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The effect of light, soil pH and stand heterogeneity on understory species composition of dry oak forests in the North Hungarian Mountains

Running title: Drivers of understory composition in temperate oak forests

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Abstract: Dry oak forests have one of the richest understory vegetation in Europe, but the environmental drivers of this community are still scarcely revealed. In this study, we assessed whether the amount of light, soil pH or stand heterogeneity affect primarily the species composition of this community. We investigaed 332 sampling plots in 40-165 year old managed and abandoned *Quercus cerris* and *Q. petraea* dominated forests in North Hungary. Presence-absence data of herbaceous species and seedlings of woody species were recorded in 28 subplots within each sampling plot. Stand structure, canopy openness and soil pH were also measured in each plot. The relationships between stand characteristics and the species assemblage were explored by redundancy analysis, while the individual responses of species and species groups were studied by generalized linear mixed models.

Multivariate methods and individual species response analyses provided similar results, the amount of light and soil pH were equally important variables (both of them explained 2.8% of species variance), while stand heterogeneity had a bit lower, albeit still significant role in determining understory species composition (1.9% of species variance explained). Seedlings of woody species preferred shaded (half-shaded) conditions, while many herbaceous species were positively related to light. The effect of the three explanatory variables was hard to separate, since they influenced each other as well. Sessile oak seedlings and herbs typical to dry forests, forest edges, grasslands and acidic soil habitats preferred light rich habitats with homogeneous stand structure and low soil pH. Mesic forest herbs and seedlings of other woody species were related to relatively high soil pH, heterogeneous stand structure and closed canopy. These two understory types were clearly separated regading composition.

This study emphasizes the importance of heterogenous light conditions and mosaic, diverse forest structure (presence of homogeneous and heterogeneous forest patches) during forest management for the maintenance of understory biodiversity.

Abbreviations: DBH – Diameter at Breast Height; OPEN – canopy openness; SOIL – soil pH; SHI – Stand Heterogeneity Index.

Nomenclature: Király (2009)

Introduction

The forests of Europe have faced considerable human impact for thousands of years (Johann et al. 2011). According to some estimates, only 0.2% of Central European deciduous forests remained in natural condition, thus species related to these forests became endangered (Hannah et al. 1995). Most of the remnant old-growth stands occur in the boreal and montane zone of Europe (Gilg 2004, Burrascano et al. 2013, Sabatini et al. 2018), there are very few natural reference stands from dry oak forests dominated by Turkey oak (*Quercus cerris*) and sessile oak (*Quercus petraea*) (Saniga et al. 2014). Because of the lack of reference stands in natural condition, we know very little about the natural dynamics and structure of these stands, although dry oak forests are very important for nature conservation and economy as well. Most of the stands that can be used as the best natural reference for this forest type are abandoned managed stands, in which natural processes dominated for decades (Korpel 1995). Regarding vegetation, the understory is the layer that best preserves the original conditions, since this is not the target of forest management; ancient forest species and species with different strategies can be found here, and even the strongly modified landscape preserves the species adapted to the former conditions in small patches.

Forest understory has a key role in the functioning of forest ecosystems (Augusto et al. 2003, Gilliam 2007, Whigham 2004). The high species richness of woodland herbs and seedlings of woody species (henceforth: seedlings) 1) contributes greatly to forest biodiversity (Gilliam 2007, von Oheimb and Hardtle 2009, Whigham 2004, Yu and Sun 2013), 2) plays an important role in nutrient cycling and energy flow (Gazol and Ibánez 2009, Gilliam and Roberts 2003, Gilliam 2007, Thomas et al. 1999, von Oheimb and Hartle 2009), 3) provides habitat for macro- and mesofauna (von Oheimb and Hartle 2009), and 4) as a potential ecological indicator, it may indicate the sustainability of forest management (Collins et al. 1985, von Oheimb and Hartle 2009). In addition, the seedlings give the basis of forest regeneration and determine the future species composition of the forest.

The amount of light reaching the understory is one of the most important environmental variables affecting herbs and seedlings; it determines cover, diversity and species composition of the understory layer (Hill 1979, Kirby 1988, Márialigeti et al. 2016, Slezák and Axmanová 2016, Van Calster et al. 2008). The canopy openness is an excellent predictor of the composition and species richness of understory in temperate forests (Hofmeister et al. 2009, Tinya et al. 2009, von Oheimb and Hardtle 2009). Light is one of the most significant drivers that define the regeneration of several woody species – the establishment, survival and growth of seedlings (Diekmann et al. 1999, Emborg et al. 2000, Pontailler et al. 1997, Tinya et al. 2009). Several authors suggested that the regeneration problems of oaks experienced in many regions may be caused by the closed canopy, the lack of light generated mainly by forest management (McDonald et al. 2008, von Oheimb and Brunet 2007).

Soil characteristics form the other group of abiotic variables that significantly affect the species richness and composition of the understory (Augusto et al. 2003, Bergès et al. 2006, Hofmeister et al. 2009, Roberts and Gilliam 1995). Soil pH is one of the most important characteristics, which is strongly related to nutrient conditions (Brosofske et al. 2001, Brunet et al. 1996, Lalanne et al. 2010, Slezák and Axmanová 2016). In many cases, species composition of herbs is used as indicator of soil acidity (Becker 1988, Brêthes 1989, Ellenberg et al. 1992). Often, species richness of the understory is positively related to soil pH in oak dominated forests (Hofmeister et al. 2009).

In forest ecosystems, stand structure considerably determines the occurrence of herbs and seedlings (Márialigeti et al. 2016, Tobisch and Standovár 2005). In managed forests, the structure and species composition of the overstory can differ significantly from the natural state (Kenderes and Standovár 2003, van Calster et al. 2008). Forest herbs adapted to special habitat conditions such as heterogeneous stand structure (regarding species composition, age and size distribution of trees); large amount of dead wood; presence of large, old trees; root plates (Whigham 2004). Most of these structural elements are missing or underrepresented in European temperate forests due to the current practices of forest management (Bengtsson et al. 2000, Peterken 1996). A heterogeneous stand structure creates environmental heterogeneity, which allows the coexistence of species with different ecological requirements. Species richness of the overstory is also an important stand characteristic, it has significant impact on the cover, richness and composition of the herbaceous layer (Gazol and Ibánez 2009, Márialigeti et al. 2016, van Calster et al. 2008).

Although it is widely accepted that these three stand characteristics are among the most important variables that define the species composition of the understory, we know very little about their relative significance in dry oak forests.

In Central-Europe, there is a long tradition of characterizing species based on their preference to different environmental conditions. These indicator values are widely used for environmental characterization of communities, especially for detecting temporal changes of vegetation (Diekmann 2003, Schaffers and Sykora 2000). These ordinal (or nominal) scale values are based on the field experience of phytosociologists (Borhidi 1995, Chytrý and Tichý 2003, Ellenberg et al. 1992, Landolt 1977, Zólyomi et al. 1967), there are very few direct environmental measurements behind this classification (Szujkó-Lacza and Fekete 1971). In this study, we revealed relationships between species and environmental variables by statistical methods.

The aim of the study was to explore the effect of light, soil pH and structural heterogeneity on the species composition of the understory, as well as on the frequency of individual species. Our hypotheses are as follows:

1) In oak-dominated, light rich forests the amount of light is less limited, hereby soil pH has higher importance in determining species composition;

2) Since the presence of arboreal species is directly affected by stand structure via propagules, stand structure is more important for seedlings, while in case of herbaceous species, where the amount of light and soil pH are more influential, stand structure has only an indirect effect.

Material and methods

Study area

The study was carried out in 40-165 year old Pannonian-Balkanic Turkey oak-sessile oak forests (91M0, Council 1992) in the North Hungarian Mountains (N 47°49’ — 48°10’, E 18°47’ — 20°42’, Fig. 1). The designated sites are managed and abandoned dry oak dominated stands in the Pilis, Börzsöny, Mátra and Bükk mountains, between 250 and 700 m a.s.l., at various aspects. The climate is continental with a mean annual precipitation of 580-700 mm (Mersich et al. 2002) and average monthly temperature of -4.6 — -1.9 ^{0}C in January and 16.6 — 20.1^{0}C in July (Mersich et al. 2002). The bedrock is mainly volcanic (andesite and andesite tufa), limestone, sandstone, shale and loess. The main soil types are leptosols and cambisols (Krasilnikov et al. 2009), with various soil depth. Besides deforestation, coppicing was the general management in oak dominated forests from the medieval times to the 19th century, completed with grazing, masting and firewood collecting (Járási 1997, Johann et al. 2011, Magyar 1993, Szabó 2005). From the 19th century these coppices and forested meadows were converted to high forests, by applying a uniform shelterwood silvicultural system with an 80-90 year rotation period (Matthews 1991). In the studied stands, dominant tree species are sessile oak (*Quercus petraea)* and Turkey oak (*Q. cerris)*, the most important subordinate tree species are *Acer campestre*, *Fraxinus excelsior* and *Sorbus torminalis*, while the main shrub species are *Cornus mas*, *Crataegus monogyna*, *Ligustrum vulgare*, *Prunus spinosa* and *Rosa canina*.

