same treatment, year, and exclosure type based on the square root transformed cover values of the herb layer species.

4. Regeneration density: number of saplings of woody species (height > 50 cm, diameter < 5 cm). They were separated from smaller individuals (seedlings, see below) as components of the advanced regeneration.

5. Turnover: the mean Euclidean distance between the same quadrats of the different years. Cover values of the herb layer species were square root transformed before the distance calculation.

The six functional groups include all the herb layer species studied and do not overlap:

1. Annual forbs: the sum of the cover of all annual and biennial forb species.

2. Perennial forbs: the sum of the cover of all perennial forbs.

3. Graminoid species: the sum of the cover of all grass (*Poaceae*) and *Cyperaceae* species (*Carex* spp., *Luzula* spp.).

4. Seedlings of woody species: the sum of all the woody species' cover in the herb layer (height ≤ 50 cm).

5. Ferns: the sum of the cover of *Athyrium filix-femina* and *Dryopteris filix-mas*.

6. Cover of *Rubus fruticosus agg.*: The semi-woody *Rubus fruticosus agg.* was handled separately from the woody species due to its different growth characteristics.

The responses of selected plant species were compared based on their cover:

1. The three plant species with the highest overall cover for all years and all treatments, *Carex pilosa, Melica uniflora, Quercus petraea* seedlings, together with *Melittis melissophyllum* ssp. *carpatica,* were selected.

2. Two disturbance-related plants, *Solidago gigantea,* a non-native invasive species, and *Calamagrostis epigeios,* a native disturbance-related weed, were selected. Monitoring their response to different forestry treatments is important from both a silvicultural and a conservational point of view.

2.4. Statistical analysis

We analysed the responses of the studied variables as dependent variables by general and generalized linear mixed effects models; LMMs and GLMMs, respectively, according to the residual error structure. The explanatory variables were the following: treatment (fixed effect with five levels: C, CC, G, P, R), game exclusion (fixed effect with two levels: fenced, unfenced), year (fixed effect with six levels: 2015, 2016, 2017, 2018, 2019, 2020), and their interactions. Block was treated as random effect with six levels. For the pre-treatment year (2014), the effects of treatment and game exclusion were tested by similar LMM and GLMM models (Table 1). Detailed model specifications for the post-treatment years, with model families, link functions, applied transformations, and the explanatory variables of the final minimum adequate models, can be found in Table 2. For model selection, backward elimination was applied based on analysis of deviance (Zuur et al., 2009). Among treatments and game exclusion types (fenced-unfenced) the differences were tested using least-squared means within years by Tukey-type pairwise comparisons (alpha = 0.05). In the case of turnover, only treatment, game exclusion, and their interaction were used as fixed terms in the LMM. Goodness-of-fit values for all models were expressed as marginal (i.e. variance explained by fixed factors) and conditional pseudo-R^2 (variance explained by both fixed and random factors) (Nakagawa and Schielzeth, 2013).

Species assemblages of the different forestry treatments were explored by principal coordinate analysis (PCoA; Podani, 2000) with Lingose correction (Borcard and Gillet, 2011), based on Bray-Curtis dissimilarities among the surveyed quadrats in each year separately. Both fenced and unfenced quadrats were used for the analyses (60 quadrats per year in total), but species with frequency < 5% were excluded. Since the first two axes explained > 50% of the total variance, two-dimensional plots were created. On the PCoA diagrams, treatments were denoted by convex hulls. The separation between the applied treatments was tested by permutational multivariate analysis of variance (PERMANOVA based on Bray-Curtis dissimilarities with 999 permutations and 'block' used as strata; Anderson, 2001).

We evaluated the connections between species having overall frequency > 5% and treatments by indicator species analysis (ISA), which is a combination of fidelity and specificity of a species to a certain treatment type (Dufrêne and Legendre, 1997). ISAs were run for all measurement years separately. As the fenced and unfenced quadrats within a plot were not independent, the randomization test of the ISA was constrained on the plot level, using the ln-transformed mean cover values of the quadrats.

The analyses were carried out in R 4.1.2 (R-Core-Team, 2022); using the package "lme4" (Bates et al., 2015) for LMMs (function "lmer") and GLMMs (function "glmer"), package MuMIn (function "r.squaredGLMM", Bartoń, 2022) for pseudo-R^2 values, package "lsmeans" for pairwised multiple comparisons (function "lsmeans", Lenth, 2016), "vegan" (Oksanen et al., 2020) for PCoAs (function "wcmdscale") and PERMANOVAs (function "adonis"), and "labdsv" for ISAs (function "indval", Roberts, 2019).

3. Results

3.1. Species richness

Altogether, 114 herb layer species were recorded during the years of the study. The treatments were already different in terms of species richness before the interventions – unplanned, due to the natural heterogeneity of the stand –, with R having a higher species number than C and G (Table 1, Fig. 2A). Species richness was significantly affected by the treatment and year factors (Table 2). C showed the lowest number of species, differing from all other treatments during the years of the study. R and CC showed the highest values throughout, although CC showed a steady decline after a large post-treatment increase in species number,

Table 1
Results of the linear and generalized linear mixed effects models (LMM or GLMM, respectively) built for the pre-treatment year (2014). Dependent variables are listed in column 'Variable'. The performed model types with the link functions are indicated in column 'Model type'. The effects of explanatory variables (Treatment, Exclosure) and their significant interactions (Interactions) were revealed by chi^2 values. Asterisks indicate the significance of the effects (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns = not significant). The models' goodness-of-fit values are expressed by marginal and conditional pseudo- R^2 (R^2_m and R^2_c, respectively).

Variable	Model type	R^2_m	R^2_c	Treatment		Exclosure		Interaction	
Species richness	GLMM	0.156	0.270	11.09	*	1.77	*ns*	-	
	(Poisson with log-link)								
Total cover	LMM	0.092	0.188	6.75	*ns*	0.01	*ns*	–	
Beta diversity	LMM	0.152	0.158	26.17	***	0.45	*ns*	–	
Regeneration density	GLMM	0.108	0.108	5.15	*ns*	0.65	*ns*	–	
	(Negative binomial with log-link)								
Annual cover	GLMM	0.122	0.309	5.25	*ns*	1.15	*ns*	–	
	(Gamma with log-link)								
Perennial forb cover	LMM	0.210	0.219	15.86	**	0.01	*ns*	–	
Graminoid cover	LMM	0.078	0.242	6.06	*ns*	0.01	*ns*	–	
Woody cover	GLMM	0.194	0.251	8.00	*ns*	1.86	*ns*	–	
	(Gamma with log-link)								
Fern	GLMM	0.085	0.123	4.92	*ns*	1.22	*ns*	–	
	(Gamma with log-link)								
Rubus fruticosus	GLMM	0.137	0.285	14.75	**	1.17	*ns*	–	
	(Gamma with log-link)								
Carex pilosa	LMM	0.101	0.101	6.27	*ns*	0.32	*ns*	–	
Melica uniflora	LMM	0.161	0.285	11.10	*	2.17	*ns*	–	
Melittis melissophyllum ssp. *carpatica*	GLMM	0.329	0.407	15.91	**	3.45	*ns*	33.26	***
	(Gamma with log-link)								
Quercus petraea	GLMM	0.059	0.235	6.28	*ns*	0.42	*ns*	–	
	(Gamma with log-link)								
Solidago gigantea	no model, zero values								
Calamagrostis epigeios	no model, zero values								

