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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).

Keywords: air temperature; relative humidity; diffuse light; stand structure; temperate mixed forests; shrub layer.

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.

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; Lin et al., 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, 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 Őrség 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).

The forest cover of the studied region is approximately 80% (Dövényi, 2010). The forests are highly heterogeneous, both tree species composition and stand structure vary among the stands. Forests are dominated by beech (*Fagus sylvatica* L.), sessile and pedunculate oak (*Quercus petraea* Matt. (Liebl.) and *Q. robur* L.), hornbeam (*Carpinus betulus* L.), Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst.). The six dominant tree species form various stands, from monodominant to highly mixed forests. The proportion of different subordinate tree species (*Betula pendula* Roth, *Populus tremula* L., *Castanea sativa* Mill., *Prunus avium* L., etc.) is relatively high (Tímár et al., 2002). Although monodominant beech, oak, and Scots pine forests are present in the region, their proportion is quite low, while mixed stands with various mixing ratios of the dominant tree species are more typical. The herb layer is usually scarce, average cover is around 5% (Márialigeti et al., 2016).

Private forests are mainly managed by a spontaneous stem selection system, while state owned forests are managed by a shelterwood forestry system, with a rotation period of 70–110 years (Matthews, 1991). A more detailed description of the studied stands and the land use history of the forests in this region can be found in the work of Király et al. (2013). Because of the different types of management, stand structure is also widely varied. In general, the forest stands managed by single stem selection have more developed shrub layers, higher tree species richness, and their canopies are more structured, both vertically and horizontally, while the shelterwood system creates forests with one or two layers, with primarily hornbeam in the subcanopy layer.

2.2 Data collection

Thirty-five forest stands (2-10 ha) were selected by stratified random sampling, using the Hungarian Forest Database (owned by the Forestry Directorate of the National Food Chain Safety Office) (Fig. 1). In the study, the mature, zonal forest stands of the region were considered as the statistical population. From the database, we selected forest stands older than 70 years, situated on gentle slopes, located in sites without direct water influence. The population of the stands was stratified, based on the combination of the main tree species. The groups were formed on the basis of the mixing ratio of the main tree species (sessile and pedunculate oak, beech, and Scots pine), so monodominant (ratio of dominant species>80%) and mixed stands became separated. The studied plots were selected randomly within each stratum. The minimum distance between selected stands was 500 m, in order to assure the spatial independence of the sampling units.

Two different plot sizes were applied for field measurements (Figure 1.A). Stand structure variables and tree species compositional data were recorded in 40 m × 40 m (0.16 ha) blocks within each selected forest stand, while ground-layer data were collected in 30 m × 30 m (0.09 ha) plots. All variables were extrapolated to 1 hectare (Table 1).

Within the larger blocks (40 m × 40 m), tree maps were created, with the exact geographical position, species identity, height, and diameter at breast height (DBH) of every individual (living trees, standing dead trees and snags as well) with DBH larger than 5 cm. *Quercus petraea*, *Q. robur* and *Q. cerris* were combined and analyzed as oaks, while less frequent tree species (e.g. *Prunus avium* and *Populus tremula*) were grouped as admixing species. The relative proportion of every tree species was calculated, based on volume. Tree volume data were computed by applying species-specific equations of standard tree volume tables (Sopp and Kolozs, 2000). Saplings and shrubs in the shrub layer (DBH <5 cm, height >0.5 m) were counted. Stem densities in different DBH categories were calculated. The Shannon diversity of the DBH categories was also computed, using the $-\sum(P_i \cdot \ln P_i)$ function, where P_i is the relative volume of DBH class *i* within the total statistical population. The length and mean diameter of lying deadwood (log) units longer than 0.5 m and thicker than 5 cm were measured. Stumps lower than 50 cm and thicker than 5 cm were also measured. The volume of snags, stumps, and lying deadwood was calculated by the cylinder formula, based on mean diameter and height or length.

The inventory of the understory layer (vegetation under 0.5 m), ground-floor bryophytes, cover type of the surface, canopy cover, and light was carried out in 30 m × 30 m plots, positioned in the centre of the 0.16-ha blocks. Absolute cover (dm^2) was estimated for herbs, bryophytes, saplings, mineral soil, deadwood, and litter within the plots. Additionally, litter characteristics (mass fraction and absolute mass of the different constituents) were measured by analyzing litter samples.

Landscape variables were computed using aerial photographs, topographic maps, and forestry data. The relative area of forests (stand age ≥20 years), different forest types (based on dominant tree species), young stands (stand age <20 years), and non-forested areas (settlements, meadows, arable lands) was estimated for an area of 300 m radius, surrounding each plot.

Micrometeorological measurements were carried out eight times between 2009 and 2011, sampling various stages of the vegetation period. Air temperature and relative humidity were measured using specific, combined sensors (Voltcraft DL-120 TH, Conrad Electronic SE, Hirschau, Germany), connected to two-channel data loggers, surrounded by radiation shields (25 cm × 30 cm white housing), and situated at 1.3 m above ground level, in the centre of the sampling units. At each plot, the microclimatic variables were recorded for 24 hours, using five-minute recording frequency. With our twelve loggers, the length of the measurement periods was 4-5 days, as we had to relocate the instruments, while two loggers were kept in permanent locations during these periods, to serve as references (see Fig. 1). The measurements of the loggers were temporally synchronized. All devices were calibrated to one chosen sensor at every measuring period. The measurements were carried out in June 2009, October 2009, June 2010, July 2010, September 2010, October 2010, March 2011, and May 2011. For every record, the mean value of the two reference loggers was subtracted from the actual values of the variables. These calculated difference values (temperature difference: dT; relative humidity difference: dRH) were introduced in order to exclude the effects of regional weather differences. Means, minimums, maximums, and ranges were calculated from these difference values for each 24-hour period.

