This manuscript contextually the same as the following paper:

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

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34   Abstract

35   In recent decades, alternative management techniques integrating conservation concerns into

36   industrial forestry have become increasingly widespread. In order to compare the effects of

37   various management methods on forest site and biodiversity, a systematic forestry experiment

38   was conducted in a managed, mature oak-hornbeam forest. The present work introduces the

39   two year responses of environmental variables and understory vegetation to different

40   silvicultural treatments. These belong either to clear-cutting (clear-cutting, retention tree

41   group), to shelterwood (preparation cutting), or to continuous cover forestry systems (gap-

42   cutting). The experiment follows a complete block design with four replicates. Light

43   availability was significantly higher in all the treatments than in the uncut control, with

44   highest values in the clear-cuts. Soil moisture was highest in the gap-cuts and clear-cuts,

45   while in the retention tree group, it did not differ from the control. Species richness, cover,

46   and height of the understory considerably differed from the control in the clear-cuts and gap-

47   cuts, while in the retention tree group, only species richness was higher. The establishment of

48   ruderal, non-forest species altered the species composition in the clear-cuts. Based on these

49   short-term responses, we conclude that as a result of the extreme environmental changes,

50   clear-cutting in oak-hornbeam forests changes the understory vegetation considerably.

51   Retention tree groups can maintain legacies of the understory composition for some years.

52   Despite the experienced high vegetation cover, gap-cutting preserves the forest characteristics

53   of the understory better than clear-cutting. These results confirm that in oak-hornbeam forests,

54   continuous cover forestry may be more sustainable from conservational aspect than clear-

55   cutting system.

56

59

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).

83   The strong microclimatic effects of these forestry practices can be somewhat mitigated by an

84   elongated regeneration period and an extended rotation age, i.e. using shelterwood system

85   instead of clear-cutting (Brose 2011). After the preparation cutting, the established,

86   moderately open stand may be favourable for light-flexible forest species, but the forest

87   character of the habitat is preserved, and there is less potential for the dispersion of non-forest

88   species than on large clearings.

89   In recent decades, alternative management techniques integrating biodiversity concerns into

90   industrial forestry have become increasingly widespread. Retention harvest (retention of

91   single trees or intact forest patches) is widely applied, especially in North America

92   (Lindenmayer et al. 2012). Green tree retention forestry can ensure the survival of the forest

93   biota (Mori and Kitagawa 2014), but its conservational effect is limited: it depends

94   considerably on the level of retention, and is especially ambiguous in the case of forest-

95   interior species (Fedrowitz et al. 2014).

96   Another widespread, nature-based forestry system is continuous cover forestry (maintained by

97   group selection or single tree selection, Pommerening and Murphy 2004). This system also

98   modifies the microclimate and the communities of the closed forest (Kern et al. 2014), but

99   Schumann et al. (2003) found in mixed coniferous-broadleaved stands that these changes are

100   less severe, and late-successional forest species can survive.

101   The comparison of the effects of different management methods on forest site, natural

102   regeneration, and forest biodiversity is equally important for forestry, conservation practices,

103   and basic research (Bauhus et al. 2009). To understand these complex relationships,

104   systematic forestry experiments are necessary (Aubry et al. 2009; de Groot et al. 2016). Many

105   studies examine the effects of a given management type on the understory, compared to the

106   below-canopy vegetation of unmanaged forests, and some analyse the effects of different

107   intensities of a given treatment (Sullivan et al. 2001; Halpern et al. 2012; de Groot et al.

108   2016), but only a few studies compare the effects of numerous different harvesting methods

109   within the same experimental framework. Most of these concern coniferous forests (Beese

110   and Bryant 1999; Jalonen and Vanha-Majamaa 2001; Huggard and Vyse 2002), and only a

111   few papers are available on deciduous stands (Philips and Shure 1990; Wender et al. 1999;

112   Jenkins and Parker 2000; Zenner et al. 2006). Moreover, the results of the different studies are

113   often contradictory considering the effects of management on understory vegetation (Duguid

114   and Asthon 2013). In some cases, no impact could be detected (Bescond et al. 2011; Zenner et

115   al. 2012), or the directions of the demonstrated effects were inconsistent (Halpern et al. 2005

116   vs. Kern et al. 2014; Godefroid et al. 2005 vs. Jenkins and Parker 2000). The results depend

117   on the vegetation zone (Kusumoto et al. 2014), forest type (Fredericksen et al. 1999),

118   successional stage and management type (Duguid and Asthon 2013), management intensity

119   (Zenner et al. 2006), forest site (Schumann et al. 2003), surrounding landscape (Halpern et al.

120   2005), and land-use history (Jenkins and Parker 2000) of the study area. Because of the

121   multitude of relevant background variables, a broad generalisation of the results is not

122   possible, and therefore, many specialised investigations are needed (Duguid and Asthon

123   2013). Furthermore, most of the studies concerning temperate deciduous forests were carried

124   out in North America (e.g. Schumann et al., 2003, Aubry et al. 2009; Fedrowitz et al. 2014),

125   or in European beech forests (Gálhidy et al. 2006, de Groot et al. 2016). Oak-dominated

126   forests are underrepresented, although they are internationally significant (Bobiec et al. 2011,

127   Bölöni et al. 2017): e.g. in Europe, mixed oak-hornbeam forests are distributed from western

128   France to the region of Kiev in Ukraine, and from southern Lithuania to the Po plains in Italy

129   (EEA Technical report No 9/2006). In Hungary, this forest type has the largest area of all the

130   forest types composed by native species, but there is little evidence of the effects of different

131   management types on the understory vegetation of these forests (Bölöni et al. 2008).