Table 2
Results of the linear and generalized linear mixed effects models (LMM or GLMM, respectively) built for the post-treatment years (2015–2020). Dependent variables are listed in column 'Variable'. Marked variables (¶) were sqrt-transformed prior to the analyses. The performed model types with the link functions are indicated in column 'Model type'. The effects of explanatory variables (T – Treatment, E – Exclosure, Y – Year) and their significant interactions (T:Y, T:E, Y:E or T:Y:E) were revealed by chi^2 values. Asterisks indicate the significance of the effects (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$). The models' goodness-of-fit values are expressed by marginal and conditional pseudo-R^2 (R^2_m and R^2_c, respectively).

Variable	Model type	R^2_m	R^2_c	Treatment		Exclosure		Year		Significant interactions		
Species richness	GLMM	0.321	0.466	160.34	***			16.75	**			
	(Poisson with log-link)											
Total cover	LMM	0.525	0.577	318.03	***			73.47	***	T:Y	39.53	**
										T:E	14.66	*
Beta diversity	LMM	0.387	0.387	383.69	***	3.75	*	107.58	***	T:Y	56.27	***
										T:E	17.25	**
Regeneration density	GLMM	0.647	0.770	181.25	***	38.74	***	95.82	***	T:Y	54.84	***
	(Negative binomial with log-link)											
Turnover¶	LMM	0.352	0.373	632.60	***	13.61	***	–		T:E	61.77	***
Annual cover	GLMM	0.435	0.514	154.04	***	5.64	*	156.48	***	T:Y	80.06	***
	(Gamma with log-link)									T:E	30.83	***
Perennial forb cover¶	LMM	0.256	0.437	132.70	***			30.41	***			
Graminoid cover	LMM	0.292	0.355	123.63	***			15.51	**	T:E	23.37	***
Woody cover	GLMM	0.524	0.583	169.22	***			204.04	***	T:Y	134.24	***
	(Gamma with log-link)											
Fern	GLMM	0.733	0.749	298.40	***	12.53	***	86.11	***	T:Y	313.80	***
	(Gamma with log-link)									T:E	91.47	***
										Y:E	11.10	*
										T:Y:E	74.34	***
Rubus fruticosus	GLMM	0.254	0.557	73.56	***	4.82	*	28.76	***	T:Y	38.26	***
	(Gamma with log-link)									T:E	22.41	***
Carex pilosa¶	LMM	0.224	0.251	107.59	***							
Melica uniflora¶	LMM	0.414	0.467	164.31	***	13.35	***	37.02	***	T:Y	64.04	***
Melittis melissophyllum ssp. *carpatica*	GLMM	0.266	0.398	142.35	***	8.98	**			T:E	145.46	***
	(Gamma with log-link)											
Quercus petraea	GLMM	0.694	0.735	315.45	***			382.83	***	T:Y	224.12	***
	(Gamma with log-link)									T:E	22.52	***
Solidago gigantea	GLMM	0.372	0.423	181.78	***			21.69	***	T:Y	80.41	***
	(Gamma with log-link)											
Calamagrostis epigeios	GLMM	0.628	0.634	332.23	***	7.08	**	82.13	***	T:Y	164.72	***
	(Gamma with log-link)									T:E	20.62	***

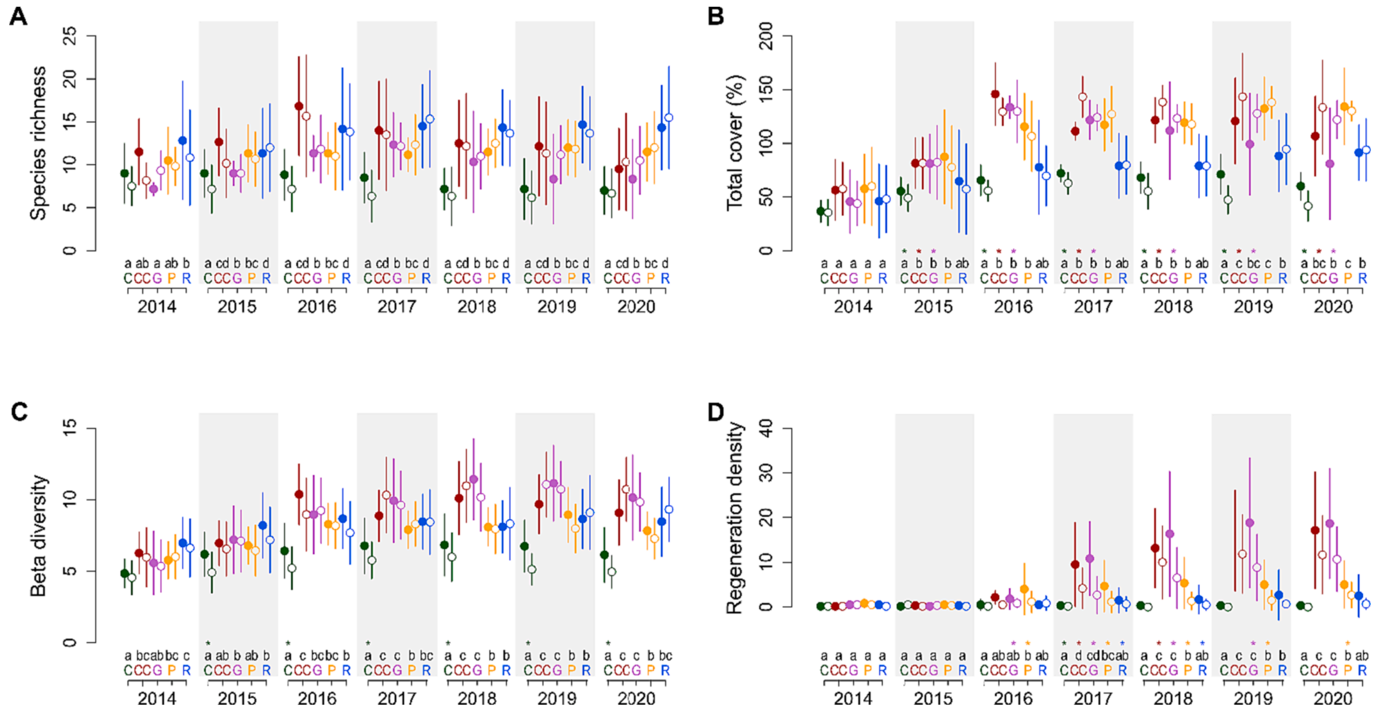

Fig. 2. Understorey variables of the five treatment types over the years studied. A) Species richness of the herb layer, B) Total cover of the herb layer (%), C) Beta diversity of the herb layer D) Regeneration density. C: Control, CC: Clear-cutting, G: Gap-cutting, P: Preparation cutting, R: Retention tree group. Different letters signify significant difference between treatments at $p < 0.05$. Full circles indicate the fenced quadrats, empty circles indicate the unfenced quadrats. Asterisks show significant exclosure effect.

while R kept the relatively higher species number over the years. G and P were characterized by intermediate values, not separated from each other (Fig. 2A, Table 2).

