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Title: Environmental drivers of the composition and diversity of the herb layer in mixed temperate forests in Hungary

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Abstract

Herbaceous understory vegetation is an important part of temperate forested ecosystems, the diversity and composition of which are strongly dependent on the conditions of the forest stand and the landscape. The aim of this study was to find the most important environmental drivers influencing understory herb layer species composition (explored with multivariate analysis), and richness and cover (analysed by linear modelling) in managed mixed forests in West Hungary. Our detailed inventory showed that the most important factors increasing the diversity and cover of the understory are light, tree species richness, and landscape diversity. Composition is also mainly influenced by light conditions and tree species richness, with minor effects of tree species composition, soil texture, and moss cover.

As the strongest influencing factors are closely linked to stand structure and tree species composition, they can either directly or indirectly be altered by forest management. In

the studied region, heterogeneous light conditions and canopy structure, the maintenance of tree species richness and forest continuity are key elements for the conservation of forest herbs. Forestry that maintains continuous forest cover and the tree selection management system can better provide these conditions than the presently widely used shelterwood management system.

Keywords (4-6): understory, vascular plants, stand structure, microclimate, soil conditions, light

Abbreviations: LAI – leaf area index, DBH – diameter at breast height, RDA – redundancy analysis, PCA – principal component analysis, GLM – general linear modelling

Introduction

Forest herbs make an important contribution to the biodiversity (e.g. Gilliam 2007; Hart and Chen 2006; Wayman and North 2007), ecosystem functioning (Allen et al. 2002; Nilsson and Wardle 2005), nutrient cycling (Muller 2014), and even biomass (Gonzalez et al. 2013) and seedling community (George and Bazzaz 2014) of temperate forests. The factors influencing their composition and diversity are therefore widely studied (e.g. Hutchinson et al. 1999; Vockenhuber et al. 2011). Although the results of these studies are remarkably heterogeneous, stand structure, light conditions, edaphic factors, site history and landscape characteristics are generally assumed to be of importance.

In managed stands, the features most directly affected by human activity are stand structure and tree species composition. These, in turn, affect understory light conditions (Lochhead and Comeau 2012; Tinya et al. 2009a), and edaphic conditions such as soil water content, pH, temperature and nutrient availability (Barbier et al. 2008; Bartels and Chen 2013; Heithecker and Halpern 2006). Although obviously not the object of harvesting practices, understory vegetation is also directly affected by forest management (Duguid and Ashton 2013).

In Hungary and across much of Europe, after the abandonment of traditional management practices in the twentieth century (Hédl et al. 2010), the shelterwood forestry system has been the dominant forest management method until recently. This management type resulted in even-aged stands with homogenous structure on a relatively coarse scale (5-10 ha; Matthews 1991; Savill 2004). In the last decades, efforts have been made to change the management structure in favour of more natural practices, such as group and stem selection

systems (Rosenvald and Lohmus 2008; Bauhus et al. 2013). Sustainable management practices aim at mimicking the natural disturbance regime as much as possible, thus maintaining the natural processes of a forest (Bauhus et al. 2013). Professional debate on possible ways to achieve this aim is intense. In some cases, even small scale clearcutting is argued to be an efficient way of forming and harvesting forests (Heinrichs and Schmidt 2009); however, some species indicate the effects of clearcuts as far as 150 m inside the remaining forest (Godefroid et al., 2005). Intensive management types cause diverse changes in the species richness of ecologically distinct species groups (on the basis of ecological traits, Kenderes and Standovár 2003), similarly to changes in plant traits during the succession of a forest (Catorci et al. 2012).

Most of the forests in West Hungary have been used in ways fars from their natural disturbance regime: clear-cut for wood, or to gain space for pastures and arable areas (Tímár et al. 2002). These actions have long-term effects, and leave their mark both on understory and overstory (e.g. Hermy and Verheyen 2007; Wulf 2003). Ancient (chronologically continuous forest cover since first written record) and recent (area utilized differently sometime throughout recorded history) woodlands host markedly different herbaceous vegetation (e.g. Hermy and Verheyen 2007, Kelemen et al. 2014). The exact type and intensity of previous land utilization of the area also has important effects (Verheyen et al. 2003), which may be detectable for millennia (Dupouey et al. 2002). The inclusion of this feature into analyses can be achieved via old maps, army surveys, and common knowledge of the area. In some cases, previous land-use seems to have an even more important influence on the current condition of the forest floor than present stand structure or microtopography (Ito et al. 2004). According to a theory, management may act through past minimum and maximum

102 canopy covers, which work as bottlenecks (Økland et al. 2003). Present management
103 obviously holds the key to the characteristics of a forest; in many cases, the typical aspects of
104 which can be assessed on the basis of the ownership of the stand (state-owned versus private
105 forests, Berges et al. 2013; Schaich and Plieninger 2013; Zmihorski et al. 2010). In our study
106 area, in private forests, management techniques are much closer to the natural disturbance
107 regime than in state-owned stands.

108 Edaphic factors, which are also strongly influenced by stand characteristics (von Arx
109 et al. 2012), naturally have strong effects on ground vegetation. The surrounding landscape,
110 serving as the species pool for the studied habitat, is also an important influential factor, and
111 can, in some cases, serve as the basis for assessing the biodiversity of poorly explored, high
112 diversity areas (Priego-Santander et al. 2013).