132   Even the characteristics of the natural understory vegetation themselves are not well-known.

133   The oak forests of Europe have been affected by humans for many centuries (traditional land-

134   use practices, e.g. coppicing, grazing, and later, intensive forest management; Parviainen

135   2005; Hofmeister et al. 2009; Bobiec et al. 2011). Besides the various land-use histories, site

136   conditions also create a substantial variability in the understory of Central European oak

137   forests. According to an investigation of a broad spectrum of different understory types, their

138   species richness and composition are mainly determined by canopy openness, altitude, soil

139   pH/base saturation gradient, plant-available phosphorus content, silt content, and topography-

140   related predictors (Slezák and Petrašová 2010; Slezák and Axmanová 2016). Oak-hornbeam

141   forests are highly closed and shaded among oak-dominated forests. Most of them are

142   managed by shelterwood forestry system. Their herb layer is characterized by relatively low

143   species richness and floristic variability, but understory cover can range from sparse to

144   continuous. Most common species are general and mesic forest species, often with a rich

145   spring geophyte aspect (Bölöni et al. 2008; Slezák and Petrášová 2010; Szmorad 2014).

146   The aim of this study is to investigate the effects of different forestry practices on the

147   understory of oak-hornbeam forests, by way of a comparative field experiment. The studied

148   silvicultural treatments were typical elements of different forestry systems: clear-cutting and

149   retention tree group (typical of the clear-cutting system), preparation cutting (typical of the

150   shelterwood system), and gap-cutting (typical of the continuous cover forestry system).

151   To evaluate the effects of each of the forestry treatments from a conservational aspect, it is

152   important to determine the reference state of the understory vegetation, which would be

153   desirable to preserve or create. A theoretical aim is to maintain the characteristics (species

154   richness, abundance, and composition) of the understory of the uncut forests. However,

155   because of the variability of oak forests – caused by land-use history and site conditions –,

156   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?

182 2. Materials and methods

183 *2.1. Study area*

184 The study was carried out in the Pilis Mountains (47°40'N, 18°54'E), the north-eastern ridge

185 of the Transdanubian Range, Hungary (Online Resource 1. Fig. A1). In terms of site

186 conditions, stand structure, composition, and prevalent management practices, the

187 investigated stand is representative of the Hungarian oak-hornbeam forests, managed by

188 shelterwood forestry system. Plots are situated on north-facing, moderate slopes (7.0–10.6°),

189 at 370–450 m a.s.l. Average annual mean temperature is 9.0–9.5°C, with a mean annual

190 precipitation of 600–650 mm (Dövényi 2010). The bedrock is limestone and sandstone with

191 loess, the most common soil type is lessivage brown forest soil (luvisol), which is slightly

192 acidic (pH of the top 20 cm layer between 4.2–5.3, Kovács et al. 2018). The study site is

193 situated in a managed sessile oak-hornbeam forest stand (Natura 2000 code: 91G0, Council

194 1992), with homogeneous site conditions. Because of the applied shelterwood system, the

195 stand is even-aged (80 years old), and has uniform structure and species composition. The

196 upper canopy layer is dominated by sessile oak (*Quercus petraea)*, while hornbeam (*Carpinus*

197 *betulus)* forms a secondary canopy layer. *Fraxinus ornus, Fagus sylvatica, Quercus cerris,*

198 and *Cerasus avium* also appear as subordinate species. The shrub layer is scarce, and the

199 understory layer consists of general and mesic forest species (dominant species are *Carex*

200 *pilosa* and *Melica uniflora*).

201

202 *2.2. Data collection*

203 Experimental silvicultural treatments were implemented in a randomized complete block

204 design, using the following treatments in four replicates (Fig. 1a, Online Resource 1. Fig. A2):

205 1. control (C): closed-canopy stand, no harvesting;

206 2. clear-cutting (CC): a circular clear-cut (diameter: 80 m), surrounded by closed stand;

207 3. gap-cutting (G): an artificial circular gap in the closed stand (diameter: 20 m,

208 approximately 1 tree height/gap diameter ratio);

209 4. preparation cutting (P): in a 80 m diameter circle, 30% (basal area) of the dominant tree

210 layer was felled in a spatially even arrangement, and the secondary canopy and shrub layer

211 were completely removed;

212 5. retention tree group (R): a circular group of retained dominant trees (diameter 20 m, 8–12

213 individuals) within the clear-cuts.

214 We devised the size and the implementation of the treatments so that they mimic the general

215 forest management processes in Hungary. In oak-hornbeam forests managed by continuous

216 cover forestry system, the applied gap size varies between 0.5-1.5 tree height/gap diameter

217 ratio (Bartha et al. 2014). This gap size is considered proper for the regeneration of oak

218 (McShea and Healy 2002). For industrial forest management, the maximum area of clear-cuts

219 in the submontane region is ruled by law, and is 5 ha (Anonymous 2017). As our

220 experimental plots are located at a Natura 2000 site, we were not allowed to create such large

221 clear-felled spaces, hence our model clear-cuts' extension is only 0.5 ha. However, we expect

222 environmental conditions in the centre of a 0.5 ha clear-cut to be similar to those of a larger

223 clearing, and we suppose that larger clear-cut areas have similar or more drastic effects than

224 our experimental ones. Data on forest structure before and after the treatments are supplied in

225 Online Resource 1. Table A1. Based on extensive sampling, understory species richness and

226 cover were homogeneous over the treatment sites before the cuttings (Aszalós et al.

227 unpublished data).