3.2. Total cover

Treatment and year were the determining factors in the change of herb layer cover, and the effect of their paired interaction was also significant (Table 2, Fig. 2B). The initial total cover of about 50% increased markedly in the first year after the interventions (in 2015) in all the treatments. Even in C, the cover increased, but this effect disappeared by the end of the study. By the second year after the intervention (in 2016), the total cover had almost tripled in CC and G before starting to decline. In P, there was a continuous increase, exceeding that of the CC and G in 2020 (Table 2, Fig. 2B). Total cover of the fenced and unfenced quadrats differed significantly in many cases, the most striking difference being for CC and G in the last two years of observation, where the cover of the fenced quadrats was significantly lower than that of the unfenced quadrats (Fig. 2B).

3.3. Beta diversity

The treatment effect on beta diversity was already significant before the interventions (Table 1), showing an initial spatial variability of the stand (Fig. 2C). All three factors and the paired interactions between treatment:year and treatment:exclosure were significant (Table 2), although the effect of treatment was much stronger than other factors. Beta diversity increased in all treatments except C after the interventions. For CC and G, beta diversity values were the highest from 2016 and remained high throughout the study. Intermediate values were calculated for P and R, with C being the lowest in all years studied (Fig. 2C). Significant exclosure effect was detected only in the case of C; the fenced quadrats showed significantly higher beta diversity than the quadrats outside the fences.

3.4. Regeneration density

The density of saplings did not differ significantly between treatments before the interventions (Fig. 2D, Table 1). All three factors were significant after the interventions, being treatment and year the most important factors (Table 2). The highest density was measured in CC and G, while intermediate values characterized P and R. The difference between treatments increased over time (Fig. 2D). Sapling densities of the fenced and unfenced quadrats differed significantly in many treatments from 2016 onwards. The largest differences were observed in the case of G, where the number of saplings in the fenced quadrats was significantly higher than that of the unfenced quadrats (Fig. 2D).

3.5. Turnover

Treatment, exclosure, and their interactions significantly affected turnover values, but the effect of treatment was much stronger than that of other factors (Table 2). Average turnover values followed the intensity of the intervention; for the whole research period, average values were the lowest in C, highest in CC, intermediate in G, and moderate in P and R (Fig. 3). However, there was no significant difference between R and C treatments.

3.6. Species groups

Of the 114 species examined, 21 annual, 59 perennial forb, 11 graminoid, 20 woody species, two ferns, and blackberry (*Rubus fruticusus agg.*) were detected.

3.6.1. Cover of annual forbs

Before the interventions, the annual cover was typically very low. It did not differ among treatments (Table 1, Fig. 4A). Strong treatment and year effect and a marginally significant exclosure effect were observed, and interactions were also significant (Table 2). In the second year after the interventions (2016), CC and G experienced a burst of annual forbs

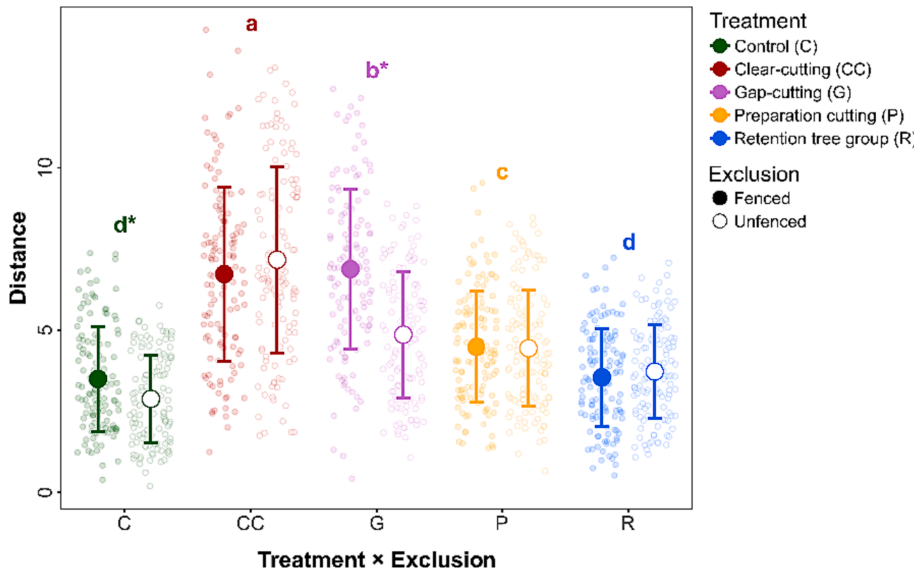

Fig. 3. Turnover values of the five treatments. Different letters show significant difference between treatments at $p < 0.05$. Full circles indicate the fenced quadrats, empty circles indicate the unfenced quadrats. Asterisks show significant exclosure effect.

(mainly in the fenced quadrats), reaching around 15% cover, but then their cover declined rapidly. Annual forbs with the highest cover were: *Galium aparine, Vicia hirsuta, Erigeron annuus, Conyza canadensis*, and *Lactuca serriola.* By the fifth year after the interventions (in 2019), treatments were no longer distinct in annual forb cover.

3.6.2. Cover of perennial forbs

There was a strong treatment effect on perennial forb cover and a significant but weaker year effect (Table 2). C showed the lowest, CC the highest perennial forb cover, distinct from all other treatments. It started to increase in the second post-treatment year (2016) in every treatment but C (Fig. 4B). By the fourth year after the interventions (in 2018), it reached its maximum in CC and G (around 40%), then gradually declined to around the intermediate value of P and R (20%), (Fig. 4B).

3.6.3. Graminoid cover

Before the intervention, the graminoid cover was around 35% on average, without significant differences among the treatments (Table 1). After the intervention, all three factors and their interactions were significant, but the treatment had the most considerable effect (Table 2). There was great variation within and between treatments (Fig. 4C). The lowest values were in C and R and the highest in CC and P. Graminoid cover reached its maximum in the second year after the interventions (in 2016), with approx. 85% in CC and G. After 2017, it differed strongly between the fenced and unfenced quadrats of G, with much lower values in the fenced ones.

