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9 **Congruence of the spatial pattern of light and understory vegetation in an old-growth,**
10 **temperate mixed forest**

11
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19
20 Abstract

21
22 Light is one of the most important drivers of understory vegetation in forests, influencing the
23 patterns of total cover as well as the abundance of individual species.

24 Based on a multi-scale approach, the relationships between the amount and pattern of relative
25 diffuse light and forest understory were studied in an old-growth, temperate mixed forest
26 (Hungary). The recorded vegetation variables were the cover of the vascular understory
27 (herbs, woody seedlings), the bryophyte layer, and some selected vascular understory species.

28 The pattern of light showed aggregations at two scales: 10×10 and 25×25 m. Both vascular
29 understory and bryophyte cover had significant positive correlations with light availability,
30 and their spatial pattern was related to it. The pattern of seedlings displayed the strongest
31 relationships with that of light at a coarser scale (25×25 m) than herbs and bryophytes (10×10
32 m). At the species level, *Festuca heterophylla*, *Fragaria vesca* and *Poa nemoralis* were
33 characterized as light-demanding herbaceous species (their spatial pattern was congruent with
34 light), *Brachypodium sylvaticum* and *Carex pallescens* were transitional, while some species
35 proved to be shade-tolerant (e.g. *Ajuga reptans*, *Dryopteris carthusiana*, *Viola*
36 *reichenbachiana*). Regarding seedlings, the patterns of *Betula pendula*, *Carpinus betulus*,
37 *Pinus sylvestris* and *Quercus petraea* were related to the pattern of light.

38 According to our observations, diversity and composition of vascular forest understory and
39 bryophytes were related to heterogeneous light conditions. Forest management should
40 maintain continuous shelter on the stand level; however, smaller gaps are necessary for the
41 survival of light-demanding forest herbs and bryophytes, and larger gaps for tree seedlings.

42

43 Keywords

44

45 Herbs, seedling, bryophyte, old-growth forest, understory light, pattern analysis, four-term
46 local quadrat covariance

47

48 Abbreviations

49 4TLQV: four-term local quadrat variance

50 4TLQC: four-term local quadrat covariance

51

52

53 Introduction

54

55 The heterogeneous spatial distribution of limiting environmental factors often creates peculiar
56 patterns of vegetation (Fortin et al. 2002). Light is one of the most important explanatory
57 variables in forests (Whigham 2004, Neufeld and Young 2014). Besides its amount and
58 quality, its heterogeneous pattern is also a determining factor for the cover and diversity of
59 understory vegetation (Canham et al. 1994). Understory light is largely determined by stand
60 structure, tree species composition and the pattern of the overstory layer (i.e. regular or
61 aggregated pattern of trees; presence and spatial arrangement of gaps in the canopy, Martens
62 et al. 2000, Valladares and Guzmán 2006).

63 Light distribution at the ground level of forests varies on several scales. There are pronounced
64 and well demonstrated differences between the light regimes of various forest types, due to
65 different stand structure and management (Bartemucci et al. 2006). Also within a single stand,
66 light conditions may be remarkably heterogeneous due to gaps, especially in forests
67 dominated by deciduous, shade-tolerant species (Muscolo et al. 2014). Finally, light
68 availability also has a fine-scale spatial pattern within mature, heterogeneous, albeit closed
69 stands, which originates in the structural and compositional heterogeneity of the overstory
70 layer. Tree pattern, age distribution, physical damage of leaves and branches, herbivory,
71 disease, crown geometry and the species-specific features of trees all add to the variability of
72 canopy and light conditions (Canham et al. 1994).

73 The light requirements of the understory species is variant, which results their different
74 responses to contrasting situations, such as various stand types (Verstraeten et al. 2014,
75 Márialigeti et al. 2016) or gap formation in homogeneous, closed forests (e. g. Collins et al.
76 1985, Gálhidy et al. 2006, Kern et al. 2014). However, measuring the fine-scale relationships

77 between irradiance and understory vegetation under a heterogeneous but closed canopy is
78 complicated. Some surveys investigated the drivers of understory species richness,
79 composition, or cover within such stands. Light usually proved to be a key factor, from many
80 environmental variables (Mrotzek et al. 1996, Chávez and Macdonald 2010, Ádám et al.
81 2013, Yu and Sun 2013, Neufeld and Young 2014, Sabatini et al. 2014). This implies that
82 forest understory species are indeed sensitive to the fine-scale variability of light conditions
83 under heterogeneous canopies.

84 Not only the composition and the amount, but also the spatial pattern of the understory can be
85 related to light. Furthermore, the light-response of the particular components of the understory
86 may manifest itself at different spatial scales. Thus, to acquire information about the
87 congruence between the pattern of understory and light, and to unfold most of these
88 relationships, spatially explicit, multi-scale pattern analysis methods are needed (Whigham
89 2004). However, there are very few studies regarding the spatial pattern of forest understory
90 (Campetella et al. 1999), and especially the spatial patterns of individual herbaceous species,
91 or their environmental drivers within a near-natural, unmanaged stand (Miller et al. 2002,
92 Scheller and Mladenoff 2002, Gazol and Ibáñez 2010). Besides light, other drivers
93 (microhabitats, substrates, soil moisture, etc.) can also determine the understory pattern
94 (Gazol and Ibáñez 2010). Understanding the spatial scale of the relationships between light
95 (or other environmental factors) and understory may help to maintain the proper scale of
96 habitat heterogeneity in forests.

97 More studies concentrate on the drivers of the survival, growth, and spatial pattern of woody
98 seedlings than those of herbs, as seedlings directly determine the structure of the next
99 generation of trees. The amount and pattern of light is also crucial for the seedlings, but the
100 strength of this effect depends on the shade-tolerance of the species, and is also influenced by
101 environmental heterogeneity (Getzin et al. 2008). Besides the effect of light and other abiotic

102 factors, the influence of biotic factors (interactions between species) is also important. The
103 relative importance of light and the biotic interactions may depend on the successional stage
104 of the stand, the investigated guilds (trees or shrubs, shade-tolerants or light-demandings, Lin
105 et al. 2014), and the age class of the seedlings (Yan et al. 2015). Kuninaga et al. (2015) and
106 Petritan et al. (2015) revealed that, because of density dependent mortality, the initially
107 clumped spatial pattern of seedlings turns to random or regular distribution. However, only a
108 few studies examine the effects of the light pattern on the spatial pattern of woody seedlings
109 (Scheller and Mladenoff 2002, Raymond et al. 2006).