228 In each of the twenty sites (five treatments in four replicates), one circular study plot with 20

229 m diameter was established. The plots were located in the centre of each treatment. In the case

230 of the clear-cuts, they were at an equal distance from the edges and the retention tree group.

231 Within the plots, understory vegetation and environmental variables were recorded in 81, 0.5

232 × 0.5 m quadrats, in a systematic grid with 2 × 2 m intervals (Fig. 1b). This arrangement

233 resulted in 1620 quadrats, located in 20 plots. Silvicultural treatments were carried out in the

234 winter of 2014-2015. Understory and environmental data were collected in the growing

235 season of 2016, i.e. in the second year after the treatments.

236 Diffuse light was measured by LAI-2000 Plant Canopy Analyzer (LI-COR Inc. 1992), in the

237 centre of each quadrat, at 1.3 m height. Measurements were carried out in July, always at

238 dusk, in order to avoid direct light getting into the sensor. A 270° view restrictor masked the

239 segment of the sky containing the sun and the operator (LI-COR Inc. 1992). Reference above-

240 canopy measurements were performed in a nearby open field.

241 Volumetric soil water content (SWC) was gauged by FieldScout TDR 300 Soil Moisture

242 Meter (Spectrum Technologies, Aurora, IL) with 7.5 cm rods (Ledieu et al. 1986). As well as

243 light, SWC was also measured in the centre of each quadrat, on three occasions: in July,

244 August, and September. Reference measurements were carried out in a closed stand, next to

245 the experimental area.

246 We surveyed the understory in the 0.5 × 0.5 m quadrats, in July. Early spring geophytes were

247 excluded from the sampling. We defined understory as all herbaceous species, plus woody

248 species shorter than 0.5 m. Percentage cover of each species, and the average height of the

249 understory for every quadrat were visually estimated. The nomenclature of plants follows

250 Király (2009). Additional information concerning the framework of the current study and

251 other investigated organism groups are available on the website of the experiment

252 (http://piliskiserlet.okologia.mta.hu/en).

253

254 *2.3. Data analysis*

255 For each quadrat, diffuse non-interceptance (DIFN, in %) was derived as the percentage of

256 diffuse light coming through the canopy. To characterize plot-level light conditions, we

257 calculated the mean of the 81, quadrat-level light values. Soil moisture was given for each

258 quadrat as relative soil water content (dSWC, in V/V%), calculated as the difference between

259 the reference and the measured values. Plot-level mean dSWC was calculated from the

260 quadrat-level, averaged values of the three measurements. Total understory cover was

261 obtained as the sum of the individual species' cover. Species were categorized as forest/non-

262 forest/indifferent species, based on the Hungarian coenosystematic classifications of the plant

263 species (Horváth et al. 1995).

264 Linear mixed-effects models were built on the quadrat level, to explore *a)* the effect of

265 silvicultural treatments on the measured environmental variables (DIFN, dSWC), *b)* the effect

266 of treatments on understory variables, and *c)* the effect of light and soil moisture, on the

267 understory variables (Zuur et al. 2009). The examined vegetation variables were species

268 richness, cover, and average height of the understory. Fixed effects were the treatments (*a* and

269 *b*) or the environmental variables (*c*). In the case of the environmental variables, the role of

270 the interaction between light and soil moisture was always tested, but we used this term in the

271 final model only where it proved to be significant. Block and plot were used as random

272 factors in a nested arrangement. In the dSWC model, data from all three measurement

273 campaigns were included; therefore, the month of measurement was also applied as a random

274 factor. In order to satisfy the requirement of normality for residual distributions, square root

275 transformation was applied for the DIFN data. In the case of significant treatment-effects

276 (P<0.05), multiple comparisons with user-defined contrasts were carried out (Bretz et al.

277 2010). To explore the role of light and soil moisture in the treatment-effects, the

278 determination coefficients (likelihood-ratio based pseudo-R-squared values) of the different

279 models were compared.

280 The relationships between treatments, environmental variables, and the species composition

281 of the understory were evaluated by redundancy analysis (RDA) on plot level, using the ln-

282 transformed cover data of the species (Borcard et al. 2011). Plot-level mean DIFN and dSWC

283 were used as canonical variables (Pearson's correlation between them: r=0.453, P=0.045). On

284 the RDA diagram, treatments were denoted by convex hulls.

285 The connections between species and treatments were evaluated by indicator species analysis

286 (ISA), which is a combination of fidelity and specificity of a species to a certain treatment

287 type (Dufrêne and Legendre 1997). As the quadrats within a plot were not independent, the

288 randomization test of the ISA was constrained on the plot level, using the ln-transformed

289 mean cover values of the quadrats.

290 All analyses were performed with R version 3.0.3 (R Development Core Team 2016). Mixed

291 modelling was conducted by the R package "nlme" (Pinheiro et al. 2013), multiple

292 comparisons by the "glht" function of the "multcomp" package (Hothorn et al. 2015).

293 Determination coefficients of the mixed models were calculated by the "MuMIn" package

294 (Bartoń 2016). We used the package "vegan" for the RDA (Oksanen et al. 2015), and

295 "labdsv" for the ISA (Roberts 2013).

296

297 3. Results

298 *3.1. Light and soil moisture in the different treatments*

299 According to the mixed models, both relative diffuse light and relative soil water content were

300 significantly related to the treatments (Table 1). The amount of light was much more variable

301 between treatments than that of soil moisture (Online Resource 2. Table A2). Light was

302 significantly higher in every treatment than in the control plots. Highest irradiation values

303 were observed in the clear-cuts (Fig. 2a, Online Resource 2. Table A2). Relative soil water

304 content was highest in the gap-cuts and in the clear-cuts, but soil moisture in the preparation

305 cuts was also significantly higher than in the control plots or in the retention tree groups (Fig.

