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Initial understory response to experimental silvicultural treatments in a temperate oak-dominated forest

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Abstract

In recent decades, alternative management techniques integrating conservation concerns into industrial forestry have become increasingly widespread. In order to compare the effects of various management methods on forest site and biodiversity, a systematic forestry experiment was conducted in a managed, mature oak-hornbeam forest. The present work introduces the two year responses of environmental variables and understory vegetation to different silvicultural treatments. These belong either to clear-cutting (clear-cutting, retention tree group), to shelterwood (preparation cutting), or to continuous cover forestry systems (gap-cutting). The experiment follows a complete block design with four replicates. Light availability was significantly higher in all the treatments than in the uncut control, with highest values in the clear-cuts. Soil moisture was highest in the gap-cuts and clear-cuts, while in the retention tree group, it did not differ from the control. Species richness, cover, and height of the understory considerably differed from the control in the clear-cuts and gap-cuts, while in the retention tree group, only species richness was higher. The establishment of ruderal, non-forest species altered the species composition in the clear-cuts. Based on these short-term responses, we conclude that as a result of the extreme environmental changes, clear-cutting in oak-hornbeam forests changes the understory vegetation considerably. Retention tree groups can maintain legacies of the understory composition for some years. Despite the experienced high vegetation cover, gap-cutting preserves the forest characteristics of the understory better than clear-cutting. These results confirm that in oak-hornbeam forests, continuous cover forestry may be more sustainable from conservational aspect than clear-cutting system.

Keywords

biodiversity; field experiment; forest herbs; forest management; light; soil moisture

1. Introduction

Forest management substantially modifies the structure and composition of forest stands, and by doing so, also forest biodiversity, which is generally lower in managed than in unmanaged forests (Paillet et al. 2010). The effects of forest management often prevail indirectly, by modifying understory microclimate and site conditions (Aussenac 2000; Ódor et al. 2013; Kovács et al. 2017). Herbaceous plant communities are sensitive to these disturbances. Their most important drivers, often highly modified by management practices, are light and soil moisture (Collins 1985; Gálhidy 2006; Slezák and Petrašová 2010; Márialigeti et al. 2016). However, the impacts of various forestry methods on site conditions and understory biodiversity differ (Duguid and Asthon 2013).

The recently widespread industrial forestry systems in Europe maintain even-aged stands, which are regenerated artificially (clear-cutting system) or naturally (shelterwood system) at the end of the rotation period (Matthews 1991). From an ecological aspect, the main disadvantage of these systems is the temporal discontinuity of the forest environment. Small and McCarthy (2002) showed that microclimate, and as a result, understory vegetation change dramatically after the final cutting. Godefroid et al. (2005) found that many forest herb species are not able to regenerate in clear-cuts of beech forests for many years because of their dispersal limitation, unsuitable forest site conditions, and strong competition from early-succession species. The understory of temperate deciduous forests is adapted to a relatively stable microclimate, maintained by fine-scale gap-dynamics, and can hardly tolerate the extreme microclimatic conditions of the clear-cuts (Bescond et al. 2011). However, the total closure of the upper canopy layer, which is typical of managed stands until the mature stage, rarely occurs in old-growth temperate forests (Saniga et al. 2014).

The strong microclimatic effects of these forestry practices can be somewhat mitigated by an elongated regeneration period and an extended rotation age, i.e. using shelterwood system instead of clear-cutting (Brose 2011). After the preparation cutting, the established, moderately open stand may be favourable for light-flexible forest species, but the forest character of the habitat is preserved, and there is less potential for the dispersion of non-forest species than on large clearings.

In recent decades, alternative management techniques integrating biodiversity concerns into industrial forestry have become increasingly widespread. Retention harvest (retention of single trees or intact forest patches) is widely applied, especially in North America (Lindenmayer et al. 2012). Green tree retention forestry can ensure the survival of the forest biota (Mori and Kitagawa 2014), but its conservational effect is limited: it depends considerably on the level of retention, and is especially ambiguous in the case of forest-interior species (Fedrowitz et al. 2014).

Another widespread, nature-based forestry system is continuous cover forestry (maintained by group selection or single tree selection, Pommerening and Murphy 2004). This system also modifies the microclimate and the communities of the closed forest (Kern et al. 2014), but Schumann et al. (2003) found in mixed coniferous-broadleaved stands that these changes are less severe, and late-successional forest species can survive.

The comparison of the effects of different management methods on forest site, natural regeneration, and forest biodiversity is equally important for forestry, conservation practices, and basic research (Bauhus et al. 2009). To understand these complex relationships, systematic forestry experiments are necessary (Aubry et al. 2009; de Groot et al. 2016). Many studies examine the effects of a given management type on the understory, compared to the below-canopy vegetation of unmanaged forests, and some analyse the effects of different intensities of a given treatment (Sullivan et al. 2001; Halpern et al. 2012; de Groot et al.

2016), but only a few studies compare the effects of numerous different harvesting methods within the same experimental framework. Most of these concern coniferous forests (Beese and Bryant 1999; Jalonen and Vanha-Majamaa 2001; Huggard and Vyse 2002), and only a few papers are available on deciduous stands (Philips and Shure 1990; Wender et al. 1999; Jenkins and Parker 2000; Zenner et al. 2006). Moreover, the results of the different studies are often contradictory considering the effects of management on understory vegetation (Duguid and Asthon 2013). In some cases, no impact could be detected (Bescond et al. 2011; Zenner et al. 2012), or the directions of the demonstrated effects were inconsistent (Halpern et al. 2005 vs. Kern et al. 2014; Godefroid et al. 2005 vs. Jenkins and Parker 2000). The results depend on the vegetation zone (Kusumoto et al. 2014), forest type (Fredericksen et al. 1999), successional stage and management type (Duguid and Asthon 2013), management intensity (Zenner et al. 2006), forest site (Schumann et al. 2003), surrounding landscape (Halpern et al. 2005), and land-use history (Jenkins and Parker 2000) of the study area. Because of the multitude of relevant background variables, a broad generalisation of the results is not possible, and therefore, many specialised investigations are needed (Duguid and Asthon 2013). Furthermore, most of the studies concerning temperate deciduous forests were carried out in North America (e.g. Schumann et al., 2003, Aubry et al. 2009; Fedrowitz et al. 2014), or in European beech forests (Gálhidy et al. 2006, de Groot et al. 2016). Oak-dominated forests are underrepresented, although they are internationally significant (Bobiec et al. 2011, Bölöni et al. 2017): e.g. in Europe, mixed oak-hornbeam forests are distributed from western France to the region of Kiev in Ukraine, and from southern Lithuania to the Po plains in Italy (EEA Technical report No 9/2006). In Hungary, this forest type has the largest area of all the forest types composed by native species, but there is little evidence of the effects of different management types on the understory vegetation of these forests (Bölöni et al. 2008).