For the estimation of the amount of light, we used the proportion of diffuse non-interceptance (DIFN). DIFN was measured once, with LAI-2000 Plant Canopy Analyser instruments (LI-COR Inc., Lincoln, USA), at 36 spots within the 30 × 30 m plots, following a systematic design (Figure 1.A), at 1.3 m height. Three measurements were taken in each locality, within a few seconds. Using parallel measurements in the nearest open areas, light conditions could be expressed as relative diffuse light, using the 2000-90 Support Software (LI-COR Inc., 1992). Derived light variables (mean, SD, coefficient of variation) for each plot were calculated from the measured light data. According to our previous study (Tinya et al., 2009b), this technique was appropriate for the estimation of the relative light in these forests. Repeated measurements were not necessary with this device.

2.3 Data analysis

As a preliminary analysis, relationships of the daily means of the measured microclimate variables (dT, dRH, DIFN) were explored by correlation analyses. The data structure of variables with high correlations (dT and dRH) was analyzed by indirect ordination (Podani, 2000). Standardized principal component analysis was only used to explore the relationship of the air temperature and relative humidity datasets (mean and range of dT, dRH), applying correlation biplots (Borcard et al., 2011). The aim of the ordination was to generalize microclimatic variables, and to compress their variance into two or three “general microclimate variables”, applicable for the further analyses.

The relationships between the two constructed generalized microclimate variables (PC1 and PC2) and the potential explanatory variables were explored by linear regression models (Faraway, 2005). Explanatory variables are summarized in Table 1. Site scores of the PC1 and PC2 axes were used as dependent microclimate variables. Linear models were used for the analysis of relative diffuse light (mean and CV) and the same environmental variable set.

Before modelling, preliminary selection and data exploration were performed. For the dT and dRH variables, the original values were used, while for the mean and CV of DIFN, natural logarithmic transformation was performed, in order to achieve normality. Each potential explanatory variable was standardized (Z-score scaling). Some explanatory variables were ln-transformed before the analysis, to meet normality criteria (as marked in Table 1). Correlation matrices were calculated and scatterplots were drawn to explore the relationships among the explanatory variables, and the correlations between the dependent and the explanatory variables. Minimal adequate models were built by backward elimination process. During the selection procedures, deviance analyses with F-test (ANOVA) were applied. In addition, log-likelihood based (AIC) model selections were also performed. Multicollinearity was tested using the variance inflation factor (VIF).

Data analyses were carried out with the R 3.0.2. software (R Development Core Team, 2015). Standardized PCA and linear models were conducted by the R package ‘vegan’ (Oksanen et al., 2015), VIFs were calculated using the ‘faraway’ package (Faraway, 2016).

3. Results

According to our results, mean air temperature of the selected stands in the growing season is 16.5°C, which corresponds with the regional average (Dövényi, 2010). Mean, minimum, maximum, and range values of our 24-hour measurements in different periods were also calculated (Table 2).

Mean and standard deviation of DIFN were 2.93 ± 2.21%, ranging from 0.62% to 10.36%. The variation coefficient of DIFN within plots (representing the heterogeneity of light within stands) averaged 0.51 (range 0.12–1.23).

Opposed to our expectations, the correlations between DIFN and the other two microclimate variables (dT, dRH) were weak in every period (Table A.1): mean of Pearson’s correlation coefficients was 0.108 for $DIFN_{ave}$ and dT_{ave}, and 0.013 for $DIFN_{ave}$ and dRH_{ave}. Significant and strong negative correlations were found between dT and dRH variables in every period (Fig. 2, Table A.2). The correlation coefficients of different periods ranged between -0.36 ($p= 0.032$) and -0.89 ($p<0.001$). The weakest correlation was detected in autumn, while values in the spring and the summer showed the strongest negative relationships (Fig. 2).

Based on the correlations, we only performed standardized principal component analysis for the strongly correlated dT and dRH variables (means and ranges for each period). The first and second PCA axis explained 27.25% and 17.69% of the total variance, respectively (Fig. 3). The highly correlated mean values (dT and dRH) were situated distantly in the multidimensional space. The first axis (PC1) displayed a gradient of the means from colder but more humid sites (negative values) to higher temperature with lower relative humidity (positive values). The second axis (PC2) could be interpreted as a gradient of the variability of measured variables: sites on the positive side of the axis had higher daily microclimatic variability.

We could separate our regression models into microclimate and light models (Table 3). In the case of the mean temperature-humidity gradient (PC1), four important explanatory variables were found, based on the linear regression model (R^2=0.61, Table 3). Humidity increased with the relative volume of hornbeam, explaining 33.3% of the total variance of the PC1 (microclimate) variable of the model. The density of shrubs and young trees (14.1% explained variance) also had a significant effect. On the contrary, the proportion of deciduous forest stands in the landscape (11.6%) and the relative volume of oaks (6.6%) decreased humidity and increased temperature. The PC2 model (reflecting microclimate variability) was weaker (R^2=0.22), and was related to litter cover, the proportion of forests in the landscape, and DBH diversity (Shannon diversity of DBH categories). All of these variables decreased the variability of humidity and temperature. Mean DIFN was decreased by total basal area (37.1%) and DBH diversity (19.7%), while it was increased by the relative proportion of oak (10.9%). The variation coefficient of relative diffuse light was decreased by average diameter (35.6%), basal area (13.5%), and proportion of beech (4.6%). The variance inflation factor was below 1.25 for every model.

4. Discussion

4.1. Correlations among microclimate variables

The temperature and humidity values provided by the eight measurement periods accomplished in mature forests in Western Hungary fit well to the previously described, moderately cool and wet climate of the region (Dövényi, 2010; Péczely, 2009). The observed relative light values in the studied stands (2.9 ± 2.21%) are corroborated by other studies. Relative light intensity in closed forests is usually under 6%, depending on their deciduous or coniferous character (Constabel and Lieffers, 1996; Emborg, 1998; Messier et al., 1998; Mihók et al., 2007).

The general negative correlation between air temperature and humidity is a well-known phenomenon (Ahrens and Henson, 2015; Anderson, 1936; Geiger et al., 1995). Moreover, based on this relationship, temperature records are often used to predict relative humidity (Andersson-Skold et al., 2008; Eskelson et al., 2013).