306 2b; Online Resource 2. Table A2).

307

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

332 and the clear-cuts were situated at opposite ends; the retention tree groups and the preparation

333 cuts highly overlapped with each other. The convex hulls of the gap-cuts and clear-cuts also

334 showed a strong separation from the other treatments, along the soil moisture gradient.

335 According to the size of the convex hulls, species composition of the control plots was the

336 most homogeneous, and that of the clear-cuts proved to be the most heterogeneous (Fig. 3).

337

338 *3.4. Indicator species*

339 The cover of individual species differed considerably by treatment (Online Resource 3. Fig.

340 A3). However, the results of the ISA revealed only 16 species significantly associated with

341 any of the treatments (Table 2). Control areas had only one indicator species (*Ligustrum*

342 *vulgare*), three species (*Campanula rapunculoides, Melica uniflora* and *Scrophularia nodosa*)

343 were associated with the gap-cuts, and 12 species were related to the clear-cuts, including

344 some graminoids (*Calamagrostis epigeios, Carex pilosa, Dactylis polygama*), and several

345 non-forest forbs (e.g. *Conyza canadensis, Erigeron annuus, Vicia hirsuta,* Table 2).

346

347 4. Discussion

348 *4. 1. Relevance and limitations of the study*

349 Our results are valid primarily in sessile oak-hornbeam forests. Nevertheless, the findings are

350 still highly relevant, since management effects in this forest type have been poorly studied,

351 compared with coniferous or beech forests. We produced a snapshot of the environmental

352 conditions and understory responses two years after the interventions, and we could already

353 observe significant differences between the effects of the treatments, even after such a short

354 period. Microclimate will change notably during the following years and decades as woody

355 species regenerate and the overstory closes. Therefore, long-term vegetation responses may

356 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

382   and retention tree groups preserve forest light conditions substantially better than clear-

383   cutting. Soil moisture was higher in the cutting treatments (clear-cuts, gap-cuts, preparation

384   cuts) than in the control, because of higher throughfall and reduced transpiration (Muscolo et

385   al. 2014).

386   Before the interventions, understory species richness and cover were homogeneous in all the

387   plots. Hence, we can declare that the differences observed in our study developed after the

388   cuttings. Two years after the interventions, species richness, cover, and height of the

389   understory were significantly higher in the treated sites than in the control plots. In their meta-

390   analysis, Duguid and Ashton (2013) showed that results about the effects of forest

391   management on understory species richness are quite contradictory. Our findings are in

392   congruence with Fredericksen et al. (1999) and Zenner et al. (2006), who also concluded that

393   understory species richness and cover increase along a harvest intensity gradient (i.e. from the

394   uncut sites, through moderate interventions such as different kinds of selection and thinning

395   practices, towards clear-cutting). The reason for this mainly lies in the higher resource

396   availability of the harvested areas (Zenner et al. 2006). In our study, the indirect effects of

397   treatments on the understory, manifested through the measured environmental factors, proved

398   to be as strong as the direct treatment–understory relationships, thus we assume that both light

399   and soil moisture are influential factors of the treatments. Comparing closed forests within a

400   relatively short light gradient (3–8%), Tinya et al. (2009) found that only the species richness

401   of understory herbs was significantly related to light, whereas their cover was independent of

402   it. However, in the present study, the huge range of light values between the five treatments

403   (0.3–90%) caused significant differences also in the cover of the understory vegetation.

404   In the clear-cuts and gap-cuts, vegetation structure also differed significantly from that of the

405   control. It was considerably denser, higher, and more stratified in the cutting treatments,

406   similarly to the findings of Fredericksen et al. (1999). Higher structural complexity is

407 particularly important for forest-dwelling animal groups living in the understory layer

408 (Ziesche and Roth 2008, Sweeney et al. 2010).

409 Not only the species richness, abundance, and structure, but also the composition and

410 heterogeneity of the understory differed between the treatments and the control. Similarly to

411 species richness and abundance, composition in the different treatments was also strongly

412 influenced both by light and soil moisture. Zenner et al. (2006) also demonstrated altered

413 understory species composition towards the more intensively harvested stands in American

414 mixed oak forests. Compositional changes in the harvested sites mainly arise from the influx

415 of new, non-forest species, the loss of the original forest species is less typical (Freedman et

416 al. 1994; Jenkins and Parker 2000; Schumann et al. 2003). In accordance with this

417 observation, in our experiment, control sites had only one indicator species, while clear-cuts

418 and gap-cuts had more.

419 The understory's response to the harvests varies largely, depending on management type

420 (Fredericksen et al. 1999; Duguid and Ashton 2013). Accordingly, we discuss the abiotic

421 environment and understory conditions of the different treatments separately.

422

423 *4.3. Uncut control*

424 In uncut sites, both irradiance and soil moisture values were low. These resulted in low

425 understory species richness, cover, and height, and homogeneous species composition in all

426 the blocks. Mature stands of oak-hornbeam and beech forests managed by shelterwood

427 forestry system are generally characterised by a homogeneous, closed canopy, which differs

428 from the natural (old-growth) stands of these communities, in which fine-scaled gap dynamics

429 results in lower canopy closure, heterogeneous stand structure and a high light heterogeneity

430 (Christensen and Emborg, 1996, Standovár and Kenderes 2003). The uncut sites in our

431 experiment represent only the between-gap matrix of these forests. At the stand scale, near-

432 natural, unmanaged forests may have higher understory cover, due to the abundance of light-

433 flexible forest species in the gaps (Collins et al. 1985), while their species richness is often

434 low (Boch et al. 2013; Schall et al. 2017). However, a common characteristic of our control

435 sites and near-natural unmanaged forests is the lack of non-forest (ruderal, meadow) species

436 (Horváth et al. 1995, Boch et al. 2013).