113 However, the diversity of understory vegetation in itself may be misleading, and is not
114 equal to forest naturalness. In disturbed or otherwise altered stands, non-forest species could
115 considerably increase these values (Hermy and Verheyen 2007; Mikoláš et al. 2014; Paillet et
116 al. 2010). Therefore, it is reasonable to handle closed-forest herbs separately from the total
117 species pool (Kelemen et al. 2014). The aim of this study is to produce a detailed analysis of
118 the understory herb layer of the studied forests, which can be used effectively in conservation
119 and management. Our questions were: (i) which environmental background factors influence
120 the composition of the understory herb layer (multivariate analysis); (ii) which are the most
121 important factors that enhance or hinder species richness and abundance of the understory
122 (linear modelling); (iii) is there a marked difference between the environmental needs of
123 closed-forest and non-forest species; and (iv) from the most influential background factors,
124 which could be altered favourably by forest management.

125

Materials and methods

Study area

Our study was carried out on 34 plots in the Őrség region, West Hungary (N46°51–55' and W16°07–23', Figure 1). Elevation of the study area is between 250 and 350 m above sea level. The bedrock in the area is alluviated gravel mixed with loess, and its topography consists of hills and wide valleys. On hills, mostly pseudogleyic brown forest soil can be found (planosols or luvisols), while in the valleys mire and meadow soils (gleysols) are common (Stefanovits et al. 1999). The soil is acidic (pH 4.0–4.8, measured in water, in the upper 10 cm) and nutrient poor. Average annual mean temperature is 9.0–9.5 °C, with a mean annual precipitation of 700–800 mm (Dövényi 2010). In the area, we can find forests of various species composition and stand structure on similar forest sites, namely on similar climatic, topographical, and bedrock conditions. The study area is dominated by beech (*Fagus sylvatica* L.), sessile and pedunculate oak (*Quercus petraea* L. and *Q. robur* L.), hornbeam (*Carpinus betulus* L.), Scots pine (*Pinus sylvestris* L.), and Norway spruce (*Picea abies* (L.) Karst.), forming monodominant and mixed stands as well. The proportion of various, subordinant tree species (birch – *Betula pendula* Roth., aspen – *Populus tremula* L., chestnut – *Castanea sativa* Mill., wild cherry – *Prunus avium* L., etc.) is relatively high (Tímár et al. 2002). The present diverse state of the forests is partly due to the special landscape history of the area. After the twelfth century, extensive farming and other activities, such as litter collection and ridging (a special form of tillage) led to the deforestation and acidification of the area and the erosion of soil. From the nineteenth century, extensive farming was

repressed, and a reforestation of the area took place, mainly by Scots pine and pioneer tree species linked to it (birch, aspen). Later, selective cutting has been applied by farmers, alongside the industrial shelterwood system in state owned forests (Gyöngyössy 2008; Tímár et al. 2002). The conditions which developed owing to these events were favourable to tree, herb, and moss species that prefer nutrient poor and disturbed conditions. Current existing forests are a fine-scale mixture of ancient and recent stands. The mixture of these pioneer species and typical species of the mesic forests together create a remarkably rich and various species composition in the region.

Data collection

We collected our data in 34 forest stands (Figure 1). These were selected by stratified random sampling from the forest stand database of the Hungarian National Forest Service. All of these stands were located on relatively level ground, devoid of direct water influence, and the age of dominant tree layer was between 70 and 100 years old. The stratification criterion was tree species composition: these stands represent different combinations of the main tree species (sessile and pedunculate oak, beech and Scots pine) of the area. Within the categories – based upon tree species composition –, random selection was carried out.

In all the stands, one 40 m x 40 m plot was selected, where all tree individuals (including snags) above 5 cm diameter at breast height (DBH) were mapped. Species identity, DBH and height of these trees were also recorded. The proportion of tree species (beech, hornbeam, oak, Scots pine, Norway spruce, subordinate trees) was expressed, based on volume. The volume of the trees was calculated by species specific equations, based on DBH

172 and tree height (Sopp and Kolozs 2000). *Quercus petraea*, *Q. robur* and *Q. cerris* were
173 merged as oaks, rare tree species were merged as subordinate trees. Tree species diversity was
174 calculated as Shannon diversity H', based on the relative volume of tree species, using natural
175 logarithm (Shannon and Weaver 1949). The volume of snags (standing dead wood) was
176 calculated, based on the measurement of individuals within the plots. For dead trees the same
177 equations were used as for living trees, for broken snags and stumps the volume was
178 calculated as a cylinder (measuring mean diameter and height). For lying dead wood, the
179 mean diameter and the length of logs larger than 5 cm in diameter were also recorded and log
180 volume (per ha) was calculated by the cylinder formula. Saplings and shrubs below 5 cm
181 DBH but above 0.5 m height were counted, by species, their densities (unit per ha) were
182 calculated.

183 The inventory of forest herbs was carried out in quadrats of 30 m x 30 m, positioned in
184 the centre of the 40 m x 40 m tree plot in June and July of 2006. This means the early spring
185 geophytes were excluded from the sample (they are relatively rare in the region). Absolute
186 cover (dm^2) was estimated for every recorded species, the nomenclature of vascular plants
187 followed Tutin et al. (1964-1993). The cover of mineral soil and bryophytes were also
188 estimated within the quadrats.

