The manuscript is contextually identical with the following paper:
Tinya. F., Márialigeti, S., Bidló, B., Ódor, P. (2019): Environmental drivers of the forest regeneration in temperate mixed forests. Forest Ecology and Management, 433:720-728.
https://doi.org/10.1016/j.foreco.2018.11.051.

Environmental drivers of the forest regeneration in temperate mixed forests

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Abstract

As modern silviculture in natural forests is based on natural regeneration, finding the most important drivers of regeneration is crucial for forestry as well as conservation. We explored the relationship between numerous environmental and land use history variables and the species richness, cover and composition of the regeneration layer, and also the cover of the dominant species of the regeneration (sessile oak, hornbeam and beech) in coniferous-deciduous mixed forests. We identified the key factors which forest management can influence to support the regeneration of mixedwoods.

Thirty-four stands were sampled, representing different tree species combinations and stand structures. We used redundancy analysis to explore the effects of the explanatory variables on the regeneration's species composition, and general linear modelling to examine their effects on its species richness and cover.

The most important drivers of species composition were tree species richness, the amount of relative diffuse light, the proportion of beech in the overstory, and the heterogeneity of the diameter of trees. The cover of the regeneration layer was positively related to the density of large trees and to the amount of relative diffuse light. Its species richness was most strongly influenced by light and tree species richness. For the cover of a particular species in the regeneration, the proportion of the conspecific species in the overstory was determinant for every species, but other, various drivers also played a role in the case of the different species.

According to our results, the community variables of the regeneration are mainly driven by the characteristics of the current forest stands, thus they are strongly influenced by management. Compositional heterogeneity of the overstory, various tree size distribution and the presence of large trees play key roles in the maintenance of a heterogeneous regeneration layer. The shelterwood forestry system is partially capable of providing these conditions, but continuous cover forestry is much more suitable to achieve them. Besides the stand structural variables, among the drivers of the individual species, various variables of forest site, landscape and land use history also occurred. Therefore, we conclude that maintaining the landscape-scale heterogeneity of forest types and management systems may promote the coexistence of various species in the region.

Keywords

mixed forest; regeneration; oak; beech; hornbeam; stand structure

1. Introduction

In the temperate region, most natural forest types (Buchwald 2005) are characterized by mixed overstory composition, as opposed to intensively managed stands (Peterken 1996). The number of tree species may differ in various forest types (Peterken 1996), but even natural stands of species-poor beech forests contain some admixing species (Czájlik et al. 2003, Feldmann et al. 2018). Mixedwoods have many advantages from both conservational and management aspects, although the effects of high tree species richness are not universal, and are sometimes contradictory (Pommerening and Murphy 2004). Mixed forests usually sustain a higher biodiversity of many different forest organism groups, because of the higher diversity of microhabitats, possible food sources and host species (Spiecker 2003, Cavard et al. 2011, Király et al. 2013). Admixing tree species are also capable of enhancing the stability of stands against biotic or abiotic stress and disturbances (Spiecker 2003, Jactel et al. 2005, Knoke et al. 2008). Moreover, based on the global meta-analysis of Zhang et al. (2012), higher tree species richness results in higher productivity. It also provides a higher level of ecosystem services (Gamfeldt et al. 2013), and may enhance adaptation to climate change (Brang et al. 2014).

Within a given climatic region (in our case, the temperate region), on the stand scale, natural regeneration is often influenced by several biotic and abiotic factors (Peterken 1996). Geomorphological characteristics, such as elevation, aspect, slope position or site productivity strongly affect saplings (Collins and Carson 2004). The species composition of the forest overstory influences the species richness and composition of the regeneration directly (via the established propagules), and, together with the stand structure, also indirectly (Ádám et al.

2013): The overstory structure of the stand (including the presence of a shrub layer) determines microclimatic conditions (Kovács et al. 2017). Among these, the effect of light conditions on regeneration is especially well studied (Emborg 1998, Gaudio et al. 2011, Parker and Dey 2008). Besides, forest stand structure and composition may also affect soil conditions, e.g. soil moisture or nitrogen availability, which also influence the regeneration (Collins and Carson 2004, Finzi and Canham 2000). Peterken (1996) emphasizes moreover the role of substrate and microsites (pits, mounds, bare soil patches, ground shaded by fallen trunks and branchwood, etc.) in the regeneration of trees. Besides physical and structural site characteristics, biotic interactions also affect forest regeneration. For example, the effects of the herbaceous understory vegetation (Jensen and Löf 2017, Mihók et al. 2005) and the presence of herbivores (Kuiters and Slim 2002, Modrý et al. 2004) are substantial.

On a coarser spatial scale, the surrounding landscape may also be an important factor in the regeneration, e.g. as a potential resource of propagules (D'Orangeville et al. 2008, Chazdon, 2017, Bobiec et al. 2018), while on a longer time scale, the disturbance regimes that establish and maintain the given forest type must be considered (Frelich 2002, Standovár and Kenderes 2003, Bobiec et al. 2011). Natural European beech forests are characterized by fine-scale gap dynamics (Standovár and Kenderes 2003, Schütz et al. 2016), while the disturbance regime sustaining oak-dominated forests is not so well defined (e.g. Vera 2000, Cowell et al. 2010, Bobiec et al. 2011 and 2018). In addition to the large number of possible factors, all the above variables may also affect regeneration through complex interactions with each other (Kuuluvainen et al. 1993, Janse-ten Klooster et al. 2007), and the relative importance of particular environmental factors varies between species (Finzi and Canham 2000, Lin et al. 2014, Modrý et al. 2004).

Human activities influence most of the drivers of the natural (not planted) regeneration, either directly or indirectly. Forest management has an evident and intensive effect on the stand level, since it strongly influences forest structure and composition. Numerous studies investigate the effects of different forestry systems on site conditions, and through these, tree regeneration (clear-cutting: Fleming et al. 1998, von Lüpke 1998; shelterwood system: Brose 2011, Modrý et al. 2004; retention harvesting: Montgomery et al. 2013; selection systems: Diaci and Firm 2011, Matonis et al. 2011). However, current regeneration may be influenced by historical land use as well as recent management, not only because past forest management determines the present-day overstory, but also via some other land use forms (coppicing, forest grazing, litter collecting) which had been modifying the forest site and the understory vegetation for a long time (Bobiec 2011, Diaci and Firm 2011).