Data collection

In this study, we used 332 sampling plots, representing 98 forest stands, as selected from the Database of Hungarian Forest Stands (NÉBIH 2018) using stratified random sampling. Dry oak forest stands were chosen based on the database, where the combined cover of Turkey and sessile oak was at least 80% and the overstory was older than 40 yr. After reconnaissance, we selected 98 stands by the following criteria: young (40-80 yr), mature (80-120 yr) and abandoned (older than 120 yr) age categories and the three mountain ranges – Pilis and Börzsöny, Mátra, Bükk – should be represented with similar stand number (Appendix A). This balanced design was not possible for abandoned stands because of their limited number in most sites, while they were overrepresented in the Bükk Mts. Sampling plots were assigned randomly within the forest stands, situated at least 40 m from roads and from each other. In most cases the abandoned forest stands had an aggregated spatial distribution. Because of their rarity, we had to assign 2-35 sampling plots in each abandoned stand, depending on its size, while in managed forests we established 1-4 plots per stand.

Sample plots were represented by their center points. The measured variables were sampled by different methods (line, relascope, circular plot based sampling), however, all of them were referenced to the plot center.

The vegetation survey was carried out once, between 2009 and 2012. The understory was studied from June to August applying systematic sampling design. At each circular sampling plot (r=8.92 m, 250 m^2) we assigned 28 subplots 0.5 m^2 in size – along three concentric circles (r = 2, 5 and 8 m respectively) – where the species list of herbs (non-arboreal vascular plants) and seedlings (arboreal species under 50 cm height) was recorded (Fig. 2), thereby we obtained local frequency data at the plot level ranging from 0 to 28 for all species.

In order to describe the main biotic and abiotic characteristics of the forest stands, we used three variables: soil pH, canopy openness and stand heterogeneity (McElhinny et al. 2006, Sabatini et al. 2015). In case of stand structure, we used a combined sampling method: trees between 5-25 cm diameter at breast high (DBH) were surveyed in the plot, while in the case of larger trees a point relascope sampling (Bitterlich sampling) with basal area factor 2 was used to identify trees added to the sample (Avery and Burkhart 2001, Bitterlich 1948, Kramer and Akça 2008, Kuusela 1966). In case of logs, we used line-intercept method with 16 m long lines starting from the center to 0^o, 120^o and 240^o directions (Ståhl et al. 2001, van Wagner

1968, Warren and Olsen 1964). For standing trees (including standing dead trees) we recorded species identity, DBH and crown position (dominant, codominant, intermediate, suppressed). For lying dead trees diameter and decay stage (using 5 categories) were recorded at the intersection of the sampling lines (Maser et al. 1979, Spetich et al. 1999). At each sampling plot, we measured the height of 1-3 dominant and 1-3 suppressed trees using Haglöf Vertex III height and distance meter (Haglöf Sweden AB 2005) and based on the measured data we estimated the height of all trees. The height of other individuals was either directly measured or estimated on the basis of tree crown positions. We measured the canopy openness by spherical densiometer at four points, 5.6 m from the center of the plot to north, east, south and west, facing to the cardinal directions (Lemmon 1956, Fig. 2). The individual measurements within a plot were averaged.

Soil samples were taken at three random points within each plot, where we excavated 500 cm^3 soil from 5 cm x 10 cm area, 10 cm depth. These individual samples were mixed and analyzed together. Soil pH was measured potentiometrically in the supernatant suspension. 10 g air-dried and sieved (< 2 mm) soil sample was weighted into glass beaker and then 25 cm^3 boiled distilled water was added. We stirred the suspension for one minute, let it stand for 12 hours, and then measured the pH of the suspension with the pH meter (Bellér 1997).

Data analysis

Stand Heterogeneity Index (SHI) was created using seven stand characteristics (living volume, number of large trees, DBH diversity, dead wood decay diversity, tree species richness, standing dead wood volume, total dead wood volume (Appendix B), following Sabatini et al. (2015). The volume of individual trees was calculated by specific equations from DBH and tree height (Sopp and Kolozs 2000). Stand structure variables of each plot were generated by the combination of the data gathered with the help of circular plot based (cp) and relascope (r) methods. All data were standardized to one hectare area. Stem number (N), basal-area (G) and volume of trees (V) were calculated according to the following formulae:

$N(cp)=n/A*10\,000$

$N(r)= \sum k/g_j$

$G(cp)= \sum N_i*(DBH_i/2)^2*\Pi$

$G(r)=mk$

$V(cp) = \sum N_i V_i$

$V(r) = \sum N_j V_j$

(n – stem number sampled by circular plot based method; m – stem number sampled by relascope method; A – area of the plot (250 m^2); k – basal area factor; g – basal-area of an individual tree; i – individual tree sampled by circular plot based method; j – individual tree sampled by relascope method).

In case of logs, we used van Wagner's (1968) formula: $V=\pi^2 * \sum d^2/8L$ (V - volume per unit area, d - diameter at intersection, L -length of sample line). We applied the Gini-Simpson diversity (evenness) index using 5 cm size categories for DBH diversity, and the five decay stage categories for dead wood decay stage diversity. Species richness means, as usual, the number of tree species in the sampling plot.

In case of four variables – living volume, number of large living trees, DBH diversity and dead wood diversity – we used unprocessed data, in case of tree species richness and standing dead wood volume we used logarithmic transformation, and square root transformation for total dead wood volume. During the calculation of the SHI the original values of the seven variables were converted to ranks between 0 and 10. In the first step, we determined the midpoints of quartiles (12.5%, 37.5%, 62.5%, 87.5%) of stand variables and assigned them the values of 2.5, 5, 7.5 and 10. Linear regression was fitted through quartiles and new scores were assigned to the observations using the regression equation. In order to avoid the distorting effect of outliers, the maximum assigned value was 10, thereby we got variables with even distribution between 0-10. (Appendix C). The scores of the seven variables were added, the total was divided by 70 and expressed as percentage.

Herbaceous species and seedlings were analyzed together, rare species – that occurred in less than 10% of sample plots – were eliminated from the analyses. The effect of the three variables (canopy openness – OPEN, soil pH – SOIL, stand heterogeneity index – SHI, Appendix D) on the understory species composition was explored by redundancy analysis (RDA), using mountain ranges as covariables (Ter Braak and Smilauer 2002). The pairwise correlations between the three explanatory variables were -0.23 for OPEN – SOIL, -0.12 for OPEN – SHI and 0.35 for SHI – SOIL. The explanatory variables were tested in separate RDA models, using a single canonical axis, which was tested by F statistics via Monte Carlo simulation (Borcard et al. 2011). The gradient length (species turnover) was determined by detrended correspondence analysis, and principal component analysis was used to compare the explained variance of unconstrained axes with the canonical axes of RDA (Borcard et al. 2011). Variation partitioning was used to reveal the individual and shared variance of OPEN, SOIL and SHI. The response (local frequency values) of individual species to the three explanatory variables was studied by general linear mixed regression models (GLMM, Zuur et al. 2009). All three explanatory variables were analyzed separately, both their linear and quadratic components were tested, while mountain ranges were used as a random factor in the models. The normality and the constancy of the residual error variance were checked by diagnostic plots.

Abbreviations of species names comprise the first four letters of the genus and the first three letters of the species names (App. E). Computations were carried out with R 3.1.2 (R Core Team 2017) using packages lattice (Sarkar 2008), permute (Simpson 2016) vegan (Oksanen et al. 2016) and nlme (Pinheiro et al. 2011).

Results

Response of the community

The gradient length of detrended correspondence analysis was 3.06 standard deviation unit. The explained variances of the first and second axes of the principal component analysis were 16.7% and 8.8%, respectively. In the redundancy analysis OPEN explained 2.8% ($F = 10.6$, $p < 0.001$), SOIL also 2.8% ($F = 10.5$, $p < 0.001$) and SHI 1.9% ($F = 7.3$, $p < 0.001$) of the species variance. In the variation partitioning the explained variance was 1.6% for OPEN, 1.8% for SOIL, 1.7% for SHI, while the shared variance was 2.2% (OPEN – SOIL: 0.6%, SOIL – SHI: 1.3%, SHI – OPEN 0.0%, OPEN – SOIL – SHI: 0.3%).

