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7 Environmental drivers of the forest regeneration in temperate mixed forests

8

9 Flóra Tinya<sup>1,\*</sup>, Sára Márialigeti<sup>2</sup>, András Bidló<sup>3</sup>, Péter Ódor<sup>1,4</sup>

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11 <sup>1</sup>MTA Centre for Ecological Research, Institute of Ecology and Botany, Alkotmány u. 2–4.,  
12 H-2163 Vácraát, Hungary

13 <sup>2</sup>Zichy P. u. 3/1, H-2040 Budaörs, Hungary

14 <sup>3</sup>Department of Forest Site Diagnosis and Classification, University of Sopron, Pf. 132, H-  
15 9401 Sopron, Hungary

16 <sup>4</sup>MTA Centre for Ecological Research, GINOP Sustainable Ecosystem Research Group,  
17 Klebelsberg K. u. 3., H-8237 Tihany, Hungary

18

19 \* Corresponding author

20 E-mail addresses: [tinya.flora@okologia.mta.hu](mailto:tinya.flora@okologia.mta.hu) (F. Tinya), [sara.marialigeti@gmail.com](mailto:sara.marialigeti@gmail.com) (S.  
21 Márialigeti), [bidlo.andras@uni-sopron.hu](mailto:bidlo.andras@uni-sopron.hu) (A. Bidló), [odor.peter@okologia.mta.hu](mailto:odor.peter@okologia.mta.hu) (P. Ódor)

22

23 Abstract

24 As modern silviculture in natural forests is based on natural regeneration, finding the most  
25 important drivers of regeneration is crucial for forestry as well as conservation. We explored  
26 the relationship between numerous environmental and land use history variables and the

27 species richness, cover and composition of the regeneration layer, and also the cover of the  
28 dominant species of the regeneration (sessile oak, hornbeam and beech) in coniferous-  
29 deciduous mixed forests. We identified the key factors which forest management can  
30 influence to support the regeneration of mixedwoods.

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

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

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

52

53 Keywords

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

55

56 1. Introduction

57 In the temperate region, most natural forest types (Buchwald 2005) are characterized by  
58 mixed overstory composition, as opposed to intensively managed stands (Peterken 1996). The  
59 number of tree species may differ in various forest types (Peterken 1996), but even natural  
60 stands of species-poor beech forests contain some admixing species (Czajlik et al. 2003,  
61 Feldmann et al. 2018). Mixedwoods have many advantages from both conservational and  
62 management aspects, although the effects of high tree species richness are not universal, and  
63 are sometimes contradictory (Pommerening and Murphy 2004). Mixed forests usually sustain  
64 a higher biodiversity of many different forest organism groups, because of the higher diversity  
65 of microhabitats, possible food sources and host species (Spiecker 2003, Cavard et al. 2011,  
66 Kiraly et al. 2013). Admixing tree species are also capable of enhancing the stability of stands  
67 against biotic or abiotic stress and disturbances (Spiecker 2003, Jactel et al. 2005, Knoke et al.  
68 2008). Moreover, based on the global meta-analysis of Zhang et al. (2012), higher tree species  
69 richness results in higher productivity. It also provides a higher level of ecosystem services  
70 (Gamfeldt et al. 2013), and may enhance adaptation to climate change (Brang et al. 2014).

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

77 2013): The overstory structure of the stand (including the presence of a shrub layer)  
78 determines microclimatic conditions (Kovács et al. 2017). Among these, the effect of light  
79 conditions on regeneration is especially well studied (Emborg 1998, Gaudio et al. 2011,  
80 Parker and Dey 2008). Besides, forest stand structure and composition may also affect soil  
81 conditions, e.g. soil moisture or nitrogen availability, which also influence the regeneration  
82 (Collins and Carson 2004, Finzi and Canham 2000). Peterken (1996) emphasizes moreover  
83 the role of substrate and microsites (pits, mounds, bare soil patches, ground shaded by fallen  
84 trunks and branchwood, etc.) in the regeneration of trees. Besides physical and structural site  
85 characteristics, biotic interactions also affect forest regeneration. For example, the effects of  
86 the herbaceous understory vegetation (Jensen and Löf 2017, Mihók et al. 2005) and the  
87 presence of herbivores (Kuiters and Slim 2002, Modrý et al. 2004) are substantial.