Certain types of industrial forestry, such as the shelterwood forestry system, have already been applying natural regeneration for a long while (Matthews 1991, Brose 2011), but recently spreading, nature-based forestry systems rely upon it particularly strongly (Peterken 1996, Pommerening and Murphy 2004, Dobrowolska 2006, Schütz et al. 2016). Thus, understanding the most important drivers of natural regeneration is essential to the application of these increasingly popular management approaches. From a conservational point of view, it is also important to explore the environmental conditions which should be preserved or enhanced during management activities, in order to support high species richness in the regeneration, and indirectly, in the future forests.

As outlined above, many studies investigate the effects of one or a few environmental factors on regeneration. However, there are few studies – especially from Europe – that compare the relative importance of different factors, measuring many potential explanatory variables. Such investigations were carried out by Bobiec et al. (2011) with oak, by Hunziker and Brang (2005) with spruce and fir, and by Kuuluvainen et al. (1993) with pine, but these studies only used variables concerning the current environment, and did not include land use history. Moreover, most of such studies investigate some treatment-effects directly, not natural processes (Fleming et al. 1998, Matonis et al. 2011). Most papers mainly focus on the saplings of the dominant tree species; only a few studies concern the role of environmental effects on the entire assemblage of the regeneration (Modrý et al. 2004, Ádám et al. 2013, Lin et al. 2014, Bose et al. 2016). This study focuses on exploring the most important environmental and land use historical factors driving natural regeneration, in a region where forests are various regarding tree species composition, stand structure, forest history, and recent management.

Our questions were the following: (1) which explanatory variables (concerning stand structure, composition, site conditions, microclimate, landscape, and land use history) influence the composition, species richness and abundance of the regeneration of coniferous-deciduous mixed forests? (2) Which are the main drivers of the saplings of the dominant tree species (sessile oak, beech, hornbeam)? Once we have the results, we also evaluate how forest management can support the regeneration of mixedwoods.

2. Material and methods

2.1. Study area

The study was carried out in the Őrség National Park, West Hungary (N 46°51’–55’, E 16°07’–23’, cca. 13 km × 24 km, Fig. 1.). The topography consists of hills and wide valleys, with elevation between 250–350 m a.s.l.. Mean annual precipitation is 800 mm, average annual mean temperature is 9.0–9.5 °C (Dövényi 2010). The bedrock is alluviated gravel mixed with loess. The soil is acidic and nutrient poor, the most common soil type on hills is pseudogleyic brown forest soil (planosols or luvisols), while in the valleys, mire and meadow soils (gleysols) can be found (Krasilnikov et al. 2009, Stefanovits et al. 1999).

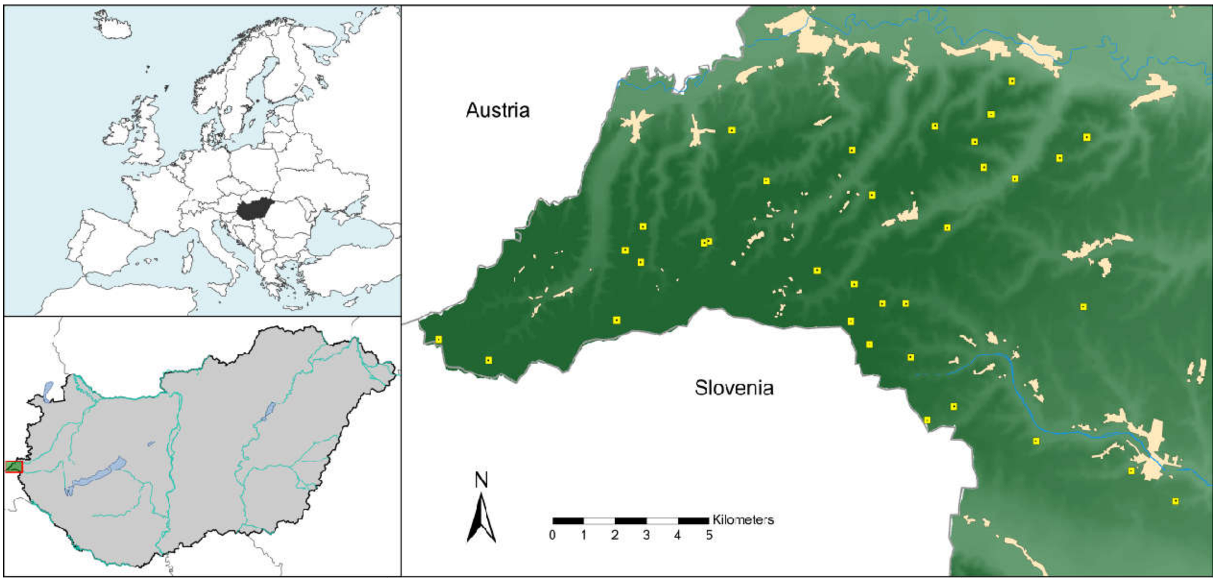

Fig. 1. The study area in the Őrség region, West Hungary (N 46°51'–55' and E 16°07'–23'); the squares show the sampling plots.

In the area, there are forests with various species composition and stand structure among similar climatic, topographical and bedrock conditions. Dominant species are beech (*Fagus sylvatica*), sessile and pedunculate oak (*Quercus petraea et Q. robur*), hornbeam (*Carpinus betulus*), Scots pine (*Pinus sylvestris*), and Norway spruce (*Picea abies*), present in both monospecific and mixed stands. The proportion of various subordinate species (*Betula pendula, Populus tremula, Castanea sativa, Prunus avium*, etc.) is relatively high (Tímár et al. 2002). Tree height varies between 20-30 m, and living stock is 300–600 m^3/ha.