Although this relationship is often observed in forest ecosystems (Baker et al., 2014; Chen et al., 1999; Ma et al., 2010), only few studies quantify the strength of their correlation. In riparian forests, Eskelson et al. (2013) detected comparable results, their correlation coefficients, calculated for mean values, ranged from -0.64 to -0.95. A similar pattern, but with weaker interactions is described in a comparative study of von Arx et al. (2012), where stronger correlations were found for night-time values than for those of daytime.

In our study, the expected relationships between light and the other two microclimate variables (temperature and humidity) were not observed. This result is slightly contradictory, because a broad set of previous studies affirmed this relationship (e.g.

Matlack, 1993). Furthermore, light is one of the major factors affecting stand scale microclimate (Fridley, 2009; Heithecker and Halpern, 2006; Rambo and North, 2009, von Arx et al., 2012). Previous studies suggest that the observed relationship between light and air temperature could be stronger if the total radiation or the direct component would been measured (Abd Latif and Blackburn, 2010; De Freitas and Enright, 1995; Ma et al., 2010). Since direct solar radiation is the primary driver of soil and air heating (Anderson et al., 2007), the diffuse component is less correlated to these (Abd Latif and Blackburn, 2010; North et al., 2005). Diffuse light is more or less constant spatially, below the canopy (Hutchison and Matt, 1977; Pukkala et al., 1991; Reifsnyder et al., 1971-1972). Its relative amount is higher in deciduous stands (Brantley and Young, 2009) than stands dominated by conifers.

The performed ordination can separate the effects of the T/RH gradients (mean and variability of temperature and humidity values). For our analysis, this was an advantageous approach, because the variability of microclimate (both minimums and maximums) is very important for the persistence of many climate-sensitive organism groups (Fenton and Frego, 2005; Halaj et al., 2008; Moning and Muller, 2009; Palo et al., 2013).

4.2. Effects of forest stand, site and landscape variables on microclimate

We hypothesized that tree species composition, stand structure, and landscape variables determine the microclimate in closed mature forests. Our results demonstrate the influence of these variables, but they also suggest that the importance of tree species in the upper canopy layer is lower than expected. In the studied closed forests, the below-canopy structural elements (subcanopy, shrub layer, DBH heterogeneity) explained a higher amount of the variance than tree species composition. However, causality cannot be stated on the basis of the relationships implicated by the regressions of the observed variables.

By the minimum adequate model for the microclimate gradient, hornbeam was the most significant driver in the maintenance of humid microclimates in mature forests with continuous canopy cover. *Carpinus betulus* creates a secondary canopy layer (with an average height of 10-15 m) in the Őrség region (Tímár et al., 2002), therefore the effect of this tree species could be more related to the vertical structure or the state of development of the subcanopy than to the physiognomy of this particular species. The moderating effect of subcanopy is also suggested by studies which measure the vertical air humidity profile in various stands (Elias et al., 1989; Gressler et al., 2015). Due to the denser foliar layer and well-developed canopy structure, midstory species could slow down evaporation, resulting in a more even temperature gradient and higher humidity below the canopy (Unterseher and Tal, 2006). The shrub layer is also an important explanatory variable for predicting microclimate. Shrubs and young trees, situated below the main canopy, increase humidity by stronger shading and by reducing wind speed by filling the trunk space with variously dense foliage, thus creating a more moderate microclimate (Bigelow and North, 2012; Campanello et al., 2007; Geiger et al., 1995). In mixed oak forests, Clinton (2003) found that the presence of *Rhododendron maxima* L. patches significantly lowered air temperatures in intact stands. Similarly, Williams and Ward (2010) found that higher shrub density results in consistently higher relative humidity. Generally, the minimums and maximums of air temperature (or humidity) are significantly influenced by shrub densities under closed canopies (Watling et al., 2011; Williams and Ward, 2010). On the contrary, the adjoining mature deciduous stands and the relative proportion of oak species could increase the average air temperature. These variables affect the microclimate through sparser canopy, lower total leaf area (Bequet et al., 2011), decreasing photosynthetic activity (Ryan et al., 1997), and greater proportion of deadwood in the crowns of living trees (Fuller et al., 2012). Furthermore, in the Őrség region, oak-dominated stands are more intensively thinned and more open than beech dominated stands, which could also increase this effect.