88 On a coarser spatial scale, the surrounding landscape may also be an important factor in the  
89 regeneration, e.g. as a potential resource of propagules (D'Orangeville et al. 2008, Chazdon,  
90 2017, Bobiec et al. 2018), while on a longer time scale, the disturbance regimes that establish  
91 and maintain the given forest type must be considered (Frelich 2002, Standovár and Kenderes  
92 2003, Bobiec et al. 2011). Natural European beech forests are characterized by fine-scale gap  
93 dynamics (Standovár and Kenderes 2003, Schütz et al. 2016), while the disturbance regime  
94 sustaining oak-dominated forests is not so well defined (e.g. Vera 2000, Cowell et al. 2010,  
95 Bobiec et al. 2011 and 2018). In addition to the large number of possible factors, all the above  
96 variables may also affect regeneration through complex interactions with each other  
97 (Kuuluvainen et al. 1993, Janse-ten Klooster et al. 2007), and the relative importance of  
98 particular environmental factors varies between species (Finzi and Canham 2000, Lin et al.  
99 2014, Modrý et al. 2004).

100 Human activities influence most of the drivers of the natural (not planted) regeneration, either  
101 directly or indirectly. Forest management has an evident and intensive effect on the stand

102 level, since it strongly influences forest structure and composition. Numerous studies  
103 investigate the effects of different forestry systems on site conditions, and through these, tree  
104 regeneration (clear-cutting: Fleming et al. 1998, von Lüpke 1998; shelterwood system: Brose  
105 2011, Modrý et al. 2004; retention harvesting: Montgomery et al. 2013; selection systems:  
106 Diaci and Firm 2011, Matonis et al. 2011). However, current regeneration may be influenced  
107 by historical land use as well as recent management, not only because past forest management  
108 determines the present-day overstory, but also via some other land use forms (coppicing,  
109 forest grazing, litter collecting) which had been modifying the forest site and the understory  
110 vegetation for a long time (Bobic 2011, Diaci and Firm 2011).

111 Certain types of industrial forestry, such as the shelterwood forestry system, have already  
112 been applying natural regeneration for a long while (Matthews 1991, Brose 2011), but  
113 recently spreading, nature-based forestry systems rely upon it particularly strongly (Peterken  
114 1996, Pommerening and Murphy 2004, Dobrowolska 2006, Schütz et al. 2016). Thus,  
115 understanding the most important drivers of natural regeneration is essential to the application  
116 of these increasingly popular management approaches. From a conservational point of view, it  
117 is also important to explore the environmental conditions which should be preserved or  
118 enhanced during management activities, in order to support high species richness in the  
119 regeneration, and indirectly, in the future forests.

120 As outlined above, many studies investigate the effects of one or a few environmental factors  
121 on regeneration. However, there are few studies – especially from Europe – that compare the  
122 relative importance of different factors, measuring many potential explanatory variables. Such  
123 investigations were carried out by Bobiec et al. (2011) with oak, by Hunziker and Brang  
124 (2005) with spruce and fir, and by Kuuluvainen et al. (1993) with pine, but these studies only  
125 used variables concerning the current environment, and did not include land use history.  
126 Moreover, most of such studies investigate some treatment-effects directly, not natural

127 processes (Fleming et al. 1998, Matonis et al. 2011). Most papers mainly focus on the  
128 saplings of the dominant tree species; only a few studies concern the role of environmental  
129 effects on the entire assemblage of the regeneration (Modrý et al. 2004, Ádám et al. 2013, Lin  
130 et al. 2014, Bose et al. 2016). This study focuses on exploring the most important  
131 environmental and land use historical factors driving natural regeneration, in a region where  
132 forests are various regarding tree species composition, stand structure, forest history, and  
133 recent management.