3.6.4. Cover of woody seedlings in the herb layer

In the pre-treatment year (2014), the cover of woody species in the herb layer was very low and did not differ across the treatments (Table 1). The effects of treatment and year factors were significant for the post-treatment years (Table 2). The years differed significantly due to the oak mast years in 2016 and 2018, as the cover increased in the following years, except in CC and G, due to weak oak acorn fall in these treatments (Fig. 4D). In 2017 and 2018, the highest woody species cover was in C, while in 2019 and 2020 it reached its maximum in P (average above 20%). Regardless of the year, it was the lowest in CC, distinct from the other treatments (Fig. 4D).

3.6.5. Cover of ferns

All factors and interactions had a significant effect on ferns, but the treatment effect was the strongest. Ferns appeared in G mainly in the inner, fenced quadrats, but only after 2018 (Fig. 4E).

3.6.6. Cover of *Rubus fruticosus agg.*

All factors had a significant effect on blackberry, and treatment was the dominant one. Its cover started to grow in CC and G from the third year after the interventions (2017 onwards, Fig. 4F); these treatments were distinct from the others. It also showed considerable variability within treatment types – from the lack of the species to the complete dominance. In CC, the influence of the exclosure factor was decisive, and blackberry grew mainly in the unfenced quadrats, but in G, both the fenced and unfenced quadrats had relatively high *Rubus fruticosus agg.* cover (Table 2).

3.7. Selected herbaceous species

Carex pilosa was present in all treatments from the beginning, with a 15.5% average cover. Its cover was affected significantly only by the treatment factor after the interventions (Table 2). It increased in all treatments as a result of the interventions but became significantly more abundant in the CC and P than in the other treatments (Fig. 5A). Occasionally, it reached 100% coverage in some CC and 90% in P quadrats. The cover of the other dominant graminoid, *Melica uniflora*, had an 18% average cover before the interventions, which already varied between the sites before the interventions (Table 1). All three factors had a significant effect for the post-treatment years, but the treatment factor had the most substantial effect (Table 2). After the interventions, *M. uniflora* became dominant in G, with a significantly higher cover than in the other treatments from 2016 (60% on average) until 2018. It reached exceptionally high cover in the unfenced quadrats of G (Fig. 5B). In CC, the opposite happened; the cover of *M. uniflora* gradually decreased. Its cover was generally higher in the unfenced quadrats in all the treatments (Fig. 5B). *Melittis melissophyllum* ssp. *carpatica* appeared almost exclusively in the fenced quadrats of P. Over the years its cover has grown steadily (Fig. 5C). Treatment and exclosure factors had a significant effect on it (Table 2). No significant difference was detected in the cover of *Quercus petraea* seedlings before the interventions (Table 1), and the cover was minimal in the first two years (Fig. 5D). From 2017 onwards, after the two masting years, oak seedlings appeared in a high number in certain treatments. The effects of treatment and year factors were significant for the post-treatment years (Table 2). Oak seedlings first

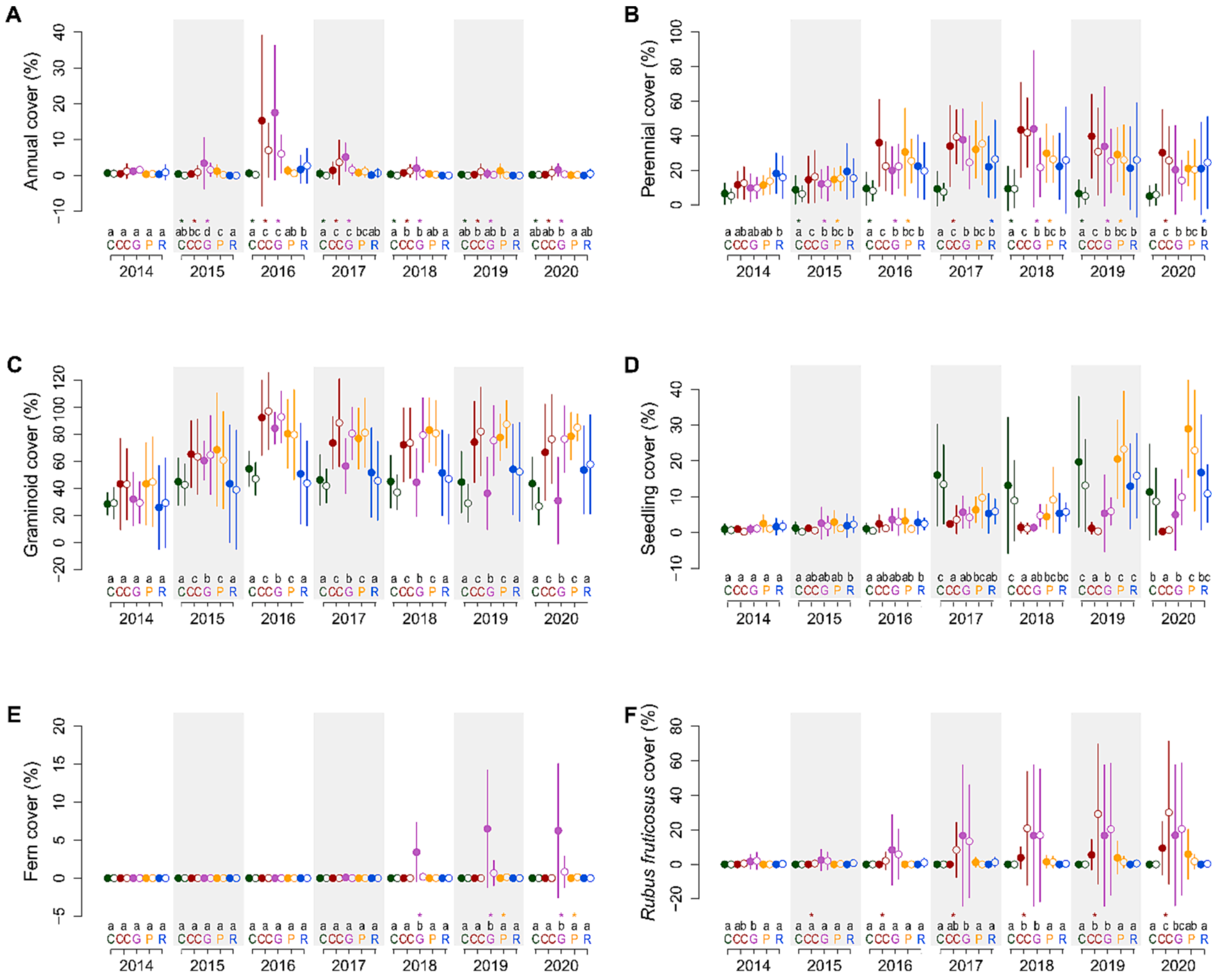

Fig. 4. Change of species groups' cover in the five treatments over the years studied. C: Control, CC: Clear-cutting, G: Gap-cutting, P: Preparation cutting, R: Retention tree group. Different letters signify significant difference between treatments at $p < 0.05$. Full circles indicate the fenced quadrats, empty circles indicate the unfenced quadrats. Asterisks show significant exclosure effect.

reached a high cover in C, then started to decrease, and by the end of the observation period, they were most abundant in P. Their cover showed intermediate values in R and remained low in CC and G (Fig. 5D).