The presence and amount of litter may be highlighted as essential factors for the microclimatic buffer capacity of closed forests. In our study, this variable is represented by total litter cover within the plots. The litter layer in forests, composed of dead leaves, bark, twigs, etc. forms a porous barrier between pedosphere and atmosphere trunk space (Matthews, 2005). Litter on the soil surface intercepts incoming radiation, slows irradiation, restrains a significant proportion of throughfall, and also modifies heat, water vapor, and carbon fluxes at the soil surface, e.g. by reducing soil evaporation (Matthews, 2005; Ogee and Brunet, 2002; Sakaguchi and Zeng, 2009, Wilson et al., 2012). The litter layer can reduce diurnal and annual thermal amplitudes in forests by decreasing the amount of solar income, and by providing insulation for the soil (Kostel-Hughes et al., 2005). The litter layer, having a great water retention capacity, is a considerable store for water, and a protracted source of water vapor (Li et al., 2013; Ogee and Brunet, 2002), thus soil moisture is typically greater, and its fluctuation is smaller under leaf litter than on bare soil (Kostel-Hughes et al., 2005). In accordance with the observations of Matlack (1993), our study proved the buffering effect of the litter layer on air temperature even at 1.3 m height. The moderating effect of forest stands on local climate is demonstrated by forest *versus* open-field, pairwise measurements (e.g. Morecroft et al., 1998; von Arx et al., 2012), and gradient studies (Chen et al., 1995). The role of the proportion of forests in the landscape and LAI is also pivotal for analyzing different, adjoining habitat types (Wright et al., 2010), or forest structure variables (Vanwalleghem and Meentemeyer, 2009). Based on these studies, besides topography, vegetation types and their various attributes are important factors in influencing the understory microclimate, especially air temperature, in complex terrains (Fridley, 2009; Saunders et al., 1998; Vanwalleghem and Meentemeyer, 2009). The relevance of adjoining habitat or land use types on forest microclimate was demonstrated in edge effect studies, where an intensified buffering effect was detected by structurally more complex adjacent matrices (Bigelow and North, 2012; Chen et al., 1995; Didham and Lawton, 1999; Dovciak and Brown, 2014; Hardwick et al., 2015; Matlack, 1993; Wright et al., 2010). Tree size diversity also decreases the variability of microclimate. Its effect is similar to that of the shrub layer and subcanopy. A higher structural heterogeneity in a given locality results in a vertically complex leaf distribution and uneven stem density with lower thermal fluxes, wind turbulence, or more shade (Bigelow and North 2012, Chen and Franklin 1995, Hardwick et al 2015), and it could play a role in achieving a higher level of thermodynamic efficiency (Norris et al., 2012). The amount of diffuse light reaching the understory depends on the complex interaction of structural elements and species-specific attributes. The near-ground level of solar radiation relates principally to canopy openness, leaf area, and crown structure (Aussenac, 2000). The interactions can be described by simple stand attributes, such as stand density, DBH, tree height, and basal area (Grayson et al., 2012; Hale, 2003; Hutchison and Matt, 1977; Stovall et al., 2009; Valladares and Guzman, 2006). Furthermore, many studies emphasized that beside stand characteristics, species-dependent variables (e.g. porosity, height, size of the canopy, and spacing) also strongly affect the transmittance, amount, quality, and temporal or spatial variability of understory light (Angelini et al., 2015; Buckley et al., 1999; Promis et al., 2009; Yirdaw and Luukkanen, 2004). For instance, the ratio of shade-tolerant tree species can reduce spatial heterogeneity of light by deeper crowns (Canham et al., 1994), and, likewise, the higher mixing ratio of broadleaved species in mixed boreal forests creates more homogenous, but higher diffuse light intensities (Messier et al., 1998). It is also noteworthy that the explanatory power of a given structural variable for below-canopy light climate depends on canopy closure, stand density, and vertical and spatial structure of the forest stands (Buckley et al., 1999; Jenkins and Chambers, 1989; Pukkala et al., 1991). Numerous studies suggested that many explanatory variables are necessary for the explanation of the variability of radiance (Lochhead and Comeau, 2012; Promis et al., 2009; Vales and Bunnell, 1988), especially in multi-aged and mixed forests (Da Silva et al., 2012). In our analysis, both basal area and tree size diversity were identified as significant variables, decreasing the amount of diffuse light. Many previous studies pointed out that the aboveground biomass is a significant background variable, determining the amount of light below the canopy (e.g. Grayson et al., 2012; Heithecker and Halpern, 2006; Hutchison and Matt, 1977; Ma et al., 2010). Basal area is a frequently used variable to predict understory light, and it is highly related to canopy closure and the gap factor (Grayson et al., 2012; Porte et al., 2004). Heterogeneous forest structure results in a higher total leaf area and a higher proportion of absorption by a multi-layered canopy with several, overlapping crowns (Aubin et al., 2009; Beaudet et al., 2004). Thus, vertical complexity and varied canopy structure reduce the amount of light (Lhotka and Loewenstein, 2006; Porte et al., 2004). The relative proportion of oak species has a positive effect on the mean amount of light because of the sparser crown structure and lower LAI of oak than beech (Genet et al., 2010; Manes et al., 2010).

The horizontal heterogeneity of the understory light climate depends on various stand characteristics. According to our models, mean DBH, basal area, and the proportion of beech decrease light variability. A negative relationship between mean DBH and the variability of light was detected in various stand types (Lochhead and Comeau, 2012; Messier et al., 1998), just as the moderating effect of big trees (Stovall et al., 2009). Light transmittance characteristics of different tree species, originating from their light demanding strategies, affect both the amount (mean) and variability of light. Shade-tolerant species (in our study, beech) react predominantly through the canopy structure, while light extinction rate per volume unit is marginal, thus a thicker crown creates a deeper shade (Canham et al., 1994).

5. Conclusions

This study is part of the research framework ŐRS-ERDŐ Project (http://orserdo.okologia.mta.hu). The aim of this project is to explore an appropriately wide range of environmental factors for explaining the diversity and species composition of various, forest-related organism groups. This multi-taxon project showed that several forest-dwelling organism groups respond to microclimate variables. For instance, the species composition of woodland herbs and epiphytic lichens are dependent on the light regime (Nascimbene et al., 2012; Tinya et al., 2009a), while the occurrence of epiphytic bryophytes and forest-dwelling spiders is determined by air humidity (Király et al., 2013; Samu et al., 2014).

In this paper, we summarized the implications of a different approach: how forest structure and landscape variables could affect microclimate variables. These results could be extended to the above mentioned assemblages, providing adoptable recommendations for forest management and nature conservation to retain the required, specific conditions for forest specialist taxa. Generally, our findings suggest that the vertical complexity and structural heterogeneity (e.g. presence of subcanopy and shrub layer) are of similar or even greater importance in determining forest microclimate than tree species composition of the overstory. The exact relative importance of the different structural elements (layers) could be tested by microclimate measurements obtained in several vertical positions, however our results based on data collected at one specific height can also demonstrate this phenomenon. A well-developed shrub layer and subcanopy were revealed to be the main drivers in maintaining a stable stand climate. These variables, together with tree size diversity, are linked to the level of self-organization and dissipative efficiency (Lin et al., 2009; Norris et al., 2012), so, beside the biodiversity maintenance aspect, they could be highly relevant regarding ecosystem functionality as well (Freudenberger et al., 2012; Frey et al., 2016). Our results, by emphasizing some structural elements, may help forest managers to make plans with conservational considerations and more complex aspects of forest sustainability in mind. The structural elements identified in this study can be protected or even restored quite cost-efficiently and rapidly by deliberate forest management practices.

These results are also important in the context of global changes. Recent studies (e.g. De Frenne et al., 2013; Frey et al., 2016; Norris et al., 2012) pointed out that some effects of the global climate change – such as “thermophilization” in forested areas – can be mitigated by more close-to-natural forest stand structures. Forest stands with higher structural and functional diversity promote thermodynamic efficiency, which contributes to the development of a more resilient ecosystem (Lin et al., 2009).

