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5

6 Initial understory response to experimental silvicultural treatments in a temperate oak-
7 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

57 Keywords

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

60 1. Introduction

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

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

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

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

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

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

181

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 $\times 0.5$ 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

308 *3.2. Understory species richness and abundance in the different treatments*

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

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

322

323 *3.3. Understory composition*

324 Using RDA ordination, we demonstrated differences in the species composition of the
325 treatment types, along the investigated environmental variables (Fig. 3). The model explained
326 25.48% of the total variance ($F=2.91$, $P=0.001$). The first canonical axis explained 19.13% of
327 the total variance ($F=4.36$, $P=0.001$), and it expressed mainly a gradient of light ($r=0.95$), but
328 soil moisture had also a strong influence ($r=0.70$). The second axis (explained variance:
329 6.35%, $F=1.45$, $P=0.108$) was primarily related to soil water content ($r=0.71$). Light and soil
330 moisture explained 17.93% ($F=3.93$, $P=0.005$) and 12.68% ($F=1.72$, $P=0.035$) of the total
331 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

357 whether closed-forest species survive in the harvested sites, and whether non-forest species
358 will be forced back as the stands close. Schumann et al. (2003) and Zenner et al. (2012)
359 conceive that forest understory can be resilient enough to regenerate after harvest, but its
360 success depends on many factors (e.g. logging technique, site characteristics or land-use
361 history). To understand the whole process, initial results are also of interest: they determine
362 the further pathway of the compositional changes, and the regeneration success of forest
363 overstory as well as understory (Grayson et al. 2012).

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

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

376

377 *4.2. General responses to the treatments*

378 Both the abiotic environment and the understory of the silvicultural treatments differed
379 significantly from those of the control. As expected, mean light was higher in all of the
380 treatments than in the control. In oak forests, Brose (2011) measured similar light values to
381 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*, *Cirsium 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 Löhmus 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.

803

| 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 | |

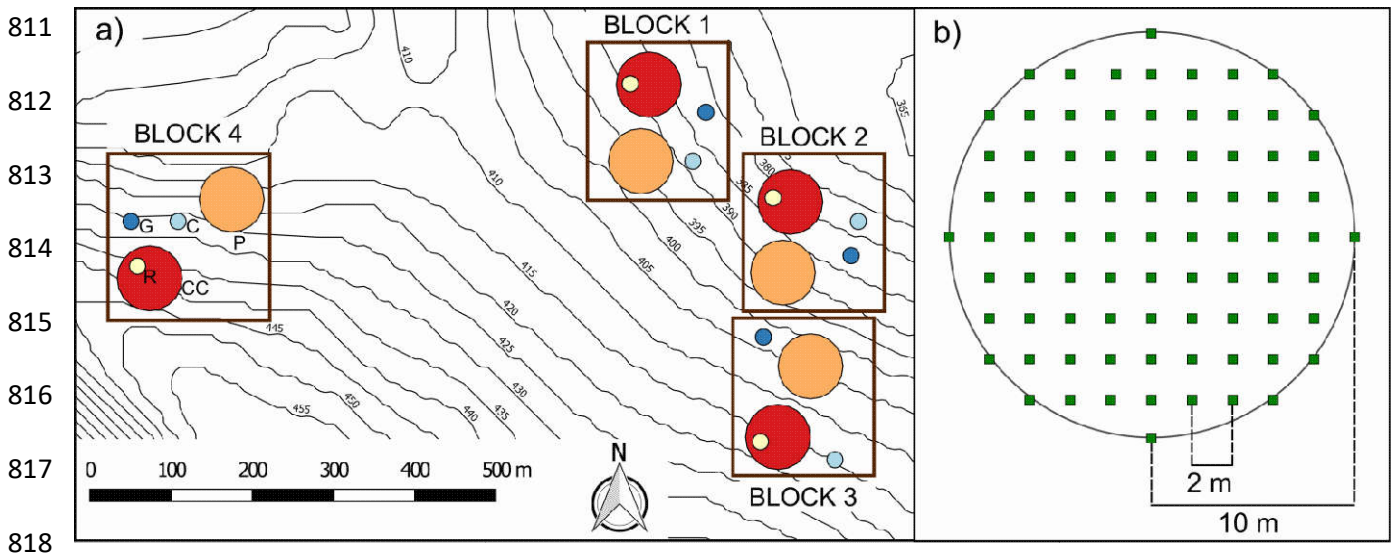
804 Table 2. Indicator species analysis of the understory species, regarding treatments. Only the
 805 species significantly related to treatments are listed. Numbers represent the cover (%) of given
 806 species in the different treatments: C = control, CC = clear-cutting, G = gap-cutting, P =
 807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

