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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.

1. 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,

Abbreviations: 4TLQV, four-term local quadrat variance; 4TLQC, four-term local quadrat covariance.

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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 Ejrnaes, 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)?

2. Materials and methods

2.1. 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 (N46°52′06″ and E16°18′13″). The elevation of the reserve is between 312 and 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 Siválk, 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).