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Table 1 Potential explanatory variables used for the linear models. Mean and range were calculated based on data from the 35 surveyed forest stands. Logarithmic data transformation was performed where necessary (noted by *ln*).

	Description	***Unit***	**Mean**	**Min**	**Max**
	Stand structure variables				
	Density of shrubs and saplings of tree species (0-5 cm DBH)	*stems/ha*	952.14	0	4706.25
	Density of mapped trees (DBH>5 cm)	*stems/ha*	591.25	218.75	1318.75
	Density of mapped trees brought into six diameter classes:				
	6<DBH<10	*stems/ha*	138.93	0	675
	11<DBH<20	*stems/ha*	126.43	0	537.5
	21<DBH<30	*stems/ha*	122.68	31.25	368.75
	31<DBH<40	*stems/ha*	134.29	62.5	256.25
	41<DBH<50	*stems/ha*	51.61	0	100
	51<DBH	*stems/ha*	17.32	0	56.25
	Basal area of mapped trees	m^2/ha	34.20	24.1	49.68
	Mean DBH of mapped trees	*cm*	26.34	13.64	40.61
	Coefficient of variation of DBH of mapped trees	*%*	48.46	17	98
	Volume of snags	m^3/ha	12.09	0	64.59
	Volume of logs	m^3/ha	10.76	1.16	35.59
	Shannon-diversity of DBH categories	-	1.27	1.04	1.51
	Tree species composition				
	Relative volume of tree species groups:				
ln	beech	*%*	27.94	0	94
ln	oaks	*%*	3.97	0	22
ln	hornbeam	*%*	26.43	0	79
ln	Scots pine	*%*	3.29	0	50
ln	spruce	*%*	36.11	1	96
ln	mixing species	*%*	1.94	0	17
	Absolute cover of different cover types of the surface				
	Total cover of shrub layer (>0.5 m and <5 cm DBH)	m^2/ha	1052.80	0	5616.11
ln	Total cover of understory layer (herbs and seedlings)	m^2/ha	740.80	19.19	4829.3
ln	Total cover of ground-floor bryophytes	m^2/ha	247.37	16.57	2201.59
ln	Total cover of deadwood	m^2/ha	261.57	79.44	730
	Total cover of litter	m^2/ha	9366.70	7814.99	9833.66
	Total cover of bare soil	m^2/ha	146.75	8.56	472.22
	Landscape variables (r=300 m)				
	Proportion of forests (>20 yr) in the landscape	*%*	89.80	56.92	100
	Proportion of predefined forest stand types (stand age >20 yr, closure >55%) in the landscape:				
	stands dominated by deciduous species	*%*	36.61	0	87.73
	stands dominated by coniferous species	*%*	42.02	0	98.12
	mixed stands	*%*	50.41	0	98.71
ln	Proportion of young stands in the landscape (<20 yr)	*%*	5.72	0	23.03
ln	Total proportion of non-forested areas	*%*	7.25	0	46.79
ln	Proportion of meadows	*%*	2.77	0	18.85
ln	Proportion of arable lands	*%*	1.09	0	17.23
ln	Proportion of settlements	*%*	0.87	0	19.79
	Attributes of the litter				
	Total dry mass of litter	*g*	147.66	105.41	243.08
	Dry mass of deciduous litter	*g*	20.53	3.17	36.19
	Dry mass of coniferous litter	*g*	8.51	0	45.94
	Dry mass of decayed litter in the litter samplings	*g*	17.48	6.38	35.52
	Dry mass of decayed twigs in the litter samplings	*g*	101.13	57.61	164.77

Table 2 Descriptive statistics of the measured air temperature (T) and relative humidity (RH) data. Captions: ‘ave’ refers to mean, ‘min’ to minimum, ‘max’ to maximum, and ‘range’ to range.

Measurement period	**RH_{ave} (%)**	**RH_{min} (%)**	**RH_{max} (%)**	**RH_{range} (%)**	**T_{ave} (°C)**	**T_{min} (°C)**	**T_{max} (°C)**	**T_{range} (°C)**
June 2009	79.86	41.47	97.07	55.60	15.80	6.46	26.15	19.70
October 2009	90.60	55.63	97.00	41.37	9.47	3.08	15.94	12.86
June 2010	73.27	43.84	95.08	51.24	21.38	13.24	31.15	17.91
July 2010	87.90	50.16	96.63	46.47	17.54	12.37	28.25	15.88
September 2010	87.77	50.86	97.03	46.17	12.56	6.75	19.02	12.27
October 2010	88.37	62.15	95.59	33.44	11.07	6.46	16.74	10.29
March 2011	60.18	22.44	94.19	71.75	9.34	-4.35	22.33	26.68
May 2011	72.91	41.10	92.85	51.74	15.64	5.95	25.64	19.69

Table 3 Explanatory variables of the minimal adequate regression models of the generalized microclimate variables (PC1 and PC2) and the relative diffuse light variables (mean and coefficient of variance). Increasing values of PC1 indicated warmer and less humid microclimate, while those of PC2 indicated higher microclimate variability. Adjusted coefficient of determination (R^2), F-statistics with p-values, sense of parameters of the variables (Estimate sign), explained variances (Variance %), and significance (p-value) are listed.