Even the characteristics of the natural understory vegetation themselves are not well-known. The oak forests of Europe have been affected by humans for many centuries (traditional land-use practices, e.g. coppicing, grazing, and later, intensive forest management; Parviainen 2005; Hofmeister et al. 2009; Bobiec et al. 2011). Besides the various land-use histories, site conditions also create a substantial variability in the understory of Central European oak forests. According to an investigation of a broad spectrum of different understory types, their species richness and composition are mainly determined by canopy openness, altitude, soil pH/base saturation gradient, plant-available phosphorus content, silt content, and topography-related predictors (Slezák and Petrašová 2010; Slezák and Axmanová 2016). Oak-hornbeam forests are highly closed and shaded among oak-dominated forests. Most of them are managed by shelterwood forestry system. Their herb layer is characterized by relatively low species richness and floristic variability, but understory cover can range from sparse to continuous. Most common species are general and mesic forest species, often with a rich spring geophyte aspect (Bölöni et al. 2008; Slezák and Petrášová 2010; Szmorad 2014).

The aim of this study is to investigate the effects of different forestry practices on the understory of oak-hornbeam forests, by way of a comparative field experiment. The studied silvicultural treatments were typical elements of different forestry systems: clear-cutting and retention tree group (typical of the clear-cutting system), preparation cutting (typical of the shelterwood system), and gap-cutting (typical of the continuous cover forestry system).

To evaluate the effects of each of the forestry treatments from a conservational aspect, it is important to determine the reference state of the understory vegetation, which would be desirable to preserve or create. A theoretical aim is to maintain the characteristics (species richness, abundance, and composition) of the understory of the uncut forests. However, because of the variability of oak forests – caused by land-use history and site conditions –, and the lack of natural references, it is hard to define the natural state of forest vegetation

(Parviainen 2005). In the present study, we used a mature, closed stand, managed by shelterwood forestry system as control, because this is the presently typical form of these forests in the region. Another reason for our choice was that we needed a stand with homogeneous stand structure and composition for the comparative experiment. This managed forest is presumably more homogeneous and closed than a natural forest would be, where fine-scale dynamics prevail (Standovár and Kenderes 2003).

In order to form a relevant conception of its response, we investigated five aspects of the understory: species richness, cover, height, composition, and indicator species. Many studies evaluate only species richness (Paillet et al. 2010), but it may be sometimes misleading. Higher species richness after treatments may result from the establishment of non-forest species occurring in meadows and ruderal areas, which is unfavourable from a conservational aspect (Boch et al. 2013). It is important to consider the changes of species composition as well: it is not only more relevant, but may also be more sensitive to the treatments (Scheller and Mladenoff 2002; Tullus et al. 2018). From a conservational aspect, the aim is not the highest possible species richness, but the preservation of the composition, abundance, and structure of the forests maintained by natural dynamics.

Site conditions and understory vegetation of the treatment sites were compared, two years after harvest, focusing on the following questions:

1. How different are the light and soil moisture conditions of the treatments from the uncut control site?
2. How do the different treatments alter the species richness, abundance, and composition of the understory vegetation, compared to the uncut stand?
3. Are the observed differences in vegetation related to the altered light and soil moisture conditions?

2. Materials and methods

2.1. Study area

The study was carried out in the Pilis Mountains (47°40'N, 18°54'E), the north-eastern ridge of the Transdanubian Range, Hungary (Online Resource 1. Fig. A1). In terms of site conditions, stand structure, composition, and prevalent management practices, the investigated stand is representative of the Hungarian oak-hornbeam forests, managed by shelterwood forestry system. Plots are situated on north-facing, moderate slopes (7.0–10.6°), at 370–450 m a.s.l. Average annual mean temperature is 9.0–9.5°C, with a mean annual precipitation of 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 4.2–5.3, Kovács et al. 2018). The study site is situated in a managed sessile oak-hornbeam forest stand (Natura 2000 code: 91G0, Council 1992), with homogeneous site conditions. Because of the applied shelterwood system, the stand is even-aged (80 years old), and has uniform structure and species composition. The upper canopy layer is dominated by sessile oak (*Quercus petraea)*, while hornbeam (*Carpinus betulus)* forms a secondary canopy layer. *Fraxinus ornus, Fagus sylvatica, Quercus cerris,* and *Cerasus avium* also appear as subordinate species. The shrub layer is scarce, and the understory layer consists of general and mesic forest species (dominant species are *Carex pilosa* and *Melica uniflora*).

2.2. Data collection

Experimental silvicultural treatments were implemented in a randomized complete block design, using the following treatments in four replicates (Fig. 1a, Online Resource 1. Fig. A2):

1. control (C): closed-canopy stand, no harvesting;
2. clear-cutting (CC): a circular clear-cut (diameter: 80 m), surrounded by closed stand;

3. gap-cutting (G): an artificial circular gap in the closed stand (diameter: 20 m, approximately 1 tree height/gap diameter ratio);

4. preparation cutting (P): in a 80 m diameter circle, 30% (basal area) of the dominant tree layer was felled in a spatially even arrangement, and the secondary canopy and shrub layer were completely removed;

5. retention tree group (R): a circular group of retained dominant trees (diameter 20 m, 8–12 individuals) within the clear-cuts.