110 Forest-dwelling bryophytes are traditionally regarded as shade-tolerant species (Proctor
111 1982). Kubásek et al. (2014) showed that the photosynthetic apparatus of bryophytes is
112 adapted for the efficient utilization of light, the intensity of which is dynamically changing in
113 the forest understory. It allows forest bryophytes to exist under the extreme ecophysiological
114 circumstances formed by the canopy shade. Among more favorable light conditions they may
115 be outcompeted by more productive, light-demanding vascular species (Bergamini et al. 2001,
116 Virtanen et al. 2000). However, results about the relationship of bryophytes and vascular
117 understory are contradictory. Other surveys showed positive interactions between bryophytes
118 and vascular plants (Márialigeti et al. 2009), because their environmental demands can be
119 similar (Lee and La Roi 1979), and herbs are also able to modify the microclimate to be more
120 favorable for bryophytes (Aude and Ernjaes 2005). However, it is logical that since
121 bryophytes live in an environment where light intensity is limited, in laboratory experiments
122 they respond to ameliorating light conditions with an increased biomass (Rincón 1993).
123 According to Márialigeti et al. (2009) and Tinya et al. (2009a) – besides the density of trees
124 and litter cover –, light influences the cover of bryophytes, especially that of species
125 inhabiting mineral soils. However, little is known about whether the pattern of bryophytes is
126 related to the pattern of light, and about the spatial scale of this possible connection.

127 This study investigates the relationships between the spatial pattern of light and the vascular
128 understory vegetation (herbs, woody seedlings) and the bryophyte layer, within a temperate
129 mixed forest stand, at different spatial scales. We focused on the following questions:

130 1. At what spatial scale is the light pattern aggregated in a temperate mixed forest with a
131 heterogeneous and species-rich canopy layer?

132 2. To what extent is the cover and spatial pattern of the vascular understory and the forest-
133 floor bryophyte layer related to light?

134 3. To what extent are the cover and the spatial pattern of particular vascular understory
135 species related to irradiance? Is it possible to classify them based on their responses to light
136 (light-demanding, transitional, shade-tolerant)?

137

138 Materials and methods

139

140 *Study area*

141 The study was carried out in the Szalafői Óserdő Forest Reserve. Its area is 89.5 ha, and it is a
142 strictly protected part of the Órség National Park, situated in the western part of Hungary (N
143 46°52'06" and E 16°18'13"). The elevation of the reserve is between 312-326 m above sea
144 level, the topography is approximately flat. Mean annual precipitation is ca. 800 mm, mean
145 annual temperature is 8.9-9.2 °C. The bedrock consists of alluviated gravel mixed with loess,
146 the soil is an acidic and nutrient poor pseudogleyic brown forest soil (planosol, Marosi and
147 Somogyi 1990, Bidló et al. 2005).

148 The reserve is a deciduous-coniferous mixed forest, with a multi-layered, old-growth stand
149 structure and heterogeneous species composition. The canopy is dominated by sessile and
150 pedunculate oak (*Quercus petraea*, *Q. robur*), Scots pine (*Pinus sylvestris*), birch (*Betula*
151 *pendula*), hornbeam (*Carpinus betulus*) and beech (*Fagus sylvatica*). The proportion of

152 subordinate tree species (*Populus tremula*, *Prunus avium*, *Pyrus pyraeaster*, etc.) is also high
153 (Király 2014). The canopy contains fine-scale gaps, but they are less clearly defined than gaps
154 in closed, monodominant stands of shade-tolerant tree species (e.g. beech), because of the
155 high tree species diversity, and the considerable light transmission of the canopy of oak and
156 pine. The relatively high species richness of the canopy has its explanation in land use history,
157 besides phytogeographic and climatic reasons. In the 18th century, for a short period of time
158 the area was used for extensive farming (Király et al. 2014). After this was abandoned, it was
159 gained back by forest, and in the 1950s it became a forest reserve, and the processes of natural
160 forest dynamics could prevail. Succession, along with the cessation of traditional forest
161 utilization, lead to changes in tree species composition. Acidophilous pioneer species (pine,
162 birch, etc.) began to vanish, and deciduous species (hornbeam, beech) are taking their place
163 (Horváth and Sivák 2014). The regeneration layer is dense and patchy, at present consisting
164 mainly of beech, hornbeam, and the saplings of the subordinate tree species. Light conditions
165 and understory vegetation seem to be also heterogeneous; the understory contains both
166 mesophilous and acidophilous species (Mázsa et al. 2014).

167

168 *Data collection*

169 A 55×55 m macroplot was set in the core of the stand. This area was dominated by oak, and
170 included birch in a high proportion, along with some other species (e.g. beech and pine, Table
171 1). The macroplot was divided into 11×11 (121) 5×5 m plots. Light measurements and
172 samplings of the understory were carried out on plot level.

173 Relative diffuse light conditions were measured with LAI-2000 Plant Canopy Analyzer (LI-
174 COR Inc. 1992). According to our previous study, this technique proved to be the best method
175 for the estimation of relative light in these forests (Tinya et al. 2009b). The measurements
176 were carried out at dusk, in order to avoid direct light getting into the sensor. A 270° view

177 restrictor masked the portion of the sky containing the sun and the operator (LI-COR Inc.
178 1992). Three instantaneous measurements were taken in the centre of each plot, at 1.3 m
179 height, immediately after each other (within some seconds). Reference above-canopy
180 measurements were taken on a nearby open field, with an identical instrument, every 15
181 seconds during the whole length of the below-canopy measurements.

182 Total absolute cover (in dm^2) of the vascular understory (woody seedlings under 0.5 m height
183 and all herbaceous species) and forest-floor bryophytes (occurring on soil or lying dead
184 wood), was estimated, visually in each of the 121 plots. In the case of herbs and woody
185 seedlings, the absolute cover of some selected species was also recorded. According to our
186 previous study, carried out in a 900 m^2 subarea within our current macroplot (Tinya et al.
187 2009a), we *a priori* chose the 11 herbaceous species with the highest cover. We recorded all
188 the tree and shrub seedlings, and on the basis of their cover and frequency values, 11 species
189 were selected for the pattern analysis (Table A.1 in supplementary material). Bryophytes were
190 not registered at the species level.