Almost the same species were related strongly to all the three variables, on the basis of their combined responses two groups of species can be recognized (Fig. 3). Species of the first one were related negatively with canopy openness and positively with soil pH and stand heterogeneity (*e.g., Acer campestre, Fraxinus excelsior, Melica uniflora, Galium odoratum, Viola odorata, Viola reichenbachiana*). The other group contains species positively related to canopy openness and negatively with soil pH and stand heterogeneity (e.g., *Hieracium racemosum, Luzula luzuloides, Poa nemoralis, Quercus petraea, Veronica chamaedrys, Vicia cassubica*).

Response of seedling species

Eleven of the 19 studied arboreal species showed significant relationship with canopy openness, 11 also with soil pH and 6 with stand heterogeneity (Table 1). Only *Rosa canina* seedlings preferred open habitats (Fig. 4), other light demanding arboreal species (*Q. petraea,* Fig. 4*; L. vulgare*) showed just unimodal response to canopy openness. Seedlings of *F. excelsior* (one of the most important subordinate tree species, Fig. 4) and three additional arboreal species preferred stands with more closed canopy. Concerning the response to soil pH, *Q. petraea* was the only arboreal species that occurred on more acidic soils (Fig. 5), while the two most frequent subordinate tree species (*A. campestre* and *F. excelsior,* Fig. 5) and most of the shrub species correlated positively with soil pH. *Acer platanoides, Cerasus avium, P. spinosa and R. canina* (Fig. 5) showed unimodal response to soil acidity. In reference to stand structural heterogeneity, only *Q. petraea* (Fig. 6) seedlings occurred more frequently in structurally homogeneous stands. Seedlings of *A. campestre, A. platanoides,* and *R. canina* (Fig. 6) preferred heterogeneous, while *F. excelsior* (Fig. 6) and *P. spinosa* moderately heterogeneous stands. None of the explanatory variables had significant effect on the occurrence of *Acer tataricum, Carpinus betulus, Fraxinus ornus*, *Malus sylvestris*, *Pyrus pyraster* and *Quercus cerris* seedlings.

Response of herbaceous species

We studied the response of 79 herbaceous species to the three variables (Table 2). Canopy openness affected significantly the occurrence of 49 of them, for 29 species openness was the most important explanatory variable. More than the half of these species occurred at open plots, 35% showed unimodal response to openness (*Poa nemoralis, Hieracium lachenalii*, Fig. 4) and only six of them preferred stands with closed canopy. Soil pH was a significant site characteristic for 39 species, and the most influential for 17 of them. The number of species belonging to the three response types was more or less balanced (Fig. 5). The occurrence of 31 species was significantly influenced by SHI, in case of 15 herbs SHI was the primary variable. More than 50% of these species preferred habitats with heterogeneous stand structure (like *Melica uniflora* Fig. 6), one third showed negative response (*Hieracium lachenalii, Poa* *nemoralis*, Fig. 6) while only 5 species belonged to the unimodal group. In case of 18 herbaceous species, none of the explanatory variables had significant effect.

Discussion

Importance of the three variables

Our first hypothesis – that soil pH is more important stand characteristic in determining species composition than canopy openness in light rich oak dominated forests – proved to be false: the two predictors had similar importance. Based on redundancy analysis, canopy openness and soil pH are more influential in determining the species composition of the understory, than stand heterogeneity. The amount of light and soil acidity have direct impact on the community, several species reach their tolerance limits along these variables. In turn, stand heterogeneity exerts indirect effects through the abiotic variables (light, soil pH, litter characteristics, microclimate, etc.), therefore this weaker relationship is understandable. According to the species level models, among the three studied stand characteristics the amount of light was the most determinant variable, followed by soil pH, and SHI had the lowest importance (49 species showed significant relationship with canopy openness, 39 with soil pH and 31 with stand heterogeneity).

There are few studies where the importance of soil pH, light and stand structure is comparable in determining species composition. The results of previous studies in mesic forests are various. Bataineh et al. (2013) found that the species composition of the regeneration stage was determined mainly by biotic factors such as the characteristics of the overstory and herb layer. Based on Márialigeti et al. (2016), the composition of the understory was influenced mainly by light conditions and tree species richness, while Tyler (1989) found soil pH as the most important variable in determining understory species composition. In case of dryer forests, the results are more uniform; soil pH seems to be the most significant stand characteristic that shapes species composition of herbs and seedlings. Brunet et al. (1997) attributed the primary importance of soil pH against the changed light conditions to forest management in dry oak forests in Sweden. Soil pH was three times more important in affecting species composition than canopy openness in Slovakian dry oak forests (Slezák and Axmanová 2016). At the local scale in a Hungarian oak dominated forest, humus content was the most determinant driver for the cover of many herbs (Szujkó-Lacza and Fekete 1971). Although the few studies of dry oak forests confirm our hypothesis, according to our results the role of light is considerable in dry forests as well. Moreover, while in mesic forests shade-tolerant herbs dominate the understory, in dry oak forests, species with various light requirements can settle and survive. In more open patches herb species typical to forest edges and grasslands occur, while in closed parts shade-tolerant species can be found as well. Thus, it seems reasonable that in addition to soil pH, canopy openness also has a significant effect on species composition.

Impact of the variables on seedling species

The second hypothesis suggesting that stand heterogeneity is more important for seedling species than for herbs has not been proven either. Stand heterogeneity was the least important among the three variables.

According to our results, seedling species – almost without exception – avoided open areas with acidic soil. Although, in general, the species richness of the understory increases with increasing light availability (Hofmeister et al. 2009, Tinya et al. 2009) and soil pH (Hofmeister et al. 2009), this phenomenon changes if seedling and herbaceous species are studied separately. Brosofske et al. (2001), Hofmeister et al. (2009) and Naveh and Whittaker (1979) published similar results: higher amounts of arboreal seedlings were found in forest stands with closed canopy. Von Oheimb and Hardtle (2009) revealed that forest management had no impact on seedling species diversity, so stand heterogeneity – in this regard – was not essential. We obtained different results: almost half of the seedlings reacted to SHI, therefore in case of some species, it can be considered as an important variable.

Sessile oak seedlings showed individual response to the studied variables, which was different from other seedlings. This species preferred moderately open areas with homogeneous stand structure and acidic soil. The relatively high light requirement needed for oak regeneration is widely known (McDonald et al. 2008, Tinya et al. 2009, von Oheimb and Brunet 2007). Several authors note that oak forests were more open habitats earlier, and they suggest that the reduced amount of light reaching the understory can cause the experienced oak regeneration problems (McDonald et al. 2008, von Oheimb and Brunet 2007). Arno et al. (2012) also report that sessile oak prefers acidic soil. Ritter et al. (2003) emphasize that litter of oak species acidifies the soil during decomposition, while De Schrijver et al. (2011) observed that soil pH of oak forests is lower than in stands dominated by several other tree species. In addition, it is conceivable that low soil pH decreases competition against seedlings of other species. The preference of homogeneous stands can be partly explained by soil pH: sessile oak prefers acidic soil, while other arboreal species avoid these stands, therefore *Q. petraea* seedlings occur in structurally more homogeneous forests. On the other hand, propagule source is very important for *Q. petraea* regeneration, it can produce notable amount of seedlings only in sessile oak dominated stands (Ádám et al. 2013, McDonald et al. 2008).

Less information is available about the habitat requirements of *Q. cerris.* In our study, none of the variables had significant effect on the occurrence of Turkey oak seedlings. Compared to sessile oak, the regeneration of Turkey oak is less problematic in Hungary, because of its more frequent seed production and wider tolerance of the seedlings (Danszky 1972).

The most important subordinate tree species – *A. campestre* and *F. excelsior* – preferred more neutral soil pH, and moderately closed, heterogeneous stands. Some authors also described similar behavior of these species (Graae and Heskjær 1997, Lalanne et al. 2010, Naqinezhad et al. 2013). The shade tolerance of *F. ecxelsior* was supported by the study of von Oheimb and Brunet (2007) as well. Both species preferred at least moderately heterogeneous stands, which is in accordance with our previous study (Ádám et al. 2013). According to our former results the admixing ratio was the most important stand characteristic for these species, that refers to the significance of the proportion of *F. excelsior* and *A. campestre* in the overstory, in other words, the importance of propagule source (Ádám et al. 2013). Von Oheimb and Hardtle (2009) noted the preference of unmanaged forests in case of *A. campestre*, which is also in accordance with stand heterogeneity.