Neither *Calamagrostis epigeios* nor *Solidago gigantea* was present in the area before the interventions. For both species, the effect of treatment and year factors were significant (Table 2). Both species became frequent from the third year after the interventions (2017) onwards in CC (Fig. 5E and 5F). *S. gigantea* was dominant in only a few quadrats, but it was still present in some of them six years after the interventions (2020). *C. epigeios* dominated only in the unfenced quadrats of CC (significant exclosure effect), with an average cover of 9% five years after the intervention, reaching 25–50% cover in some quadrats.

3.8. Species composition

Multivariate analyses (PCoA models) showed that after the interventions, understorey communities differed significantly between treatments over the years studied (Fig. 6). Based on the PERMANOVAs, the separation hardly changed after 2017 (pseudo-F values varied between 4.19 and 4.78 in these years but were ≤ 3.51 before 2017). From 2018 onwards, plots of CC were separated from those of C, P, and R. The plots of these three treatments overlapped, while the plots of G overlapped with both CC and the other three treatments. G showed the highest heterogeneity (compositional beta diversity), but CC was also heterogeneous (Fig. 6).

CC had the largest number of indicator species (Table 3). They formed a diverse group of species, including light-flexible forest perennial species e.g., *Euphorbia amygdaloides, Carex pilosa, Epilobium montanum, Veronica officinalis, Hypericum hirsutum,* and shade-tolerant forest perennials, e.g., *Ajuga reptans, Viola reichenbachiana,* as well as disturbance-related light-demanding species, e.g., *Calamagrostis epigeios, Cirsium arvense*, and the invasive *Solidago gigantea* (Collins et al., 1985, Tinya et al., 2019, Heinken et al., 2022). The light-flexible forest species were mainly associated with CC in the second and third years after the interventions (2016, 2017, see Table 3). Annual light-demanding species, e.g., *Vicia hirsuta*, the invasive *Conyza canadensis,* and *Erigeron annuus,* were also typical CC species. The annual forbs were indicator species only in the second year after the interventions (2016), the only year they appeared in large numbers and then disappeared (Fig. 4A). Among the graminoids, *Carex pilosa* showed a CC preference. Few species were associated with G. Here, *Melica uniflora*, one of the dominant grass species, was preferential in almost all years of the study, while the annual *Galium aparine* appeared in the second year but later declined (Table 3). Also, only a few species were associated with P, such as *Melittis melissophyllum* ssp. *carpatica*, a tall forest herb, which was the indicator species of this treatment type in all studied years (Table 3). Both C and P

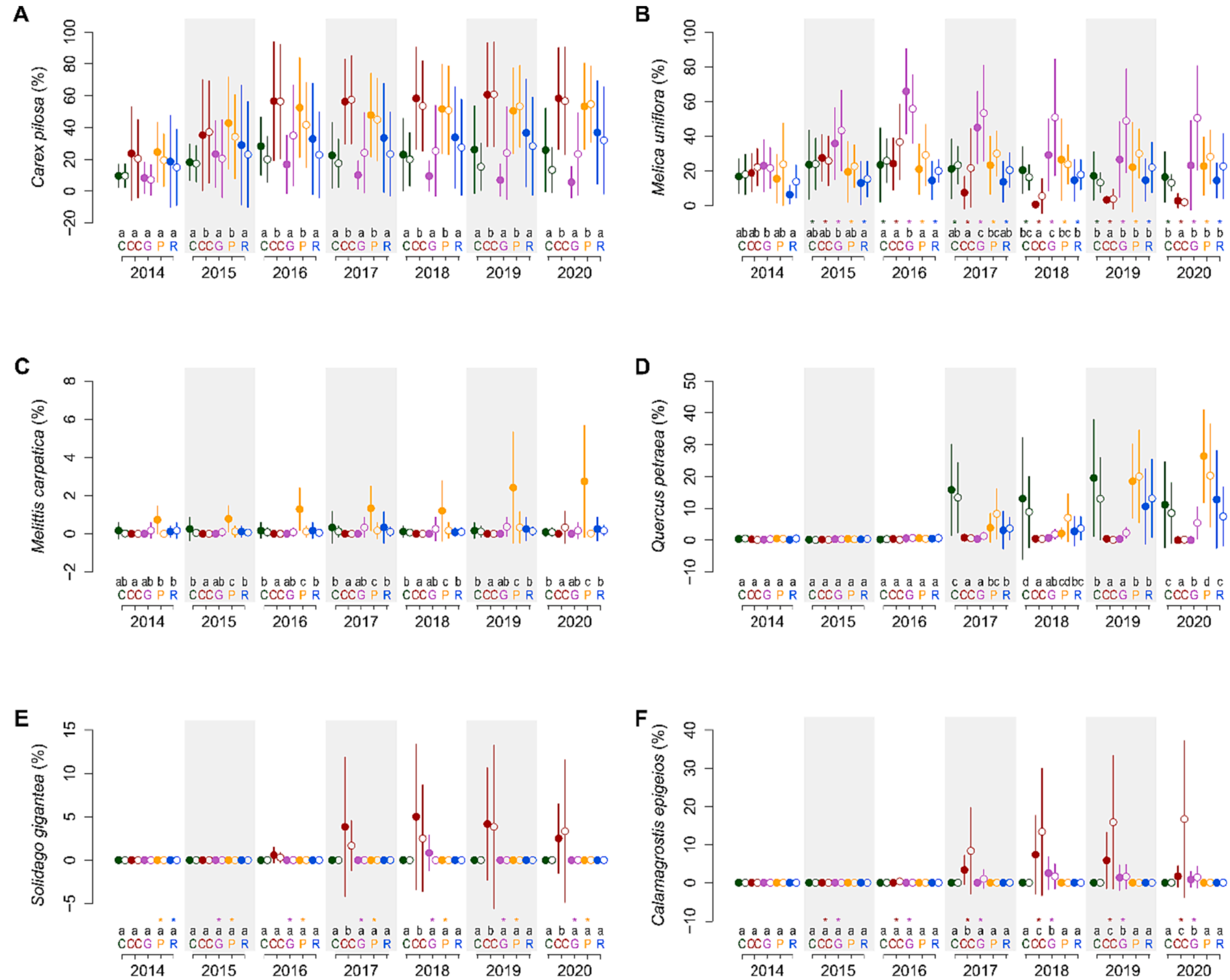

Fig. 5. Change of selected species' cover in the five treatments over the years studied. C: Control, CC: Clear-cutting, G: Gap-cutting, P: Preparation cutting, R: Retention tree group. Different letters signify significant difference between treatments at $p < 0.05$. Full circles indicate the fenced quadrats, empty circles indicate the unfenced quadrats. Asterisks show significant exclosure effect.

were associated with *Quercus petraea* (Table 3) in different years; C in 2017 and 2018, and P in 2019 and 2020. Indicator species of R were a heterogeneous group of perennial forb species usually inhabiting forest edges or drier, more open, and rocky habitats, such as *Crataegus monogyna, Dactylis polygama, Hedera helix, Viola alba,* and *Waldsteinia geoides*. Also, *Anemone ranunculoides* was associated with R in all studied years (Table 3).

