



Stand structural drivers of microclimate in mature temperate mixed forests



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ABSTRACT

The complex interactions between stand characteristics and forest site variables result in specific understory microclimate conditions, which are essential for many forest-dwelling organism groups.

The main aim of our study was to evaluate the relative importance of stand structure variables and landscape elements that account for the microclimate in closed, managed, mature forest stands. The relationships between different microclimatic variables were also analyzed. 35, 70–100 year-old deciduous-coniferous mixed forest stands were selected in Western Hungary. Air temperature, relative humidity, and relative diffuse light were measured at eight sampling periods between 2009 and 2011.

Below-canopy air temperature and humidity showed a strong negative correlation, but diffuse light was independent. The mean values of air temperature and humidity depended on stand structure elements, chiefly on the subcanopy and shrub layer, while their variance was lowered by litter cover. The amount of diffuse light was negatively affected by tree diameter, basal area and tree size diversity.

Our results suggest that structural elements have a stronger influence on microclimate conditions than tree species composition of the overstory. The midstory and the shrub layer play key roles in maintaining the special microclimate of forests with continuous canopy-cover. Our results can provide adoptable aspects for forest management and nature conservation for the maintenance of the specific conditions favorable to sensitive forest specialist taxa (e.g. forest herbs, forest-dwelling ground beetles, epiphytic bryophytes, and lichens).

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1. Introduction

The characteristics and pattern of local scale climate are essential to the habitat requirements of different species within a given region (Kearney et al., 2014; Suggitt et al., 2011). These features are also responsible for providing the potential of persistence and dispersal for climate-sensitive organisms (Frey et al., 2016). Microclimate is relevant in modifying and maintaining species composition and community structure (Aude and Lawesson, 1998; Kearney et al., 2014; Moning and Muller, 2009), and influencing demography, individual behavior (Latimer and Zuckerberg, 2016), and ecological interactions (Ackerly et al., 2010). From a broader viewpoint, creating a particular microclimate is an important

regulatory function of ecosystems, depending on structural and network complexity (Jorgensen, 2006; Lin et al., 2009; Lin et al., 2011; Norris et al., 2012). Thermodynamic efficiency, which is strongly determined by the self-organization of the ecosystems (Lin et al., 2009), is especially important. A well-developed structure and the optimum functional status enhance energy capture and maximize the buffer capacity regarding external fluxes (Freudenberger et al., 2012; Lin et al., 2009, 2011).

Forest ecosystems modify climatic parameters within a given locality and create a special microclimate through a complex interaction of topography, vegetation composition, and structure. According to Aussenac (2000), factors regulating the microclimate under closed forest canopy can be classified hierarchically. Higher-level components, such as regional climate and topography (elevation, exposure, etc.) are substantial, and affect microclimate fundamentally (Holst et al., 2004). These factors determine edaphic conditions and the structure of natural vegetation, which becomes altered by forest management practices. The effects of lower-level factors, such as soil and stand characteristics (humus content, amount of litter, species composition, age and vertical structure,

Abbreviations: CV, coefficient of variation; DBH, diameter at breast height; DIFN, diffuse non-interceptance; dRH, difference of relative humidity from the reference value; dT, difference of temperature from the reference value; LAI, leaf area index.

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cover of herb layer, etc.) are additional, and these drivers impinge by modifying the base conditions created by higher level elements (Gehlhausen et al., 2000; Weng et al., 2007).

Forest canopy is a key driver in the regulation of the climate of the stand, by influencing energy, water vapor, and carbon exchange between the trunk space and the atmosphere (Chen et al., 1999; De Frenne et al., 2013; Renaud et al., 2011; von Arx et al., 2012). Beside the (partial) shielding effect, canopy, together with tree stems, also reduces air mixing (Baker et al., 2016; Chen et al., 1999; Geiger et al., 1995). Compared to open areas, the microclimate conditions of forest stands are moderated, and have lower annual and seasonal variability (Ewers and Banks-Leite, 2013; von Arx et al., 2013). In comparison to non-forested areas with similar site conditions, below-canopy climates are characterized by lower maximum temperatures and wind speeds, with higher minimum temperatures and humidity values (Chen et al., 1999; Geiger et al., 1995; Renaud et al., 2011). This balancing effect is present not only in widespread closed forests; it is perceptible within patchy, spatially complex landscapes as well (Baker et al., 2016; Giambelluca et al., 2003; Hesslerová et al., 2013). Beside forest canopy, vegetation structure (i.e. vertical and horizontal complexity) and composition are also crucial factors in creating and maintaining the fine-scale climate of forested landscapes (Frey et al., 2016; Latimer and Zuckerberg, 2016; Suggitt et al., 2011). The amount, condition and distribution of the biomass have a great influence on thermodynamic efficiency: a well-developed and self-organized ecosystem receives, absorbs, and dissipates incoming solar energy more efficiently (Lin et al., 2011; Norris et al., 2012). The importance of structural complexity was demonstrated by comparing old-growth forests and plantations with similar canopy cover, where site-scale thermal buffering was connected to higher biomass, well developed vertical stratification, and dense canopy (Frey et al., 2016; Lin et al., 2009).