189 Relative diffuse light was calculated based on parallel measurements carried out in the
190 quadrats and in nearby open fields with LAI-2000 Plant Canopy Analyzer instruments
191 (LICOR Inc. 1992a, 1992b; Tinya et al. 2009a, 2009b). In each quadrate, 36 light
192 measurements were taken in a systematically arranged grid, at 1.3 m height, using 5 m
193 intervals. For quadrate level light conditions, the mean and coefficient of variation of the 36
194 relative diffuse light values were calculated.

Land cover types in a 300 m radius area around each plot were estimated with the help of aerial photos, maps and the forest stand database. Regenerating forests (<20 years), forests (older than 20 years), and non-forested areas (meadows and arable lands) were distinguished. Landscape diversity was calculated as the Shannon diversity H' of land cover types. The land use history of the plots and their surroundings (300 m radius) was estimated, based on the Second Military Survey of the Habsburg Empire from 1853 (Arcanum 2006). The existence of forests in the plots (as a presence/absence variable) was recorded, and the proportion of forested areas in the historical landscape (in a circle of 300 m radius) was calculated.

Litter was collected from 5 systematically arranged, 30 x 30 cm areas from all quadrats. Litter weight, proportion of coniferous litter, litter pH (in water), organic carbon content and nitrogen content were measured. In the same points, soil samples were collected from the 0-10 cm layer. The following variables were measured from soil samples: pH in water using hydrolytic and exchangeable acidity measured by titration (Bellér 1997); clay (<0,002 mm), silt (0,002 – 0,02 mm) and sand (0,02-2 mm) fractions determined by sedimentation process (Cools and De Vos 2010); organic carbon and nitrogen content analysed by dry combustion elementary analysis using Elementar vario EL III CNS equipment (Elementar Analysensysteme GmbH 2000); ammonium-lactate/acetic-acid (AL-) extractable phosphorus and potassium content (Bellér 1997).

Air humidity and temperature were measured in the middle of the quadrats, at 1.3 m height, using Voltcraft DL-120 TH data loggers, in 24-hour measurements with a 5-minute recording frequency. The measurements of all quadrats were carried out within a five-day period. During this period, two reference plots were measured permanently. Eight temperature and air humidity measurements were carried out during three vegetation periods (June and

October 2009; June, August, September and October 2010; March and May 2011). For air humidity and temperature, differences were calculated from the two reference plots. Relative daily mean and range values were expressed for both variables and averaged over the eight measurements. The geographical positions of the plots were given in meters, based on the Hungarian Geographical Projection (EOV). For a summary of the potential explanatory variables, see Table 1.

Data analysis

Data structure was explored by ordination (Podani 2000; ter Braak and Smilauer 2002). In order to gain insight into the relations of the species and sites, we carried out principal component analysis (PCA), and to determine the gradient length along the axes, detrended correspondence analysis (DCA). As the gradient lengths were less than three standard deviation units, redundancy analysis (RDA) was conducted, in order to identify the effects of explanatory variables on species composition (Table 1).

We carried out all analyses with log-transformed cover data of herbaceous species. Only species with a frequency larger than three were included. PCA and RDA were centred by species. Some explanatory variables were ln-transformed before the analyses, to fulfil normality conditions (proportions of tree species, light variables), and all explanatory variables were standardized (zero mean, one standard deviation). Within the RDA model, the explanatory variables were forward selected manually, by F-statistics via Monte Carlo simulation (number of permutations was 499), and only significant ($p<0.05$) variables were selected for the model. The significance of canonical axes was tested by similar Monte Carlo

241 simulations. Latitude data, determining the geographical position of the plots, was used as a
242 covariable within the RDA model.

243 To explore the effect of the explanatory variables on species richness and cover,
244 general linear modelling (GLM) was used (Faraway 2005), using identity link function and
245 Gaussian error structure. Ruderal and meadow-inhabiting species were separated from closed-
246 forest herbs during the analysis; this classification is indicated in Table 1 in Online Resource
247 1. The classification was based on the habitat preference characterization of the species of the
248 Hungarian Flora (Simon 1992). Total species richness, and species richness of closed-forest
249 species were analysed separately, and the same approach was used for cover.

250 The dependent variables of the GLM models were ln-transformed before the analyses,
251 for a better fit of the model residuals to normality conditions. Linearity between the
252 dependent and explanatory variables and constancy of the residual error variance were also
253 checked after model selection. Before the statistical selection procedure, pairwise correlations
254 and visual relationships between dependent and explanatory variables were investigated, and
255 intercorrelations among explanatory variables were also considered. For the statistical
256 selection procedure, only those explanatory variables were selected which showed a strong
257 and consistent relationship with the dependent variable, and the intercorrelations with other
258 explanatory variables were weak ($r_{abs}<0.5$). Although Poisson error structure is widely used
259 for species richness models, we have chosen the Gaussian error structure because of better
260 model diagnostics and coefficients of determination (Faraway 2005).

261 For multivariate analyses, Canoco for Windows 4.5 (ter Braak and Smilauer 2002), for
262 all other analyses, R version 2.11.1 (R Development Core Team 2011) was used.

263

264 Results

265

266 We recorded a total of 134 species, 99 of which were labelled ‘closed-forest species’
267 (Simon 1992, Online Resource 1). Mean cover of the herbaceous layer in the plots was
268 4.08%, with high standard deviation (7.22% dm^2). Species with the highest cover values were
269 common woodland species, such as *Rubus fruticosus*, *Oxalis acetosella*, *Pteridium aquilinum*,
270 *Galeopsis pubescens*, *Galium odoratum* and *Ajuga reptans*.