437

438 *4.4. Clear-cutting*

439 Because of the relatively small size of the clear-cut sites (0.5 ha), relative diffuse light did not

440 reach 100%, even in the centre of the clear-felled areas. But even so, this was prominently the

441 brightest treatment. Compared with the control sites, the lack of trees also caused significantly

442 higher soil moisture. However, the soil was slightly less moist than in the gap-cuts, because of

443 the stronger drying effect of wind and solar radiation.

444 Presumably as a result of the high light and soil moisture values, cover, height, and species

445 richness of the understory were considerably larger in the clear-cuts than in the control sites.

446 Higher species richness was mainly caused by the occurrence of non-forest (ruderal and

447 meadow) species (Horváth et al. 1995), from which some also proved to be indicators of the

448 clear-cuts (e.g. *Vicia hirsuta*, *Cirsum spp.*). Most of these are referred to as sun-species, with

449 metabolism adapted to high-intensity light environments (Collins et al. 1985). Among these

450 non-forest species, annual weeds (e.g. *Conyza canadensis, Erigeron annuus*) had high

451 abundance two years after the interventions, but perennials (e.g. *Calamagrostis epigeios,*

452 *Solidago gigantea*) also occurred. We expect the dynamic spreading of the latter species

453 group in the course of the next years. Forest species were also present in the clear-cuts; some

454 of them had such high abundance that they became clear-cut indicators. Most of these (e.g.

455 *Carex pilosa, Euphorbia amygdaloides*) are light-flexible plants, which are photosynthetically

456 adaptable over a broad range of light intensity. However, some typically shade-tolerant herbs

457 (e.g. *Ajuga reptans*) were also abundant here, in the lowermost layer of the understory,

458 sheltered by taller, dominant species (Collins et al. 1985).

459 As a result of these differences from the uncut stand, we conclude that species composition

460 lost its original forest character. Contrarily, Halpern et al. (2005) found that during the first

461 two years, only a few new species colonized the harvested areas, and forest species were still

462 dominant. According to the RDA, species composition of the four clear-cut plots was more

463 heterogeneous than that of the controls. The possible reason for the high beta-diversity of the

464 clear-cut sites may be that while closed canopy moderates the abiotic differences among the

465 four blocks, clear-cutting enhances them; or that the establishment of new species after

466 harvest is quite stochastic.

467 Clear-cuts in practice are usually larger than our experimental sites. We suppose that in larger

468 cutting areas, differences from the uncut control are similar or even more pronounced than

469 those observed in our experiment (Philips and Shure 1990; Huggard and Vyse 2002).

470 Microclimate is expected to be more extreme, and dispersal from the surroundings is expected

471 to be more limited. Hence we assume an even more intensive alteration of understory species

472 composition (retreat of forest species and establishment of non-forest species).

473

474 *4.5. Gap-cutting*

475 Gaps were much less light than clear-cuts. Because of higher throughfall, the local lack of tree

476 transpiration, and the shading effect of the surrounding stand, soil moisture was the highest in

477 gap-cuts from all our treatments (Gálhidy et al. 2006; Muscolo et al. 2014).

478 Understory height was the largest in gap-cuts, and cover and species richness were also

479 significantly higher than in the control sites. These results are in congruence with the increase

480 of understory cover and species richness reported from gaps in beech stands (Gálhidy et al.

481 2006). We suppose that high species richness was caused by the introduction of some

482   moisture-demanding, disturbance-tolerant species (e.g. *Scrophularia nodosa* and *Campanula*

483   *rapunculoides*, which proved to be indicators of the gaps).

484   Species composition of the gap-cuts differed substantially from that of the control, although

485   this difference was less pronounced than in the case of the clear-cuts. In gaps, light-flexible

486   species were more abundant than shade-tolerants (Collins et al. 1985). However, these light-

487   flexible species can be also categorized as forest species (Horváth et al. 1995), because they

488   may occur also in the natural gaps established during the small forest cycle, which is

489   characteristic for the Central, Eastern and Southern European forests (Schmidt-Vogt 1991 as

490   cited in Schuck et al. 1994). Thus we can state that in gaps only the dominance relations of

491   forest species has rearranged. The establishment of non-forest species was less characteristic,

492   therefore we conclude that gap-cutting is more apt for preserving forest understory than clear-

493   cutting. Similarly, Schumann et al. (2003) found that gap-cutting did not negatively impact

494   the presence of species in the understory in oak-pine forests.

495   Besides the low presence of non-forest species, another important aspect of gap-based

496   continuous cover forestry is that at the stand scale, between the gaps, the closed-forest

497   environment is constantly present. Thus the typical understory species composition of the

498   uncut forest (dominated by shade-tolerant species) can also be preserved.

499

500   *4.6. Preparation cutting*

501   Because of the evenly distributed, partial elimination of trees, the light and soil moisture

502   conditions of the preparation-cuts differed moderately but significantly from the control. We

503   also found an intermediate but significant divergence from the control's understory species

504   richness, cover, and height. A slight difference in species composition was also detected:

505   some open-forest species (e.g. *Poa nemoralis*, *Campanula persicifolia*) were more abundant

506   here than at other sites. According to Halpern et al. (2005, 2012) and Zenner et al. (2006),

507 retaining trees in a dispersed spatial arrangement has a buffering effect on the forest site and

508 understory, even if the level of retention is much lower than the one tested in our study.