The present diversity of the forests in the area is partly caused by the special landscape history (Tímár et al. 2002, Markovics 2016): From the 13th century, extensive farming and other land-use activities, such as litter collection and ridging (a special form of tillage) resulted in the deforestation and acidification of the area, and strong soil erosion. From the 19th century, extensive farming was repressed. Reforestation in the area began, mainly by Scots pine and pioneer tree species (*Betula pendula, Populus tremula*). Farmers traditionally applied spontaneous selective cutting: firewood was selectively logged every year, but trees for timber were retained for longer. This practice caused a continuous, intensive forest use, which maintained a continuous, uneven aged forest cover. The various routines of the farmers resulted in a high spatial heterogeneity of management. Besides logging, forests were also used in some other ways. Grazing, litter and moss collection were commonly practiced. The developing conditions were favourable to species that prefer nutrient poor and disturbed conditions. Later, from the middle of the 20^{th} century, forest management became heterogeneous in a new way: private forests continued to be managed by a spontaneous selection system, but in the state-owned stands, industrial shelterwood or clear-cutting system was applied (Matthews 1991, Tímár et al. 2002, Markovics 2016). Currently, ancient and recent stands form a fine-scale mixture in the region. The coexistence of pioneer and late successional forest species creates a remarkably rich and various species composition. However, the cessation of traditional forest utilization (spontaneous selection, grazing, litter collecting), and the consequential succession of the forests lead to changes in tree species composition. Deciduous species (hornbeam, beech) are taking over from the vanishing acidophilous pioneer species (Tímár et al. 2002). The understory is formed by mesophilic and acidophilic species, and the shrub layer mainly consists of the saplings of beech, hornbeam and admixing species. Herbaceous cover and the amount of tree saplings highly vary among the stands.

2.2. Data collection

In this study, the abundance and species composition of the regeneration layer were used as dependent variables, while the potential explanatory variables were related to tree species composition of the overstory, stand structure, microclimate, soil conditions, landscape, and forest history (Table 1).

Explanatory variables	Minimum	Mean	Maximum
Overstory tree species composition			
Tree species richness	2.00	5.59	10.00
Tree species Shannon diversity (H')	0.19	0.90	1.95
Relative volume of beech (%)	0.00	28.75	94.33
Relative volume of hornbeam (%)	0.00	3.57	21.80
Relative volume of oaks (*Q. petraea, Q. robur* and *Q. cerris, %*)	1.16	37.16	96.46
Relative volume of Scots pine (%)	0.00	26.49	78.60
Relative volume of Norway spruce (%)	0.00	1.93	14.43
Relative volume of other mixing trees (%)	0.00	1.87	17.29
Stand structure			
Density of trees (stems/ha)	218.75	593.93	1318.75
Density of large trees (>50 cm DBH, stems/ha)	0.00	16.54	56.25
Basal area of trees (m^2/ha)	24.10	34.08	49.68
Mean DBH of trees (cm)	13.64	26.30	40.61
Variation coefficient of DBH	0.17	0.48	0.98
Volume of snags (m^3/ha)	0.00	12.17	64.59
Volume of logs (m^3/ha)	1.16	10.15	35.59
Density of shrubs (>50 cm height, <5 cm DBH, stems/ha)	0.00	947.43	4706.25
Forest floor			
Cover of mineral soil (m^2/ha)	8.56	145.85	472.22
Cover of litter (m^2/ha)	7814.99	9391.93	9833.66
Forest site characteristics			
Litter weight (g/900 cm^2)	105.41	148.32	243.08
Proportion of deciduous litter (%)	5.54	15.07	32.80
Litter pH	4.86	5.29	5.68
Litter nitrogen content (%)	0.83	1.28	1.84
Soil pH	3.96	4.32	4.84
Soil hydrolitic acidity (0-10 cm)	20.68	30.45	45.22
Soil fine texture (clay and silt) proportion (%, 0-10 cm)	27.60	52.06	68.60
Soil carbon content (%, 0-10 cm)	3.30	6.49	11.54
Soil nitrogen content (%, 0-10 cm)	0.11	0.22	0.34
Soil phosphorus content (mgP_2O_5/100g, 0-10 cm)	1.96	4.32	9.35
Microclimate			

Mean relative diffuse light (%)	0.62	2.97	10.36
Variation coefficient of relative diffuse light	0.12	0.50	1.23
Temperature difference (K)	-0.93	-0.08	0.73
Temperature range difference (K)	-0.42	0.90	2.35
Air humidity difference (%)	-1.83	0.79	3.32
Air humidity range difference (%)	-2.27	1.80	6.58
Landscape			
Proportion of forests in the landscape (%)	56.92	89.64	100.00
Proportion of open areas in the landscape (%)	0.00	4.86	45.25
Landscape diversity (H')	0.11	1.11	1.86
Land use history (1853)			
Proportion of forests in the landscape in 1853 (%)	24.03	75.98	100.00
Proportion of arable lands in the landscape in 1853 (%)	0.00	16.64	61.27
Plot was forest (binary)	0	0.79	1
Plot was arable land (binary)	0	0.18	1

Table 1. Potential explanatory variables. Minimum, mean and maximum values are given for the 34 studied plots.

Thirty-four stands were selected by stratified random sampling from the stand structural database of the Hungarian National Forest Service (Table 1., Fig. 1.). The stratification criterion was tree species composition; the selected stands represent different combinations of the main tree species of the area (oak, beech, Scots pine, Norway spruce and hornbeam). Further criteria of the site selection were as follows: age of dominant trees between 70 and 100 years, relatively level ground, absence of direct water influence, and spatial independence of other sites (distance min. 500 m). From the categories – based upon tree species composition –, sample sites were selected randomly. In this way, the sample was representative for the mixed forests of the Őrség region. Such mixed forests are common in many of the lowland and hilly regions of Europe. Most of the investigated stands were managed by various forestry systems (spontaneous or standardized selection, or shelterwood forestry systems), but we also sampled two unmanaged reserves. Through its impact on the stand structure and tree species composition, management had an indirect effect on the studied regeneration, however, direct human effects did not influenced the survey: We chose only closed, mature stands, which have not been cut for several decades. Regeneration in the investigated stands was natural, not influenced by artificial reproduction, cleaning or nursing. Mean canopy openness was 10.9%, canopy openness of the individual sites ranged from 4.0 to 23.2%.