In case of shrub species, some general behavioral patterns can be observed. Every species avoided acidic soil, the two forest edge species (*P. spinosa, R. canina*) showed unimodal response to soil pH, whereas the typical forest species (*C. mas, C. laevigata, E. verrucosus, L. vulgare*) occurred in stands with high soil pH, which is more or less in accordance with published results (Brunet et al. 1996, Lalanne et al. 2010, Naqinezhad et al. 2013, Slezák and Axmanová 2016). Canopy openness also had significant impact on almost all shrub species. In general, they preferred closed stands, except for *R. canina*; even species typical of open habitats and forest edges showed unimodal response. Although less information is available about these species, the negative response of *C. monogyna* and *L. vulgare* to canopy openness was observed by Brunet et al. (1996), Slezák and Axmanová (2016) and Tinya et al. (2009), while the lack of response of *P. spinosa* seedlings was revealed by Tinya et al. (2009) as well. Márialigeti et al. (2016) also found positive relationship with light in case of *R. canina* seedlings. Stand heterogeneity had significant effect on the fewest shrub species, all of which avoided homogeneous forest stands.

Impact of the variables on herbaceous species

According to the second hypothesis, in case of herbaceous species canopy openness and soil pH were more important than stand heterogeneity. Interestingly, SHI plays a more significant role for herbs than seedlings.

Herbaceous species showed various responses to the studied stand characteristics, however, some response combinations were completely missing. None of the studied 79 herb species preferred acidic soil with heterogeneous stand structure or with closed canopy, and they avoided homogeneous stands with relatively neutral soil. It is conceivable that these habitat types do not exist under natural circumstances of this forest type. Most of the arboreal species avoid stands with low soil pH, thus subordinate tree species and the second canopy layer are missing; the soil is poor in nutrients (Ponge et al. 1997). Accordingly, the growth of trees is slower, consequently even old forests in natural condition have relatively homogeneous stand structure. In contrast, several arboreal species prefer high soil pH, trees and shrubs grow faster; in natural state these forests have therefore multi-layered overstory comprised of several species and trees of various size. In these forests, homogeneous structure is created by forest management. Furthermore, the almost complete lack of herbs preferring closed canopy is conspicuous, it can be partly caused by stronger competition with seedlings in these shaded stands. Despite their small density, these species show a uniform behavoiur: *Buglossoides purpurocaerulea*, *Campanula rapunculoides*, *Clematis vitalba*, *Melica uniflora* and *Scutellaria altissima* also preferred closed, heterogeneous stands with higher soil pH. In case of these species, closely unimodal light response would be expected (except *Melica uniflora*), while their soil reaction values are in accordance with our results.

Considering the half-shaded areas, in homogeneous stands with acidic soil and sessile oak dominance in the overstory the typical herbaceous species are *Carex digitata*, *Luzula luzuloides*, *Poa nemoralis* and *Veronica chamaedrys.* Their light requirement indicator values are more or less in accordance with our measurement results (although *Carex digitata* and

Luzula luzuloides are known as shade-tolerant species). Soil reaction indicator values are less consistent with our data; according to the indicator values *Poa nemoralis* is neutral, while *Veronica chamaedrys* is a basifrequent species.

The majority of the species showed positive relationship to light. Herbs typical to open stands with acidic soil are *Cardaminopsis arenosa, Genista tinctoria, Hypericum perforatum, Poa angustifolia*, *Silene nutans, Trifolium medium* and *Vicia cassubica*. According to the indicator values, it was expected that *Cardaminopsis arenosa*, *Silene nutans*, *Trifolium medium* and *Vicia cassubica show* a unimodal response, but all of them preferred these light rich areas. Except *Genista tinctoria*, all these species are known as neutral regarding soil reaction, however, based on our models they are rather acidofrequent species. *Clinopodium vulgare, Dactylis polygama, Fragaria vesca, Tanacetum corymbosum* and *Vincetoxicum hirundinaria* preferred moderately high soil pH and opened canopy. The soil reaction values of this group are mostly in accordance with our measurements (*Clinopodium vulgare* and *Vincetoxicum hirundinaria* are known as rather basifrequent species). All members of this group are half shadow herbs based on their light requirement values. In contrast, they preferred light rich stands.

As to the assessment of light indicator values, it should be noted that our study was carried out in shaded forest habitats. Therefore, it is understandable that for the light demanding species canopy openness was the most limiting factor and half-shadow species often showed strong light preference. Since the estimation of soil preference of herbs is quite difficult based on field observations, it is not surprising that our result differed from the soil reaction indicator values in several cases.

Two types of dry oak forest understories

Although the community-level responses of species were similar to the results of individual models, the latter can help to get a more complete picture of oak forest understory organization. According to our results based on the species composition of the understory, two types of dry oak forests can be distinguished. The basis of the separation is soil pH, which largely determines stand heterogeneity, and through this, the amount of light reaching the understory. In stands with low soil pH, *Q. petraea* dominates the overstory, shrub and subordinate tree species are almost completely absent, the second canopy layer is missing and the shrub layer is undeveloped. On acidic and nutrient poor soil, the trees stand farther apart and grow slowly. In these stands, more light reaches the understory due to the homogeneous stand structure, the one-layered overstory and the sparsely standing trees. These conditions are favorable for sessile oak seedlings and herb species of dry, open, acidic forests. Most of the shrub and tree species prefer more neutral soil conditions. Under natural circumstances, these stands are characterized by dense shrub layer, multi-layered overstory and faster growth of the trees, which result in heterogeneous stand structure in terms of species composition, stem size and vertical layers as well. Due to the densely standing trees and the multiple canopy layer, less light reaches the understory which is dominated by seedlings and mesic forest herbs. Under natural conditions, fine scaled disturbance creates small canopy gaps. In these temporarily opened patches, light-demanding species preferring neutral soil conditions can establish. Naturally, the two types of dry oak forests are not clearly separated from each other; several transitional forms occur between the two extreme cases.

Conclusions

Multivariate analysis revealed that the amount of light and soil acidity are equally important in determining the species composition in Turkey oak – sessile oak forests. The individual models gave a more detailed and complex picture of the species' behavior and the organization of dry oak forests. In the case of species models, canopy openness was the most important stand characteristic, while soil pH was only the second. On the basis of both analyses, SHI has a bit lower, but still significant impact on the understory. However, the impact of the three stand characteristics cannot be separated; they affect each other and form the structure and species composition of the forest together. On acidic soil homogeneous, light rich habitat develops, where species typical of dry forests, forest edges, grasslands and acidic soil habitats can survive and establish. Most of the seedling species and mesic forest herbs prefer neutral soil, heterogeneous stand structure and closed canopy. In order to preserve the dry oak forest communities, light rich, sessile oak dominated stands with sparsely standing trees and heterogeneous, species-rich patches with developed shrub layer have to be created and maintained.

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Tables

Table 1. Interactions between explanatory variables and tree seedlings based on linear models. Linear positive ("+"), linear negative ("-") and quadratic unimodal ("^2") responses are separated: Open – canopy openness; Soil – soil pH; SHI – Stand Heterogeneity Index. Abbreviations with bold and italic font show the most important variable for the species.

Open "+"	Open "-"	Open "^2"	Soil "+"	Soil "-"	Soil "^2"	SHI "+"	SHI "-"	SHI "^2"	NS
Rosacan	Cornmas	Acercam	***Acercam***	Querpet	***Acerpla***	Acercam	Querpet	***Fraxexc***	Acertat
	Cratmon	Acerpla	***Cornmas***		***Ceraavi***	Acerpla		Prunspi	Carpbet
	Euonver	***Cratlae***	Cratlae		***Prunspi***	***Rosacan***			Fraxorn
	Fraxexc	***Liguvul***	Euonver		Rosacan				Malusyl
		Querpet	Fraxexc						Pyrupyr
		Sorbtor	Liguvul						Quercer

Table 2. Interactions between explanatory variables and herbaceous species based on linear models. Linear positive ("+"), linear negative ("-") and quadratic unimodal ("^2") responses are separated: Open – canopy openness; Soil – soil pH; SHI – Stand Heterogeneity Index. Abbreviations with bold and italic font show the most important variable for the species.