191 The nomenclature of vascular plants follows Tutin et al. (1964-1993). We did not discriminate
192 between *Q. petraea* and *Q. robur*, because of the many transitional forms (both were
193 considered *Q. petraea*). Understory estimations were carried out in the summer of 2006 and
194 2007, light was measured in August 2007.

195

196 *Data analysis*

197 Diffuse non-interceptance was derived from the light data measured for each plot, with the
198 LAI-2000 File Viewer 1.06 software (LI-COR Inc. 2005). It was calculated as the percentage
199 of diffuse light measured under the canopy, compared to the diffuse light values measured by
200 another instrument located in open field.

201 To investigate the correlation between light and understory variables (total cover of the
202 vascular understory and the bryophyte layer, cover of the investigated species) at the finest
203 scale, Pearson correlation was calculated. The significance of the correlation was tested by a
204 modified t-test (CRH test), because the sampling units – being situated on a grid – were not
205 spatially independent (Rosenberg and Anderson 1998-2011). This test is based on the
206 estimation of spatial autocorrelation by Moran's I. Holm's correction of the p values was
207 applied for multiple pairwise correlation tests (Holm 1979). In the case of some species,
208 natural logarithm transformation was used before the calculations, in order to satisfy the
209 requirement of normal distribution. The transformation of light values was not necessary, as
210 they fulfilled the normality condition.

211 The individual patterns of the variables (both light and understory variables) were
212 investigated by four-term local quadrat variance (4TLQV) analysis (Dale 1999). Local
213 quadrat variance methods were developed to identify spatial patterns in data of contiguous
214 sampling units, by computing the variance using various sizes of adjacent blocks (Fortin et al.
215 2002). The basic method is the two-term local quadrat variance, applicable for transects;
216 4TLQV is an extension of this to surfaces (Dale 1999). The 4TLQV analysis combines four
217 blocks into a square of blocks, and calculates the variance between one block and the average
218 of the three adjacent blocks. Then this procedure is repeated with every possible position and
219 orientation of the square of blocks. In the following steps, this calculation is performed for a
220 range of block sizes (blocks of 1, 4, 9, 16, etc. original quadrats). The result is a plot of variance
221 against block size. Peaks of the 4TLQV plots indicate the scale of aggregated pattern in the data, i.e.
222 the average size of the patches (Dale 1999). In our 121 plots five different spatial steps could be
223 investigated: 5×5, 10×10, 15×15, 20×20 and 25×25 m, but the first scale (5×5 m) was never
224 evaluated, because it does not provide reliable results (Campbell et al. 1998).

225 After analyzing the individual patterns, covariances between light pattern and the pattern of
226 understory (total cover and cover of particular species) were calculated by the four-term local

227 quadrat covariance (4TLQC) method (Dale 1999). It is very similar to 4TLQV, but instead of
228 examining the quadrat variance of a single variable, it calculates the covariance of two
229 variables. Peaks of the 4TLQC plots show the spatial scale at which the patterns of the two
230 variables are most strongly related, either positively or negatively.

231 The significance of the variance and covariance peaks was tested by Monte-Carlo simulations, based
232 on 999 unrestricted permutations of the original data, for both 4TLQV and 4TLQC
233 (Rosenberg and Anderson 1998-2011). The data of the 5×5 m plots were permuted
234 independently from their spatial position. Quadrat (co)variance analysis was carried out for
235 each spatial arrangement of the data gained by the permutations, in the same way as for the
236 original pattern. Thus we determined a null distribution for all spatial scales, which represents
237 a 95% confidence interval. Significant peak(s) of the 4TLQV (above the 95% confidence
238 level) indicate the characteristic scale(s) of the pattern. If two variables (e.g. light and a
239 species) have significant 4TLQV peaks at the same scale, and their 4TLQC analyses also
240 display a significant maximum at that scale, the two patterns are positively related. When the
241 4TLQV analyses of two variables indicates the same characteristic area, but their 4TLQC
242 shows a significant minimum value (below the 95% confidence level), the patterns of these
243 two variables are negatively related. The permutation test is one-tailed for 4TLQV, while two-
244 tailed for 4TLQC.

245 Vascular understory species were classified according to their relation to light. Species the
246 pattern of which was related to the light pattern were considered 'light-demanding species'. If
247 the pattern of a species was independent from that of light, but its cover significantly
248 correlated with the amount of light, it was labelled 'transitional'. Species which did not show
249 any relation to light were evaluated as 'shade-tolerants'.

250 For the visual representation of the pattern of light and understory cover in the plots,
251 abundance maps were drawn with ArcView GIS, Version 3.3 (Environmental Systems

252 Research Institute, Inc. 1992-2002). Descriptive statistics were calculated with SPSS 14.0
253 (SPSS Inc. 1989-2005), correlations and pattern analyses were carried out with PASSaGE 2.0
254 (Rosenberg and Anderson 2011).

255

256 Results

257

258 *Descriptive statistics*

259 Mean diffuse interceptance and its standard deviation were 7.34 ± 4.4 %, the minimum and
260 maximum values of it were 0.40 and 22.30 %, respectively (Table A.1). The total cover of the
261 vascular understory layer in the block was 21.99 ± 15.0 %, and it ranged from 0.28 to
262 72.56 %. The cover of bryophytes was 6.42 ± 6.6 %. Its minimum was 0.12 %, but in one of
263 the plots it exceeded 35.90 %. Herbaceous and seedling species with the largest cover were
264 *Rubus fruticosus* agg. and *Carpinus betulus*, respectively (Table A.1).

265

266 *Correlations between light and understory variables*

267 The cover of the vascular understory and the bryophyte layer showed significant positive
268 correlations with light ($R=0.459$, $p<0.01$; $R=0.521$, $p<0.01$, respectively, Table 2).
269 Herbaceous species showed stronger correlations with irradiance than seedling species. At the
270 5×5 m scale, five herbaceous species (*Carex pallescens*, *Brachypodium sylvaticum*, *Poa*
271 *nemoralis*, *Fragaria vesca* and *Festuca heterophylla*) and one seedling species (*Betula*
272 *pendula*) correlated significantly with light (Table 2).