Explanatory variables	**Estimate sign**	**Variance %**	**F-value**	**p-value**
PC 1 ~ “Warm and less humid microclimate” R^2=0.61, F(4,30)=14.3, p<0.001				
Relative volume of hornbeam (%)	-	33.31	29.04	<0.001
Density of shrubs and trees (0-5 cm DBH)	-	14.05	12.25	0.002
Proportion of deciduous stands in the landscape (r=300 m)	+	11.62	10.14	0.003
Relative volume of oak species (%)	+	6.62	7.76	0.023
PC 2 ~ “Higher daily microclimate range” R^2=0.22, F(3,31)=4.19, p=0.013				
Total cover of litter	-	11.09	4.83	0.036
Proportion of forests in the landscape (r=300 m)	-	9.74	4.24	0.048
Shannon-diversity of DBH categories	-	8.02	3.49	0.071
Mean of relative diffuse light R^2=0.65, F(3,31)=21.64, p<0.001				
Total basal area of mapped trees (m^2/ha)	-	37.06	35.55	<0.001
Shannon-diversity of DBH categories	-	19.67	18.87	<0.001
Relative volume of oak species (%)	+	10.95	10.50	0.003
CV of relative diffuse light R^2=0.49, F(3,31)=11.94, p<0.001				
Average DBH (cm)	-	35.56	23.76	<0.001
Total basal area of mapped trees (m^2/ha)	-	13.48	9.01	0.005
Relative volume of beech (%)	-	4.56	3.05	0.091

Figure 1. (A, B) Geographical position of the studied area (Őrség, Hungary). (C) Distribution of sampling plots, represented by squares. Location of reference loggers marked by points. Settlements are delineated by polygons.

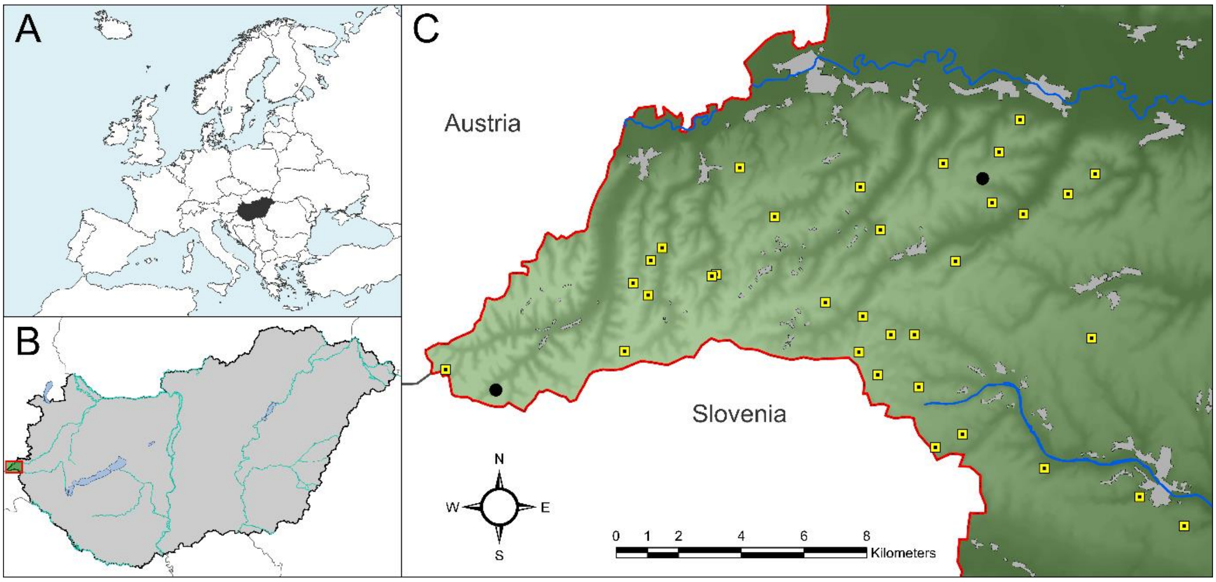


Figure 2. Scatterplots of the daily means of the differences of relative humidity (dRH) and temperature (dT) in different measurement periods, and for the mean of all periods ('Mean'). Coefficients of correlation and significance levels are indicated. Significance levels are marked as ** for p<0.05 and *** for p<0.001.