We devised the size and the implementation of the treatments so that they mimic the general forest management processes in Hungary. In oak-hornbeam forests managed by continuous cover forestry system, the applied gap size varies between 0.5-1.5 tree height/gap diameter ratio (Bartha et al. 2014). This gap size is considered proper for the regeneration of oak (McShea and Healy 2002). For industrial forest management, the maximum area of clear-cuts in the submontane region is ruled by law, and is 5 ha (Anonymous 2017). As our experimental plots are located at a Natura 2000 site, we were not allowed to create such large clear-felled spaces, hence our model clear-cuts' extension is only 0.5 ha. However, we expect environmental conditions in the centre of a 0.5 ha clear-cut to be similar to those of a larger clearing, and we suppose that larger clear-cut areas have similar or more drastic effects than our experimental ones. Data on forest structure before and after the treatments are supplied in Online Resource 1. Table A1. Based on extensive sampling, understory species richness and cover were homogeneous over the treatment sites before the cuttings (Aszalós et al. unpublished data).

In each of the twenty sites (five treatments in four replicates), one circular study plot with 20 m diameter was established. The plots were located in the centre of each treatment. In the case of the clear-cuts, they were at an equal distance from the edges and the retention tree group. Within the plots, understory vegetation and environmental variables were recorded in 81, 0.5

× 0.5 m quadrats, in a systematic grid with 2 × 2 m intervals (Fig. 1b). This arrangement resulted in 1620 quadrats, located in 20 plots. Silvicultural treatments were carried out in the winter of 2014-2015. Understory and environmental data were collected in the growing season of 2016, i.e. in the second year after the treatments.

Diffuse light was measured by LAI-2000 Plant Canopy Analyzer (LI-COR Inc. 1992), in the centre of each quadrat, at 1.3 m height. Measurements were carried out in July, always at dusk, in order to avoid direct light getting into the sensor. A 270° view restrictor masked the segment of the sky containing the sun and the operator (LI-COR Inc. 1992). Reference above-canopy measurements were performed in a nearby open field.

Volumetric soil water content (SWC) was gauged by FieldScout TDR 300 Soil Moisture Meter (Spectrum Technologies, Aurora, IL) with 7.5 cm rods (Ledieu et al. 1986). As well as light, SWC was also measured in the centre of each quadrat, on three occasions: in July, August, and September. Reference measurements were carried out in a closed stand, next to the experimental area.

We surveyed the understory in the 0.5 × 0.5 m quadrats, in July. Early spring geophytes were excluded from the sampling. We defined understory as all herbaceous species, plus woody species shorter than 0.5 m. Percentage cover of each species, and the average height of the understory for every quadrat were visually estimated. The nomenclature of plants follows Király (2009). Additional information concerning the framework of the current study and other investigated organism groups are available on the website of the experiment (http://piliskiserlet.okologia.mta.hu/en).

2.3. Data analysis

For each quadrat, diffuse non-interceptance (DIFN, in %) was derived as the percentage of diffuse light coming through the canopy. To characterize plot-level light conditions, we calculated the mean of the 81, quadrat-level light values. Soil moisture was given for each quadrat as relative soil water content (dSWC, in V/V%), calculated as the difference between the reference and the measured values. Plot-level mean dSWC was calculated from the quadrat-level, averaged values of the three measurements. Total understory cover was obtained as the sum of the individual species' cover. Species were categorized as forest/non-forest/indifferent species, based on the Hungarian coenosystematic classifications of the plant species (Horváth et al. 1995).

Linear mixed-effects models were built on the quadrat level, to explore *a)* the effect of silvicultural treatments on the measured environmental variables (DIFN, dSWC), *b)* the effect of treatments on understory variables, and *c)* the effect of light and soil moisture, on the understory variables (Zuur et al. 2009). The examined vegetation variables were species richness, cover, and average height of the understory. Fixed effects were the treatments (*a* and *b*) or the environmental variables (*c*). In the case of the environmental variables, the role of the interaction between light and soil moisture was always tested, but we used this term in the final model only where it proved to be significant. Block and plot were used as random factors in a nested arrangement. In the dSWC model, data from all three measurement campaigns were included; therefore, the month of measurement was also applied as a random factor. In order to satisfy the requirement of normality for residual distributions, square root transformation was applied for the DIFN data. In the case of significant treatment-effects ($P<0.05$), multiple comparisons with user-defined contrasts were carried out (Bretz et al. 2010). To explore the role of light and soil moisture in the treatment-effects, the determination coefficients (likelihood-ratio based pseudo-R-squared values) of the different models were compared.

The relationships between treatments, environmental variables, and the species composition of the understory were evaluated by redundancy analysis (RDA) on plot level, using the ln-transformed cover data of the species (Borcard et al. 2011). Plot-level mean DIFN and dSWC were used as canonical variables (Pearson's correlation between them: r=0.453, P=0.045). On the RDA diagram, treatments were denoted by convex hulls.

The connections between species and treatments were evaluated 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). As the 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.

All analyses were performed with R version 3.0.3 (R Development Core Team 2016). Mixed modelling was conducted by the R package "nlme" (Pinheiro et al. 2013), multiple comparisons by the "glht" function of the "multcomp" package (Hothorn et al. 2015). Determination coefficients of the mixed models were calculated by the "MuMIn" package (Bartoń 2016). We used the package "vegan" for the RDA (Oksanen et al. 2015), and "labdsv" for the ISA (Roberts 2013).

3. Results

3.1. Light and soil moisture in the different treatments

According to the mixed models, both relative diffuse light and relative soil water content were significantly related to the treatments (Table 1). The amount of light was much more variable between treatments than that of soil moisture (Online Resource 2. Table A2). Light was significantly higher in every treatment than in the control plots. Highest irradiation values were observed in the clear-cuts (Fig. 2a, Online Resource 2. Table A2). Relative soil water content was highest in the gap-cuts and in the clear-cuts, but soil moisture in the preparation cuts was also significantly higher than in the control plots or in the retention tree groups (Fig. 2b; Online Resource 2. Table A2).