4. Discussion

Our results showed that year and treatment were significant factors for almost all the variables tested, highlighting considerable differences between treatments and between years of observations. Other studies also support strong post-treatment successional changes and high variability (Small and McCarthy, 2002, Beese et al., 2022) – hence the need for long-term studies of forest vegetation and understorey responses on forestry treatments (North et al., 1996, Pretzsch et al., 2019). The high variance may be partly due to differences in understory vegetation prior to the interventions, which were also reported in this study. The pre-disturbance status of forest stands and understorey community can significantly impact post-treatment patterns (Kermavnar et al., 2021).

The interventions resulted in a rapid increase in total understorey cover, mainly in favour of graminoid and perennial species. The extent of the increase in herb layer cover depended primarily on the intensity of the treatment, corresponding to the amount of additional light received (CC > G > P > R > C order, Kovács et al., 2018, Kovács et al., 2020), as it was also found by other authors (Kutnar et al., 2015). We observed the most rapid total herb layer cover growth in CC and G, followed by a decline from the third year onwards as saplings grew up and closed the regeneration layer, especially in fenced areas, where ungulates were excluded. The turnover values, i.e., the rate of compositional change, also decreased in the same order as the treatment intensity.

4.1. Control plots

As expected, the closed forest C plots were the most conservative ones; the number of herb layer species has hardly changed, species turnover has been minimal over the years, and there were virtually no saplings. However, there have been changes over the years. Due to a moderate canopy-affecting ice break in the winter of 2014 and the two masting years, the total cover and beta diversity increased. This alteration was mainly due to changes in the cover of *Carex pilosa* and *Quercus petraea* seedlings. The latter was found to be the only indicator species of C. By 2020, the canopy closure had reduced the total herb layer cover to

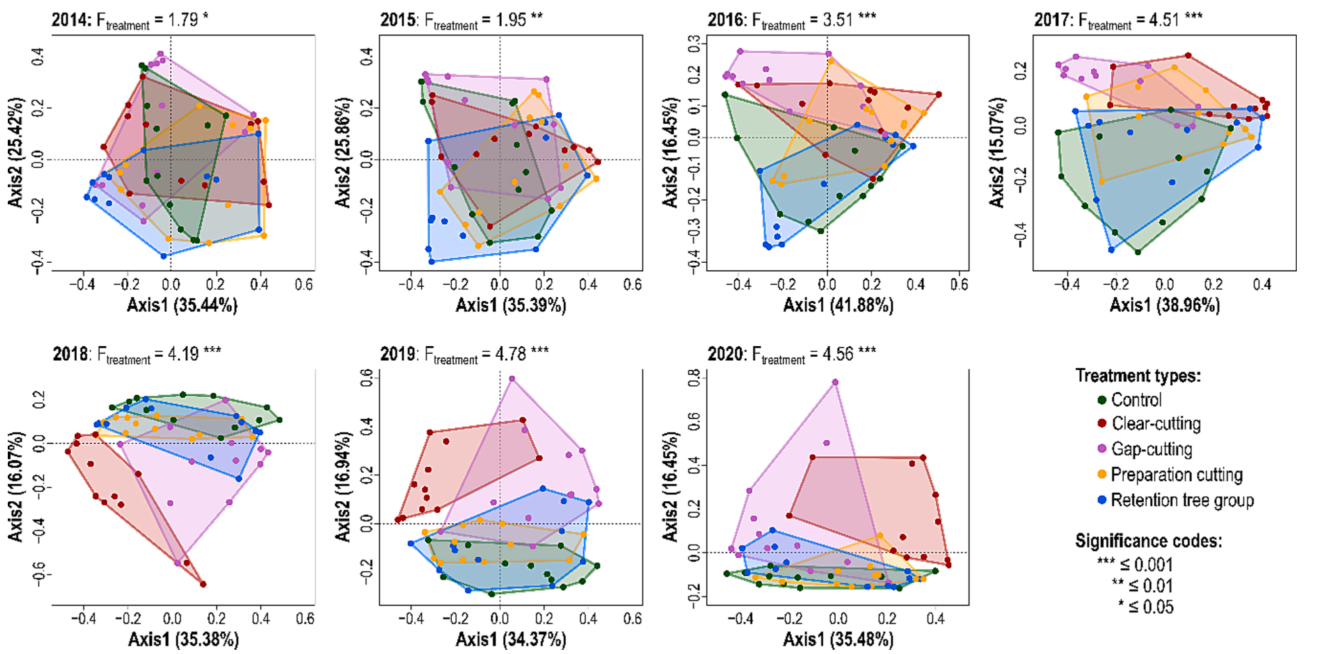

Fig. 6. Ordination plots of the four treatment types and the control according to the principal coordinate analysis (PCoA) based on Bray-Curtis dissimilarity matrices. PCoAs were performed for the individual years (2014–2020) separately. Explained variance of the axes (axis 1 and 2) are shown as proportion of the total inertia. For visualization of the heterogeneity of the treatments, convex hulls were also drawn. C: Control, CC: Clear-cutting, G: Gap-cutting, P: Preparation cutting, R: Retention tree group.

Table 3
Summary of the indicator species analysis of the understorey species by treatments. Only species significantly related to treatments in a given year are listed. Tr: treatments with the highest indicator values; IndVal (%): indicator value related to treatment. C: control, CC: clear-cutting, G: gap-cutting, P: preparation cutting, R: retention tree group. Asterisks indicate the significance of the effects (** 0.001 < p < 0.01, * 0.01 < p < 0.05).