273

274 *Pattern analysis*

275 When investigating the spatial pattern of light, 4TLQV showed two significant peaks, at
276 10×10 m and 25×25 m (Fig. 1.a). Total cover 4TLQV analysis of both plant groups displayed

277 a high, significant peak at 10×10 m, indicating that the cover of both the vascular understory
278 layer and the bryophytes shows an aggregated pattern at that scale (Fig. 1.b and c, Table 2).
279 According to the 4TLQC analysis, both vascular understory and bryophyte cover have a
280 maximal covariance with light at the same scale as their maximal individual variance (i.e. at
281 10×10 m, Fig. 1.b and c, Table 2), which suggests that their pattern is strongly related to that
282 of light. Comparing their maps to the map of light visually confirms these connections, their
283 patterns are quite similar (Fig. A.1.a, b and c in supplementary material).

284 Regarding the individual species, *Festuca heterophylla*, *Fragaria vesca*, *Poa nemoralis*, *Viola*
285 *reichenbachiana*, *Brachypodium sylvaticum* and *Dryopteris carthusiana* had aggregated
286 patterns (i.e. the peak of 4TLQV) at finer scales (10×10 or 15×15 m, Fig. 2.a, b, Table 2).
287 Other species' patches manifested at coarser scales: *Ajuga reptans* at 20×20 m, and *Mycelis*
288 *muralis* and *Rubus fruticosus* agg. at 25×25 m. The distribution of *Athyrium filix-femina* and
289 *Carex pallescens* proved random distribution at every scale (Table 2).

290 According to the 4TLQC analyses, the spatial arrangement of *Festuca heterophylla*, *Fragaria*
291 *vesca* and *Poa nemoralis* was positively related to light pattern at 10×10 m, and *Rubus*
292 *fruticosus* agg. was negatively related at 25×25 m (Fig. 2. a, Table 2). The patterns of other
293 herbs did not show significant covariances with light; however, some of them did display a
294 spatial pattern, but this was independent from light (*Ajuga reptans*, *Dryopteris carthusiana*,
295 *Mycelis muralis* and *Viola reichenbachiana*, Fig. 2.b, Table 2). Based on the correlation and
296 the pattern analysis, *Festuca heterophylla*, *Fragaria vesca*, and *Poa nemoralis* were evaluated
297 as light-demanding species, *Brachypodium sylvaticum* and *Carex pallescens* as transitional,
298 while all the other species proved to be shade-tolerant (Table 2).

299 As regards seedlings, the pattern of *Betula pendula*, *Carpinus betulus*, *Daphne mezereum*,
300 *Pinus sylvestris* and *Quercus petraea* had peaks at the coarsest scale (25×25 m, Fig. 2.c, Fig.
301 A.1.f, Table 2), while *Frangula alnus* at 15×15 m. The patterns of the other seedlings did not

302 differ significantly from the random distribution. Investigating the 4TLQC graphs, *Betula*
303 *pendula*, *Carpinus betulus*, *Pinus sylvestris* and *Quercus petraea* had significant positive
304 covariance peaks with light at the same scale as their own variance peaks (i.e. at 25×25 m,
305 Fig. 2.c, Table 2). The pattern of *Daphne mezereum* displayed a significant negative
306 relationship to the pattern of light at 25×25 m.

307 Based on the correlation and the pattern analysis, *Betula pendula*, *Carpinus betulus*, *Pinus*
308 *sylvestris*, and *Quercus petraea* seedlings were categorized as light-demanding, while all
309 other seedlings as shade-tolerants.

310 The visual evaluation of the maps also supported these results: the maps of the positively
311 related species were similar to the light map (e.g. *Fragaria vesca*, Fig. A.1.a and d). On the
312 contrary, species that did not show significant covariance with light had different patterns also
313 according to the maps (e.g. *Viola reichenbachiana*, Fig. A.1.a and e). Species with coarser
314 scale patterns (e.g. *Quercus petraea*) have larger patches on their maps than species with finer
315 scale patterns (Fig. A.1.d and f).

316

317 Discussion

318

319 *Understory light pattern in the investigated forest reserve*

320 Diffuse radiation in the understory of the Szalafői Óserdő Forest Reserve is quite high and
321 variable (from 0.4 % to 22 %), compared to managed stands in the region (Tinya et al. 2009a).

322 The explanation for this is simple: old-growth stands with near-natural forest dynamics and
323 variable tree species composition have heterogeneous light conditions, due to the mortality of
324 old trees, and to the heterogeneous canopy layer (Roburn 2003).

325 The pattern of light had significant aggregation peaks at two different scales (10×10 and
326 25×25 m). We can interpret the coarser aggregation of the light pattern as a consequence of

327 the usual patch size of regeneration in canopy gaps formed by individual or multiple treefall
328 (Král et al. 2014). We suppose that the finer scale of the light pattern is caused by openings
329 (imperfect insertion) between the canopies of neighboring individual trees, which corresponds
330 with the results of Kuuluvainen et al. (1998).

331

332 *Relationships between light and vascular understory cover*

333 We demonstrated a significant correlation between the amount of relative diffuse light and the
334 total cover of the vascular understory layer. This relationship was stronger than the
335 correlations of the majority of the individually examined species. This result may seem
336 contradictory, as total vascular understory cover contains shade-tolerant species as well. A
337 potential explanation is that a few species reached extremely high cover at higher light
338 conditions. On the other hand, most of the species – including the shade-tolerant ones – prefer
339 more open areas, although the light response of shade-tolerant species is less pronounced than
340 that of light-demanding ones, because of their weaker competitive ability (Plue et al. 2013).

341 Besides total cover, also the spatial pattern of the vascular understory was related to light. The
342 patches of the understory emerged at 10×10 m, matching the scale of the light pattern. This
343 relationship was also confirmed by the light–vascular understory cover 4TLQC diagram, and
344 the visible similarity of their spatial patterns on the maps. Chazdon (1988) also stated that
345 heterogeneous stand structure and variable light conditions may cause greater heterogeneity in
346 the pattern of understory vegetation. However, Miller et al. (2002) and Roburn (2003) did not
347 find light to be a key factor in the determination of the understory pattern in old-growth
348 stands. Roburn (2003) supposed that overstory openness and light availability can only predict
349 forest understory composition across a broader range of light conditions (e.g. from closed
350 forest to partial cutting). Contrarily, we found a strong relationship between the patterns of

351 light and vascular understory within a near-natural forest stand, characterized by fine-scale
352 structural heterogeneity.