3.2. Understory species richness and abundance in the different treatments

We recorded altogether 123 plant species in the understory (Online Resource 2. Table A3). The mixed models showed significant relationships between the treatments and understory species richness, cover, and height (Table 1, Fig. 2c, d, e). Species richness was highest in the clear-cuts, and it differed significantly from the control plots in all of the other treatments as well (Fig. 2c, Online Resource 2. Table A4). The mean values of the treatments' understory cover were arranged in the same order as the species richness values, with clear-cuts having the highest cover, but for this variable, the retention tree group did not significantly differ from the control (Fig. 2d, Online Resource 2. Table A4). Understory height was largest in the gap-cuts, but it was also significantly larger in the clear-cuts and the preparation cuts than in the control plots (Fig. 2e, Online Resource 2. Table A4).

Understory species richness, cover, and height were all significantly related not only to the treatments, but also to light and relative soil water content. Based on the R^2 values, the effect of the environmental variables was similar to the effects of the treatments (Table 1).

3.3. Understory composition

Using RDA ordination, we demonstrated differences in the species composition of the treatment types, along the investigated environmental variables (Fig. 3). The model explained 25.48% of the total variance (F=2.91, P=0.001). The first canonical axis explained 19.13% of the total variance (F=4.36, P=0.001), and it expressed mainly a gradient of light (r=0.95), but soil moisture had also a strong influence (r=0.70). The second axis (explained variance: 6.35%, F=1.45, P=0.108) was primarily related to soil water content (r=0.71). Light and soil moisture explained 17.93% (F=3.93, P=0.005) and 12.68% (F=1.72, P=0.035) of the total variance, respectively. Most of the treatments separated along the light gradient. The controls and the clear-cuts were situated at opposite ends; the retention tree groups and the preparation cuts highly overlapped with each other. The convex hulls of the gap-cuts and clear-cuts also showed a strong separation from the other treatments, along the soil moisture gradient. According to the size of the convex hulls, species composition of the control plots was the most homogeneous, and that of the clear-cuts proved to be the most heterogeneous (Fig. 3).

3.4. Indicator species

The cover of individual species differed considerably by treatment (Online Resource 3. Fig. A3). However, the results of the ISA revealed only 16 species significantly associated with any of the treatments (Table 2). Control areas had only one indicator species (*Ligustrum vulgare*), three species (*Campanula rapunculoides, Melica uniflora* and *Scrophularia nodosa*) were associated with the gap-cuts, and 12 species were related to the clear-cuts, including some graminoids (*Calamagrostis epigeios, Carex pilosa, Dactylis polygama*), and several non-forest forbs (e.g. *Conyza canadensis, Erigeron annuus, Vicia hirsuta*, Table 2).

4. Discussion

4. 1. Relevance and limitations of the study

Our results are valid primarily in sessile oak-hornbeam forests. Nevertheless, the findings are still highly relevant, since management effects in this forest type have been poorly studied, compared with coniferous or beech forests. We produced a snapshot of the environmental conditions and understory responses two years after the interventions, and we could already observe significant differences between the effects of the treatments, even after such a short period. Microclimate will change notably during the following years and decades as woody species regenerate and the overstory closes. Therefore, long-term vegetation responses may differ considerably from short-term responses (Halpern et al. 2012). It is still uncertain whether closed-forest species survive in the harvested sites, and whether non-forest species will be forced back as the stands close. Schumann et al. (2003) and Zenner et al. (2012) conceive that forest understory can be resilient enough to regenerate after harvest, but its success depends on many factors (e.g. logging technique, site characteristics or land-use history). To understand the whole process, initial results are also of interest: they determine the further pathway of the compositional changes, and the regeneration success of forest overstory as well as understory (Grayson et al. 2012).

In the present study, we investigated only one component of the forest biota: understory vegetation. Obviously, this single assemblage cannot be considered as an indicator of the entire forest biodiversity (Sabatini et al. 2016). Every organism group responds differently to the treatments, as they react to various effects of the cuttings. However, the response of the understory is relevant, since it constitutes a large proportion of forest biodiversity (Lorenz et al. 2006; Gilliam 2007; Mölder et al. 2008), and its changes strongly affect many other organism groups (e.g. herbivores and other animals using understory vegetation as habitat). Through competitive interactions, the herb layer is also an important determinant of tree regeneration (Gilliam 2007).

We investigated the response of the understory only at within-stand scale. However, Schall et al. (2017) showed that at coarser scales, the effects of treatments on forest organism groups may be quite different.

4.2. General responses to the treatments

Both the abiotic environment and the understory of the silvicultural treatments differed significantly from those of the control. As expected, mean light was higher in all of the treatments than in the control. In oak forests, Brose (2011) measured similar light values to ours in closed stands, preparation cuts and clear-cut plots. Gap-cutting, preparation cutting and retention tree groups preserve forest light conditions substantially better than clear-cutting. Soil moisture was higher in the cutting treatments (clear-cuts, gap-cuts, preparation cuts) than in the control, because of higher throughfall and reduced transpiration (Muscolo et al. 2014).

Before the interventions, understory species richness and cover were homogeneous in all the plots. Hence, we can declare that the differences observed in our study developed after the cuttings. Two years after the interventions, species richness, cover, and height of the understory were significantly higher in the treated sites than in the control plots. In their meta-analysis, Duguid and Ashton (2013) showed that results about the effects of forest management on understory species richness are quite contradictory. Our findings are in congruence with Fredericksen et al. (1999) and Zenner et al. (2006), who also concluded that understory species richness and cover increase along a harvest intensity gradient (i.e. from the uncut sites, through moderate interventions such as different kinds of selection and thinning practices, towards clear-cutting). The reason for this mainly lies in the higher resource availability of the harvested areas (Zenner et al. 2006). In our study, the indirect effects of treatments on the understory, manifested through the measured environmental factors, proved to be as strong as the direct treatment–understory relationships, thus we assume that both light and soil moisture are influential factors of the treatments. Comparing closed forests within a relatively short light gradient (3–8%), Tinya et al. (2009) found that only the species richness of understory herbs was significantly related to light, whereas their cover was independent of it. However, in the present study, the huge range of light values between the five treatments (0.3–90%) caused significant differences also in the cover of the understory vegetation.