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

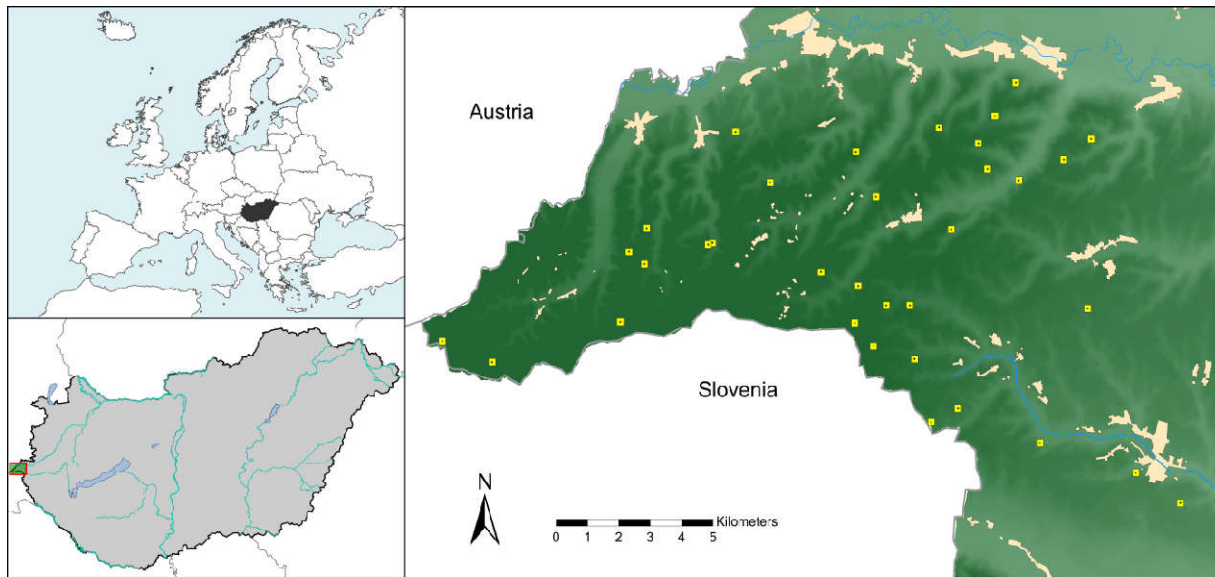
140

## 141 2. Material and methods

### 142 2.1. Study area

143 The study was carried out in the Órség National Park, West Hungary (N 46°51'–55', E  
144 16°07'–23', cca. 13 km × 24 km, Fig. 1.). The topography consists of hills and wide valleys,  
145 with elevation between 250–350 m a.s.l.. Mean annual precipitation is 800 mm, average  
146 annual mean temperature is 9.0–9.5 °C (Dövényi 2010). The bedrock is alluviated gravel  
147 mixed with loess. The soil is acidic and nutrient poor, the most common soil type on hills is  
148 pseudogleyic brown forest soil (planosols or luvisols), while in the valleys, mire and meadow  
149 soils (gleysols) can be found (Krasilnikov et al. 2009, Stefanovits et al. 1999).

150



151

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

154

155 In the area, there are forests with various species composition and stand structure among  
 156 similar climatic, topographical and bedrock conditions. Dominant species are beech (*Fagus*  
 157 *sylvatica*), sessile and pedunculate oak (*Quercus petraea* et *Q. robur*), hornbeam (*Carpinus*  
 158 *betulus*), Scots pine (*Pinus sylvestris*), and Norway spruce (*Picea abies*), present in both  
 159 monospecific and mixed stands. The proportion of various subordinate species (*Betula*  
 160 *pendula*, *Populus tremula*, *Castanea sativa*, *Prunus avium*, etc.) is relatively high (Tímár et al.  
 161 2002). Tree height varies between 20–30 m, and living stock is 300–600 m<sup>3</sup>/ha.