353

354 *Relationships between light and cover of particular understory species*

355 Light-demanding, transitional and shade-tolerant species could be distinguished among
356 vascular understory species, on the basis of their correlation and spatial covariance with light.

357 *Festuca heterophylla*, *Fragaria vesca* and *Poa nemoralis* proved to be light-demanding herbs.

358 Their cover correlated with light, and their spatial pattern was also related to the light pattern.

359 All of these species matched the finer scale (10×10 m) pattern of the irradiance, which implies

360 that they prefer small open areas in the forests (Gálhidy et al. 2006). This scale of light

361 heterogeneity is presumably caused by the arrangement of the individual trees. We considered

362 *Brachypodium sylvaticum* and *Carex pallescens* transitional species, because their cover

363 correlated with light availability at the 5×5 m scale, but their spatial pattern did not follow the

364 pattern of light.

365 *Ajuga reptans*, *Mycelis muralis*, *Rubus fruticosus* agg., *Viola reichenbachiana* and the two

366 ferns (*Athyrium filix-femina* and *Dryopteris carthusiana*) proved to be shade-tolerant – neither

367 their cover nor their spatial pattern was positively related to light. Most of these species are

368 typically closed forest species, which usually occur in the shady parts of the stands (Schmidt

369 et al. 2003, Gálhidy et al. 2006, Tinya et al. 2009a). However, *Rubus fruticosus* agg. is often

370 considered as a light-flexible species, frequently invading the clear-cut areas (Gálhidy et al.

371 2006, Plue et al. 2013). It is a long-lived, clonal plant, which is capable of intensive horizontal

372 growth (Klimešová and de Bello 2009). It can efficiently allocate photosynthates and nutrients

373 between ramets, thus ramets in the light can feed ramets in the shade. It usually prefers more

374 open stands (based on the comparison of many forest stands in this region, Tinya et al.

375 2009a), but within one stand it can also survive in the shade of the dense regeneration patches.

376 The pattern of woody seedlings had a significant covariance with the light pattern on the
377 coarser scale (25×25 m), which is probably caused by the gaps and regeneration patches.
378 Consequently, the patterns of tree and shrub seedlings are affected by the environmental
379 patterns at a coarser scale than herbs.

380 From the seedlings, four species had light-related spatial arrangements: *Betula pendula*, *Pinus*
381 *sylvestris*, *Quercus petraea* and *Carpinus betulus*. The first three of these are also
382 characterized as light-demanding by other studies (Farque et al. 2001, Kimmins 2003). The
383 fourth, *Carpinus betulus*, however, is usually regarded as a shade-tolerant tree species
384 (Ellenberg et al. 1992). Analyzing many forest stands in the region, we found that its cover
385 did not correlate with light (Tinya et al. 2009a). However, within this heterogeneous stand it
386 could reach a higher cover in plots situated under the gaps of collapsing birches and pines
387 than under closed canopies (Modrý et al. 2004).

388 Tree species that were not related to light in this study (*Fagus sylvatica*, *Picea abies*, *Prunus*
389 *avium*, *Pyrus pyraeaster*) are usually considered as shade-tolerant, based on other investigations
390 (Emborg 1998, Modrý et al. 2004). The shade-tolerance of *Prunus avium* is quite
391 contradictory in the literature: according to its Ellenberg-light values, it is supposed to be
392 shade-tolerant (Ellenberg et al. 1992), but Petrokas (2010) describes it as a shade-intolerant,
393 colonizing species of the initial succession stages, which may also become a component of
394 climax or close-to-climax mesophilous forest ecosystems.

395 The spatial pattern of anemochorous species (*Betula pendula*, *Pinus sylvestris*, *Carpinus*
396 *betulus*, *Picea abies*, etc.) can be easily explained by their light-demand. However, in the case
397 of seedlings of species with heavy seeds (e.g. *Quercus petraea*, *Fagus sylvatica*), distribution
398 of overstory trees (Ádám et al. 2013), and dispersion by animals must also be considered.
399 Dow and Ashley (1996) found that only half of the *Quercus* seeds were dispersed under the
400 crown of their maternal parent, so they concluded that long-distance seed dispersal may be

401 more common than has been previously reported. Sunyer et al. (2015) stated that rodents
402 carry most of the seeds to more open areas, but the spatial patterns of acorn
403 dispersal/predation had no direct effect on recruitment. So we think that within a forest with
404 such a fine-scale heterogeneity, acorns are not really dispersal-limited.

405 The examined shrub species were not positively related to the pattern of light in our study.
406 Some of them had a patchy distribution, but it was independent from the light pattern. This
407 result contradicts Lin et al. (2014), who found that from woody seedlings, light was more
408 important for shrubs than trees. The pattern of shrub species or their relationship to light is
409 probably strongly influenced by other environmental variables in our case.

410

411 *Relationship between light and bryophyte cover*

412 The cover of forest-floor bryophytes showed a strong correlation with relative irradiance at
413 the plot level. Similarly to herbs, the cover of bryophytes also displayed an aggregation at
414 10×10 m, i.e. it followed the finer scale of the light patterns, which we suppose to be
415 determined by the small openings between individual trees. Söderström and Jonsson (1989)
416 found a similar spatial scale (15 m) for the patches of the bryophyte species *Ptilidium*
417 *pulcherrimum*.

418 The important role of the radiation on the cover, species composition and species richness of
419 terricolous bryophytes was also demonstrated in managed forests of the region (Márialigeti et
420 al. 2009, Tinya et al. 2009a). The light-sensitivity of bryophytes is supported by other
421 laboratory and field studies as well (Rincón 1993, Halarewicz and Pruchniewicz 2015).
422 However, some surveys showed that there are interactions between light and other
423 environmental drivers of bryophytes (Caners et al 2013). Investigating more stands in the
424 region, Márialigeti et al. (2009) concluded that bryophyte cover was more strongly
425 determined by the amount of litter than light, as an accumulated layer of litter inhibits the

426 development of a bryophyte layer. In our stand, we recorded remarkably high bryophyte cover
427 principally in gaps under dead birches, where the amount of litter was relatively low. Thus it
428 is possible that litter had a more important effect on the pattern of bryophytes than light, but
429 this was not investigated. Further studies are necessary to decide whether light indeed
430 determines the pattern of bryophytes, or this relationship is indirect.