In the clear-cuts and gap-cuts, vegetation structure also differed significantly from that of the control. It was considerably denser, higher, and more stratified in the cutting treatments, similarly to the findings of Fredericksen et al. (1999). Higher structural complexity is particularly important for forest-dwelling animal groups living in the understory layer (Ziesche and Roth 2008, Sweeney et al. 2010).

Not only the species richness, abundance, and structure, but also the composition and heterogeneity of the understory differed between the treatments and the control. Similarly to species richness and abundance, composition in the different treatments was also strongly influenced both by light and soil moisture. Zenner et al. (2006) also demonstrated altered understory species composition towards the more intensively harvested stands in American mixed oak forests. Compositional changes in the harvested sites mainly arise from the influx of new, non-forest species, the loss of the original forest species is less typical (Freedman et al. 1994; Jenkins and Parker 2000; Schumann et al. 2003). In accordance with this observation, in our experiment, control sites had only one indicator species, while clear-cuts and gap-cuts had more.

The understory's response to the harvests varies largely, depending on management type (Fredericksen et al. 1999; Duguid and Ashton 2013). Accordingly, we discuss the abiotic environment and understory conditions of the different treatments separately.

4.3. Uncut control

In uncut sites, both irradiance and soil moisture values were low. These resulted in low understory species richness, cover, and height, and homogeneous species composition in all the blocks. Mature stands of oak-hornbeam and beech forests managed by shelterwood forestry system are generally characterised by a homogeneous, closed canopy, which differs from the natural (old-growth) stands of these communities, in which fine-scaled gap dynamics results in lower canopy closure, heterogeneous stand structure and a high light heterogeneity (Christensen and Emborg, 1996, Standovár and Kenderes 2003). The uncut sites in our experiment represent only the between-gap matrix of these forests. At the stand scale, near-natural, unmanaged forests may have higher understory cover, due to the abundance of light-flexible forest species in the gaps (Collins et al. 1985), while their species richness is often low (Boch et al. 2013; Schall et al. 2017). However, a common characteristic of our control sites and near-natural unmanaged forests is the lack of non-forest (ruderal, meadow) species (Horváth et al. 1995, Boch et al. 2013).

4.4. Clear-cutting

Because of the relatively small size of the clear-cut sites (0.5 ha), relative diffuse light did not reach 100%, even in the centre of the clear-felled areas. But even so, this was prominently the brightest treatment. Compared with the control sites, the lack of trees also caused significantly higher soil moisture. However, the soil was slightly less moist than in the gap-cuts, because of the stronger drying effect of wind and solar radiation.

Presumably as a result of the high light and soil moisture values, cover, height, and species richness of the understory were considerably larger in the clear-cuts than in the control sites. Higher species richness was mainly caused by the occurrence of non-forest (ruderal and meadow) species (Horváth et al. 1995), from which some also proved to be indicators of the clear-cuts (e.g. *Vicia hirsuta*, *Cirsum spp.*). Most of these are referred to as sun-species, with metabolism adapted to high-intensity light environments (Collins et al. 1985). Among these non-forest species, annual weeds (e.g. *Conyza canadensis, Erigeron annuus*) had high abundance two years after the interventions, but perennials (e.g. *Calamagrostis epigeios, Solidago gigantea*) also occurred. We expect the dynamic spreading of the latter species group in the course of the next years. Forest species were also present in the clear-cuts; some of them had such high abundance that they became clear-cut indicators. Most of these (e.g. *Carex pilosa, Euphorbia amygdaloides*) are light-flexible plants, which are photosynthetically adaptable over a broad range of light intensity. However, some typically shade-tolerant herbs (e.g. *Ajuga reptans*) were also abundant here, in the lowermost layer of the understory, sheltered by taller, dominant species (Collins et al. 1985).

As a result of these differences from the uncut stand, we conclude that species composition lost its original forest character. Contrarily, Halpern et al. (2005) found that during the first two years, only a few new species colonized the harvested areas, and forest species were still dominant. According to the RDA, species composition of the four clear-cut plots was more heterogeneous than that of the controls. The possible reason for the high beta-diversity of the clear-cut sites may be that while closed canopy moderates the abiotic differences among the four blocks, clear-cutting enhances them; or that the establishment of new species after harvest is quite stochastic.

Clear-cuts in practice are usually larger than our experimental sites. We suppose that in larger cutting areas, differences from the uncut control are similar or even more pronounced than those observed in our experiment (Philips and Shure 1990; Huggard and Vyse 2002). Microclimate is expected to be more extreme, and dispersal from the surroundings is expected to be more limited. Hence we assume an even more intensive alteration of understory species composition (retreat of forest species and establishment of non-forest species).

4.5. Gap-cutting

Gaps were much less light than clear-cuts. Because of higher throughfall, the local lack of tree transpiration, and the shading effect of the surrounding stand, soil moisture was the highest in gap-cuts from all our treatments (Gálhidy et al. 2006; Muscolo et al. 2014).

Understory height was the largest in gap-cuts, and cover and species richness were also significantly higher than in the control sites. These results are in congruence with the increase of understory cover and species richness reported from gaps in beech stands (Gálhidy et al. 2006). We suppose that high species richness was caused by the introduction of some moisture-demanding, disturbance-tolerant species (e.g. *Scrophularia nodosa* and *Campanula rapunculoides*, which proved to be indicators of the gaps).