162 The present diversity of the forests in the area is partly caused by the special landscape history  
 163 (Tímár et al. 2002, Markovics 2016): From the 13<sup>th</sup> century, extensive farming and other land-  
 164 use activities, such as litter collection and ridging (a special form of tillage) resulted in the  
 165 deforestation and acidification of the area, and strong soil erosion. From the 19<sup>th</sup> century,  
 166 extensive farming was repressed. Reforestation in the area began, mainly by Scots pine and  
 167 pioneer tree species (*Betula pendula*, *Populus tremula*). Farmers traditionally applied  
 168 spontaneous selective cutting: firewood was selectively logged every year, but trees for timber

169 were retained for longer. This practice caused a continuous, intensive forest use, which  
170 maintained a continuous, uneven aged forest cover. The various routines of the farmers  
171 resulted in a high spatial heterogeneity of management. Besides logging, forests were also  
172 used in some other ways. Grazing, litter and moss collection were commonly practiced. The  
173 developing conditions were favourable to species that prefer nutrient poor and disturbed  
174 conditions. Later, from the middle of the 20<sup>th</sup> century, forest management became  
175 heterogeneous in a new way: private forests continued to be managed by a spontaneous  
176 selection system, but in the state-owned stands, industrial shelterwood or clear-cutting system  
177 was applied (Matthews 1991, Tímár et al. 2002, Markovics 2016). Currently, ancient and  
178 recent stands form a fine-scale mixture in the region. The coexistence of pioneer and late  
179 successional forest species creates a remarkably rich and various species composition.  
180 However, the cessation of traditional forest utilization (spontaneous selection, grazing, litter  
181 collecting), and the consequential succession of the forests lead to changes in tree species  
182 composition. Deciduous species (hornbeam, beech) are taking over from the vanishing  
183 acidophilous pioneer species (Tímár et al. 2002). The understory is formed by mesophilic and  
184 acidophilic species, and the shrub layer mainly consists of the saplings of beech, hornbeam  
185 and admixing species. Herbaceous cover and the amount of tree saplings highly vary among  
186 the stands.

187

## 188 *2.2. Data collection*

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

193



<b>Explanatory variables</b>	<b>Minimum</b>	<b>Mean</b>	<b>Maximum</b>
<b>Overstory tree species composition</b>			
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 ( <i>Q. petraea</i> , <i>Q. robur</i> and <i>Q. cerris</i> , %)	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
<b>Stand structure</b>			
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 <sup>2</sup> /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 <sup>3</sup> /ha)	0.00	12.17	64.59
Volume of logs (m <sup>3</sup> /ha)	1.16	10.15	35.59
Density of shrubs (>50 cm height, <5 cm DBH, stems/ha)	0.00	947.43	4706.25
<b>Forest floor</b>			
Cover of mineral soil (m <sup>2</sup> /ha)	8.56	145.85	472.22
Cover of litter (m <sup>2</sup> /ha)	7814.99	9391.93	9833.66
<b>Forest site characteristics</b>			
Litter weight (g/900 cm <sup>2</sup> )	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 <sub>2</sub> O <sub>5</sub> /100g, 0-10 cm)	1.96	4.32	9.35
<b>Microclimate</b>			

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
<b>Landscape</b>			
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
<b>Land use history (1853)</b>			
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