Open "+"	Open "-"	Open "^2"	Soil "+"	Soil "-"	Soil "^2"	SHI "+"	SHI "-"	SHI "^2"	NS
Ajugrep	Buglpur	***Allipet***	Buglpur	Campper	Clinvul	Allipet	Caredig	Campper	Betooff
Astrgly	Camprap	Bromram	***Camprap***	Cardare	***Dactpol***	***Anthram***	Caremic	Carepai	Brachpin
Brachsyl	***Caremic***	***Campper***	Chaetem	Caredig	***Fragves***	***Bromram***	Genitin	***Luzucam***	Caremon
Cardare	Clemvit	***Caredig***	Clemvit	***Galisch***	Galiodo	***Buglpur***	Hierlac	***Poaang***	Festrup
Carepai	Meliuni	***Crucgla***	***Convmaj***	Genitin	***Hierlac***	Camprap	Hierrac	***Vicicas***	Galiapa
Clinvul	Scutalt	***Cruclae***	***Geumurb***	***Hiermur***	***Hierrac***	***Chaetem***	***Hylotel***		Glechhir
Dactpol		***Festhet***	Meliuni	Hypeper	***Lychvis***	***Clemvit***	Luzuluz		Lathver
Euphcyp		***Galimol***	***Origvul***	Luzucam	Tanacor	***Digigra***	Lychvis		Melimel
Falldum		***Galiodo***	***Primver***	***Luzuluz***	***Verooff***	Galiodo	Poanem		Moehtri
Fragves		Hierlac	Scutalt	Poaang	Vinchir	Geumurb	Verocha		Mycemur
Genitin		Hierrac	Secuvar	Poanem		***Lathnig***			Polyodo
Hylotel		Luzuluz	***Torijap***	***Silenut***		***Meliuni***			Pulmmol
Hypeper		***Poanem***	***Violodo***	Trifmed		***Scutalt***			Rubus
Lapscom		***Silevul***	Violrei	Verocha		***Vinchir***			Sanieur
Origvul		***Verocha***		Vicicas		Violodo			Stelhol
Poaang		Violodo				***Violrei***			Symptub
Secuvar		Violrei							Vicitet
Silenut									Violhir
Tanacor									
Teuccha									
Trifalp									
Trifmed									
Verbcha									
Verooff									
Vicicas									
Vinchir									

Figures

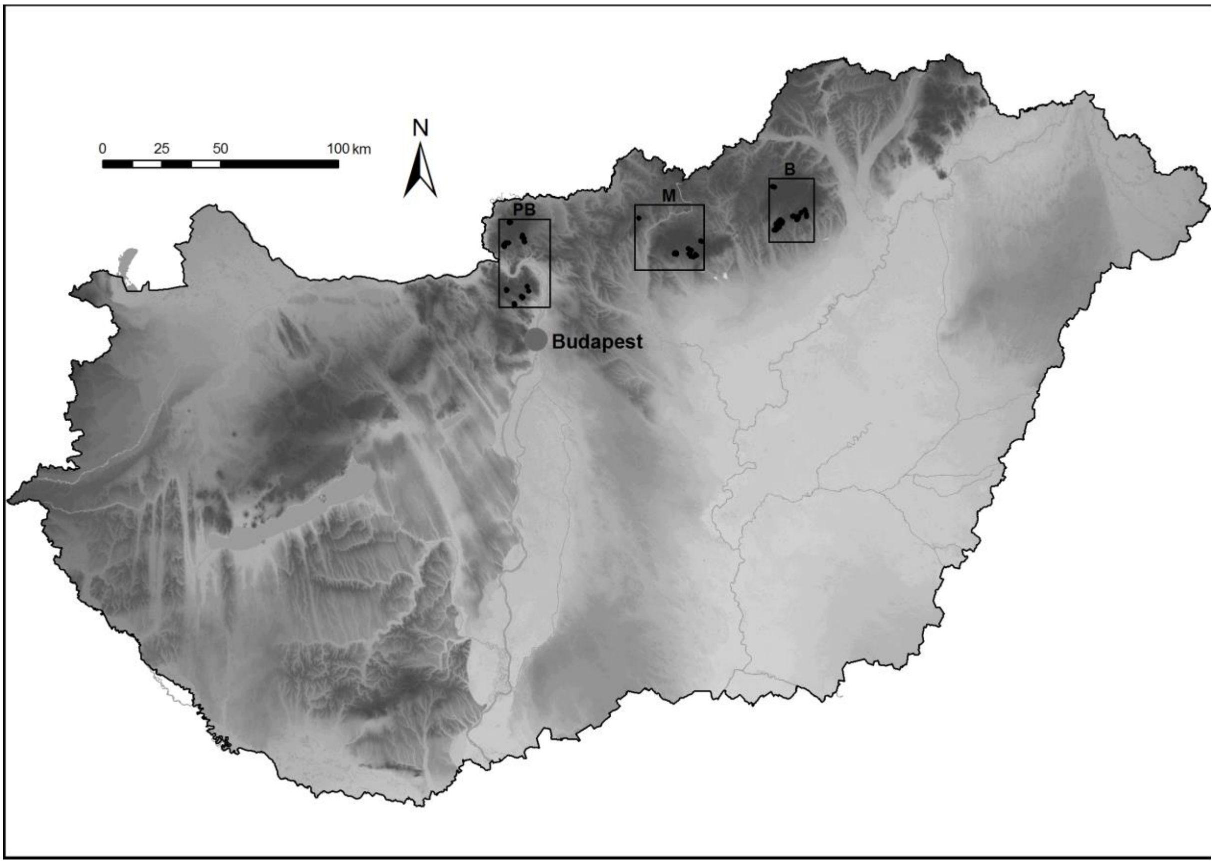

Figure 1. Occurrences of the sample plots in Hungary. The studied mountain ranges are Pilis-Börzsöny (PB), Mátra (M) and Bükk (B).

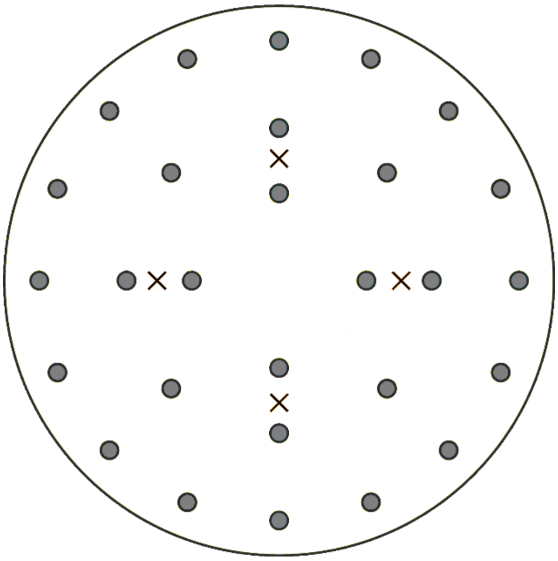

Figure 2: Sampling arrangement. The whole plot (r = 8.92 m, 250 m^2) were used for overstory, the 28 subplots (r = 0.4 m, grey circles) for understory, the four x symbols show positions of canopy openness measurements.