431

432 *General considerations*

433 Our results indicate that in an old-growth, temperate, mixed forest, understory light and
434 vegetation (total cover and the cover of some species) have aggregated spatial patterns. The
435 covariances show that the spatial arrangement of the forest understory is related to light
436 pattern. We determined that the patterns of herbs and bryophytes were associated to the finer-
437 scale (5×5 m) pattern of light, while the spatial patterns of woody seedlings followed its
438 coarser (25×25 m) aggregations.

439 However, the existence of a significant covariance between light and understory does not
440 mean that light produces these understory patterns. Besides light, some other environmental
441 variables are also potential drivers of the understory, but the relationships between the
442 irradiance and understory pattern are remarkable. Further experiments are needed to
443 understand the relative importance of light and the other drivers in determining the spatial
444 patterns of understory vegetation.

445 Land use history and topography may be important in determining understory composition,
446 but they presumably act on coarser spatial scales than the ones applied in our study (Gazol
447 and Ibáñez 2010). Stand structure and composition, soil characteristics, dead wood, and
448 microtopography may also influence understory vegetation (Scheller and Mladenoff 2002,
449 Sabatini et al. 2014, McIntosh et al. 2016). It is possible to calculate correlations between
450 several explanatory and understory variables simultaneously; however, investigating the

451 relations between the spatial patterns of many environmental and understory variables at the
452 same time is much more complicated. In a previous study, we revealed the key drivers of the
453 herbaceous understory in this region, based on the correlations of observational data
454 (Márialigeti et al. 2016). Outranking some other significant explanatory variables (e.g. tree
455 species richness and composition, landscape diversity, soil texture, and bryophyte cover),
456 light proved to be the most important driver of the diversity, cover and composition of the
457 herbaceous understory. Tinya et al. (2009a) also found that light explains much of the
458 differences between the understory compositions of many forest stands in the region.
459 However, the other, above mentioned environmental variables and some biotic processes may
460 also affect the spatial pattern of the understory (Miller et al. 2002, Chávez and Macdonald
461 2010, Gazol and Ibáñez 2010).

462 In summary, investigating the relationships between light conditions and the forest understory
463 is important, not only for scientific reasons, but also concerning forest management and
464 nature conservation. To be able to predict the understory response to management, it is vital to
465 understand how light characteristics (which are indirectly determined by forest management)
466 affect the understory vegetation. The individual components of the understory are related to
467 light to various degrees and at different spatial scales, so in order to preserve a diverse
468 understory, it is necessary to maintain or establish variable light conditions, while creating
469 homogeneous, closed forests should be avoided (Chávez and Macdonald 2010). However, it is
470 important to sustain the shaded light regime on the stand level, because excessively open
471 conditions cause the appearance and spreading of non-forest species (weeds, species of
472 meadows and clear-cuts, Tinya et al. 2009a, Márialigeti et al. 2016). Heterogeneous overstory
473 layers and small gaps of various sizes – which appear where single trees or small groups of
474 trees have been harvested – enable the spreading of the forest understory and natural forest
475 regeneration.

476

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478

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487

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679

680 Tables

681 Table 1. Stand composition and structure characteristics of the investigated block, based on
682 the survey of trees larger than 5 cm DBH (diameter at breast height).

683

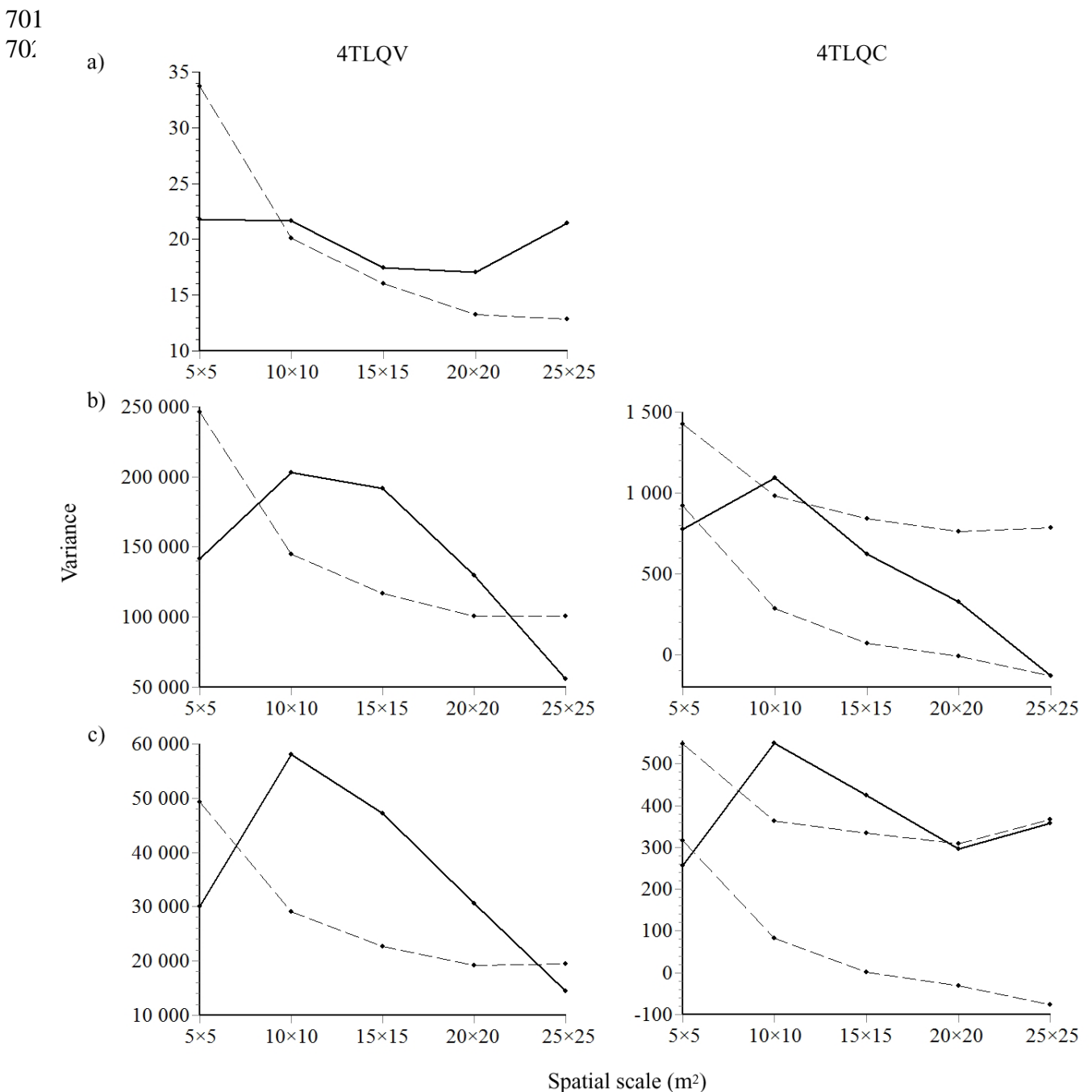
Species	Rel. abundance (%)	Mean DBH (cm)	Mean height (m)
<i>Betula pendula</i>	19.01	22.81 ± 6.22	10.48 ± 7.40
<i>Carpinus betulus</i>	3.52	14.64 ± 7.96	9.60 ± 6.12
<i>Corylus avellana</i>	0.70	7.30 ± 0.00	50.00 ± 0.00
<i>Fagus sylvatica</i>	7.04	24.53 ± 15.48	15.75 ± 6.68
<i>Pinus sylvestris</i>	6.34	35.99 ± 7.71	22.31 ± 3.20
<i>Prunus avium</i>	2.11	26.77 ± 7.77	20.00 ± 1.50
<i>Quercus cerris</i>	2.82	30.68 ± 18.35	17.00 ± 7.79
<i>Quercus petraea</i>	58.45	33.22 ± 11.09	20.23 ± 5.09
Total		29.79 ± 11.87	17.65 ± 7.03