194

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

197

198 Thirty-four stands were selected by stratified random sampling from the stand structural  
199 database of the Hungarian National Forest Service (Table 1., Fig. 1.). The stratification  
200 criterion was tree species composition; the selected stands represent different combinations of  
201 the main tree species of the area (oak, beech, Scots pine, Norway spruce and hornbeam).  
202 Further criteria of the site selection were as follows: age of dominant trees between 70 and  
203 100 years, relatively level ground, absence of direct water influence, and spatial independence  
204 of other sites (distance min. 500 m). From the categories – based upon tree species  
205 composition –, sample sites were selected randomly. In this way, the sample was  
206 representative for the mixed forests of the Órség region. Such mixed forests are common in  
207 many of the lowland and hilly regions of Europe. Most of the investigated stands were

208 managed by various forestry systems (spontaneous or standardized selection, or shelterwood  
209 forestry systems), but we also sampled two unmanaged reserves. Through its impact on the  
210 stand structure and tree species composition, management had an indirect effect on the  
211 studied regeneration, however, direct human effects did not influenced the survey: We chose  
212 only closed, mature stands, which have not been cut for several decades. Regeneration in the  
213 investigated stands was natural, not influenced by artificial reproduction, cleaning or nursing.  
214 Mean canopy openness was 10.9%, canopy openness of the individual sites ranged from 4.0  
215 to 23.2%.

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

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

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

243 We estimated the cover of mineral soil and litter within the quadrats. Litter was collected  
244 from five 30 cm × 30 cm areas from every plot: the centre, and along the four diagonals, from  
245 halfway between the centre and the corners. Measured litter variables were weight, proportion  
246 of deciduous litter, pH (in water) and nitrogen content. Five soil samples per plot were  
247 collected from the same locations as the litter samples. The following variables were  
248 measured from the upper 10 cm of the samples: pH in water, clay (<0,002 mm) and silt (0,002  
249 – 0,02 mm) fractions determined by sedimentation process (Cools and De Vos 2010), organic  
250 carbon and nitrogen content analysed by dry combustion elementary analysis using Elementar  
251 vario EL III CNS equipment (Elementar Analysensysteme GmbH, Langenselbold, Germany),  
252 and ammonium-lactate/acetic-acid (AL-) extractable phosphorus content (Bellér 1997). Air  
253 humidity and temperature were measured in one point per plot (in the centre), at 1.3 m height,  
254 with Voltcraft DL-120 TH data loggers (Conrad Electronic SE, Hirschau, Germany).  
255 Measurements were taken eight times, in three growing seasons (June and October 2009;  
256 June, August, September and October 2010; March and May 2011). Each time, 5-minute  
257 recording frequency was applied, for 24 hours. Every site was measured within a five-day

258 period. During this period, two reference plots were measured permanently. Differences from  
259 the reference were calculated for the measured values of the quadrats. Relative daily mean  
260 and range values were expressed for both variables, and averaged over the eight measurement  
261 periods. See more methodological details of the microclimate measurements in Kovács et al.  
262 (2017). Diffuse light was measured in all the 36 quadrats per plot, with LAI-2000 Plant  
263 Canopy Analyzer instruments (LICOR Inc. 1992, Tinya et al. 2009a). Relative diffuse light  
264 values were calculated by using data from parallel reference measurements, carried out in  
265 nearby open fields. Repeated measurements are not necessary with this device. Plot-level light  
266 conditions were calculated as the mean and coefficient of variation of the 36 relative diffuse  
267 light values taken in each of the plots' quadrats.

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

277

### 278 *2.3. Data analysis*

279 All analyses were conducted with ln-transformed cover data of the species. Some explanatory  
280 variables were also ln-transformed, to fulfil normality conditions. All explanatory variables  
281 were standardized. For the statistical selection procedure, we selected only those explanatory  
282 variables which showed a strong and consistent relationship with the dependent variable, and

283 the intercorrelations with other explanatory variables were weak ( $R < 0.5$ , Borcard et al. 2011,  
284 Faraway 2005).

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

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

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

306

307 3. Results

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

318

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

319

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

323

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

329 5.67% (F=2.05, p=0.002). The whole model explained 34.31% of the variance (F=3.79,  
 330 p=0.001).