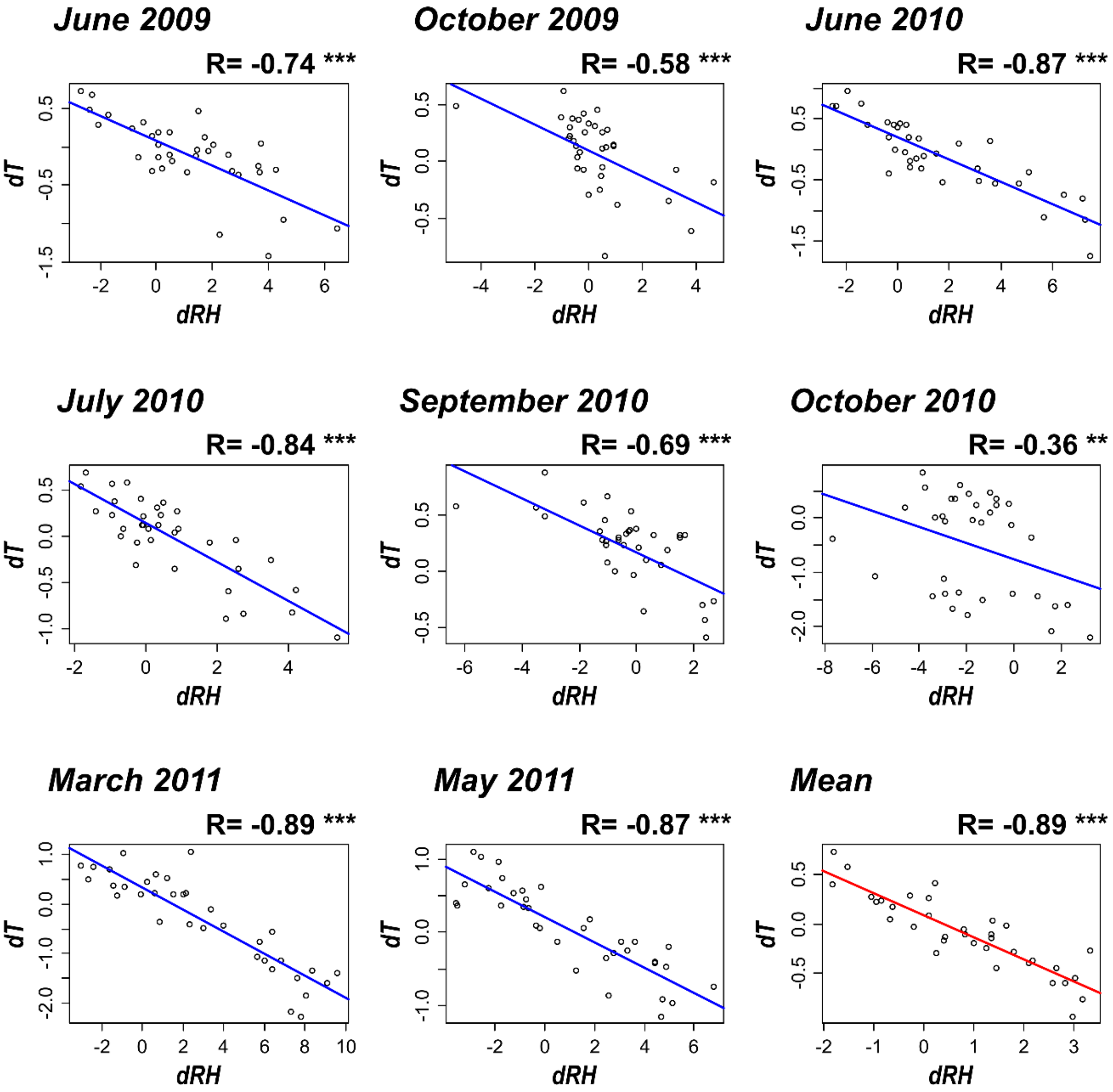
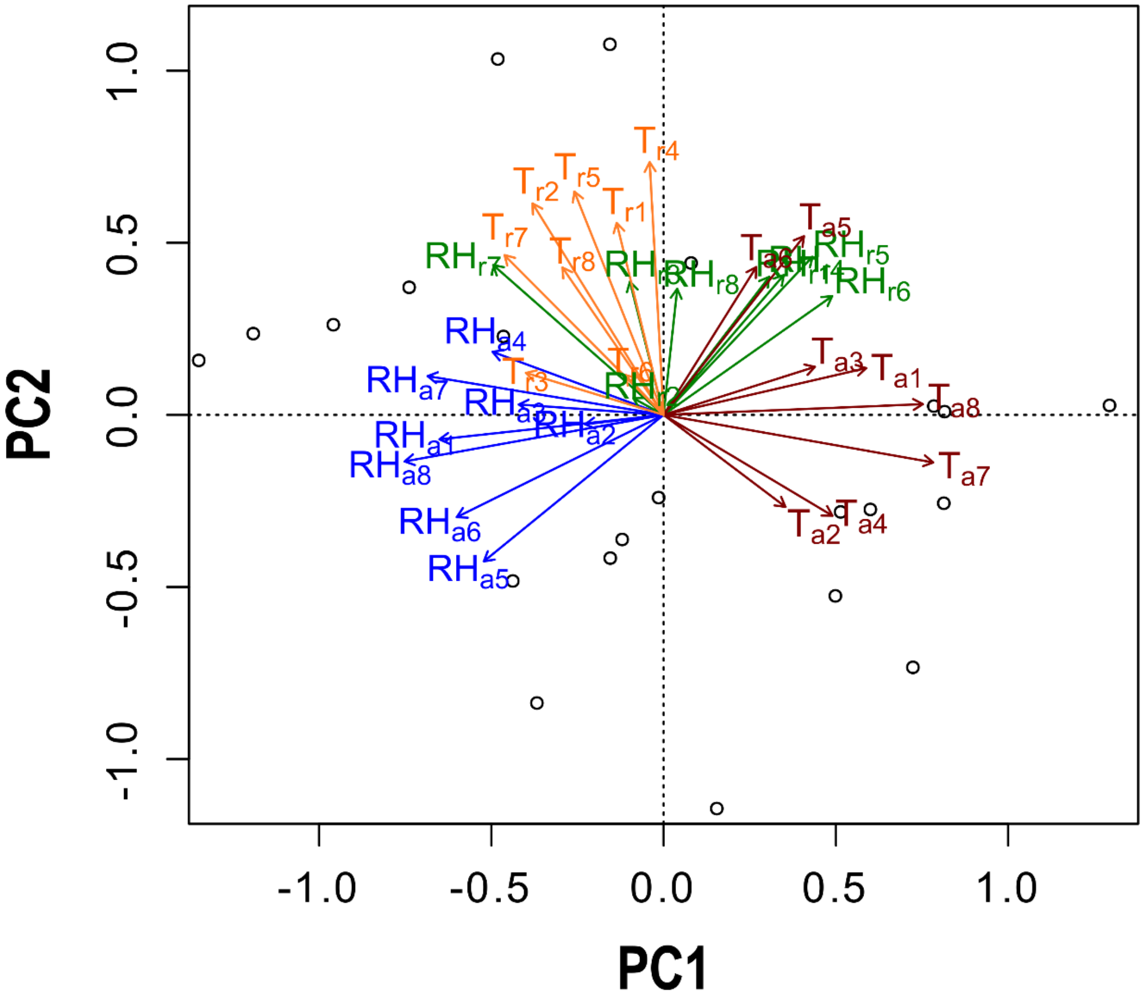


Figure 3. Standardized principal component analysis for 32 microclimate variables (dT marked as 'T' and dRH marked as 'RH'). The first two axes explained 44.95% (27.3% for PC1 and 17.7% for PC2) of the total variance. Captions: 'a' refers to mean, while range is indexed with 'r'. Inferior numbers (1-8) refer to the measurement period (see Table 1).



Appendix

Supplementary material to the manuscript of Kovács, B.[1,2], Tinya, F.[1] and Ódor, P.[1] "Stand structural drivers of microclimate in mature temperate mixed forests".