We designated one 40 m × 40 m block in each stand, representative of the stand's general tree species composition, canopy closure and structure, and not containing forest paths or other human disturbances. In this block, all tree individuals above 5 cm diameter at breast height (DBH) were mapped. Species identity, DBH, and height of each tree individual were recorded. The mean DBH of the upper canopy layer was about 40 cm. We determined the density of large trees, which were defined as trees with DBH larger than 50 cm. We calculated the relative volume of each tree species (beech, hornbeam, oaks, Scots pine, Norway spruce, subordinate trees), using specific equations based on DBH and tree height (Sopp and Kolozs 2000). *Quercus petraea, Q. robur and Q. cerris* were merged as oaks, because distinction of *Q. petraea* and *Q. robur* was difficult due to hybridisation, and *Q. cerris* was rare. Other rare tree species were merged as other admixing trees. Tree species Shannon diversity (H') was calculated, based on the relative volume of tree species, using natural logarithm (Shannon and Weaver 1949). DBH and length of snags and logs were also measured, and their volume was calculated. Density of shrubs (woody plants higher than 0.5 m, but with DBH below 5 cm) was calculated.

From the entire range of the regeneration, in this paper we focus only on seedlings as dependent variables, defined as woody plants (both tree and shrub species) shorter than 0.5 m.

The drivers of the shrub layer were not analysed, since we assumed that it is much more exposed to human management than smaller seedlings, thus its natural drivers cannot be explored in this way. Its reason is that, according to the forestry practice in Hungary, managers may clean the shrub layer – both shrub species and undesirable admixing tree species – to keep the stands clean. The inventory of the seedlings was carried out in 30 m × 30 m plots, positioned in the centre of each 40 m × 40 m block. Plots were divided into 36 contiguous 5 m × 5 m quadrats, where absolute cover (dm^2) of every species from the seedling category was estimated visually. We did not discriminate between *Quercus petraea* and *Q. robur* seedlings (considering both as *Q. petraea*). Nomenclature of plants follows Tutin et al. (1964-1993).

We estimated the cover of mineral soil and litter within the quadrats. Litter was collected from five 30 cm × 30 cm areas from every plot: the centre, and along the four diagonals, from halfway between the centre and the corners. Measured litter variables were weight, proportion of deciduous litter, pH (in water) and nitrogen content. Five soil samples per plot were collected from the same locations as the litter samples. The following variables were measured from the upper 10 cm of the samples: pH in water, clay (<0,002 mm) and silt (0,002 – 0,02 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, Langenselbold, Germany), and ammonium-lactate/acetic-acid (AL-) extractable phosphorus content (Bellér 1997). Air humidity and temperature were measured in one point per plot (in the centre), at 1.3 m height, with Voltcraft DL-120 TH data loggers (Conrad Electronic SE, Hirschau, Germany). Measurements were taken eight times, in three growing seasons (June and October 2009; June, August, September and October 2010; March and May 2011). Each time, 5-minute recording frequency was applied, for 24 hours. Every site was measured within a five-day period. During this period, two reference plots were measured permanently. Differences from the reference were calculated for the measured values of the quadrats. Relative daily mean and range values were expressed for both variables, and averaged over the eight measurement periods. See more methodological details of the microclimate measurements in Kovács et al. (2017). Diffuse light was measured in all the 36 quadrats per plot, with LAI-2000 Plant Canopy Analyzer instruments (LICOR Inc. 1992, Tinya et al. 2009a). Relative diffuse light values were calculated by using data from parallel reference measurements, carried out in nearby open fields. Repeated measurements are not necessary with this device. Plot-level light conditions were calculated as the mean and coefficient of variation of the 36 relative diffuse light values taken in each of the plots' quadrats.

We estimated the proportion of different land cover types in a 300 m radius area around every plot based on aerial photos, maps and the forest stand database. We calculated landscape diversity based on the relative proportion of each cover type, using the Shannon index. Regenerating areas (tree age <20 years), forests (tree age >20 years) and non-forested areas (meadows and arable lands) were distinguished. We characterized the land use history of the plots and their surroundings (300 m radius) using the Second Military Survey of the Habsburg Empire from 1853 (Arcanum 2006). The presence or absence of forests and arable lands in the plots was recorded, and the proportion of forested areas and arable fields in the historical landscape was calculated.

2.3. Data analysis

All analyses were conducted with ln-transformed cover data of the species. Some explanatory variables were also ln-transformed, to fulfil normality conditions. All explanatory variables were standardized. For the statistical selection procedure, we selected only those explanatory variables which showed a strong and consistent relationship with the dependent variable, and the intercorrelations with other explanatory variables were weak (R<0.5, Borcard et al. 2011, Faraway 2005).

To identify the effects of explanatory variables on species composition, redundancy analysis (RDA) was carried out (Borcard et al., 2011). Only species occurring at least in three plots were included. Explanatory variables were forward selected; significance of the model and the canonical axes was tested by F-statistics (Monte Carlo simulation with 10000 permutations).

We explored the effects of the explanatory variables on the species richness and the cover of the regeneration layer by general linear modelling (Faraway 2005). The minimal adequate model was built with backward elimination, using deviance analysis with F-test (ANOVA). After model selection, linearity between the dependent and explanatory variables and constancy of the residual error variance were checked. We created similar general linear models for the cover data of the three most frequent and abundant species in the regeneration (sessile oak, hornbeam and beech). Although coniferous species constituted more than 20% of the stand volume, none of them was abundant in the regeneration layer. In all of the three models, the effect of the conspecific trees (the relative volume of the same species in the overstory layer) proved to be significant. As we assumed that this effect is related to the propagule limitation of the species, which may mask the effects of other explanatory variables, we also created partial linear models using the conspecific species as covariables (Legendre and Legendre 2003). This way we were able to explore the proportion of the variation of the response variable attributed to the other factors, excluding the effects of conspecific trees.