271 The PCA (see Fig. 1 in Online Resource 3) revealed that most species are placed in
272 one direction, in accordance with a distinction between species-rich and species-poor sites.
273 The first axis explains 31.0% of the total variance, the second 12.4%.

274 In the RDA, the amount of diffuse light was the most important factor, but tree species
275 richness, the relative volume of hornbeam, the proportion of fine-texture particles of the soil
276 and moss cover were also significant (Table 2, Figure 2). The first RDA axis explained
277 19.1%, the second 8.9% of the species variance, respectively, the first ($F=6.25$, $p=0.002$) and
278 all other canonical axes ($F=3.67$, $p=0.002$) had significant effects.

279 Herbaceous species preferring open areas (meadows, as *Juncus effusus* and *Agrostis*
280 *stolonifera*, or clearcuts, as *Calamagrostis epigeios*) and several acidophilous species (e.g.
281 *Luzula pilosa*, *Melampyrum pratense*) correlate most strongly with light (Figure 2). Many
282 acidophilous species, however, are most strongly correlated with moss cover (*Calluna*
283 *vulgaris*, *Sieglingia decumbens*, *Carex pilulifera*), itself also influenced by light availability.
284 The variables referring to tree species composition (i.e. tree species richness and the amount
285 of hornbeam) seemed to have a stronger effect on the herb species of closed forests (such as
286 *Sanicula europaea*, *Ajuga reptans*, *Viola reichenbachiana*, *Maianthemum bifolium*, *Athyrium*

filix-femina). The proportion of fine-texture ingredients in the soil act in the opposite direction to tree species richness, and hardly any species prefer the sites with a high clay and silt ratio (*Veronica chamaedrys, Luzula luzuloides, Epipactis helleborine*).

In the linear regression models, significant background factors were principally the same for all four explored dependent variables (species richness and cover of all the species and closed-forest species; Table 3). The dependent variables were strongly correlated (after log-transformation, total cover and species richness: $r=0.845$; $p<0.001$; cover and species richness of closed-forest species: $r=0.843$; $p<0.001$; illustrated in Figures 6 and 7 in Online Resource 8 and 9, respectively). In the model for both total and closed-forest herb cover, the relative amount of diffuse light, tree species richness, and landscape diversity proved significant with a positive sign, while the proportion of clay and silt in the soil had a negative effect. The explained variance, by chance, was 46% for both of these models. In the case of species richness, again the same explanatory variables were the most effective for both studied groups (all and closed-forest species), namely the amount of relative diffuse light, tree species richness and landscape diversity, all with positive signs. The explained variance is 45% for total species richness and 41% for closed-forest species richness.

Scatterplots with correlation coefficients between the dependent and the selected explanatory variables and a table of the correlations can be found in Table 2 in Online Resource 2, and in Figures 2–5 in Online Resource 4–7, respectively.

Discussion

Direct and indirect effects of the significant environmental drivers

Our results show that from all the background factors examined in our study, the amount of diffuse light, tree species richness, the relative volume of hornbeam, silt and clay ratio of the soil, moss cover, and landscape diversity are the most important factors correlating with the diversity and cover of the herbaceous layer. This means that the different aspects of the understory herb layer, i.e. species composition (explored by RDA), and species richness and cover (examined by GLM) are all chiefly influenced by the same environmental background factors. Most of these are not only directly operating agents, but rather factors influenced by the same mechanisms as understory vegetation (Roberts and Gilliam 2014).

In our study, the most important driver was light. Light conditions on deciduous forest floors are evidently determined by canopy structure, or, more specifically, canopy openness. Whereas in such environments light is the most important limiting factor (Neufeld and Young 2014), its measurement is loaded with technical difficulties (e.g. Tinya et al. 2009a, 2009b). For this study, we used LAI measurements, where the relative proportion of light is calculated by a comparison between values recorded in open areas and the forest site, at the same time.

The effect of light is not straightforward, because the abundance or diversity of the understory is not necessarily in direct proportion to light availability. In the study of Härdtle et al. (2003), light conditions were the most important drivers in acidophytic beech-oak forests, while on more neutral forest sites, different soil properties proved more determinant. Other studies have also come to the conclusion that the effects of light – or canopy openness –

conditions depend on edaphic conditions (e. g. Tyler 1989; Van Couwenberghe et al. 2011). In our case, however, light was more important than soil conditions; the reason for this may lie, at least in part, in our sampling arrangements (stratified random method, resulting in similar edaphic conditions at all sites). Besides, the quality of soil itself is not independent of light availability (Strandberg et al. 2005; Van Calster et al. 2007) either.