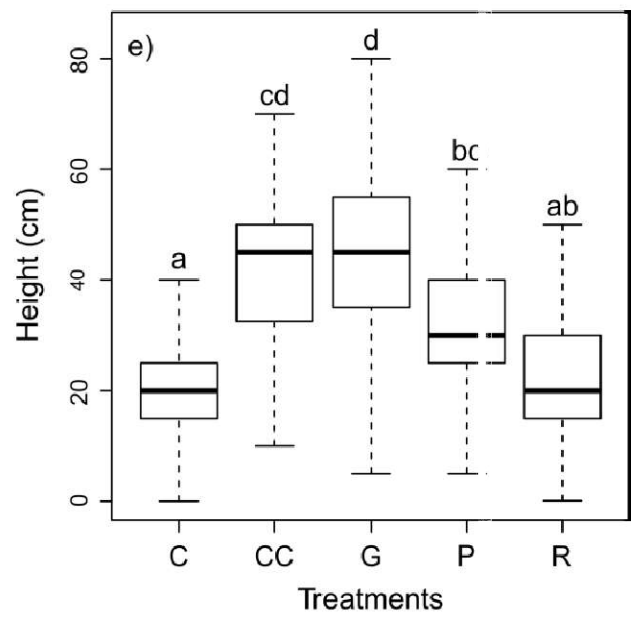
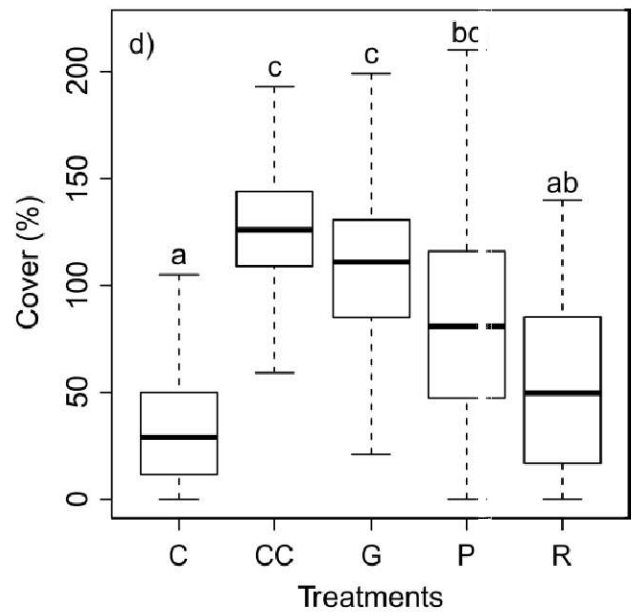
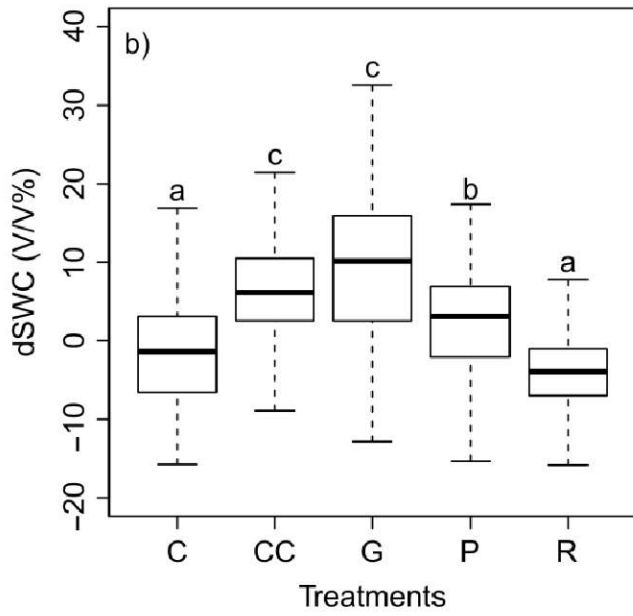
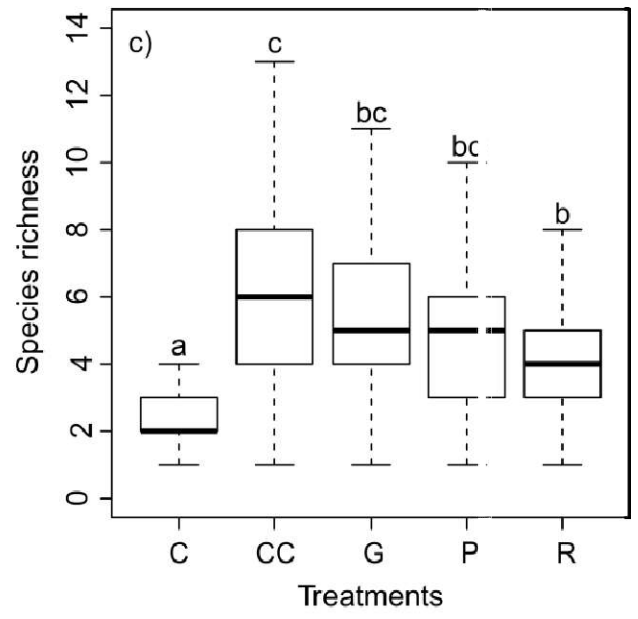
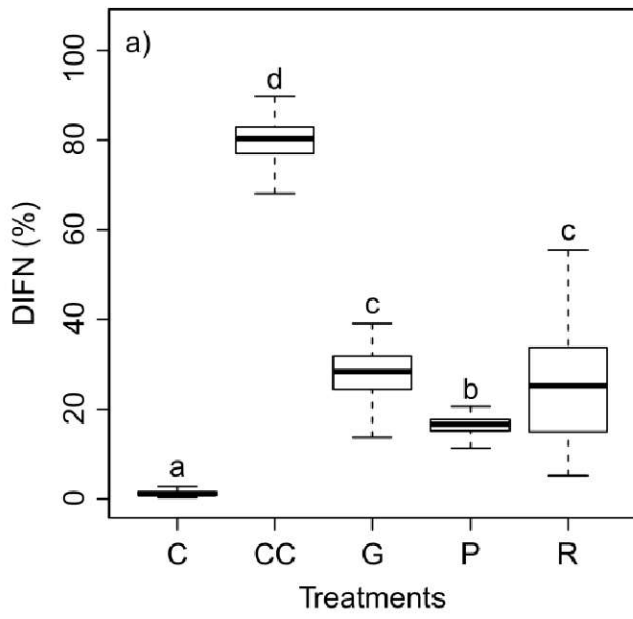
| Species | C | CC | G | P | R | Ind. treatm. | Indval (%) |
|--------------------------------|-------|-------|-------|-------|-------|--------------|------------|
| <i>Ligustrum vulgare</i> | 0.13 | 0.00 | 0.02 | 0.00 | 0.00 | C | 66.3* |
| <i>Campanula rapunculoides</i> | 0.00 | 0.01 | 0.08 | 0.00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