509 However, we emphasize that this is a relatively short, transitional stage within the

510 shelterwood system. After 5–15 years, preparation cutting is followed by the final cutting,

511 which leaves behind only a few legacy trees or retention tree groups within the felling area

512 (Matthews 1991).

513

514 *4.7. Retention tree groups*

515 In retention tree groups, the average light was similar to that of the gap-cuts. Soil moisture

516 was slightly but significantly lower than in the control, because of the intensive transpiration

517 of the remaining trees and the drying effect of the surrounding clear-cut. Presumably because

518 of the low soil moisture, cover and height of the understory did not differ from the control. At

519 the same time, new, non-forest species were established, supposedly facilitated by the higher

520 amount of light, the proximity of the clear-cut, and the lack of extremely abundant forest herb

521 species. These species usually occurred with a very low abundance, thus they did not change

522 the species composition considerably, but they caused a significant difference in species

523 richness from the control.

524 Neither the preparation cuts, nor the retention tree groups had any indicator species. Both had

525 transient assemblages, between the control and the open areas (gap-cuts, clear-cuts), and no

526 specific species pool. Understory species richness, cover, and height were also similar in these

527 two treatments. Halpern et al. (2005) also found that two years after the cutting, the pattern of

528 retention (aggregated vs. dispersed) had little effect on the general response of the understory.

529 Further study should concern the spatial pattern of the abiotic environment and the understory

530 in the differently treated areas. Despite similar average values, the spatial pattern of the

531 microclimatic variables may be considerably different in the various treatments, which in turn

532 may cause variable vegetation patterns (Grayson et al. 2012).

533

534 5. Conclusions

535 Natural mesophilous forests are driven by fine-scale gap dynamics (Standovár and Kenderes

536 2003). In these forests, closed-canopy areas with low understory cover are disrupted by gaps

537 with denser vegetation. Consequently, homogeneous, closed forests are not favourable from a

538 conservational aspect. The environmental conditions in the gaps of our experiment may be

539 similar to those of natural gaps, thus, besides their economic role, they may be a means to

540 recover the near-natural state of the understory vegetation. Local increase in the abundance of

541 light-flexible forest species fits into the natural dynamics of these forests, while in the uncut

542 parts of the stand, the dominance of shade-tolerant species remains.

543 The extreme environment of the clear-cuts is quite contrasting with the conditions of any kind

544 of uncut stands. Here, not only the species richness and the abundance, but also the species

545 composition of the understory changes drastically. Increased species richness in this case

546 cannot be considered favourable from a conservational point of view: as a result of the

547 intensive establishment of non-forest species, the understory vegetation loses its forest

548 character, even if shade-tolerant species can survive. Vegetation of clear-cuts is not analogous

549 with the understory of any stage of the natural stand dynamics of oak-hornbeam forests.

550 If clear-cutting is applied, retention tree groups are efficient for preserving the legacy of the

551 forest understory composition for some years, but to evaluate the duration of this sheltering

552 effect, long-term studies are necessary (Rosenvald and Lõhmus 2008). Semi-open stands,

553 similar to our preparation cuts, develop in various management systems (e.g. shelterwood

554 system, dispersed retention harvest). The uniform, slight increase in irradiance and moderate

555 changes in soil moisture cause only modest alterations in the understory, which keeps its

556 forest character, but open-forest species spread at the shade-tolerant species' cost.

557 Final cutting in the shelterwood and clear-cutting systems produces conditions that are too

558 open for any kind of forest understory vegetation (i.e. herb layer of sites with closed or semi-

559 open canopy or gaps). Meanwhile, in the mature stage of these systems, the homogeneous,

560 closed canopy favours only shade-tolerant species. The continuous cover forestry system,

561 which creates illuminated gaps in a shaded matrix, is better suited to the preservation of the

562 heterogeneous vegetation (composition and structure) of the near-natural forest.