All analyses were performed with R version 3.4.0 (The R Foundation for Statistical Computing 2016). We used the package “vegan” for the RDA (Oksanen et al. 2015).

3. Results

Altogether, 39 woody species (28 tree and 11 shrub species) were recorded in the regeneration layer. Mean and standard deviation of woody species richness in the plots was 9.71±4.35. Minimum species number was 3, maximum 19. Mean and standard deviation of regeneration cover in the plots was 3.00±2.63%, with a minimum of 0.10% and a maximum of 10.07%. The main deciduous tree species of the region (beech, hornbeam and sessile oak) proved to be the most frequent and abundant species within the seedlings (Table 2., Table 3.). Hornbeam had about seven times larger proportion in the regeneration than in the canopy. The cover of Scots pine seedlings was very low, although it was the third most abundant species in the overstory. Norway spruce was the most abundant coniferous species in the regeneration, its proportion was similar to that in the overstory (Table 2.).

Species	**Rel. volume in canopy layer (%)**	**Rel. cover in regeneration layer (%)**
Beech	28.75	37.95
Hornbeam	3.57	26.25
Oaks (*Q. petraea, Q. robur* and *Q. cerris*)	37.16	22.02
Scots pine	26.49	0.31
Norway spruce	1.93	1.88
Other admixing trees	1.87	8.37

Table 2. Proportion of the main tree species in the overstory and in the regeneration layer. In the overstory, it is expressed as the relative volume of the species, in the case of the regeneration layer relative cover is shown.

According to the RDA, the most important drivers of the species composition were tree species richness, the amount of relative diffuse light, the proportion of beech in the overstory, and the heterogeneity of tree diameters (Table 4., Fig. 2.). The trends of light and DBH-heterogeneity were similar. Three RDA axes were significant: the first axis explained 18.45% of the species variance (F=8.14, p=0.001), the second 7.85% (F=3.46, p=0.001), and the third

5.67% (F=2.05, p=0.002). The whole model explained 34.31% of the variance (F=3.79, p=0.001).

Code	Species	Cover (m^2/ha)	Frequency
abialb	*Abies alba*	0.02	1
acecam	*Acer campestre*	0.72	2
acepla	*Acer platanoides*	0.06	1
acepse	*Acer pseudolatanus*	7.80	5
betpen	*Betula pendula*	6.61	5
carbet	*Carpinus betulus*	3299.62	32
cassat	*Castanea sativa*	38.83	7
corave	*Corylus avellana*	142.83	17
corsan	*Cornus sanguinea*	18.44	6
cramon	*Crataegus monogyna*	18.89	14
euoeur	*Euonymus europaeus*	0.67	1
fagsyl	*Fagus sylvatica*	3030.91	31
fraaln	*Frangula alnus*	34.68	13
fraexc	*Fraxinus excelsior*	10.28	3
jugreg	*Juglans regia*	0.67	1
juncom	*Juniperus communis*	5.11	3
lardec	*Larix decidua*	3.78	1
ligvul	*Ligustrum vulgare*	79.33	4
malsyl	*Malus sylvestris*	2.44	3
picabi	*Picea abies*	92.64	26
pinsyl	*Pinus sylvestris*	10.89	14
popcan	*Populus canescens*	4.44	1
poptre	*Populus tremula*	7.35	7
pruavi	*Prunus avium*	117.48	24
pruspi	*Prunus spinosa*	14.64	8
pyrpyr	*Pyrus pyraster*	39.89	17
quecer	*Quercus cerris*	25.17	3
quepet	*Quercus petraea*	2185.52	34
querub	*Quercus rubra*	9.44	7
rhacat	*Rhamnus catharticus*	8.78	8
robpse	*Robinia pseudoacacia*	111.89	1
salcap	*Salix caprea*	13.61	6
sorauc	*Sorbus aucuparia*	0.11	1
sortor	*Sorbus torminalis*	9.83	1
taxbac	*Taxus baccata*	0.19	1
tilcor	*Tilia cordata*	822.50	5
tilpla	*Tilia platyphyllos*	4.06	6
ulmgla	*Ulmus glabra*	0.89	1

vibopu	*Viburnum opulus*	22.06	6

Table 3. List of the recorded woody species in the regeneration layer. Frequency is the number of occurrences among the investigated 34 plots.

Variable	**Variance (%)**	**F-value**	**p**
Tree species richness	8.61	3.80	0.002
Relative diffuse light	8.19	3.61	0.001
Relative volume of beech	6.05	2.67	0.014
Variation coefficient of DBH	4.31	1.90	0.040

Table 4. Explained variance (%) of the significant explanatory variables in the redundancy analysis (RDA).