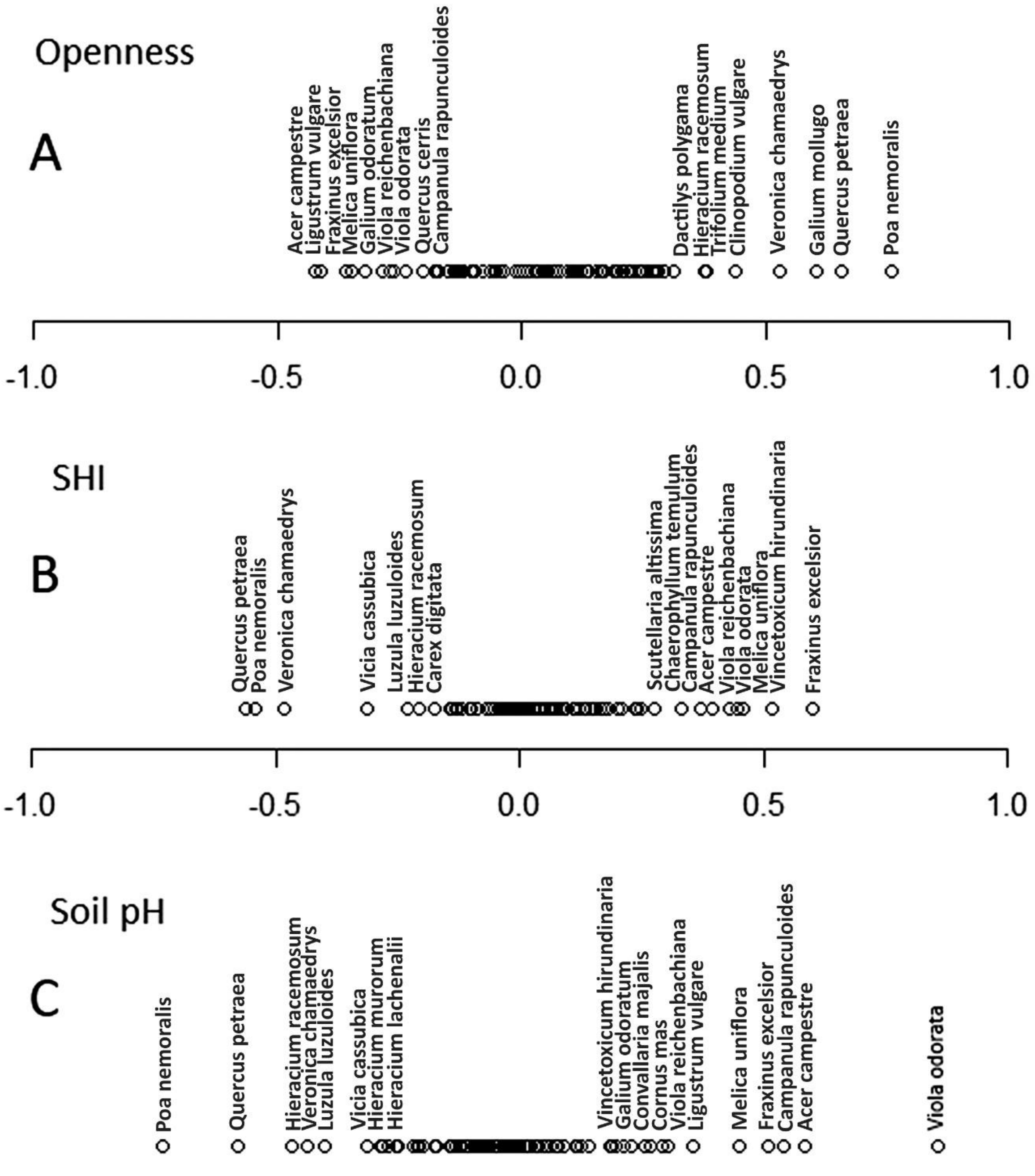

Figure 3. The scores of seedling and herbaceous species on the Canopy openness (A), Stand Heterogeneity Index (B) and Soil pH (C) canonical RDA axes (Appendix F). In redundancy analysis, the variance covered by Canopy openness and soil pH was 2.8 %, and 1.9 % in case of Stand Heterogeneity Index. Species occurring at the two ends of the gradient are listed.

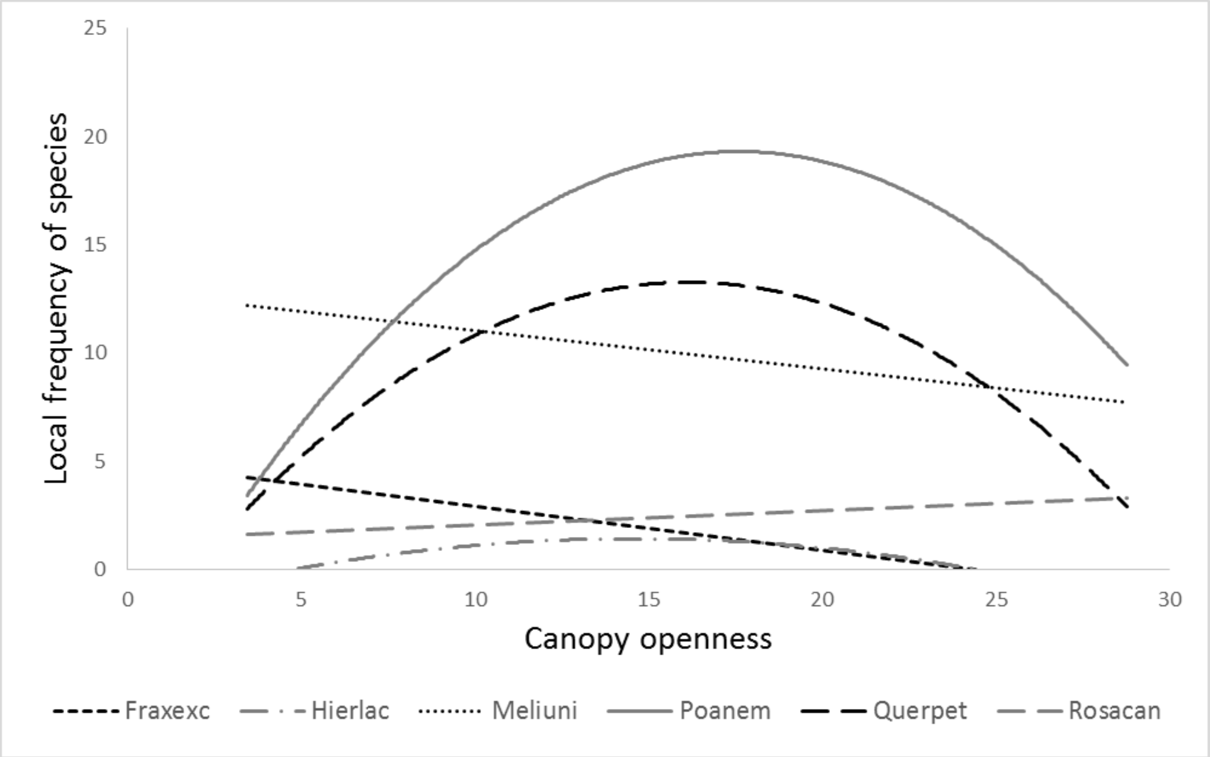

Figure 4. The local frequency of some species depending on the canopy openness (astrgly – *Astragalus glycyphyllos*, clinvul – *Clinopodium vulgare*, fraxexc – *Fraxinus excelsior*, hierlac – *Hieracium lachenalii*, poanem – *Poa nemoralis*, querpet – *Quercus petraea*)

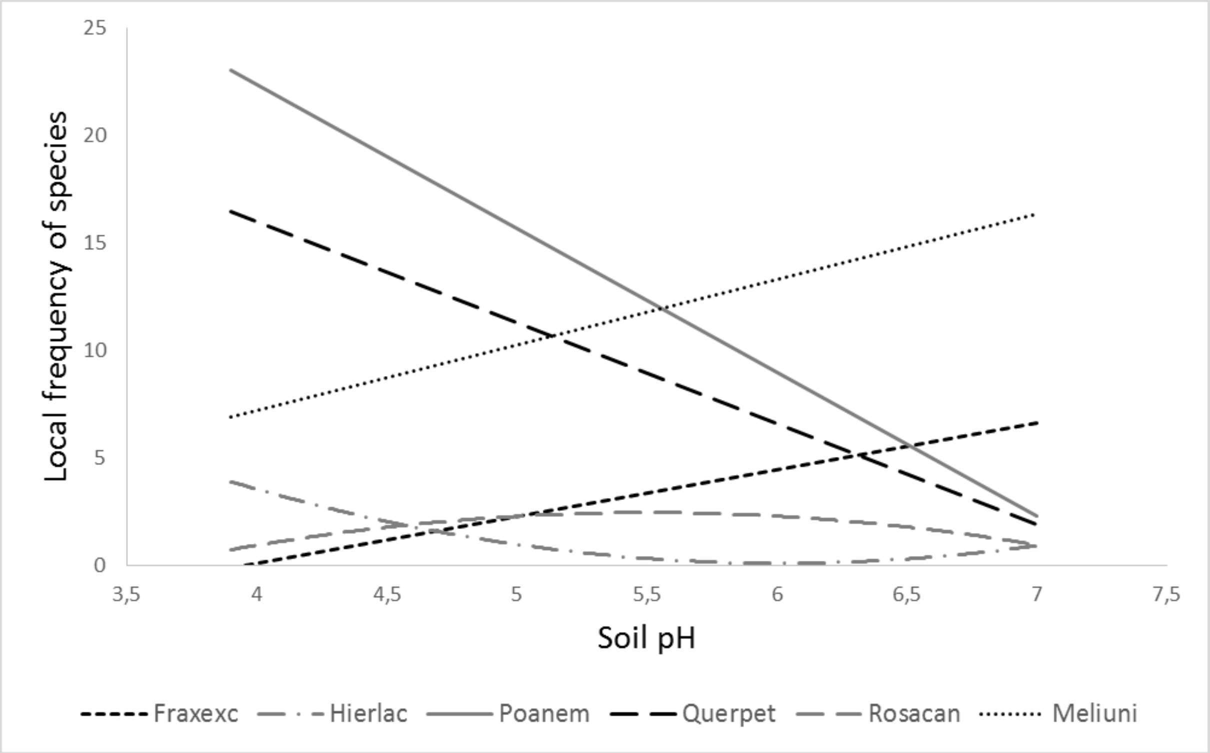

Figure 5. The local frequency of some species depending on the soil pH (astrgly – *Astragalus glycyphyllos*, clinvul – *Clinopodium vulgare*, fraxexc – *Fraxinus excelsior*, hierlac – *Hieracium lachenalii*, poanem – *Poa nemoralis*, querpet – *Quercus petraea*)