563

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799 Tables

800 Table 1. Mixed effects models for the investigated environmental and understory variables.

801 Random factor: block/plot (and month/block/plot in the treatment–relative soil water content

802 model). To relative diffuse light values, square root transformation was applied.
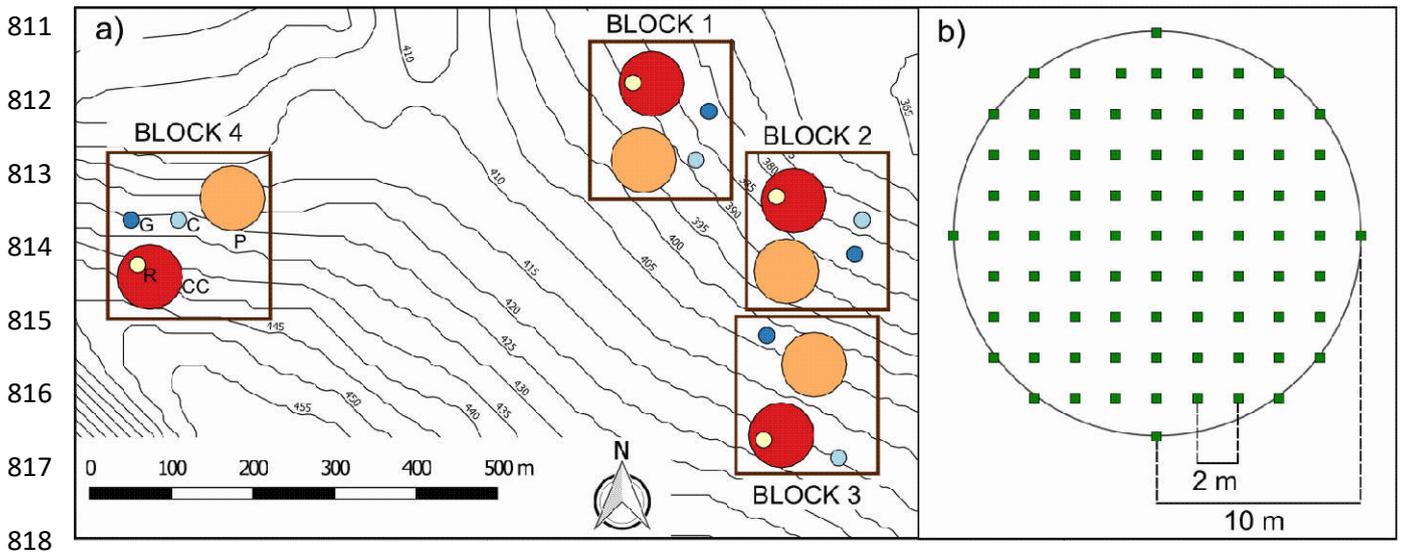
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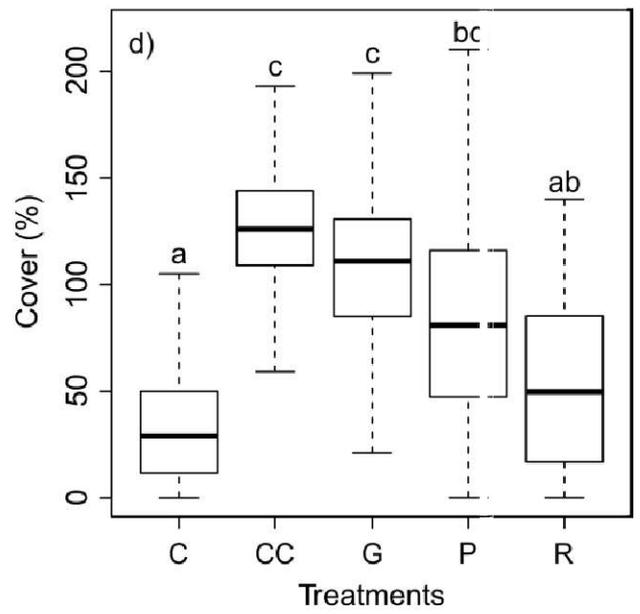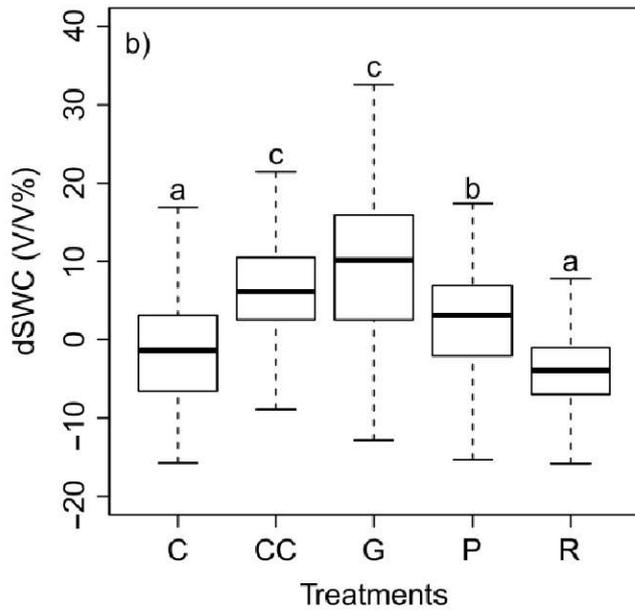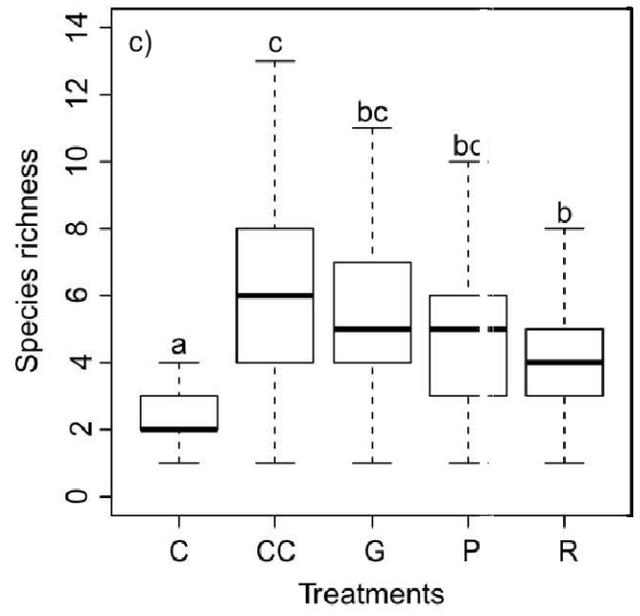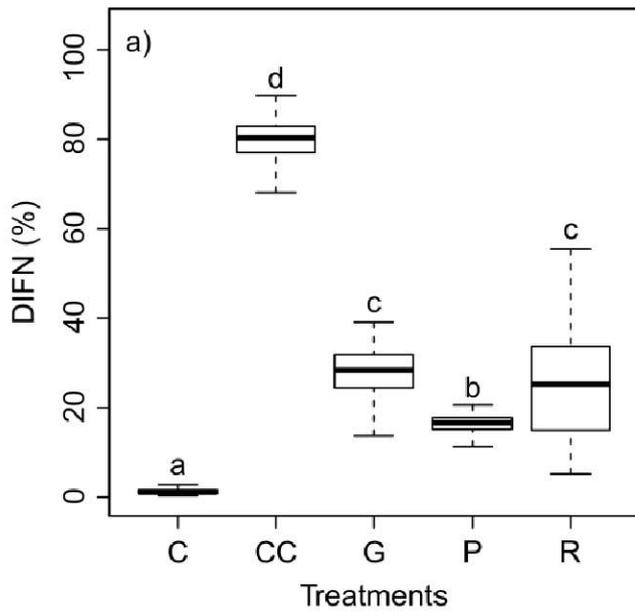| Dependent variables	Fixed effect	F-value	P	R^2_{pseudo}
Rel. diffuse light	Treatment	421.71	<0.0001	0.944
Rel. soil water content	Treatment	33.18	<0.0001	0.626
Species richness	Treatment	9.54	0.001	0.42
Understory cover	Treatment	8.54	0.0017	0.618
Understory height	Treatment	13.75	0.0002	0.538
Species 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	