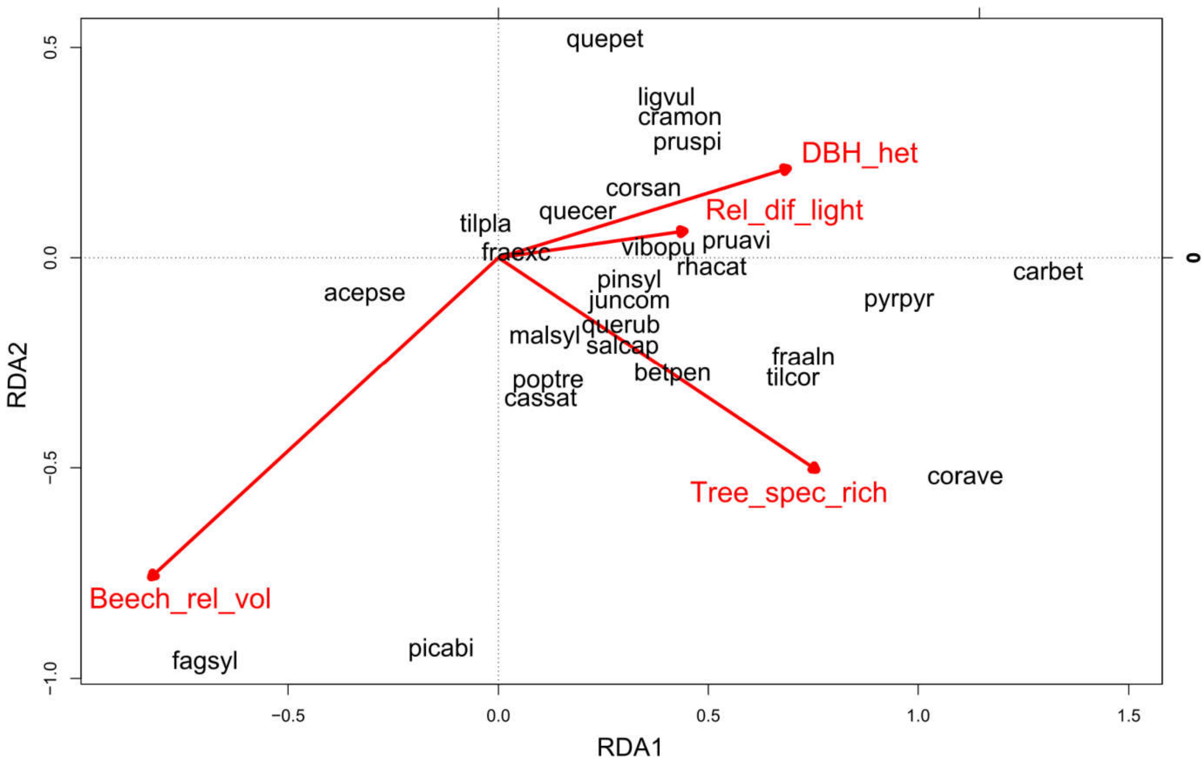

Fig 2. Distribution of species (black) and explanatory variables (red) at the first and second redundancy analysis axes. Beech_rel_vol: relative volume of beech; DBH_het: variation

coefficient of diameter at breast height; Rel_dif_light: mean relative diffuse light; Tree_spec_rich: tree species richness. Species abbreviation consists of the first three letters of the genus and the species names. See full names in the Table 3.

Carpinus betulus, *Corylus avellana* and *Pyrus pyraster* were the most strongly related to sites with high tree species richness, large amount of light, and with heterogeneous tree size distribution, but most of the species (both trees and shrubs) also preferred these stands. *Tilia platyphyllos* and *Fraxinus excelsior* were indifferent to these variables, while *Fagus sylvatica*, *Picea abies* and *Acer pseudoplatanus* regenerated mainly in structurally homogeneous and shady, beech dominated stands (Fig. 2.).

The linear models showed that the cover of the regeneration is mainly related to the density of large trees (DBH >50cm) and to the amount of relative diffuse light, while for regeneration species richness, light and tree species richness were the most important variables (Table 5.). Explained variances were 31% and 41% for cover and species richness, respectively. For the cover of sessile oak, hornbeam and beech regeneration, the proportion of the conspecific species in the overstory was determinant. Besides this evident relationship, for oaks, the amount of light, and in the partial model, some site characteristics (soil phosphorus content [positive effect] and litter pH [negative effect]) were also important. The proportion of arable land in the landscape in the past also had a negative effect on oak regeneration. The explained variance was 52% in the full model, and 38% in the partial model. For hornbeam, the proportion of arable land in the past was more important than the presence of the species in the canopy, and this species was strongly related to sites with high tree species richness. When excluding conspecific trees in the partial model, besides arable land cover in the past, the amount of diffuse light had a significant positive effect. The full model explained 43%, and the partial model 45% of the variance. The cover of beech regeneration was positively related to beech proportion in the overstory and to the proportion of mature forests in the landscape, and negatively to litter nitrogen content and the proportion of arable land in the historical landscape (explained variance: 55%). In the partial model, the density of large trees, soil phosphorus content, and tree size had significant positive, while litter nitrogen content negative effects (explained variance: 36%).

Variable	Sense	Variance (%)	F value, significance
Cover of the regeneration; R^2 = 0.31			
Density of large trees (DBH >50 cm)	+	18.80	9.03**
Mean relative diffuse light	+	16.65	8.00**
Species richness of the regeneration; R^2 = 0.41			
Mean relative diffuse light	+	28.24	15.90***
Tree species richness in the overstory	+	16.7	9.40**
Cover of sessile oak; R^2 = 0.52			
Relative volume of oaks	+	39.33	26.87***
Mean relative diffuse light	+	15.29	10.45**
Partial model for sessile oak; R^2 = 0.38			
Soil phosphorus content	+	18.15	9.64**
Proportion of arable lands in1853	-	15.51	8.24**
pH of litter	-	9.85	5.23*
Cover of hornbeam; R^2 = 0.43			
Proportion of arable lands in 1853	+	22.72	13.25**
Relative volume of hornbeam	+	15.41	8.99**
Tree species richness in the overstory	+	10.43	6.08*
Partial model for hornbeam; R^2 = 0.45			
Proportion of arable lands in 1853	+	35.96	21.38***
Mean relative diffuse light	+	14.00	7.03*
Cover of beech; R^2 = 0.55			
Relative volume of beech	+	30.40	22.38***
Proportion of mature forests in the landscape	+	13.81	10.17**
Litter nitrogen content	-	9.58	7.04*
Proportion of arable lands in 1853	-	6.84	5.04*

Partial model for beech; R^2 = 0.36			
Density of large trees	+	17.95	9.34**
Litter nitrogen content	-	8.94	4.65*
Soil phosphorus content	+	8.69	4.52*
Mean DBH of trees	+	8.66	4.50*

Table 5. Significant explanatory variables of the different regression models. R^2: adjusted coefficient of determination of the models; Sense: the sense of the parameter of the variables in the regression equation; Variance %: 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. Partial models show the effect of the different explanatory variables once the effect of the mother trees (relative volume of the given tree species in the overstory) has been taken into account.

