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

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Abstract

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

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

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

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

Keywords

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

Abbreviations

4TLQV: four-term local quadrat variance

4TLQC: four-term local quadrat covariance

Introduction

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

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

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

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

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

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

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

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

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

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

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

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

Materials and methods

Study area

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

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

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

Data collection

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

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

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

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

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

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

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

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

For the visual representation of the pattern of light and understory cover in the plots, 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

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

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

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

Discussion

Understory light pattern in the investigated forest reserve

Diffuse radiation in the understory of the Szalafői Őserdő Forest Reserve is quite high and variable (from 0.4 % to 22 %), compared to managed stands in the region (Tinya et al. 2009a). The explanation for this is simple: old-growths stands with near-natural forest dynamics and variable tree species composition have heterogeneous light conditions, due to the mortality of old trees, and to the heterogeneous canopy layer (Roburn 2003).

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

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

Relationships between light and vascular understory cover

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

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

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

Relationships between light and cover of particular understory species

Light-demanding, transitional and shade-tolerant species could be distinguished among vascular understory species, on the basis of their correlation and spatial covariance with light. *Festuca heterophylla*, *Fragaria vesca* and *Poa nemoralis* proved to be light-demanding herbs. Their cover correlated with light, and their spatial pattern was also related to the light pattern. All of these species matched the finer scale (10×10 m) pattern of the irradiance, which implies that they prefer small open areas in the forests (Gálhidy et al. 2006). This scale of light heterogeneity is presumably caused by the arrangement of the individual trees. We considered *Brachypodium sylvaticum* and *Carex pallescens* transitional species, because their cover correlated with light availability at the 5×5 m scale, but their spatial pattern did not follow the pattern of light.

Ajuga reptans, Mycelis muralis, Rubus fruticosus agg., *Viola reichenbachiana* and the two ferns (*Athyrium filix-femina* and *Dryopteris carthusiana*) proved to be shade-tolerant – neither their cover nor their spatial pattern was positively related to light. Most of these species are typically closed forest species, which usually occur in the shady parts of the stands (Schmidt et al. 2003, Gálhidy et al. 2006, Tinya et al. 2009a). However, *Rubus fruticosus agg.* is often considered as a light-flexible species, frequently invading the clear-cut areas (Gálhidy et al. 2006, Plue et al. 2013). It is a long-lived, clonal plant, which is capable of intensive horizontal growth (Klimešová and de Bello 2009). It can efficiently allocate photosynthates and nutrients between ramets, thus ramets in the light can feed ramets in the shade. It usually prefers more open stands (based on the comparison of many forest stands in this region, Tinya et al. 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 pyraster*) 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

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

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

Relationship between light and bryophyte cover

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

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

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

General considerations

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

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

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

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

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

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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)**
Betula pendula	19.01	22.81 ± 6.22	10.48 ± 7.40
Carpinus betulus	3.52	14.64 ± 7.96	9.60 ± 6.12
Corylus avellana	0.70	7.30 ± 0.00	50.00 ± 0.00
Fagus sylvatica	7.04	24.53 ± 15.48	15.75 ± 6.68
Pinus sylvestris	6.34	35.99 ± 7.71	22.31 ± 3.20
Prunus avium	2.11	26.77 ± 7.77	20.00 ± 1.50
Quercus cerris	2.82	30.68 ± 18.35	17.00 ± 7.79
Quercus petraea	58.45	33.22 ± 11.09	20.23 ± 5.09
Total		29.79 ± 11.87	17.65 ± 7.03