Species composition of the gap-cuts differed substantially from that of the control, although this difference was less pronounced than in the case of the clear-cuts. In gaps, light-flexible species were more abundant than shade-tolerants (Collins et al. 1985). However, these light-flexible species can be also categorized as forest species (Horváth et al. 1995), because they may occur also in the natural gaps established during the small forest cycle, which is characteristic for the Central, Eastern and Southern European forests (Schmidt-Vogt 1991 as cited in Schuck et al. 1994). Thus we can state that in gaps only the dominance relations of forest species has rearranged. The establishment of non-forest species was less characteristic, therefore we conclude that gap-cutting is more apt for preserving forest understory than clear-cutting. Similarly, Schumann et al. (2003) found that gap-cutting did not negatively impact the presence of species in the understory in oak-pine forests.

Besides the low presence of non-forest species, another important aspect of gap-based continuous cover forestry is that at the stand scale, between the gaps, the closed-forest environment is constantly present. Thus the typical understory species composition of the uncut forest (dominated by shade-tolerant species) can also be preserved.

4.6. Preparation cutting

Because of the evenly distributed, partial elimination of trees, the light and soil moisture conditions of the preparation-cuts differed moderately but significantly from the control. We also found an intermediate but significant divergence from the control's understory species richness, cover, and height. A slight difference in species composition was also detected: some open-forest species (e.g. *Poa nemoralis*, *Campanula persicifolia*) were more abundant here than at other sites. According to Halpern et al. (2005, 2012) and Zenner et al. (2006), retaining trees in a dispersed spatial arrangement has a buffering effect on the forest site and understory, even if the level of retention is much lower than the one tested in our study. However, we emphasize that this is a relatively short, transitional stage within the shelterwood system. After 5–15 years, preparation cutting is followed by the final cutting, which leaves behind only a few legacy trees or retention tree groups within the felling area (Matthews 1991).

4.7. Retention tree groups

In retention tree groups, the average light was similar to that of the gap-cuts. Soil moisture was slightly but significantly lower than in the control, because of the intensive transpiration of the remaining trees and the drying effect of the surrounding clear-cut. Presumably because of the low soil moisture, cover and height of the understory did not differ from the control. At the same time, new, non-forest species were established, supposedly facilitated by the higher amount of light, the proximity of the clear-cut, and the lack of extremely abundant forest herb species. These species usually occurred with a very low abundance, thus they did not change the species composition considerably, but they caused a significant difference in species richness from the control.

Neither the preparation cuts, nor the retention tree groups had any indicator species. Both had transient assemblages, between the control and the open areas (gap-cuts, clear-cuts), and no specific species pool. Understory species richness, cover, and height were also similar in these two treatments. Halpern et al. (2005) also found that two years after the cutting, the pattern of retention (aggregated vs. dispersed) had little effect on the general response of the understory. Further study should concern the spatial pattern of the abiotic environment and the understory in the differently treated areas. Despite similar average values, the spatial pattern of the microclimatic variables may be considerably different in the various treatments, which in turn may cause variable vegetation patterns (Grayson et al. 2012).

5. Conclusions

Natural mesophilous forests are driven by fine-scale gap dynamics (Standovár and Kenderes 2003). In these forests, closed-canopy areas with low understory cover are disrupted by gaps with denser vegetation. Consequently, homogeneous, closed forests are not favourable from a conservational aspect. The environmental conditions in the gaps of our experiment may be similar to those of natural gaps, thus, besides their economic role, they may be a means to recover the near-natural state of the understory vegetation. Local increase in the abundance of light-flexible forest species fits into the natural dynamics of these forests, while in the uncut parts of the stand, the dominance of shade-tolerant species remains.

The extreme environment of the clear-cuts is quite contrasting with the conditions of any kind of uncut stands. Here, not only the species richness and the abundance, but also the species composition of the understory changes drastically. Increased species richness in this case cannot be considered favourable from a conservational point of view: as a result of the intensive establishment of non-forest species, the understory vegetation loses its forest character, even if shade-tolerant species can survive. Vegetation of clear-cuts is not analogous with the understory of any stage of the natural stand dynamics of oak-hornbeam forests.

If clear-cutting is applied, retention tree groups are efficient for preserving the legacy of the forest understory composition for some years, but to evaluate the duration of this sheltering effect, long-term studies are necessary (Rosenvald and Lõhmus 2008). Semi-open stands, similar to our preparation cuts, develop in various management systems (e.g. shelterwood system, dispersed retention harvest). The uniform, slight increase in irradiance and moderate changes in soil moisture cause only modest alterations in the understory, which keeps its forest character, but open-forest species spread at the shade-tolerant species' cost.

Final cutting in the shelterwood and clear-cutting systems produces conditions that are too open for any kind of forest understory vegetation (i.e. herb layer of sites with closed or semi-open canopy or gaps). Meanwhile, in the mature stage of these systems, the homogeneous, closed canopy favours only shade-tolerant species. The continuous cover forestry system, which creates illuminated gaps in a shaded matrix, is better suited to the preservation of the heterogeneous vegetation (composition and structure) of the near-natural forest.

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Tables

Table 1. Mixed effects models for the investigated environmental and understory variables. Random factor: block/plot (and month/block/plot in the treatment–relative soil water content model). To relative diffuse light values, square root transformation was applied.

Dependent variables	Fixed effect	F-value	P	R^2_{pseudo}
Rel. diffuse light	Treatment	421.71	<0.0001	0.944
Rel. soil water content	Treatment	33.18	<0.0001	0.626
Species richness	Treatment	9.54	0.001	0.42
Understory cover	Treatment	8.54	0.0017	0.618
Understory height	Treatment	13.75	0.0002	0.538
Species richness	Environmental variables (Chi^2=59.65, P<0.0001)			0.433
	Rel. diffuse light	44.03	<0.0001	
	Rel. soil water content	27.29	<0.0001	
Understory cover	Environmental variables (Chi^2=177.78, P<0.0001)			0.653
	Rel. diffuse light	71.17	<0.0001	
	Rel. soil water content	120.58	<0.0001	
	Rel. diffuse light: rel. soil water content	4.47	0.0347	
Understory height	Environmental variables (Chi^2=64.73, P<0.0001)			0.549
	Rel. diffuse light	24.03	<0.0001	
	Rel. soil water content	45.35	<0.0001	

Table 2. Indicator species analysis of the understory species, regarding treatments. Only the species significantly related to treatments are listed. Numbers represent the cover (%) of given species in the different treatments: C = control, CC = clear-cutting, G = gap-cutting, P = preparation cutting, R = retention tree group. Ind. treatm: treatments with the highest indicator values. Indval (%): indicator value related to treatment.