Numerous studies focus on only one or a few explanatory factors influencing certain microclimate variables such as temperature, relative humidity, and incoming radiation (Chen et al., 1999; Davies-Colley et al., 2000; Morecroft et al., 1998; Renaud and Rebetez, 2009). The variability of microclimatic characteristics depends on several different factors, such as topographic conditions, soil properties, forest type, stand structure, or distance from forest edge. Elevation, slope and aspect (Holst et al., 2005; Ma et al., 2010; Weng et al., 2007) are essential for incoming radiation, soil and air temperature. Forest type can affect both relative humidity and air temperature (von Arx et al., 2012). Adjacent land use type determines microclimate mainly in the transition zones, and this factor influences several variables (light, VPD, temperature), not just mean values, but also ranges (Denyer et al., 2006; Matlack, 1993; Wright et al., 2010). Forest structure (e.g. vertical complexity, spatial pattern) can directly affect the amount and variability of light (Sprugel et al., 2009; Tinya et al., 2009a; Valladares and Guzman, 2006), while litter has effect on soil and below-canopy energy fluxes indirectly. Litter layer is a heat and water reservoir that can alter below-canopy microclimate resulting in reduced soil evaporation, lowered capillary rise, or altered albedo and vertical vapor transfer (Matthews, 2005; Ogee and Brunet, 2002; Sakaguchi and Zeng, 2009). Due to the complex relationships between microclimate and habitat elements, during statistical analyses, it is useful to select the influential factors for microclimate from many potential explanatory variables (e.g. Dovciak and Brown, 2014; Holst et al., 2004; Ma et al., 2010; Matlack, 1993; von Arx et al., 2012).

A notable proportion of studies on forest microclimate focuses on the description of the spatial or temporal patterns of microclimate variables in a selected stand type (e.g. Carlson and Groot, 1997; Friedland et al., 2003; Holst et al., 2004). Beside these, numerous studies compare contrasting environments, such as open areas and closed forest stands (e.g. Morecroft et al., 1998), different forest types (e.g. Norris et al., 2012) and environmental gradients from

non-forested sites towards forest interiors (e.g. Chen et al., 1999). Another general aspect is studying the changes of macroclimatic variables after severe changes of the canopy cover, caused by natural disturbances (Abd Latif and Blackburn, 2010), management practices (Heithecker and Halpern, 2006), or habitat fragmentation, explored by the edge effect (Wright et al., 2010). On the other hand, fewer studies investigate the relationships between the below-canopy microclimate and the stand characteristics or landscape variables in mature forests (Frey et al., 2016; Heithecker and Halpern, 2006; Matlack, 1993; von Arx et al., 2012, 2013).

The identification of those attributes in forest stands that create a particular microclimate may help to maintain ecosystem structure and function in forests, and improve conservation and management practices preserving biodiversity and mitigation strategies against the effects of local and global changes. The aim of this study was to evaluate the relative importance of a wide set of stand structure variables and landscape factors explaining microclimatic conditions under continuously closed canopies. For the analysis, managed, mature forests with various tree species compositions were chosen, where stand characteristics were strongly influenced by a long history of previous forest utilization. Explanatory variables influencing forest microclimate (including temperature, relative humidity and relative diffuse light) were explored at both stand level (e.g. species composition, vertical structure) and landscape level (adjacent land use types). We focused on the following questions and hypotheses:

- 1) To what extent are the variables of temperature, relative humidity, and light correlated?

Based on previous studies (Anderson, 1936; Geiger et al., 1995), our hypothesis is that air temperature and humidity are consistently negatively correlated. We also expect significant relationships between light and the other two variables: positive correlation with temperature, and negative correlation with air humidity.

- 2) Instead of using numerous, separately measured microclimate variables, is it possible to use only a few, derived, generalized ones?

As we assumed that the original microclimate variables strongly correlate, it is expected that their multidimensional space could be effectively reduced by ordination methods, to derive general microclimate variables.

- 3) From several variables of tree species composition, stand structure, landscape, and ground layer, which factors are the most influential on microclimate?

According to our expectations, the microclimate of mature, closed forests is mainly determined by tree species composition and stand structure (shrub layer density, vertical canopy structure, amount of large trees, deadwood).

2. Material and methods

2.1. Study area

The study was conducted in the Órség National Park, Western Hungary (46°51'–55' N, 16°70'–23' E; Fig. 1). Mean annual temperature in the area is 9.1–9.8 °C, and precipitation is 700–800 mm per year. Elevation ranges from 250 to 380 m above sea level, with a gentle topography. The most common landscape elements are hills, orientated northwest-southeast, divided by valleys formed by rivers. Acidic and nutrient poor soils (pH 4.0–4.8) with pseudogley or lessivage (planosols or luvisols) (Krasilnikov et al., 2009) are the most frequent soil types, on a bedrock of alluvial gravel mixed with sand and loess (Dövényi, 2010).

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