Species	2015			2016			2017			2018			2019			2020		
	Tr	IndVal		Tr	IndVal		Tr	IndVal		Tr	IndVal		Tr	IndVal		Tr	IndVal	
Ajuga reptans	CC	30.19	*	CC	40.11	**	CC	32.21	**	CC	41.45	**	CC	34.5	**			
Anemone ranunculoides	R	25.87	*	R	24.55	*	R	25.65	*	R	26.19	*	R	26.03	*	R	26.43	*
Calamagrostis epigeios							CC	43.96	**	CC	35.1	**	CC	38.2	**	CC	37.12	**
Carpinus betulus							G	33.29	*	P	30.87	*	P	32.72	*	P	30.67	*
Carex pilosa							CC	26.52	**				CC	26.49	*	P	26.88	*
Cirsium arvense				CC	41.67	**	CC	26.14	*	CC	28.41	**	CC	32.72	**			
Conyza canadensis				CC	40.94	**												
Crataegus monogyna				R	33.33	**												
Dactylis polygama																R	23.22	*
Epilobium montanum				CC	29.56	**												
Erigeron annuus				CC	30.75	**												
Euphorbia amygdaloides				CC	30.81	**	CC	36.13	**	CC	38.71	**						
Galium aparine				G	41.54	**	G	33.14	**									
Galium schulthesii							P	29.14	*									
Hedera helix	R	26.2	*	R	23.8	*												
Hypericum hirsutum				CC	22.12	*												
Hypericum perfoliatum				CC	29.13	*												
Melittis melissophyllum	P	29.96	*	P	33.13	**	P	26.53	*	P	25.58	*	P	30.74	*	P	30.08	*
Melica uniflora	G	23.71	*	G	25.33	**	G	25.8	**				G	25.69	*	G	25.57	*
Quercus petraea							C	40.1	**	C	34.69	**	P	35.96	**	P	40.47	**
Rosa canina				CC	24.46	*										CC	23.74	*
Rubus fruticosus																		
Solidago gigantea				CC	33.33	**	CC	33.33	**	CC	20.52	*						
Veronica officinalis							CC	26.28	*				R	23.44	*			
Vicia hirsuta				CC	52.36	**												
Viola alba							R	24.8	*	R	29.38	*						
Viola reichenbachiana				CC	30.98	*	CC	32.06	*									
Waldsteinia geoides				R	33.33	**												

its original level, with most of the oak seedlings not surviving as a consequence of the light deficit (Tinya et al., 2020). In the unfenced quadrats, the cover was significantly lower than in the fenced quadrats by the end of the study due to the strong impact of wild ungulates, like the browsing of red and roe deer and the trampling of wild boars. These results show that ice break and masting years created dynamics in closed forests, but their effects have levelled out over the years. In contrast, the effect of wild ungulates exerted continuous pressure on the understorey, keeping its cover low. The strong impact of overstocked wildlife on regeneration and understorey is also found in other areas of the country and is a common phenomenon in the temperate region (Ramirez et al., 2018). A systematic literature review by Ramirez et al., (2018) showed that in 70% of the evaluated cases, wild ungulates have a negative effect on tree regeneration, forest development and functioning, and eventually, their browsing can lead to total regeneration failure (Palmer et al., et al., 2004).

4.2. Clear-cut plots

The most significant changes in almost all variables were in CC, and its species composition differed the most from the other treatments. One year after the interventions, increased irradiance and heat load, elevated soil moisture levels, high soil temperature, low mean air humidity, and the highest daily temperature and air humidity variability characterized these treatments (Kovács et al., 2018, Kovács et al., 2020), triggering rapid changes in the understorey. Temperate forest forbs are generally adapted to high and stable air humidity (Lendzion and Leuschner, 2009, Leuschner and Lendzion, 2009), hence low air humidity and high vapour pressure deficit of CC might be a strong stressor for many forest species. By the end of the survey, several forest species (*Melica uniflora, Dactylis polygama, Euphorbia amygdaloides, Galium odoratum, Stellaria holostea*) had practically disappeared from CC.

Species richness and total herb layer cover increased significantly after the clear-cutting. Graminoids (mainly *Carex pilosa*) and annual forbs were the main species to increase. The total herb layer cover started to decline slowly after 2016 in the fenced quadrats due to the closure of the emerging woody regeneration. Beta diversity and the rate of species turnover in CC were the highest among the treatments, and both variables were particularly elevated in the unfenced quadrats, underlining the high variability between both quadrats and years. The establishment of tree saplings (firstly hornbeam) was particularly rapid in fenced quadrats, where wild ungulates could not harm them. From 2018 onwards, the species composition separated from the other treatments, showing some overlap only with G. A large proportion of the several species associated with CC were annual and perennial light-demanding species, including disturbance-related (*Cirsium arvense, Calamagrostis epigeios*) and invasive species (*Erigeron annuus, Conyza canadensis, Solidago gigantea*).

Change in canopy openness due to human intervention is a strong driver of species richness (Pastur et al., 2002, Kirby, 2015, Dormann et al., 2020). Silvicultural treatments often lead to an increase in species diversity, mainly due to the emergence of light-demanding and disturbance-related species (Zenner et al., 2006, Kirby, 2015, Dormann et al., 2020), but in some cases, especially in larger openings, invasive species also appear (Pastur et al., 2002, Small and McCarthy, 2002, Kirby, 2015). This post-disturbance colonization of early-successional, disturbance-related species is a common phenomenon in clear-cut areas (Brunet et al., 1996, Kirby, 2015, Kermavnar et al., 2018). In some cases, invasive species can appear in large numbers (Halada et al., 2010, Godefroid et al., 2005a), and plant functional groups with a high conservation value, such as ancient-forest species retreat (Kenderes and Standovár, 2003, Godefroid et al., 2005b). Graminoids and perennial forbs also often exhibit a notable increase in clear-cut areas (Kirby, 2015, Kermavnar et al., 2018), leading to a significant increase in species richness (Brunet et al., 1996). Kirby (2015) detected 1.5 to 3 times higher species richness in the first two growing seasons in clear-cuts compared to the undisturbed stands in English oak-dominated woodlands. Species richness doubled in our case. The expansion of pre-treatment resident species, coupled with non-forest perennials and early-successional, disturbance-related species, not only elevates the species richness but usually lead to a very large number of clear-cut indicator species. Kermavnar et al., (2018) investigated the understorey vegetation responses on different forest management intensities in Illyrian beech forests of Slovenia, and they found that a high number of species significantly associated with the 100% felling intensity (47 out of 251) due to the post-colonization of early-successional, non-forest species. As disturbances by management generally increase plant species richness, the consequent increase in species number indicates disturbance rather than naturalness, as pointed out by Schmidt (2005) and Boch et al., (2013).

4.3. Gaps

The observed rapid changes of understorey variables and their high variability were almost as characteristic of G as of CC. The increase in the number of species in G was not as quick as in CC, but by the end of the study, there was roughly the same number of species in the herb layer in both treatments. The main contributors to the increase in total herb layer cover were *Melica uniflora* (the second most common herb layer species across all treatments and all years, indicator species of G treatment) and blackberry. In line with our result on the rapid total herb layer cover increase in G and CC treatments, other authors also found a strong correlation between herb layer cover and light availability, such as in three ecoregions in Germany (Dormann et al., 2020), in Slovenian beech stands (Kermavnar et al., 2018), in Hungarian mixed temperate (Márialigeti et al., 2016), beech (Gálhidy et al., 2006, Kelemen et al., 2012), and oak forests (Ádám et al., 2013). The increase in cover was mainly due to the expansion of graminoids and perennial forbs in the treatments of the present study, as observed by other authors as well (Kermavnar et al., 2018, Kirby, 2015).