Table 2. Relationships of total understory cover and the cover of individual species with relative diffuse light. Corr. coeff.: Pearson correlation between light and understory variables (n=121). Corrected p: significance values corrected with Moran's I because of the spatial autocorrelation, and with Holm-correction for multiple testing. 4TLQV, 4TLQC: Scale of significant peaks (at $p<0.05$ level, in m) of four-term local quadrat variance and four-term local quadrat covariance between the pattern of light and understory variables. 4TLQC peaks were listed only if their scale agreed with the scale of the 4TLQV peaks. "Direction" means the sign of the 4TLQC value. Relation to light: shade = shade-tolerant, light = light-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						
Ajuga reptans	0.19	1	20×20			shade
Athyrium filix-femina	0.15	1				shade
Brachypodium sylvaticum	0.51	0.000	15×15			transitional
Carex pallescens	0.57	0.000				transitional
Dryopteris carthusiana	0.09	1	15×15			shade
Festuca heterophylla	0.41	0.002	10×10	10×10	+	light
Fragaria vesca	0.44	0.001	10×10	10×10	+	light
Mycelis muralis	0.27	0.696	25×25			shade
Poa nemoralis	0.47	0.000	10×10	10×10	+	light
Rubus fruticosus agg.	0.27	0.303	25×25	25×25	-	shade
Viola reichenbachiana	0.29	0.161	10×10			shade
Seedling species						
Betula pendula	0.44	0.003	25×25	25×25	+	light
Carpinus betulus	0.14	1	25×25	25×25	+	light
Daphne mezereum	-0.12	1	25×25	25×25	-	shade
Fagus sylvatica	0.07	1				shade
Frangula alnus	0.04	1	15×15			shade
Picea abies	0.21	0.255				shade
Pinus sylvestris	0.29	0.133	25×25	25×25	+	light
Prunus avium	0.19	0.485				shade
Pyrus pyraster	-0.03	1				shade
Quercus petraea	0.35	0.256	25×25	25×25	+	light
Viburnum opulus	0.07	1				