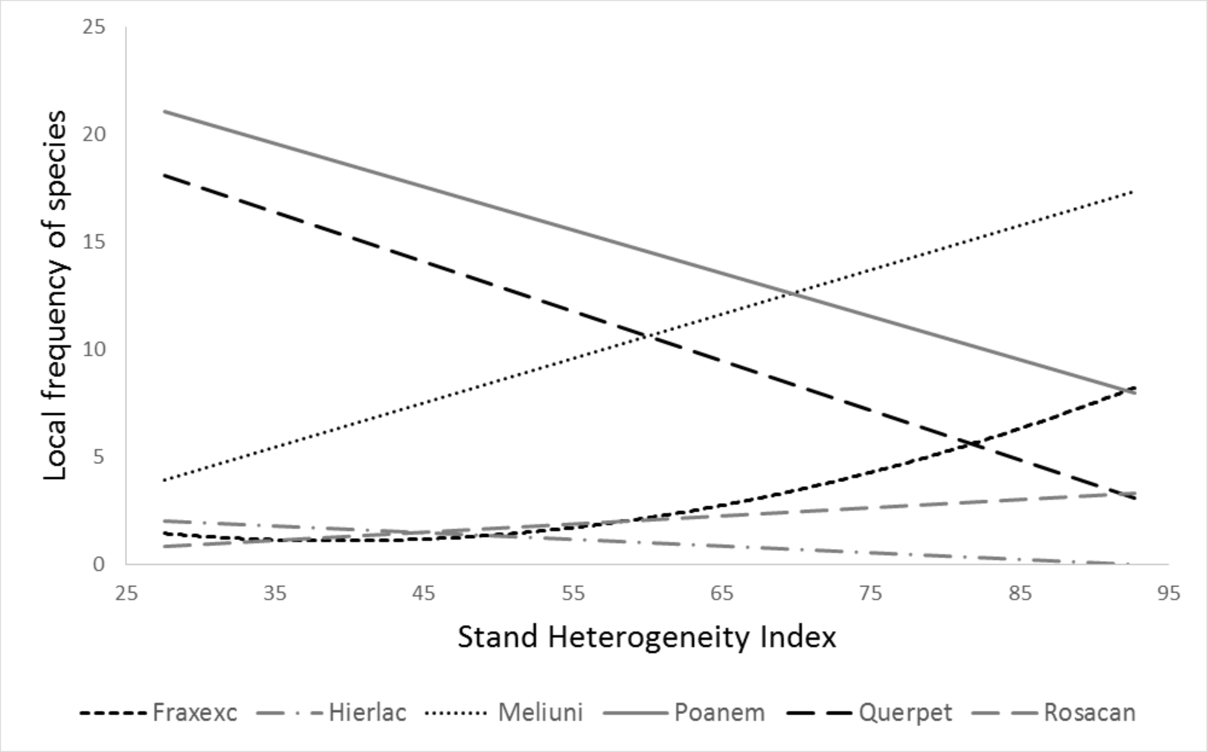

Figure 6. The local frequency of some species depending on Stand Heterogeneity Index (astrgly – Astragalus glycyphyllos, clinvul – Clinopodium vulgare, fraxexc – Fraxinus excelsior, hierlac – Hieracium lachenalii, poanem – Poa nemoralis, querpet – Quercus petraea)

Appendices

Table S1. Plot numbers per age classes and mountain ranges.

Age Classes	**Pilis-Börzsöny**	**Mátra**	**Bükk**
40-80	30	20	43
80-120	23	18	38
120-	27	15	118

Table S2. Values of the stand structural variables used for the Stand Heterogeneity Index.

Variable	**Unit**	**Min**	**Average**	**Max**
Living volume	m^3/ha	125	298	587
Number of large living trees (DBH > 40 cm)	stem/ha	0	3.6	17
DBH diversity (Gini-Simpson index)	-	0.32	0.73	0.88
Dead wood decay stage diversity (Gini-Simpson index)	-	0	0.22	0.74
Tree species richness	-	1	3.3	11
Standing dead wood volume	m^3/ha	0	10.0	130.6
Total deadwood volume	m^3/ha	0	27.6	380.2

Table S3. Linear regression equations of the variables of Stand Heterogeneity Index for converting original values (X) to ranks (Score) between 0 and 10. R^2 means the coefficient of determination of the regression models.

Variable	**Regression equation**	**R^2**
Living volume	Score = -4.850 + 0.038*X	0.994
Number of large living trees (DBH > 40 cm)	Score = 3.571 + 0.765*X	0.918
DBH diversity (Gini-Simpson index)	Score = -18.760 + 33.760*X	0.990
Dead wood decay stage diversity (Gini-Simpson index)	Score = 3.715 + 12.326*X	0.898
Tree species richness (log)	Score = 2.414 + 9.860*log(X)	0.990
Standing deadwood volume (log)	Score = 3.831 + 4.421*log(X)	0.895
Total deadwood volume (sqrt)	Score = 1.641 + 1.116*sqrt(X)	0.992

Table S4. Values of the used environmental variables.

Abbreviation	**Description of the variable**	**Min**	**Average**	**Max**
Open	Average canopy openness (%)	3.5	10.8	27.8
Soil	pH of the upper 10 cm of soil	3.9	5.2	7.0
SHI	Stand Heterogeneity Index (%)	27.6	61.5	92.7

Table S5. List of the species, their abbreviations, frequency values and response types. Open: canopy openness, Soil: soil pH, SHI: Stand Heterogeneity Index, 2: quadratic unimodal response, P: positive linear response, N: negative linear response.

Abbreviation	**Binomial name**	**Frequency (%)**	**Open**	**Soil pH**	**SHI**
Acercam	Acer campestre	70.2	2	P	P
Acerpla	Acer platanoides	15.4	2	2	P
Acertat	Acer tataricum	11.1			
Ajugrep	Ajuga reptans	31.9	P		
Allipet	Alliaria petiolata	20.5	2		P
Anthram	Anthericum ramosum	23.2			P
Astrgly	Astragalus glycyphyllos	41.6		P	
Betooff	Betonica officinalis	15.7			
Bracpin	Brachypodium pinnatum	21.7			
Bracsyl	Brachypodium sylvaticum	29.8	P		
Bromram	Bromus ramosus	31.3	2		P
Buglpur	Buglossoides ~~purpurocaerulea~~purpurocaeruleum	19.9	N	P	P
Campper	Campanula persicifolia	36.7	2	N	2
Camprap	Campanula rapunculoides	44.9	N	P	P
Cardare	Cardaminopsis arenosa	13.3	P	N	
Caredig	Carex digitata	14.5	2	N	N
Caremic	Carex michelii	37.0	N		N
Caremon	Carex montana	9.9			
Carepai	Carex pairaei	50.3	P		2
Carpbet	Carpinus betulus	44.0			
Ceraavi	Cerasus avium	28.9		2	
Chaetem	Chaerophyllum temulum	29.5		P	P
Clemvit	Clematis vitalba	25.6	N	P	P
Clinvul	Clinopodium vulgare	81.0	P	2	
Convmaj	Convallaria majalis	19.3		P	
Cornmas	Cornus mas	46.4	N	P	
Cratlae	Crataegus laevigata	15.1	2	P	
Cratmon	Crataegus monogyna	49.4	N		
Crucgla	Cruciata glabra	29.8	2		
Cruclae	Cruciata laevipes	13.6	2		
Dactpol	Dactylis polygama	89.5	P	2	
Digigra	Digitalis grandiflora	21.7			P
Euonver	Euonymus verrucosus	14.5	N	P	
Euphcyp	Euphorbia cyparissias	31.6	P		
Falldum	Fallopia dumetorum	58.1	P		
Festhet	Festuca heterophylla	35.24	2		
Festrup	Festuca rupicola	10.8			
Fragves	Fragaria vesca	68.1	P	2	
Fraxexc	Fraxinus excelsior	49.01	N	P	2
Fraxorn	Fraxinus ornus	15.4			
Galiapa	Galium aparine	19.6			

Galimol	Galium mollugo	50.0	2		
Galiodo	Galium odoratum	16.6	2	2	P
Galisch	Galium schultesii	66.3		N	
Genitin	Genista tinctoria	23.12	P	N	N
Geumurb	Geum urbanum	59.6		P	P
Glechir	Glechoma hirsuta	18.4			
Hierlac	Hieracium lachenalii	23.5	2	2	N
Hiermur	Hieracium murorum	25.0		N	
Hierrac	Hieracium racemosum	37.0	2	2	N
Hylotel	Hylotelephium telephium	13.9	P		N
Hypeper	Hypericum perforatum	27.7	P	N	
Lapscom	Lapsana communis	46.7	P		
Lathnig	Lathyrus niger	34.6			P
Lathver	Lathyrus vernus	31.9			
Liguvul	Ligustrum vulgare	49.4	N	P	
Luzucam	Luzula campestris	11.4		N	2
Luzuluz	Luzula luzuloides	12.7	2	N	N
Lychvis	Lychnis viscaria	15.1		2	N
Malusyl	Malus sylvestris	11.1			
Melimel	Melittis melissophyllum	37.7			
Meliuni	Melica uniflora	74.4	N	P	P
Moehtri	Moehringia trinervia	22.9			
Mycemur	Mycelis muralis	15.4			
Origvul	Origanum vulgare	15.1	P	P	
Poaang	Poa angustifolia	15.1	P	N	2
Poanem	Poa nemoralis	88.2	2	N	N
Polyodo	Polygonatum odoratum	18.7			
Primver	Primula veris	14.2		P	
Prunspi	Prunus spinosa	60.8		2	2
Pulmmol	Pulmonaria mollissima	11.1			
Pyrupyr	Pyrus pyraster	15.4			
Quercer	Quercus cerris	62.0			
Querpet	Quercus petraea	85.5	2	N	N
Rosacan	Rosa canina	76.2	P	2	P
Rubufru	Rubus fruticosus	27.1			
Sanieur	Sanicula europea	12.0			
Scutalt	Scutellaria altissima	13.0	N	P	P
Secuvar	Securigera varia	16.9	P	P	
Silenut	Silene nutans	31.9	P	N	
Silevul	Silene vulgaris	16.3	2		
Sorbtor	Sorbus torminalis	32.2	2		
Stelhol	Stellaria holostea	37.7			
Symptub	Symphytum tuberosum	37.3			
Tanacor	Tanacetum corymbosum	58.1	P	2	
Teuccha	Teucrium chamaedrys	14.8	P		
Torijap	Torilis japonica	16.3		P	
Trifalp	Trifolium alpestre	25.9	P		
Trifmed	Trifolium medium	43.7	P	N	
Verbcha	Verbascum chaixii	13.0	P		
Verocha	Veronica chamaedrys	82.8	2	N	N