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

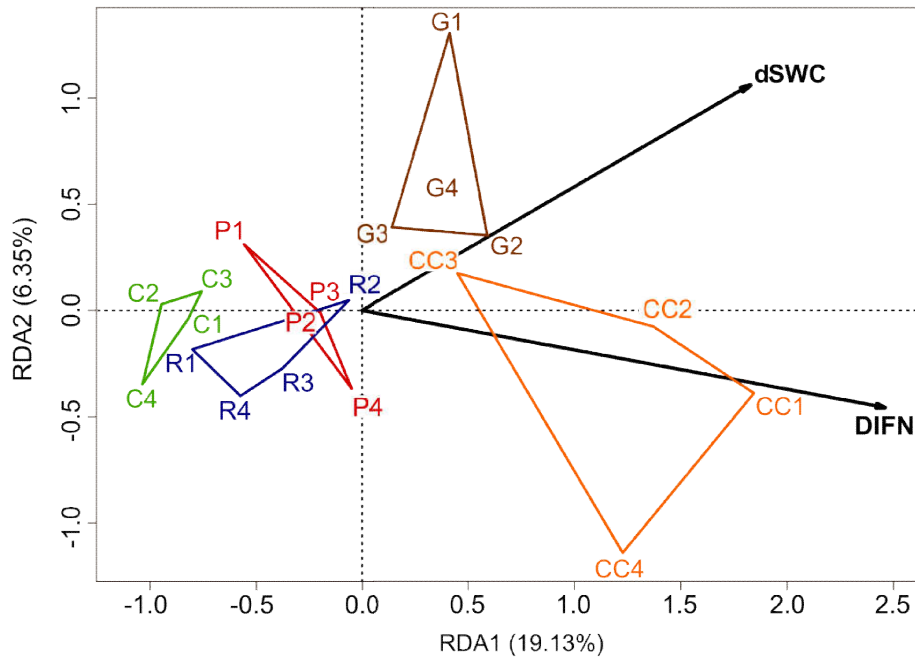
809

810 Figures





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



830

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