Species	C	CC	G	P	R	Ind. treatm.	Indval (%)
Ligustrum vulgare	0.13	0.00	0.02	0.00	0.00	C	66.3*
Campanula rapunculoides	0.00	0.01	0.08	0.00	0.00	G	69.1*
Melica uniflora	15.66	25.87	45.82	23.42	15.73	G	24.3**
Scrophularia nodosa	0.00	0.45	1.06	0.05	0.02	G	60.1*
Ajuga reptans	0.27	3.61	1.53	0.42	0.19	CC	48.1**
Calamagrostis epigeios	0.00	0.95	0.00	0.00	0.00	CC	99.5**
Carex pilosa	11.75	65.16	31.88	34.19	27.34	CC	25.4*
Centaurium erythraea	0.00	0.02	0.00	0.00	0.00	CC	75.0*
Cirsium arvense	0.00	0.36	0.04	0.00	0.00	CC	66.1*
Conyza canadensis	0.00	2.45	0.01	0.00	0.01	CC	73.8*
Dactylis polygama	0.04	3.35	0.40	0.63	0.45	CC	54.4**
Erigeron annuus	0.00	0.78	0.11	0.00	0.00	CC	83.7**
Euphorbia amygdaloides	0.03	1.16	0.81	0.14	0.02	CC	53.1*
Hypericum perforatum	0.00	0.96	0.59	0.05	0.13	CC	53.4*
Solidago gigantea	0.00	0.16	0.00	0.00	0.00	CC	75.0*
Vicia hirsuta	0.00	1.65	0.51	0.04	0.16	CC	60.1*

** $0.001 < P < 0.01$, * $P < 0.05$

Figures

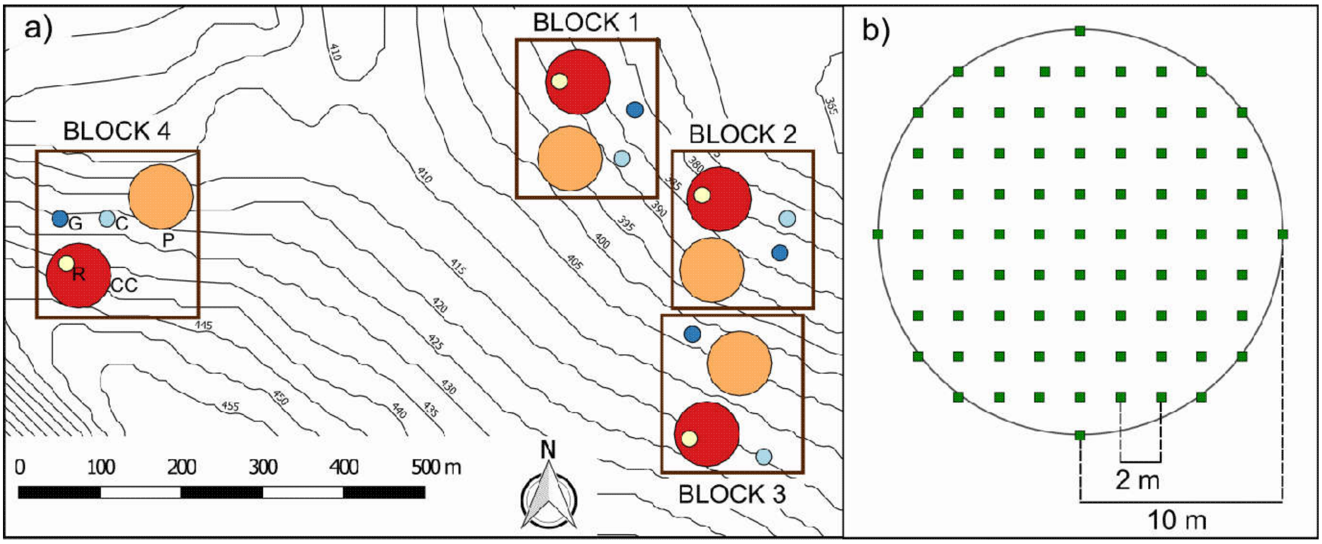

Fig. 1 Sampling design. a) Arrangement of the silvicultural treatments. C (light blue) = control, CC (red) = clear-cutting, G (dark blue) = gap-cutting, P (orange) = preparation cutting, R (yellow) = retention tree group. b) Sampling grid with 81 0.5 × 0.5 m quadrats within a plot