Verooff	Veronica officinalis	30.4	P	2	
Vicicas	Vicia cassubica	18.4	P	N	2
Vicitet	Vicia tetrasperma	11.1			
Vinchir	Vincetoxivum hirundinaria	39.8	P	2	P
Violhir	Viola hirta	12.7			
Violodo	Viola odorata	57.5	2	P	P
Violrei	Viola reichenbachiana	45.8	2	P	P

Table S6. Position of the species along the environmental variables as redundancy analysis axes.

Abbreviation	Binomial name	Openness	Soil pH	SHI
Acercam	Acer campestre	-0,42	0,58	0,39
Acerpla	Acer platanoides	0,04	0,06	0,07
Acertat	Acer tataricum	-0,05	0,01	-0,06
Ajugrep	Ajuga reptans	0,29	-0,08	-0,08
Allipet	Alliaria petiolata	0,12	0,08	0,14
Anthram	Anthericum ramosum	0,13	-0,02	0,11
Astrgly	Astragalus glycyphyllos	0,23	0,09	0,06
Betooff	Betonica officinalis	-0,01	0,02	0,01
Bracpin	Brachypodium pinnatum	-0,12	0,20	0,06
Bracsyl	Brachypodium sylvaticum	0,19	0,01	0,06
Bromram	Bromus ramosus	-0,13	0,10	0,24
Buglpur	Buglossoides purpurocaerulea	-0,17	0,20	0,23
Campper	Campanula persicifolia	0,26	-0,19	0,00
Camprap	Campanula rapunculoides	-0,23	0,46	0,36
Cardare	Cardaminopsis arenosa	0,16	-0,14	-0,10
Caredig	Carex digitata	0,17	-0,19	-0,18
Caremic	Carex michelii	-0,17	0,03	-0,13
Caremon	Carex montana	0,06	-0,05	-0,03
Carepai	Carex pairaei	0,20	0,08	0,00
Carpbet	Carpinus betulus	0,06	0,01	0,04
Ceraavi	Cerasus avium	0,00	0,02	-0,05
Chaetem	Chaerophyllum temulum	-0,09	0,21	0,32
Clemvit	Clematis vitalba	-0,17	0,14	0,17
Clinvul	Clinopodium vulgare	0,44	-0,02	0,13
Convmaj	Convallaria majalis	-0,13	0,26	0,08
Cornmas	Cornus mas	-0,20	0,28	0,09
Cratlae	Crataegus laevigata	-0,11	0,09	-0,01
Cratmon	Crataegus monogyna	-0,13	0,17	0,10
Crucgla	Cruciata glabra	0,27	-0,04	-0,11
Cruclae	Cruciata laevipes	0,07	0,03	0,07
Dactpol	Dactylis polygama	0,38	-0,21	-0,04
Digigra	Digitalis grandiflora	0,10	0,09	0,16
Euonver	Euonymus verrucosus	-0,14	0,11	-0,07
Euphcyp	Euphorbia cyparissias	0,21	0,05	-0,05
Falldum	Fallopia dumetorum	0,17	0,07	0,16
Festhet	Festuca heterophylla	0,11	-0,13	0,01
Festrup	Festuca rupicola	0,01	-0,02	-0,06
Fragves	Fragaria vesca	0,28	-0,06	0,00
Fraxexc	Fraxinus excelsior	-0,36	0,43	0,59

Fraxorn	Fraxinus ornus	0,05	0,07	-0,03
Galiapa	Galium aparine	-0,04	0,02	0,04
Galimol	Galium mollugo	0,61	-0,09	-0,13
Galiodo	Galium odoratum	-0,32	0,25	0,23
Galisch	Galium schultesii	0,01	-0,23	0,20
Genitin	Genista tinctoria	0,32	-0,21	-0,15
Geumurb	Geum urbanum	0,02	0,21	0,19
Glechir	Glechoma hirsuta	-0,10	0,14	0,07
Hierlac	Hieracium lachenalii	0,14	-0,30	-0,15
Hiermur	Hieracium murorum	0,25	-0,31	0,03
Hierrac	Hieracium racemosum	0,38	-0,54	-0,22
Hylotel	Hylotelephium telephium	0,08	-0,04	-0,08
Hypeper	Hypericum perforatum	0,21	-0,13	-0,05
Lapscom	Lapsana communis	0,25	-0,08	0,02
Lathnig	Lathyrus niger	-0,03	0,07	0,14
Lathver	Lathyrus vernus	-0,03	0,02	-0,06
Liguvul	Ligustrum vulgare	-0,41	0,31	-0,14
Luzucam	Luzula campestris	0,06	-0,08	-0,02
Luzuluz	Luzula luzuloides	0,30	-0,45	-0,24
Lychvis	Lychnis viscaria	0,10	-0,22	-0,11
Malusyl	Malus sylvestris	-0,05	0,01	-0,02
Melimel	Melittis melissophyllum	-0,05	0,08	0,09
Meliuni	Melica uniflora	-0,35	0,39	0,45
Moehtri	Moehringia trinervia	-0,01	-0,02	0,09
Mycemur	Mycelis muralis	0,01	0,01	0,07
Origvul	Origanum vulgare	0,14	0,10	0,06
Poaang	Poa angustifolia	0,12	-0,12	-0,14
Poanem	Poa nemoralis	0,76	-0,86	-0,49
Polyodo	Polygonatum odoratum	0,05	-0,04	0,03
Primver	Primula veris	-0,12	0,13	0,04
Prunspi	Prunus spinosa	0,05	0,08	0,03
Pulmmol	Pulmonaria mollissima	-0,04	0,03	-0,01
Pyrupyr	Pyrus pyraster	0,04	0,05	-0,03
Quercer	Quercus cerris	-0,26	0,02	0,01
Querpet	Quercus petraea	0,66	-0,59	-0,57
Rosacan	Rosa canina	0,13	0,03	0,20
Rubufru	Rubus fruticosus	-0,05	0,00	0,08
Sanieur	Sanicula europea	-0,09	0,09	0,12
Scutalt	Scutellaria altissima	-0,15	0,17	0,27
Secuvar	Securigera varia	0,22	0,12	0,02
Silenut	Silene nutans	0,24	-0,27	-0,05
Silevul	Silene vulgaris	0,07	-0,05	0,06
Sorbtor	Sorbus torminalis	0,06	0,01	-0,01
Stelhol	Stellaria holostea	-0,07	-0,04	-0,07
Symptub	Symphytum tuberosum	-0,06	-0,07	-0,15

Tanacor	Tanacetum corymbosum	0,25	-0,02	0,07
Teuccha	Teucrium chamaedrys	0,14	0,04	0,02
Torijap	Torilis japonica	0,11	0,12	-0,15
Trifalp	Trifolium alpestre	0,28	-0,12	-0,05
Trifmed	Trifolium medium	0,38	-0,20	0,11
Verbcha	Verbascum chaixii	0,16	0,03	-0,01
Verocha	Veronica chamaedrys	0,53	-0,51	-0,55
Verooff	Veronica officinalis	0,12	-0,26	0,00
Vicicas	Vicia cassubica	0,20	-0,36	-0,32
Vicitet	Vicia tetrasperma	0,04	0,02	-0,03
Vinchir	Vincetoxivum hirundinaria	0,25	0,25	0,51
Violhir	Viola hirta	-0,03	0,05	0,04
Violodo	Viola odorata	-0,27	0,73	0,44
Violrei	Viola reichenbachiana	-0,28	0,28	0,42