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

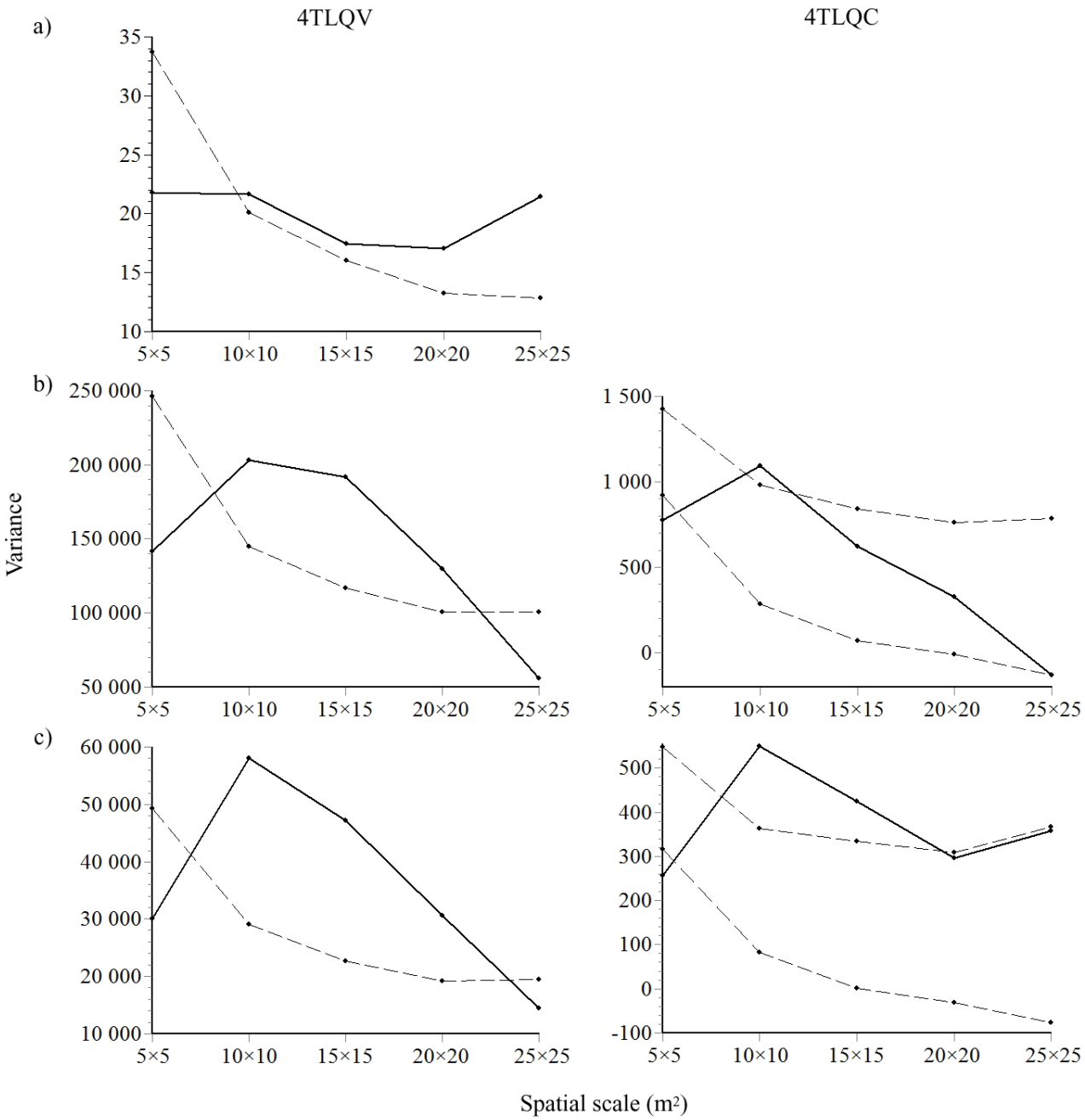
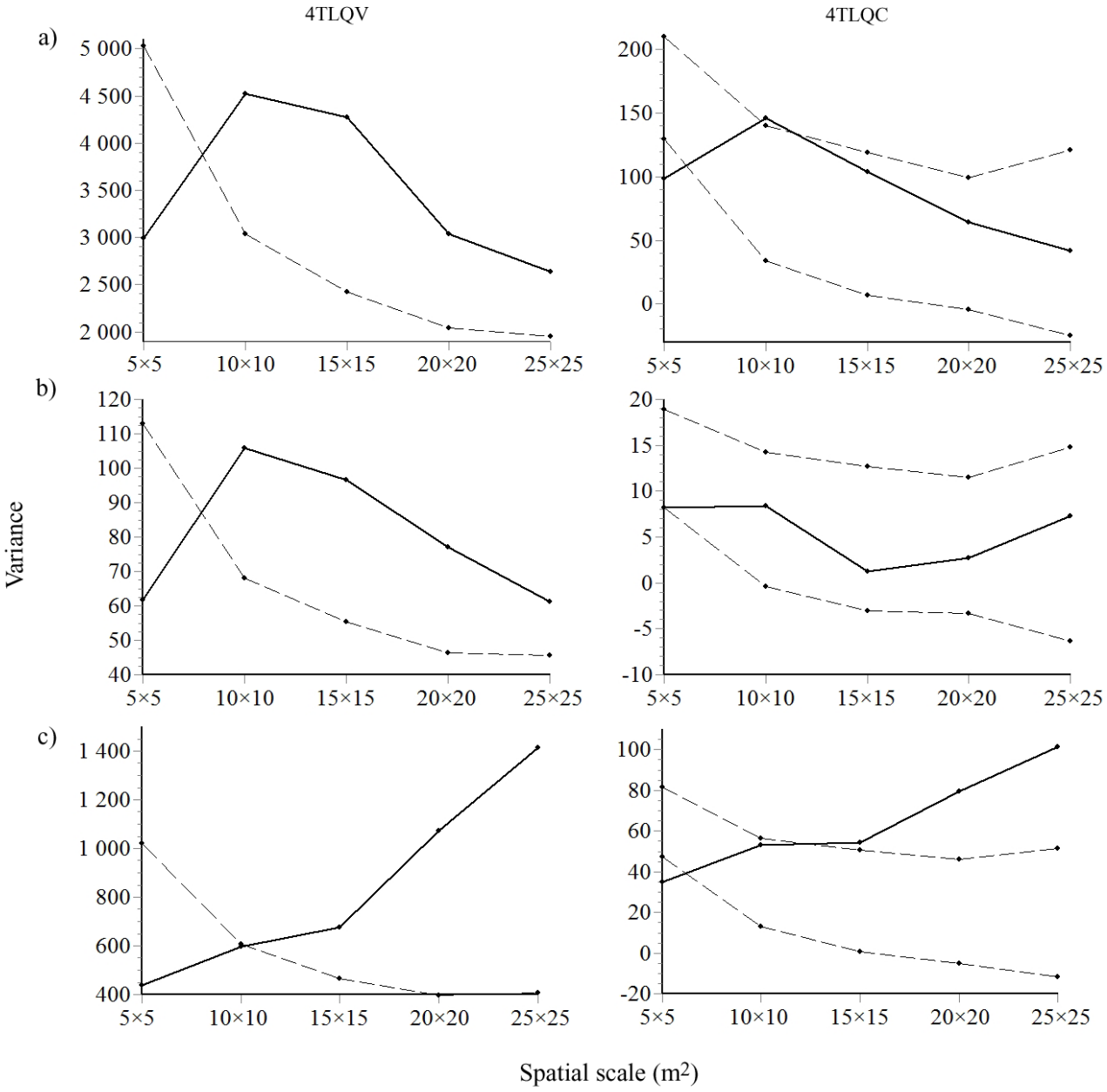