4. Discussion

4.1. Effects of the environmental and land use history factors

According to our results, community variables (species richness, composition and cover) of the regeneration could be mostly explained by the features of the current forest stand. Other studies found that the overstory accounted for the composition of the regeneration to a similar extent (Ádám et al. 2013, McKenzie et al. 2000). The only significant microclimatic variable was relative diffuse light, which is directly determined by the overstory layer. Characteristics of the forest floor, forest site, landscape and land use history were not key drivers of the community characteristics of the regeneration layer.

Tree species richness was one of the most important drivers of regeneration, similarly to the results of Ádám et al. (2013) in oak forests. It explained the largest proportion of the variance in the composition (RDA) model, and was the second most important variable in the species richness model. The seedlings of admixing tree species (e.g. *Pyrus pyraster, Tilia cordata,* *Betula pendula*) were particularly strongly related to stands with high tree species richness. The obvious explanation for this phenomenon seems to be the effect of the parent trees. This may partly be true, as in the case of the individually investigated species, especially the two species with large fruits (sessile oak and beech), relative volume of the given species in the overstory was a main driver of the regeneration. However, this cannot be the only reason, as in many stands, different species occurred in the regeneration than in the overstory layer. As forest stands with different species compositions create a heterogeneous, fine-scaled mosaic in the area, propagule limitation is presumably not too strong for most of the species, even if they are not present in a given stand. This can be especially relevant for anemochor trees, such as *Carpinus, Tilia, Betula* and *Pinus*. Thus we may suppose that besides providing propagules, tree species richness also increases the structural diversity of the stand. According to the heterogeneity-diversity hypothesis, heterogeneous environment ensures more niches, which decreases interspecific competition (Wilson 2000). Heterogeneous tree species composition can create various light conditions and microsites for the regeneration of many different woody species (Tinya et al. 2016). The presence of light in every model of the community variables, and of structural variables in the various models (DBH-heterogeneity in the RDA, density of large trees in the cover model) also support this explanation.

Our results about the role of light for the cover of the regeneration correspond well to those known from literature. Light can directly promote the growth of seedlings, increasing the cover of the regeneration (Finzi and Canham 2000, Ostrogović et al. 2010, Ligot et al. 2013). However, only a few studies investigated the drivers of the diversity of the whole regeneration assemblage (Ádám et al. 2013, Lin et al. 2014, Bose et al. 2016), and we could not find any demonstrating a significant relationship between light and regeneration diversity. This means that our result, namely, the positive effect of light on the species richness of the regeneration provides novel insight into this relation. A possible explanation for this result is that in highly closed stands, the low amount of light limits not only the growth, but even the establishment of many woody species.

Based on the ordination, the effects of light and DBH-heterogeneity on the composition of the seedlings cannot readily be distinguished. Most of the shrub species (e.g. *Corylus avellana, Frangula alnus, Crataegus monogyna, Prunus spinosa*) prefer stands with open canopies and heterogeneous stand structure. This is in agreement with Tinya et al. (2009b), who investigated the light-demands of particular species in these forests. Ádám et al. (2013) also found that structural heterogeneity of the stand is among the main drivers of the regeneration.

The density of large trees proved to be the main driver of regeneration cover. Large trees promote regeneration both by propagule production and by enhancing microsite heterogeneity. They often have broken parts in their canopy, where more light can penetrate. The presence of large trees may also indicate less intensive management (e.g. continuous cover forestry instead of industrial shelterwood forestry system, Pommerening and Murphy 2004), which results in lower tree density, and a more aggregated distribution of resources. The enhanced structural heterogeneity of the stands may be favourable for regeneration.

The relative volume of beech in the overstory had a negative effect on the regeneration. Apart from beech, only two species (*Picea abies* and *Acer pseudoplatanus*) were positively related to beech stands, both shade-tolerant (Hunziker and Brang 2005, Modrý et al. 2004). The regeneration layer of beech-dominated forests is usually species-poor, basically due to the homogeneous stand structure and low light level of managed beech stands. However, even in gaps of the canopy layer, where structural heterogeneity and irradiance are higher, species richness of the regeneration rises only to 5-6 species (Feldmann et al. 2018, Mountford et al. 2006, Schnitzler and Closset 2003).

Considering the individual responses of the dominant species of the regeneration (sessile oak, beech and hornbeam), we find that the relative volume of a given species in the overstory layer is always a significant driver of the seedling cover. Conspecific trees in the canopy layer can affect the regeneration directly as propagule sources (parent trees), but there may also be an indirect relationship: it is possible that the local environment facilitates the regeneration of the same species as earlier, 70-100 years ago, when the current forest stand was established. However, variance explained by the conspecific trees varies for the different species, and there are also substantial differences between the other explanatory variables relevant for the species, in accordance with their specific demands (Lin et al. 2014). We generally observed that forest site, landscape and land use history variables influence the cover of the individual species much more strongly than the assemblage-level variables (species richness, cover and composition) of the regeneration.

Based on our results, parent trees are extremely important for the establishment of sessile oak in the regeneration. This contradicts some studies, which found no relationship between oak regeneration and the presence of the species in the overstory (Mosandl and Kleinert 1998, Dobrowolska 2006). It is often explained by the acorn-dispersing ability of European jays (*Garrulus glandarius*) for long distances (Kollmann and Schill 1996, Mosandl and Kleinert 1998), but according to Bobiec et al. (2018), the role of jays is more prominent in landscapes with more non-forest habitats than in closed forests. In our case, the strong correspondence of oak regeneration with the parent trees suggest that in this region, oak regenerates mainly from the acorns of the local mother trees, which is in agreement with the findings of Ádám et al. (2013). The second significant explanatory variable for oak was relative diffuse light. This species is generally considered light-demanding (Ligot et al. 2013, Van Couwenberghe et al. 2013, Sevillano et al. 2016, Schütz et al. 2016), but many studies showed that young seedlings of oaks are shade-tolerant, and need direct light only some years after germination (Ostrogović et al. 2010, von Lüpke 1998). According to our results, small seedlings (<50 cm height) may already be light-demanding.