331

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



332

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

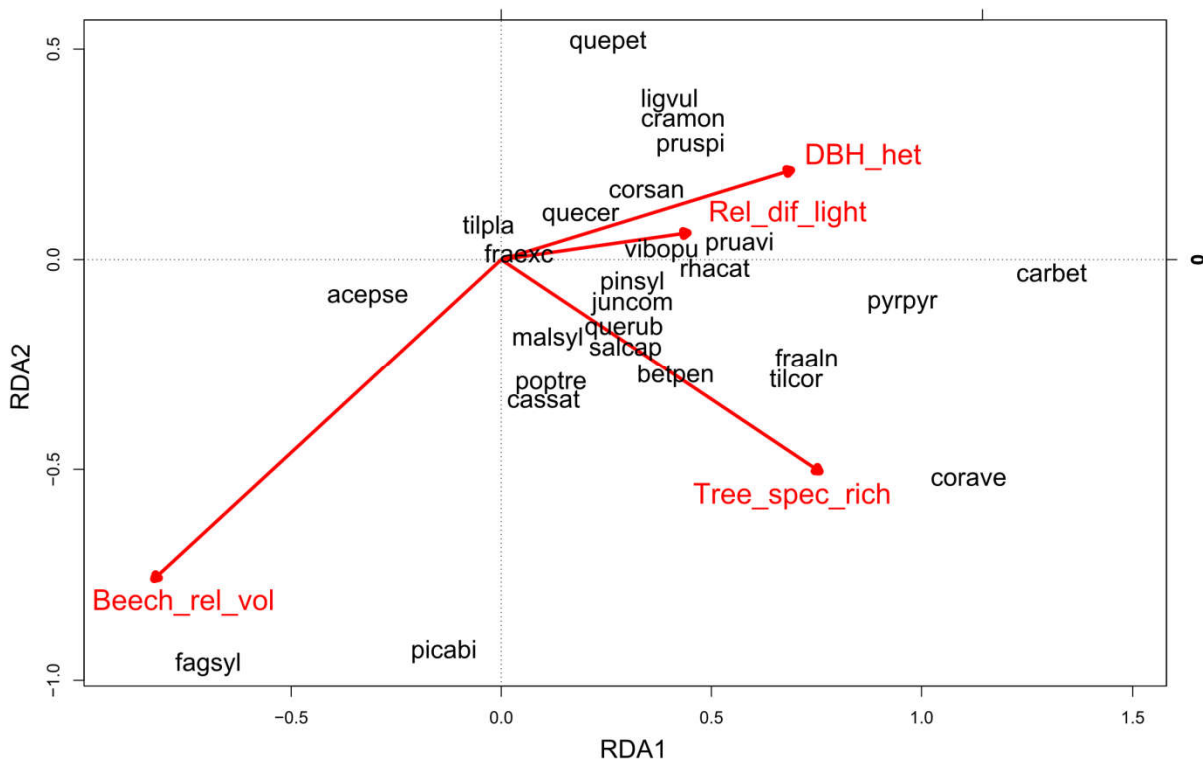
335

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

336

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

339



340

341 Fig 2. Distribution of species (black) and explanatory variables (red) at the first and second  
 342 redundancy analysis axes. Beech\_rel\_vol: relative volume of beech; DBH\_het: variation

343 coefficient of diameter at breast height; Rel\_dif\_light: mean relative diffuse light;  
344 Tree\_spec\_rich: tree species richness. Species abbreviation consists of the first three letters of  
345 the genus and the species names. See full names in the Table 3.