Our studies were carried out in slightly acidic forests, and acidofrequent (e.g. *Luzula pilosa*, *Melampyrum pratense*) and non-forest (e.g. *Juncus effusus*, *Calamagrostis stolonifera*) species showed the strongest connection with light conditions. In our linear analyses, we found that light had a greater effect on total cover than on the cover of closed-forest species; however, even in the case of closed-forest species, light was the most important background factor, positively influencing both cover and species richness. This result is slightly contradictory. Studies on the subject tend to show that whereas total forest floor herb cover is increased by light, a denser canopy increases the proportion of forest dwelling species, which are more shade-tolerant (e.g. Schmidt et al. 2014; Vockenhuber et al. 2011). In our study area, most of the stands are highly closed (managed, even-aged stands, many of them dominated by beech), thus light availability is generally so low that, even for closed-forest species, this is the most important limiting factor. Similar findings have been reported elsewhere: Plue et al (2013) conclude that even though the production of closed-forest species tends to improve with decreasing light conditions, this is only valid up to a given point; from then on, even these shade-tolerant species react strongly to small, favourable changes in light conditions. In the course of our project, Tinya et al (2009a) explored in detail the effects of light on different understory species groups in the same forest stands. Their results show that a group of species, termed light-flexible species – mainly closed-forest species – correspond positively to

353 light availability on a relatively small spatial scale. These species may be important in
354 emphasising the importance of light availability in our models as well.

355 In the studied area, more acidic soils are linked to sparse pine forests, where ground
356 floor light conditions are better. In these stands, ground floor mosses are also more abundant
357 (Márialigeti et al. 2009). In the same stands, light conditions proved to be determinant in the
358 diversity and composition of epiphytic lichens (Király et al. 2013; Nascimbene et al. 2012;
359 Ódor et al. 2013) as well.

360 Terricolous bryophyte cover correlates strongly and positively with herb cover and
361 species richness. Bryophyte and herbaceous species may act similarly to the same background
362 conditions, apart from light availability (see also Tinya et al. 2009a), soil and litter properties,
363 and microclimate. We recorded a number of features of these edaphic conditions (see Table
364 1). However, their correlations with the examined characteristics of the understory were weak
365 and not significant. This implies that if understory herbs and bryophytes do indeed react to
366 similar background factors, then these factors must be more complex than the ones we could
367 measure.

368 It is possible that bryophytes directly facilitate the growth of vascular plants, by
369 making the microenvironment more favourable. This has been known in more nutrient-limited
370 habitats (peatlands – Groeneveld et al. 2007, cave entrances – Ren et al. 2010), and the same
371 mechanisms may be at work in temperate forests as well.

372 Historic reasons may also be significant. Plots with former litter collection and
373 foraging had become more acidic, which was beneficial to many bryophyte and herb species,
374 and usually implied better light conditions as well (because of the presence of coniferous tree
375 species).

376 Apart from light, other microclimatic conditions (such as temperature and air-
377 humidity) were not highly influential for understory herbs. These factors are more effective in
378 the case of cryptogamic organisms, such as epiphytic lichens and bryophytes (Király et al.
379 2013; Ódor et al. 2013) and terricolous saprotrophic and mycorhizza fungi (Kutszegi et al.
380 2015).

381 Light availability may be the most important among the influencing factors
382 determined by stand structure, but it is not the only one. We found that other characteristics of
383 the stand structure also play important roles in the cover and species richness of the
384 understory vegetation. As our sites host a wide variety of tree species and a broad range of
385 their different compositions, we were able to study their influence.

386 Tree species richness acts as a positive factor for herb composition, species richness
387 and cover. In the multivariate analysis, the presence of hornbeam is also a significant factor.
388 Hornbeam is economically not preferred, but in many of our sites it is nearly the only species
389 which forms a second canopy layer. It is possible that the presence of the second canopy
390 layer, and not hornbeam itself has relevant effects. Cook (2015), although admitting to the
391 scarcity of literary data, hints that the abundance of canopy layers (shrubs, saplings or
392 midstory) may create diverse resource limitations, thus enhancing the ecological possibilities
393 of understory herbs. Although a second canopy layer reduces forest floor light availability and
394 contributes to higher litter production, its presence or absence on a sub-patch scale creates
395 highly variable microenvironments.

396 Stand structure and tree species composition directly determine litter properties and
397 strongly influence the soil (e.g. Arno et al. 2012; Augusto et al. 2003) and microclimate of the
398 site. The amount and composition of litter are fundamental for understory vegetation. In most

of our forest patches, beech was dominant: on many locations, the plots consisted of even-aged beech trees, with vast amounts of litter and practically no understory (either herbaceous or bryophyte). Mölder et al. (2008), facing similar problems, found no significant effects of light conditions on the herb layer (its diversity or productivity), whereas the proportion of beech was crucial. They assumed that beech has indirect effects on ground floor vegetation through soil pH and litter production. Mölder et al. (2014) also point out that the growing proportion of beech, induced by the cessation of traditional management methods (in their case, coppicing with standards) acts negatively on the ground floor vegetation. Durak (2012) also notes the negative effect of beech and the strong connections between understory and overstory diversity. These findings correspond well to the conditions in our research sites: in our case, the unique variability of stand structure and composition has been brought about by centuries of various management types, and is jeopardized by the introduction of the shelterwood system.

Vockenhuber et al. (2011) also examined both understory herbaceous plant species richness and cover, and their results highly correspond with ours. Both cover and species richness were enhanced by tree species diversity, and both responded negatively to increasing canopy cover.

Based on our study, it is expected that mixed forest stands help to maintain the biodiversity of the herb layer. Tree species richness was a crucial factor both for the total and only forest herb species richness. The importance of the heterogeneity of the tree species is also stressed in Macdonald and Fenniak (2007). They show that understory vegetation is linked to canopy composition and also edaphic conditions, with mixed and conifer forests differing significantly from broadleaved forests. Many studies show the great importance of

422 canopy structure in maintaining understory diversity (e.g. Chávez and Macdonald 2010,
423 2012). As patches with different canopy types maintain various understory vegetation, all
424 canopy patch types are important to maintain overall understory diversity.