The regeneration advancement of tree saplings in the fenced quadrats was very pronounced from the third year after the intervention (2017). In particular, hornbeam saplings grew rapidly and in large numbers (Tinya et al., 2020), and as a result, the understorey cover within the fenced quadrats started to decline sharply. In the fenced quadrats, however, a moist, cool microclimate (Kovács et al., 2020) was created by the regeneration layer of tree saplings, favoring ferns' emergence. The beta diversity was similarly high as in CC, but the inter-annual variation (i.e., turnover) was slightly lower. In parallel, the overall species composition showed the highest diversity of all treatments. Light-demanding species, including the disturbance-related *Calamagrostis epigeios* and the invasive *Solidago gigantea*, were uncommon in G. Battles et al., (2001) have come to similar conclusions in their study of Sierra Nevada forests in California – the proportion of early-successional and introduced exotic species was lower in forests managed by group and single-tree selection systems than in more intensively managed forest pairs, such as shelterwoods and plantations.

Overall, the high amount of additional light triggered a significant understorey response in G with an increase in species number and total cover, a significant increment in the regeneration layer, and high turnover and beta diversity. However, the highest soil moisture value of all treatments was found in the gaps, providing a cool and humid environment (Kovács et al., 2018, Kovács et al., 2020). Compared to clear-cuts, in gaps, higher soil moisture and lower light levels were probably responsible for the lower amount of disturbance-related and light-demanding plants, including invasive species. In general, although the vegetation cover and species richness increased, the composition preserved the forest characteristics of G contrary to CC.

4.4. Preparation cuts

The number of species in P has increased slightly over the years, while the total cover has increased steadily, reaching the highest values of all treatments by 2020. Graminoids, perennial forbs, and tree seedlings, including oak and hornbeam, were associated with P and reached high cover values by 2020. Only a few exceeded the height of 50 cm among the seedlings. Probably, the moderate amount of additional light received was sufficient for seedling survival and understorey cover growth but was not yet enough for sapling emergence and closure (Tinya et al., 2020).

The medium values in turnover suggest a slightly but constantly changing ecological condition in P reflected in the herb layer composition. The original humid forest microclimate was just moderately altered in P (Kovács et al., 2018). Craig and Macdonald (2009) investigated the effect of different levels of preparation cutting on understorey in boreal mixedwood forests. Their results were similar to those presented here, despite the different forest types. The cover of understorey vegetation, especially graminoids, increased with increasing harvesting intensity; however, species richness and herb layer composition did not change markedly (Craig and Macdonald, 2009).

4.5. Retention tree groups

Despite the warm and relatively dry microclimate of R (Kovács et al., 2018), the total cover of the herb layer grew over the years due to the increased cover of graminoids and seedlings (especially oaks). By 2020, R had the highest average species number, hosting a heterogeneous group of perennial forb species, many of them being the indicator species of this treatment type. However, despite the relatively high bare soil cover (Tinya et al., 2020), disturbance-related, invasive, or other exotic species did not appear in this treatment. Such habitats can maintain high species diversity, higher than the surrounding closed forests or clear-cuts (North et al., 1996). Tree retentions usually host less early-successional, disturbance-related herbs both in terms of plant abundance and richness (Halpern et al., 2005, Nelson and Halpern, 2005) and higher cover of shade-tolerant species, important for maintaining understorey diversity in the landscape (North et al., 1996, Nelson and Halpern, 2005, Beese et al., 2022). In addition to the shade-tolerant species, light-flexible and light-demanding species of the open areas and dry forest stands can also survive, which ensures the high species richness of such habitats. This result underlines the importance of retention tree groups, which in some cases can also act as a "lifeboat" (Franklin et al., 1997, Macdonald and Fenniak, 2007, Rosenvald and Lõhmus, 2008) in an intensively managed landscape by facilitating the re-development of important habitat structures and composition (Keeton and Franklin, 2005, Craig and Macdonald, 2009, Johansson et al., 2013). However, this effect is not universal for all organism groups, e.g., for soil organisms sensitive to soil moisture and temperature conditions, the retention tree groups in this experiment were unfavourable (Elek et al., 2018, Boros et al., et al., 2019).

5. Conclusions and management implications

Overall, the understorey variables had a large temporal variability over the years observed. The variables are likely to continue to change dynamically in the coming years, with the direction and intensity of change varying from treatment to treatment, which underlines the importance of long-term research.

The high beta diversity and turnover values indicated the large spatial and temporal variation in CC plots. Many new species appeared after this treatment, and many were disturbance-related and invasive species, as has been detected by several other studies on temperate European forests (Godefroid et al., 2005a, Halada et al., 2010, Kirby, 2015). In line with the results of the review by Savilaakso et al., (2021), despite the substantial amount of incoming light, G could guard the forest flora better than CC by resisting disturbance-related, light-demanding, and invasive herb layer species, most probably due to their humid air conditions and high soil moisture content (Kovács et al., 2020). Silvicultural practices prior to the final cutting, i.e., preparation cutting, can be essential in managed landscapes; the increased amount of light and the relatively humid and cool climate mimic the conditions after a mild natural disturbance, which supports the survival and growth of forest shrubs, herbaceous plants, and tree saplings. R maintained a diverse flora in the presented experiment – disturbance-related and invasive species have been unable to penetrate these habitats.

Based on our results, we formulate the following management implications. The vast majority (73%) of temperate and boreal forests of Europe are managed under rotation forestry systems, resulting in a mosaic of different aged even-aged forest patches at the landscape level. In contrast, selection systems, which maintain uneven-aged stands, are employed only approx. across 10% of European countries (Aszalós et al., 2022). Increasing the share of selection systems and other continuous cover forestry methods is crucial to preserve the forest herb layer at the landscape scale (Brang et al., 2014, Kern et al., 2014, Kutnar et al., 2015), specifically in countries where uneven-aged management is highly underrepresented. In a shelterwood system, we suggest leaving at least one decade between preparation cut and final felling. This light-rich condition benefits many forest herb layer species and helps to survive and strengthen tree saplings, e.g., in our case, oak saplings. Rotation forestry with large cutting areas is not recommended or should be kept at low landscape rates because these areas are highly exposed to disturbance-related and invasive species. Leaving retention tree groups with different patterns and sizes, however, as many authors have noted (Macdonald and Fenniak, 2007, Rosenvald and Lõhmus, 2008, Lencinas et al., 2011), can be crucial to the survival of numerous forest species, and therefore including them to forest management planning is highly recommended. Reduction of cutting areas, retention of tree groups, promotion of uneven-aged structure, and the extension of preparation cut phase all contribute to the maintenance of the forest microclimate and, through this, to the conservation of forest understorey vegetation and to the control of disturbance-related and invasive plant species.

Declaration of Competing Interest

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Data availability

https://osf.io/549wm/

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