346

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

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

368 related to beech proportion in the overstory and to the proportion of mature forests in the  
 369 landscape, and negatively to litter nitrogen content and the proportion of arable land in the  
 370 historical landscape (explained variance: 55%). In the partial model, the density of large trees,  
 371 soil phosphorus content, and tree size had significant positive, while litter nitrogen content  
 372 negative effects (explained variance: 36%).  
 373

<b>Variable</b>	<b>Sense</b>	<b>Variance (%)</b>	<b>F value, significance</b>
<b>Cover of the regeneration; R<sup>2</sup> = 0.31</b>			
Density of large trees (DBH >50 cm)	+	18.80	9.03**
Mean relative diffuse light	+	16.65	8.00**
<b>Species richness of the regeneration; R<sup>2</sup> = 0.41</b>			
Mean relative diffuse light	+	28.24	15.90***
Tree species richness in the overstory	+	16.7	9.40**
<b>Cover of sessile oak; R<sup>2</sup> = 0.52</b>			
Relative volume of oaks	+	39.33	26.87***
Mean relative diffuse light	+	15.29	10.45**
<b>Partial model for sessile oak; R<sup>2</sup> = 0.38</b>			
Soil phosphorus content	+	18.15	9.64**
Proportion of arable lands in 1853	-	15.51	8.24**
pH of litter	-	9.85	5.23*
<b>Cover of hornbeam; R<sup>2</sup> = 0.43</b>			
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*
<b>Partial model for hornbeam; R<sup>2</sup> = 0.45</b>			
Proportion of arable lands in 1853	+	35.96	21.38***
Mean relative diffuse light	+	14.00	7.03*
<b>Cover of beech; R<sup>2</sup> = 0.55</b>			
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*

---

374

375 Table 5. Significant explanatory variables of the different regression models.  $R^2$ : adjusted  
376 coefficient of determination of the models; Sense: the sense of the parameter of the variables  
377 in the regression equation; Variance %: the percentage of the explained variance by the  
378 variable within the model. The significance of explained variance was tested by F statistics  
379 \*\*\*  $p < 0.001$ ; \*\*  $p < 0.01$ ; \*  $p < 0.05$ . Partial models show the effect of the different explanatory  
380 variables once the effect of the mother trees (relative volume of the given tree species in the  
381 overstory) has been taken into account.

382

383 4. Discussion

384 4.1. *Effects of the environmental and land use history factors*

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

392 Tree species richness was one of the most important drivers of regeneration, similarly to the  
393 results of Ádám et al. (2013) in oak forests. It explained the largest proportion of the variance  
394 in the composition (RDA) model, and was the second most important variable in the species  
395 richness model. The seedlings of admixing tree species (e.g. *Pyrus pyraeaster*, *Tilia cordata*,

396 *Betula pendula*) were particularly strongly related to stands with high tree species richness.  
397 The obvious explanation for this phenomenon seems to be the effect of the parent trees. This  
398 may partly be true, as in the case of the individually investigated species, especially the two  
399 species with large fruits (sessile oak and beech), relative volume of the given species in the  
400 overstory was a main driver of the regeneration. However, this cannot be the only reason, as  
401 in many stands, different species occurred in the regeneration than in the overstory layer. As  
402 forest stands with different species compositions create a heterogeneous, fine-scaled mosaic  
403 in the area, propagule limitation is presumably not too strong for most of the species, even if  
404 they are not present in a given stand. This can be especially relevant for anemochor trees,  
405 such as *Carpinus*, *Tilia*, *Betula* and *Pinus*. Thus we may suppose that besides providing  
406 propagules, tree species richness also increases the structural diversity of the stand. According  
407 to the heterogeneity-diversity hypothesis, heterogeneous environment ensures more niches,  
408 which decreases interspecific competition (Wilson 2000). Heterogeneous tree species  
409 composition can create various light conditions and microsites for the regeneration of many  
410 different woody species (Tinya et al. 2016). The presence of light in every model of the  
411 community variables, and of structural variables in the various models (DBH-heterogeneity in  
412 the RDA, density of large trees in the cover model) also support this explanation.

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

421 closed stands, the low amount of light limits not only the growth, but even the establishment  
422 of many woody species.