425 Whereas soil properties are usually found among the most important factors for
426 understory vegetation (e.g. Chavez and Macdonald 2010, 2012; Härdtle et al. 2003; Ikauniece
427 et al. 2013; Van Couwenberghe et al. 2011), in our study, their significance was low.
428 Although, as mentioned above, we have recorded several characteristics of the soil (including
429 potassium and phosphorous content), these have not shown significant correlations with the
430 examined variables. The reason for this may be the complexity of the interactions between
431 trees and herbs, or the agency of some other edaphic factor, e.g. manganese, which, according
432 to Muller (2014), may be a good indicator of general soil fertility. Finally, again, as in the
433 case of bryophytes, it is also possible that herbs and trees react similarly to background
434 factors (Gilliam and Roberts 2014).

435 In the case of cover (both total and closed-forest species), however, silt and clay
436 content of the soil was a significant and negative background factor. The reason for this may
437 be that increasing silt and clay content cause pseudogleyization and poorer water conditions,
438 which is not favourable to herb cover. This background factor had no significant effect on
439 species richness, but a few species favour sites with higher silt and clay ratio. De
440 Keersmaeker et al. (2004) suggest that soil properties (carbon, moisture, nitrogen,
441 phosphorous) may be related to forest age. The forest stands in which our investigation has
442 been carried out were selected to be more or less of the same age (70-100 yr), so this variation
443 is absent from our analyses; this may in part account for the lack of correlations.

Tree species composition also affects soil properties: Arno et al. (2012) demonstrated the varying effects of oak and poplar on the development of soil and understory vegetation in an experiment. They found that the soil differs under these two species, establishing the dissimilarities in understory vegetation. The positive effect of tree species richness on understory vegetation may also be conveyed through mixed litters, which are known to decompose more rapidly than litter from a single species (Gartner and Cardon 2004). The resulting fast nutrient cycling enhances the resources available to the understory layer.

Landscape diversity was an important factor for both cover and species richness for all and wood inhabiting species as well. Landscape diversity is generally thought to enhance species richness by acting as species pool for various species groups. High landscape diversity means that the forests are surrounded by other landscape types (mainly meadows and arable lands). The vicinity of these landscape elements can increase the species richness of the forests, adding many (primarily not forest specialist) species to the species pool. It is interesting that understory cover showed even stronger correlations with landscape diversity than species richness; the reason for this is not known.

Land-use history was not an influential factor in species composition. It is possible that during the periods of intensive utilization, the species sensitive to these effects partly disappeared (as suggested in the case of epiphytes in Király et al. 2013), which means that the continuity of the forest (important for several, closed-forest species, e.g. Hermy et al. 1999) had been broken in the past (bottleneck effect, Økland et al. 2003), and its effects cannot be properly shown today.

Implications for conservation and management

The effects of changes in forest management are widely felt throughout the forests of Central Europe. The effects of the cessation of traditional management (e.g. coppicing in Germany, Mölder et al. 2014, and the Czech Republic, Vild et al. 2013, Hédl et al. 2010; leaving up chestnut forests in Bulgaria, Zlatanov et al. 2013) are revealed by several studies (this phenomenon is valid not only in forests, but other ecosystems as well, e.g. hayfields in Romania, Baur et al. 2006). The exact ecological mechanisms of the changes are often unclear; however, Kopecký et al. (2013) have demonstrated non-random extinction from the former species pool; a process that is hardly reversible. In our case, the unique versatility of the studied region is largely the result of past management practices (felling and using as arable lands, fodder removal). Diversity is largely kept up by present, close-to-nature management practices, typically in small, private forests (Schaich and Plieninger 2013). On the other hand, in our region, the shelterwood system has caused and is causing the homogenisation of stands (species composition as well as stand structure), which, according to our results, is disadvantageous for the diversity and productivity of the herbaceous vegetation.

Our results show that the most important factors affecting the composition, species richness, and cover of understory herbs act on the stand level. We have also shown that the amount (and variability) of light is important, along with the presence of the second canopy layer and the diversity of tree species. Most of the relevant factors, such as canopy cover and tree species composition, can be directly affected by forest management. The analysis of species composition revealed that although light increases the diversity of forest herbs, too open conditions are favoured mainly by non-forest species (plants of the meadows and weeds

of arable lands and clear-cuts). For the biodiversity of forest herbs, forest management should maintain heterogeneous light conditions including gaps and canopy openings, but the general light regime should be characterised as a high forest, to prevent the dominance of non-forest species. Management should also maintain high tree species diversity, including the mixed occurrence of the dominant species (Scots pine, beech, oaks) and a high proportion of non-dominant tree species, so as to enhance microenvironmental diversity (e.g. Arno et al. 2012) and, via litter mixing, promote nutrient cycling (Gartner and Cardon 2004). The presence of the secondary canopy layer (dominated by hornbeam) is also very important, as it also adds to the diversity of available resources (Cook 2015). These conditions can be provided by various types of management maintaining continuous forest cover, such as tree selection or group selection management systems (Matthews 1991).