684 Table 2. Relationships of total understory cover and the cover of individual species with
685 relative diffuse light. Corr. coeff.: Pearson correlation between light and understory variables
686 (n=121). Corrected p: significance values corrected with Moran's I because of the spatial
687 autocorrelation, and with Holm-correction for multiple testing. 4TLQV, 4TLQC: Scale of
688 significant peaks (at p<0.05 level, in m) of four-term local quadrat variance and four-term
689 local quadrat covariance between the pattern of light and understory variables. 4TLQC peaks
690 were listed only if their scale agreed with the scale of the 4TLQV peaks. "Direction" means
691 the sign of the 4TLQC value. Relation to light: shade = shade-tolerant, light = light-
692 demanding species, transitional means intermediate relations.

Understory variables	Corr. coeff.	Corrected p	4TLQV	4TLQC	Direction of covar.	Relation to light
Understory cover	0.46	0.000	10×10	10×10	+	
Bryophyte cover	0.52	0.000	10×10	10×10	+	
Herbaceous species						
<i>Ajuga reptans</i>	0.19	1	20×20			shade
<i>Athyrium filix-femina</i>	0.15	1				shade
<i>Brachypodium sylvaticum</i>	0.51	0.000	15×15			transitional
<i>Carex pallescens</i>	0.57	0.000				transitional
<i>Dryopteris carthusiana</i>	0.09	1	15×15			shade
<i>Festuca heterophylla</i>	0.41	0.002	10×10	10×10	+	light
<i>Fragaria vesca</i>	0.44	0.001	10×10	10×10	+	light
<i>Mycelis muralis</i>	0.27	0.696	25×25			shade
<i>Poa nemoralis</i>	0.47	0.000	10×10	10×10	+	light
<i>Rubus fruticosus agg.</i>	0.27	0.303	25×25	25×25	-	shade
<i>Viola reichenbachiana</i>	0.29	0.161	10×10			shade
Seedling species						
<i>Betula pendula</i>	0.44	0.003	25×25	25×25	+	light
<i>Carpinus betulus</i>	0.14	1	25×25	25×25	+	light
<i>Daphne mezereum</i>	-0.12	1	25×25	25×25	-	shade
<i>Fagus sylvatica</i>	0.07	1				shade
<i>Frangula alnus</i>	0.04	1	15×15			shade
<i>Picea abies</i>	0.21	0.255				shade
<i>Pinus sylvestris</i>	0.29	0.133	25×25	25×25	+	light
<i>Prunus avium</i>	0.19	0.485				shade
<i>Pyrus pyraster</i>	-0.03	1				shade
<i>Quercus petraea</i>	0.35	0.256	25×25	25×25	+	light
<i>Viburnum opulus</i>	0.07	1				