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Table A.1 Correlations between diffuse light (mean and CV), air temperature (dT) and relative humidity (dRH) variables of the different measurement periods (2009-2011). Pearson’s coefficients of correlation and significance levels are indicated. Significance levels are marked as ** for $p<0.05$ and *** for $p<0.001$. Captions: ’ave’ refers to mean, ’min’ to minimum, ‘max’ to maximum, ‘range’ to range.

ln $DIFN_{ave}$

versus	**dRH_{ave}**	**dRH_{min}**	**dRH_{max}**	**dRH_{range}**	**dT_{ave}**	**dT_{min}**	**dT_{max}**	**dT_{range}**
June 2009	-0.154	-0.114	0.171	0.178	0.239	-0.125	0.433 **	0.420 *
October 2009	0.047	0.096	0.032	-0.098	0.065	-0.069	0.114	0.132
June 2010	0.186	0.295 *	0.118	-0.228	-0.071	0.055	-0.145	-0.138
July 2010	0.122	-0.103	0.374 **	0.199	0.020	-0.096	0.122	0.147
September 2010	-0.255	-0.340 **	-0.186	0.328 *	0.388 **	0.151	0.467 **	0.200
October 2010	-0.299 *	-0.218	-0.285 *	0.135	0.100	0.249	-0.058	-0.277
March 2011	-0.102	-0.282	0.128	0.258	0.097	0.023	0.128	0.066
May 2011	-0.195	-0.262	-0.112	0.166	0.299 *	0.214	0.307 *	-0.003

ln $DIFN_{CV}$

versus	**dRH_{ave}**	**dRH_{min}**	**dRH_{max}**	**dRH_{range}**	**dT_{ave}**	**dT_{min}**	**dT_{max}**	**dT_{range}**
June 2009	0.148	0.067	0.015	-0.052	-0.230	-0.256	0.083	0.262
October 2009	0.040	0.109	-0.025	-0.128	-0.051	-0.164	0.041	0.176
June 2010	0.107	0.060	0.125	0.029	-0.133	-0.317 *	0.110	0.268
July 2010	0.173	0.177	0.114	-0.147	-0.055	-0.058	-0.127	-0.038
September 2010	0.279	0.194	0.294 *	-0.155	-0.037	-0.170	-0.005	0.133
October 2010	0.163	0.007	0.211	0.087	-0.288 *	-0.346 **	-0.175	0.201
March 2011	0.310 *	0.296 *	0.291 *	0.185	-0.203	-0.169	-0.061	0.104
May 2011	0.324 *	0.182	0.398 **	0.081	-0.195	-0.068	0.076	0.097

Table A.2 Pairwise correlations between air temperature (dT) and relative humidity (dHR) variables in the different measurement periods (2009-2011). Pearsons's coefficients of correlation and significance levels are indicated. Significance levels are marked as ** for p<0.05 and *** for p<0.001. Captions: 'ave' refers to mean, 'min' to minimum, 'max' to maximum, and 'range' to range.

Period		dRH_{ave}	dRH_{max}	dRH_{min}	dRH_{ave}
June 2009	dT_{ave}	-0.744 ***	-0.028	-0.413 **	0.347 **
	dT_{max}	-0.409 **	0.370 **	-0.450 **	0.563 ***
	dT_{min}	-0.394 **	-0.335 **	-0.116	-0.054
	dT_{ran}	0.007	0.536 ***	-0.241	0.458 **
October 2009	dT_{ave}	-0.575 ***	-0.450 **	-0.388 **	0.315 *
	dT_{max}	-0.571 ***	-0.504 **	-0.703 ***	0.652 ***
	dT_{min}	-0.382 **	-0.233	-0.259	0.227
	dT_{ran}	0.020	-0.078	-0.172	0.171
June 2010	dT_{ave}	-0.874 ***	-0.704 ***	-0.554 ***	0.069
	dT_{max}	-0.368 **	-0.206	-0.818 ***	0.721 ***
	dT_{min}	-0.567 ***	-0.528 **	-0.087	-0.300 *
	dT_{ran}	0.065	0.159	-0.545 ***	0.701 ***
July 2010	dT_{ave}	-0.837 ***	-0.482 **	-0.437 **	0.311 *
	dT_{max}	-0.388 **	0.350 **	-0.765 ***	0.853 ***
	dT_{min}	-0.661 ***	-0.724 ***	-0.188	0.000
	dT_{ran}	0.237	0.752 ***	-0.347 **	0.540 ***
September 2010	dT_{ave}	-0.689 ***	-0.412 **	-0.527 **	0.487 **
	dT_{max}	-0.484 **	-0.183	-0.655 ***	0.662 ***
	dT_{min}	-0.258	-0.421 **	-0.275	0.218
	dT_{ran}	-0.126	0.212	-0.229	0.279
October 2010	dT_{ave}	-0.362 **	-0.288 *	-0.116	0.011
	dT_{max}	-0.196	-0.014	-0.183	0.216
	dT_{min}	-0.433 **	-0.483 **	-0.102	-0.095
	dT_{ran}	0.267	0.444 **	-0.036	0.245
March 2011	dT_{ave}	-0.900 ***	-0.799 ***	-0.391 **	-0.687 ***
	dT_{max}	-0.046	-0.083	-0.305 *	0.042
	dT_{min}	-0.779 ***	-0.870 ***	-0.251	-0.823 ***
	dT_{ran}	0.641 ***	0.695 ***	0.011	0.739 ***
May 2011	dT_{ave}	-0.866 ***	-0.473 **	-0.529 **	0.182
	dT_{max}	-0.459 **	0.114	-0.552 ***	0.564 ***
	dT_{min}	-0.557 ***	-0.717 ***	-0.098	-0.353 **
	dT_{ran}	0.195	0.642 ***	-0.228	0.599 ***

Figure A.1. (A) Graphical scheme of the applied recording arrangements. Land-use types were calculated (proportion of different categories) by digitizing aerial photographs of a 300 m circular area around the study sites. (B) The two different plot sizes of the field measurements: stand structure variables (living trees and deadwood) and tree species composition were recorded in 40 m × 40 m blocks within each selected forest stand, while ground-layer data were collected in 30 m × 30 m plots. Microclimate measurements were carried out in the centre of the blocks (signed by circle). Light measurements were performed in the centre of the 36, 5 m × 5 m subplots within each 30 m × 30 m plot (signed by “x”).