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773

774 Table 1. Potential explanatory variables. Minimum, mean and maximum values of the 34
775 studied plots are given where appropriate.
776

Explanatory variable	Minimum	Mean	Maximum
Tree species composition			
Tree species richness	2.0	5.6	10.0
Tree species Shannon diversity *H'*	0.2	0.9	2.0
Proportion of tree species (beech, hornbeam, oaks, Scots pine, subordinate trees)	-	-	-
Stand structure			
Mean DBH (cm)	13.6	26.3	40.6
Coefficient of variation of DBH	0.2	0.5	1.0
Sapling density (stems/ha)	0	947.4	4706.3
Basal area of mapped trees (m^2/ha)	24.1	34.1	49.7
Snag volume (m^3/ha)	0.0	12.2	64.6
Log volume (m^3/ha)	1.2	10.1	35.6
Forest floor			
Bryophyte cover (m^2/ha)	2.9	4.7	7.7
Cover of mineral soil (m^2/ha)	8.6	145.8	472.2
Cover of litter (m^2/ha)	7815.0	9391.9	9833.7
Cover of deadwood (m^2/ha)	4.4	5.4	6.6
Light conditions			
Mean relative diffuse light	0.5	1.3	2.4
Coefficient of variation of relative diffuse light	0.1	0.4	0.8
Landscape variables			
Landscape diversity *H'*	0.1	1.1	1.9
Proportion of forests (%)	56.9	89.6	100.0
Land use history (1853)			
Proportion of forests in the landscape (%)	24.0	76.6	100.0
Forest site characteristics			
Litter $pH_{(in\ water)}$	4.9	5.3	5.7
Litter weight (g, 30cm x 30cm)	105.4	148.3	243.1
Proportion of deciduous litter (%)	5.5	15.1	32.8
Litter carbon content (%)	42.9	65.8	78.1
Litter nitrogen content (%)	0.8	1.3	1.8
Soil $pH_{(in\ water)}$	4.0	4.3	4.8
Soil texture (clay and silt %)	27.6	52.1	68.6
Soil carbon content (%)	3.3	6.5	11.5
Soil nitrogen content (%)	0.1	0.2	0.3

Soil AL-extractable phosphorous content (mg P_2O_5/100g)	2.0	4.3	9.4
Soil AL-extractable potassium content (mg K_2O/100g)	4.0	7.7	13.1
Microclimate			
Temperature difference (K)	-0.9	-0.1	0.7
Temperature range difference (K)	-0.4	0.9	2.3
Air humidity difference (%)	-1.8	0.8	3.3
Air humidity range difference (%)	-2.3	1.8	6.6

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779 Table 2. Explained variance (%) of the canonical variables in the RDA model, and the
780 correlation of the explanatory variables with the axes. The effect of the explanatory variables
781 was tested by F-test. **: p<0.01; *: p<0.05.
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	Var (%)	F-test	Axis1	Axis2	Axis3	Axis4
Relative diffuse light	15	5.98**	0.88	-0.13	-0.41	0.17
Tree species richness	7	3.13**	0.22	0.19	0.91	-0.13
Hornbeam (relative volume)	6	2.47*	-0.18	0.73	0.14	-0.24
Soil fine texture proportion	4	2.08*	-0.12	-0.31	-0.15	-0.92
Moss cover	4	2.03*	0.73	-0.39	0.24	0.35

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Table 3. Significant explanatory variables of the different regression models. "R^{2}" is the adjusted coefficient of determination of the models, "Sense" is the sense of the parameter of the variables in the regression equation, "Variance %" is the percentage of the explained variance by the variable within the model. The significance of explained variance was tested by F statistics, ***: p<0.001; **: p<0.01; *: p<0.05; .: p<0.1.

Total cover; R^2=0.46			
Variable	Sense	Variance %	F-value, significance
Relative diffuse light	+	21.16	13.01**
Landscape diversity	+	11.88	7.31*
Tree species richness	+	10.13	6.23*
Fine texture proportion	-	9.68	5.95*

Cover of closed-forest species; R^2=0.46			
Variable	Sense	Variance %	F-value, significance
Relative diffuse light	+	17.97	11.05**
Landscape diversity	+	12.62	7.76**
Tree species richness	+	11.64	7.16*
Fine texture proportion	-	10.61	6.52*

Total species richness; R^2=0.45			
Variable	Sense	Variance %	F-value, significance
Relative diffuse light	+	21.69	12.94**
Tree species richness	+	21.29	12.70**
Landscape diversity	+	6.71	4.00.

Closed-forest species richness; R^2=0.41			
Variable	Sense	Variance %	F-value, significance
Relative diffuse light	+	23.06	12.97**
Tree species richness	+	17.10	9.62**
Landscape diversity	+	6.48	3.65.