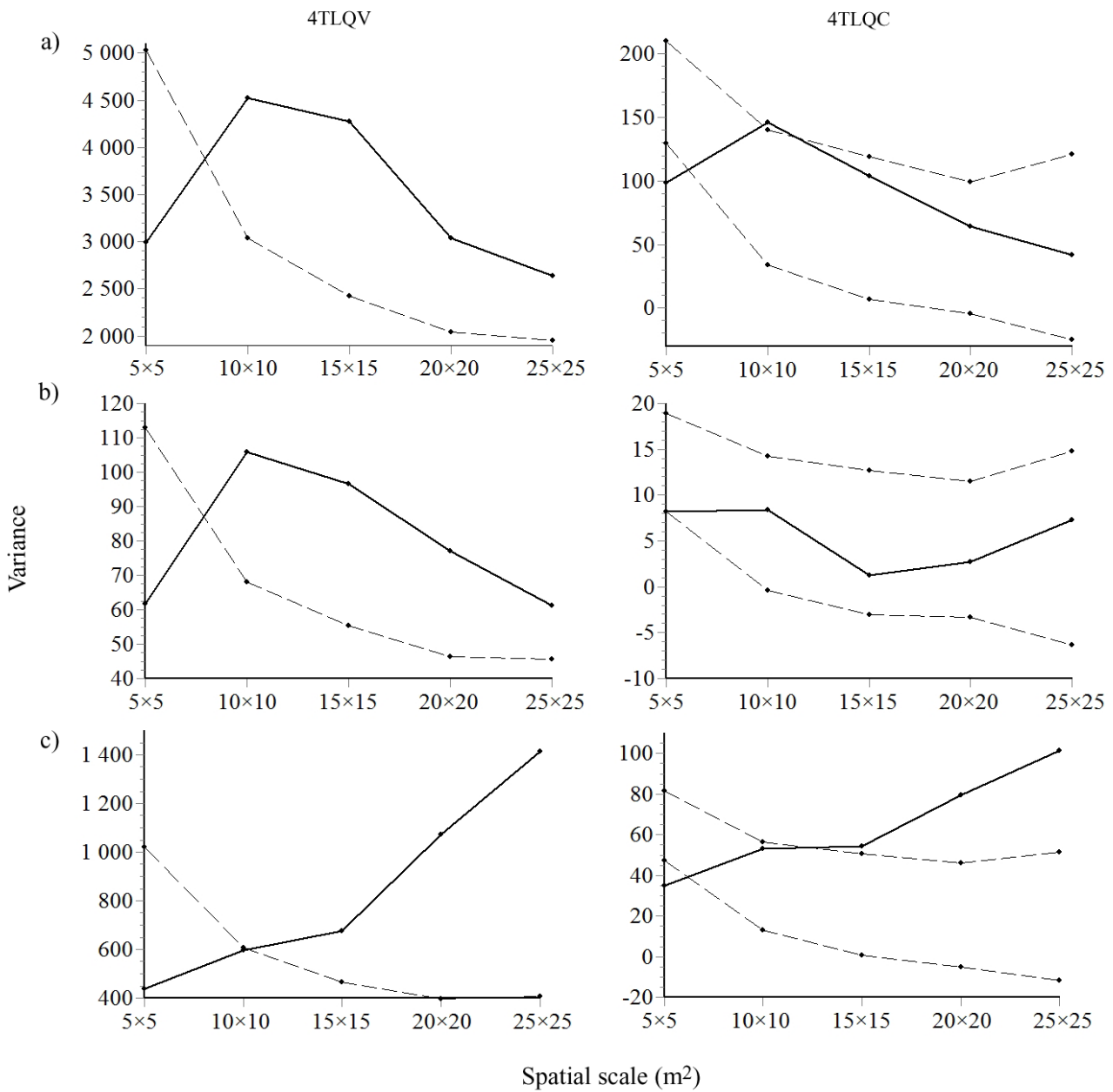
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694 Figure 1. Four-term local quadrat variance (4TLQV) graphs of light (diffuse non-
 695 interceptance), understory and bryophyte cover, and four-term local quadrat covariance
 696 (4TLQC) graph between light and the understory variables. a) diffuse non-interceptance;
 697 cover of b) understory layer, c) bryophytes. Solid line: observed pattern, dashed line:
 698 boundary of the confidence interval of 95% according to the resampling test. (During the
 699 permutations 95% of the resulted random variances were within the dashed lines.) A peak of
 700 the observed pattern can be considered significant if it is above the confidence interval.



703 Figure 2. Four term local quadrat variance (4TLQV) graphs of some species covers and four-
 704 term local quadrat covariance (4TLQC) graphs between light (diffuse non-interceptance) and
 705 the cover of these species. a) a light-related species, *Fragaria vesca*, b) a species not related to
 706 irradiance, *Viola reichenbachiana*, c) seedlings of a light-related woody species, *Quercus*
 707 *petraea*. Solid line: observed pattern, dashed line: boundary of the confidence interval of 95%
 708 according to the resampling test.

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Supplementary materials

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Congruence of the spatial pattern of light and understory vegetation in an old-growth

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temperate mixed forest

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723 Table A.1. Proportion of relative diffuse light in the investigated block, cover of understory

724 and bryophyte layer, and cover and frequency (max. 121) of the selected species. SD:

725 standard deviation.

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	Mean	SD	Cover		Frequency
			Minimum	Maximum	
Rel. diff. light (%)	7.34	4.41	0.40	22.30	
Understory layer (%)	21.99	14.97	0.28	72.56	
Bryophyte layer (%)	6.42	6.58	0.12	35.90	
Herbaceous species					
<i>Ajuga reptans</i>	0.53	1.00	0.00	6.80	62
<i>Athyrium filix-femina</i>	0.16	0.70	0.00	5.40	14
<i>Bracypodium sylvaticum</i>	3.47	5.14	0.00	28.00	102
<i>Carex pallescens</i>	0.57	1.01	0.00	7.20	92
<i>Dryopteris carthusiana</i>	0.17	0.57	0.00	4.80	23
<i>Festuca heterophylla</i>	0.64	1.89	0.00	12.00	47
<i>Fragaria vesca</i>	1.87	2.14	0.00	10.00	99
<i>Mycelis muralis</i>	0.33	0.39	0.00	1.96	98
<i>Poa nemoralis</i>	1.22	3.77	0.00	32.00	54
<i>Rubus fruticosus</i> agg.	7.09	7.02	0.00	32.12	111
<i>Viola reichenbachiana</i>	0.24	0.32	0.00	1.28	97
Woody seedling species					
<i>Betula pendula</i>	0.09	0.22	0.00	1.52	39
<i>Carpinus betulus</i>	5.12	6.24	0.00	32.00	112
<i>Daphne mezereum</i>	0.05	0.15	0.00	0.88	18
<i>Fagus sylvatica</i>	0.30	0.99	0.00	8.80	47
<i>Frangula alnus</i>	0.05	0.12	0.00	0.92	34
<i>Picea abies</i>	0.03	0.07	0.00	0.40	48
<i>Pinus sylvestris</i>	0.01	0.04	0.00	0.28	31
<i>Prunus avium</i>	0.07	0.17	0.00	1.56	61
<i>Prunus spinosa</i>	0.04	0.16	0.00	1.20	14
<i>Quercus petraea</i>	0.84	0.96	0.00	4.48	110
<i>Viburnum opulus</i>	0.10	0.25	0.00	1.20	26

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728 Figure A.1. Maps of some investigated variables in the block. a) light (diffuse non-
729 interceptance); cover of b) understory layer, c) bryophytes, d) a light-related species, *Fragaria*
730 *vesca*, e) a species not related to irradiance, *Viola reichenbachiana*, and f) seedlings of a light-
731 related woody species, *Quercus petraea*. The deeper colours show higher values of the
732 variables, dividing the range of the variables to 10 intervals.