After excluding the effects of parent trees by partial modelling, we find that some forest site and land use history variables are also important for the *Quercus* seedlings' cover. It was positively related to low litter pH, in congruence with its ecological indicator value for acidity (Horváth et al. 1995), and the findings of Ádám et al. (2013). In the studied region, low litter pH is mainly associated with pine forests (Ódor et al. 2015). Von Lüpke (1998) also found that oaks regenerate well under pine forests, because of their favourable light conditions and suitable soils. We also found that the proportion of historical arable lands in the surrounding area had a negative effect on the cover of oak seedlings. We suppose that as oaks are dispersal-limited, slowly growing species, thus temporal continuity of the forest landscape is especially important to them.

The drivers of hornbeam regeneration are strikingly different from those of the oaks. The most important factor was the proportion of arable lands in the surrounding area in the past, but in this case, it had a positive sign. This result implies that hornbeam does not require long-term forest continuity, but prefers secondary forested landscapes. Historically, after the cessation of farming, secondary succession began in the region with the establishment of pine forests (Tímár et al. 2002, Markovics 2016). Hornbeam is a well-dispersing, anemochorous species. Its regeneration is not strongly dependant on the presence of parent trees in the stand, thus it is able to colonize the pioneer pine forests. The prevalent process of the region, namely, the diminishing of pine and the increase of hornbeam (and other deciduous species) in the regeneration layer was well visible in our study. This can be explained by both the natural process of succession, and the altered disturbance regimes of these forests (cessation of grazing, litter and moss collection).

As hornbeam seedlings occur not only in pine stands, but also in oak-hornbeam forests, the relative volume of hornbeam trees in the canopy is also present in the model. Since oak-hornbeam forests have high canopy closure and low understory light (Bölöni 2008), hornbeam is considered to be a shade-tolerant species (Modrý et al. 2004). However, if we extract the effect of hornbeam trees from the model, we find that hornbeam regeneration is also driven by light. This can be seen on the ordination plot as well. Tinya et al. (2009b and 2016) also found that when comparing numerous stands, hornbeam seems to be shade-tolerant (since it often occurs in closed, dark oak-hornbeam stands), but its within-stand spatial pattern is positively related to light. This species was indifferent to site conditions: none of the forest site variables was present in the model.

The cover of beech seedlings had remarkably various drivers: overstory, forest site, landscape and land use history variables all influenced its abundance. As this species has large fruits, it is also dispersal-limited (Mihók et al. 2005). In accordance with this, the relative volume of beech in the overstory was the first driver of the regeneration's cover, but, compared to oak, with a weaker effect. This is presumably due to the different size of their fruit, and the ensuing difference in their dispersal ability. Beech seedling cover was positively related to the proportion of mature forests in the landscape, and negatively to the proportion of arable lands in the past. This demand for spatial and temporal forest continuity may also be explained by the dispersal-limitation.

In the partial model for beech regeneration, overstory structural variables also appeared: the density of large trees and the mean DBH of trees enhanced the cover of beech seedlings. Larger trees promote regeneration by their heavy propagule production, and by the establishment of various microsites. However, microsite-variability in this case does not indicate heterogeneous light conditions, because this species proved to be completely independent from irradiance (light was absent even from the partial model). The observed shade-tolerance of beech is in accordance with many previous studies (Emborg 1998, Modrý 2004, Schnitzler and Closset 2003, Ligot et al. 2013).

As our project was an observational study and not an experiment, it has its limitations. We cannot confirm any cause-and-effect relationships; we can only describe correlations between the regeneration and the potential explanatory variables. The relationships may also be indirect, e.g. if the regeneration and the explanatory variables are driven by the same, not measured environmental variable. To verify the explored relationships, experimental studies are necessary, for which the current research is a good starting point.

4.2. Implications for conservation and management

According to our results, community variables of the regeneration are mainly driven by the characteristics of the current forest stands, thus they can be strongly influenced by management. Compositional and structural heterogeneity of the overstory layer plays a key role in the maintenance of a heterogeneous regeneration. Large tree species richness ensures propagule sources for the regeneration of various tree species, and in addition, it results in heterogeneous light conditions and microsites for the tree and shrub seedlings. Heterogeneous age distribution and the presence of large trees in the stands also increase the number of potential sites for the establishment of regeneration. The maintenance of these stand structural and compositional factors can serve multiple purposes, since they also help the preservation of the diversity of other forest organism groups (birds, spiders, bryophytes, lichens, fungi, herbs), as explored in other investigations within the same project (Márialigeti et al. 2009, Király and Ódor 2010, Nascimbene et al. 2012, Király et al. 2013, Ódor et al. 2013, Samu et al. 2014, Kutszegi et al. 2015, Mag and Ódor 2015, Márialigeti et al. 2016).

With some amount of extra effort, high tree species diversity can be maintained in the course of the shelterwood forestry system. However, most of the listed aims (heterogeneous tree size distribution, large trees, various light conditions) are much better achieved by continuous cover forestry. This management system is traditionally applied in the region (in the form of spontaneous selection), but from a conservational aspect, the increase of its ratio would be desirable, in the form of standardized selective cutting, which adapts knowledge from spontaneous selection into the planning process.

A high variety of drivers proved to be of importance for the different species, and besides the stand structural variables, some forest site, landscape and land use history variables also affected their occurrence. Therefore, it is reasonable to suggest that maintaining the landscape-scale heterogeneity of forest types and management systems helps the coexistence of various species in the region. Retaining unmanaged stands within the landscape is also highly important, because in these forests, natural processes can prevail, which usually lead to heterogeneous structure and composition, and a rich regeneration layer.

If forest management is able to ensure the establishment of a complex regeneration layer, forest stand heterogeneity can be maintained for the future, from which the entire forest biota will benefit.

Acknowledgement

We thank Balázs Németh, István Mazál, László Bodonczi, Zsuzsa Mag and Ákos Molnár for their help in the field survey and Tibor Standovár for the light measuring instruments. Bence Kovács contributed to the microclimate-analysis. The project was funded by the Hungarian Science Foundation (OTKA 79158), the National Research, Development and Innovation Fund of Hungary (PD 123811, GINOP-2.3.2-15-2016-00019), and the Őrség National Park Directorate.

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