793 **Fig. 1** Study area: Őrség region, West Hungary (N46°51–55’ and W16°07–23’); the dots
794 show our plots.
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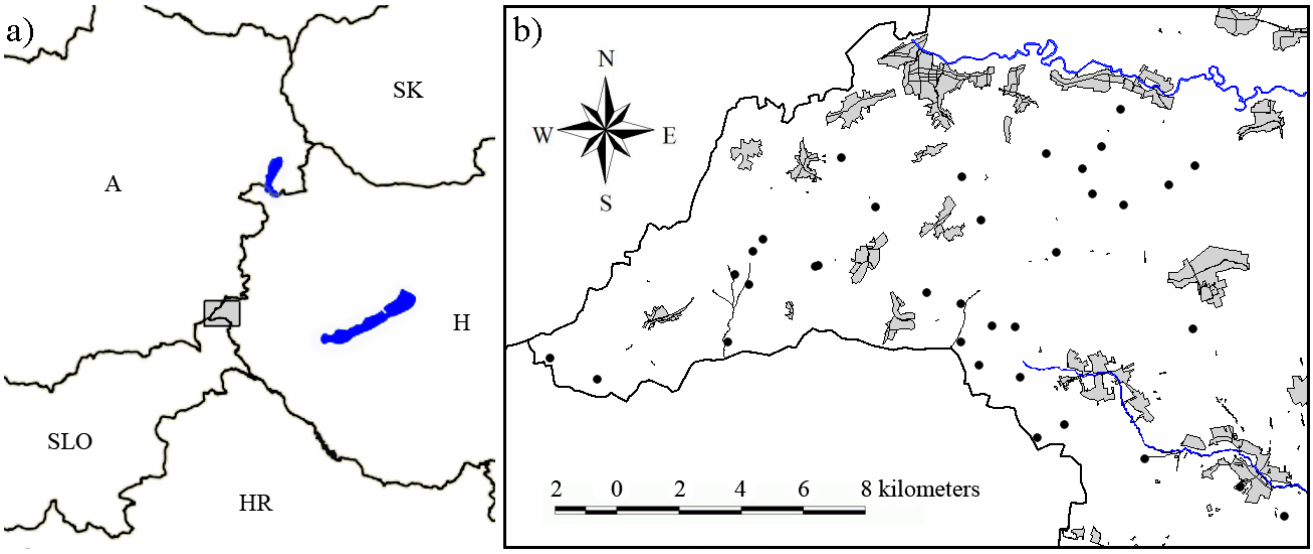

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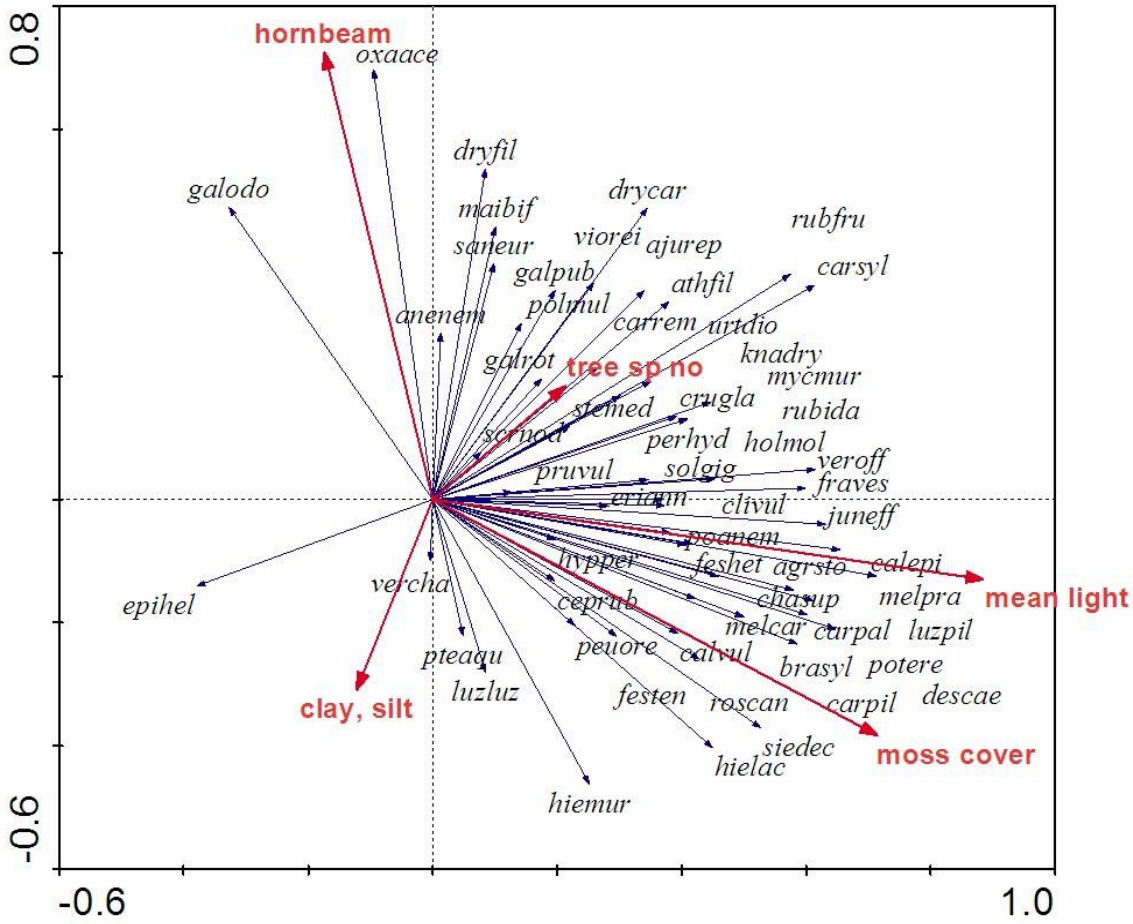
799 **Fig. 2** Species (black) and environmental variables (red) biplot of the redundancy analysis

800 (RDA)



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