804   Table 2. Indicator species analysis of the understory species, regarding treatments. Only the

805   species significantly related to treatments are listed. Numbers represent the cover (%) of given

806   species in the different treatments: C = control, CC = clear-cutting, G = gap-cutting, P =

807   preparation cutting, R = retention tree group. Ind. treatm: treatments with the highest indicator

808   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*

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

809

810 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

823
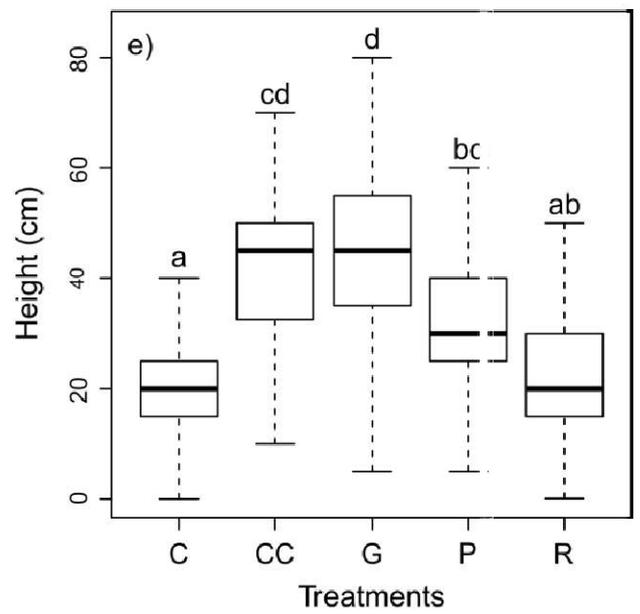
824 **Fig. 2** Boxplots of the investigated environmental and understory variables in the different

825 treatments, on quadrat level. a) relative diffuse light (DIFN, %), b) relative soil water content

826 (dSWC, V/V%), c) species richness, d) total cover (%), and e) average height of the

827 understory (cm). C = control, CC = clear-cutting, G = gap-cutting, P = preparation cutting, R

828 = retention tree group. Different letters mean significant differences at P<0.05 level. Outliers

829 are not shown
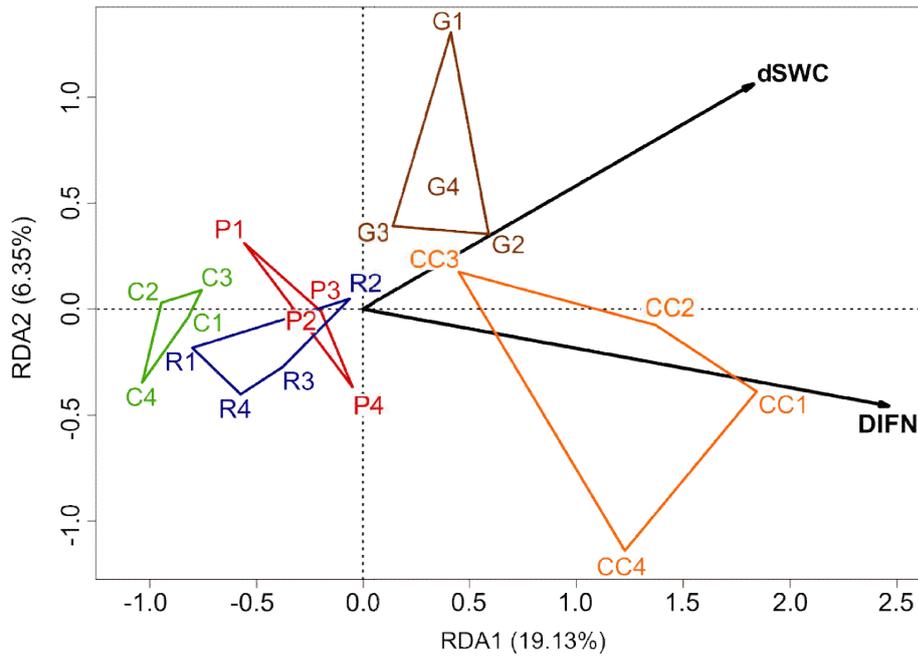
Fig. 3 RDA scatterplot of the understory in the different treatments, on plot level. C (green) = control, CC (orange) = clear-cutting, G (brown) = gap-cutting, P (red) = preparation cutting, R (blue) = retention tree group. Explanatory variables are represented by arrows. dSWC = relative soil water content, DIFN = relative diffuse light. Explained variances (%) of the axes are indicated