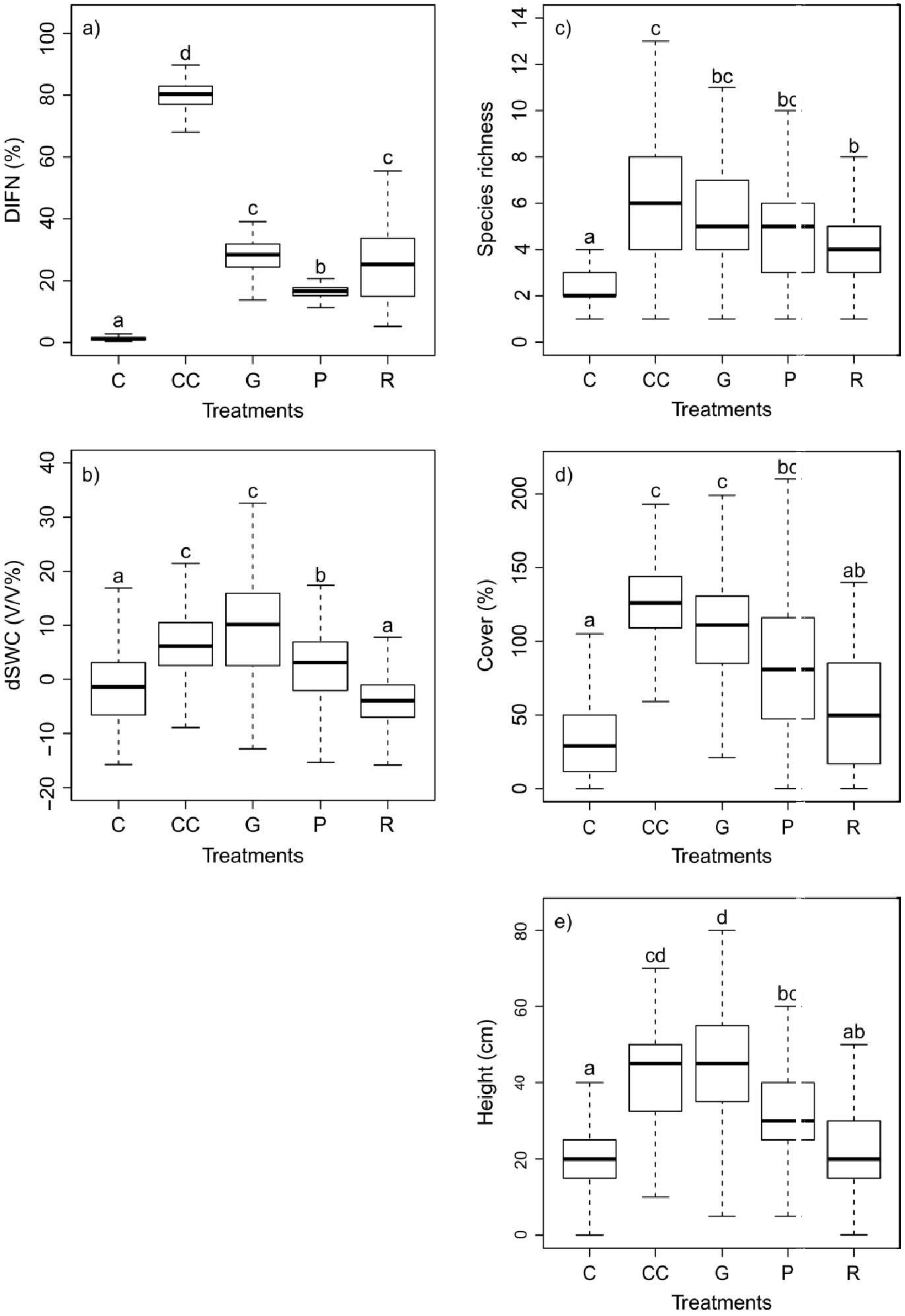
a)
DIFN (%)
0
20
40
60
80
100
a
d
c
b
c
C
CC
G
P
R
Treatments
b)
dSWC (V/V%)
−20
−10
0
10
20
30
40
a
c
c
b
a
C
CC
G
P
R
Treatments
c)
Species richness
0
2
4
6
8
10
12
14
a
c
bc
bc
b
C
CC
G
P
R
Treatments
d)
Cover (%)
0
50
100
150
200
a
c
c
bc
ab
C
CC
G
P
R
Treatments
e)
Height (cm)
0
20
40
60
80
a
cd
d
bc
ab
C
CC
G
P
R
Treatments

Fig. 2 Boxplots of the investigated environmental and understory variables in the different treatments, on quadrat level. a) relative diffuse light (DIFN, %), b) relative soil water content (dSWC, V/V%), c) species richness, d) total cover (%), and e) average height of the understory (cm). C = control, CC = clear-cutting, G = gap-cutting, P = preparation cutting, R = retention tree group. Different letters mean significant differences at $P<0.05$ level. Outliers are not shown

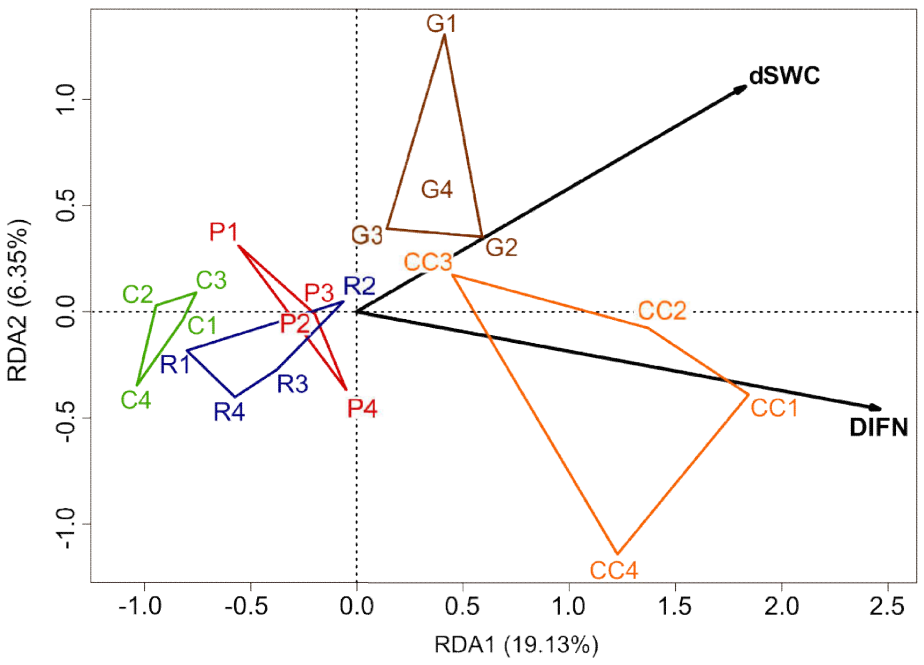

Fig. 3 RDA scatterplot of the understory in the different treatments, on plot level. C (green) = control, CC (orange) = clear-cutting, G (brown) = gap-cutting, P (red) = preparation cutting, R (blue) = retention tree group. Explanatory variables are represented by arrows. dSWC = relative soil water content, DIFN = relative diffuse light. Explained variances (%) of the axes are indicated