Figure 2. Four term local quadrat variance (4TLQV) graphs of some species covers and four-term local quadrat covariance (4TLQC) graphs between light (diffuse non-interceptance) and the cover of these species. a) a light-related species, *Fragaria vesca*, b) a species not related to irradiance, *Viola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



Supplementary materials

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

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Table A.1. Proportion of relative diffuse light in the investigated block, cover of understory and bryophyte layer, and cover and frequency (max. 121) of the selected species. SD: standard deviation.

	Cover				Frequency
	Mean	**SD**	**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					
Ajuga reptans	0.53	1.00	0.00	6.80	62
Athyrium filix-femina	0.16	0.70	0.00	5.40	14
Bracypodium sylvaticum	3.47	5.14	0.00	28.00	102
Carex pallescens	0.57	1.01	0.00	7.20	92
Dryopteris carthusiana	0.17	0.57	0.00	4.80	23
Festuca heterophylla	0.64	1.89	0.00	12.00	47
Fragaria vesca	1.87	2.14	0.00	10.00	99
Mycelis muralis	0.33	0.39	0.00	1.96	98
Poa nemoralis	1.22	3.77	0.00	32.00	54
Rubus fruticosus agg.	7.09	7.02	0.00	32.12	111
Viola reichenbachiana	0.24	0.32	0.00	1.28	97
Woody seedling species					
Betula pendula	0.09	0.22	0.00	1.52	39
Carpinus betulus	5.12	6.24	0.00	32.00	112
Daphne mezereum	0.05	0.15	0.00	0.88	18
Fagus sylvatica	0.30	0.99	0.00	8.80	47
Frangula alnus	0.05	0.12	0.00	0.92	34
Picea abies	0.03	0.07	0.00	0.40	48
Pinus sylvestris	0.01	0.04	0.00	0.28	31
Prunus avium	0.07	0.17	0.00	1.56	61
Prunus spinosa	0.04	0.16	0.00	1.20	14
Quercus petraea	0.84	0.96	0.00	4.48	110
Viburum opulus	0.10	0.25	0.00	1.20	26
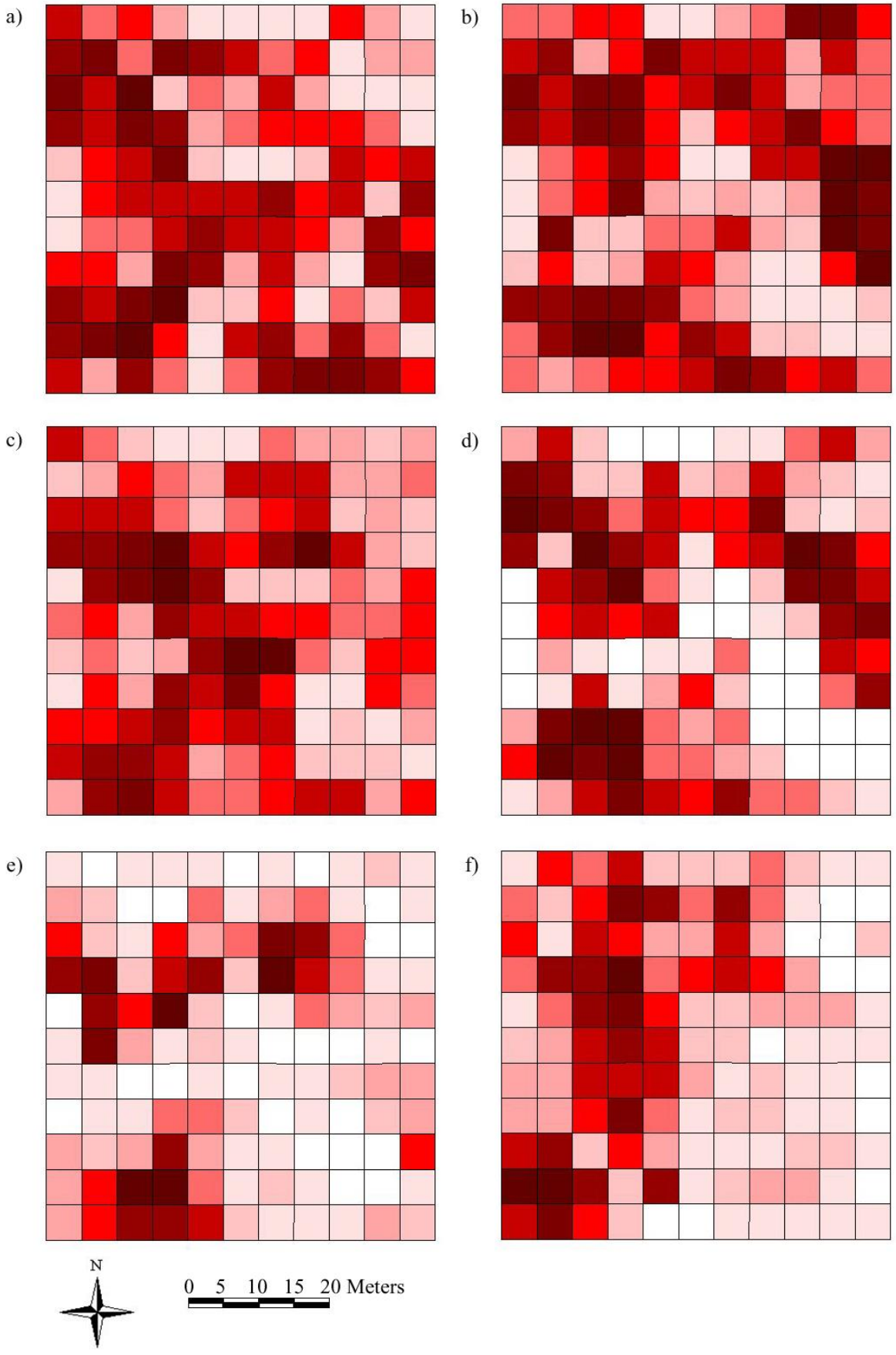
Figure A.1. Maps of some investigated variables in the block. a) light (diffuse non-interceptance); cover of b) understory layer, c) bryophytes, d) a light-related species, *Fragaria vesca*, e) a species not related to irradiance, *Viola reichenbachiana*, and f) seedlings of a light-related woody species, *Quercus petraea*. The deeper colours show higher values of the variables, dividing the range of the variables to 10 intervals.