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

429 The density of large trees proved to be the main driver of regeneration cover. Large trees  
430 promote regeneration both by propagule production and by enhancing microsite  
431 heterogeneity. They often have broken parts in their canopy, where more light can penetrate.

432 The presence of large trees may also indicate less intensive management (e.g. continuous  
433 cover forestry instead of industrial shelterwood forestry system, Pommerening and Murphy  
434 2004), which results in lower tree density, and a more aggregated distribution of resources.

435 The enhanced structural heterogeneity of the stands may be favourable for regeneration.

436 The relative volume of beech in the overstory had a negative effect on the regeneration. Apart  
437 from beech, only two species (*Picea abies* and *Acer pseudoplatanus*) were positively related  
438 to beech stands, both shade-tolerant (Hunziker and Brang 2005, Modrý et al. 2004). The  
439 regeneration layer of beech-dominated forests is usually species-poor, basically due to the  
440 homogeneous stand structure and low light level of managed beech stands. However, even in  
441 gaps of the canopy layer, where structural heterogeneity and irradiance are higher, species  
442 richness of the regeneration rises only to 5-6 species (Feldmann et al. 2018, Mountford et al.  
443 2006, Schnitzler and Closset 2003).

444 Considering the individual responses of the dominant species of the regeneration (sessile oak,  
445 beech and hornbeam), we find that the relative volume of a given species in the overstory

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

456 Based on our results, parent trees are extremely important for the establishment of sessile oak  
457 in the regeneration. This contradicts some studies, which found no relationship between oak  
458 regeneration and the presence of the species in the overstory (Mosandl and Kleinert 1998,  
459 Dobrowolska 2006). It is often explained by the acorn-dispersing ability of European jays  
460 (*Garrulus glandarius*) for long distances (Kollmann and Schill 1996, Mosandl and Kleinert  
461 1998), but according to Bobiec et al. (2018), the role of jays is more prominent in landscapes  
462 with more non-forest habitats than in closed forests. In our case, the strong correspondence of  
463 oak regeneration with the parent trees suggest that in this region, oak regenerates mainly from  
464 the acorns of the local mother trees, which is in agreement with the findings of *Ádám et al.*  
465 (2013). The second significant explanatory variable for oak was relative diffuse light. This  
466 species is generally considered light-demanding (Ligot et al. 2013, Van Couwenberghe et al.  
467 2013, Sevillano et al. 2016, Schütz et al. 2016), but many studies showed that young seedlings  
468 of oaks are shade-tolerant, and need direct light only some years after germination  
469 (Ostrogović et al. 2010, von Lüpke 1998). According to our results, small seedlings (<50 cm  
470 height) may already be light-demanding.

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

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

493 As hornbeam seedlings occur not only in pine stands, but also in oak-hornbeam forests, the  
494 relative volume of hornbeam trees in the canopy is also present in the model. Since oak-  
495 hornbeam forests have high canopy closure and low understory light (*Bölöni 2008*), hornbeam



496 is considered to be a shade-tolerant species (Modrý et al. 2004). However, if we extract the  
497 effect of hornbeam trees from the model, we find that hornbeam regeneration is also driven by  
498 light. This can be seen on the ordination plot as well. Tinya et al. (2009b and 2016) also found  
499 that when comparing numerous stands, hornbeam seems to be shade-tolerant (since it often  
500 occurs in closed, dark oak-hornbeam stands), but its within-stand spatial pattern is positively  
501 related to light. This species was indifferent to site conditions: none of the forest site variables  
502 was present in the model.

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

512 In the partial model for beech regeneration, overstory structural variables also appeared: the  
513 density of large trees and the mean DBH of trees enhanced the cover of beech seedlings.  
514 Larger trees promote regeneration by their heavy propagule production, and by the  
515 establishment of various microsites. However, microsite-variability in this case does not  
516 indicate heterogeneous light conditions, because this species proved to be completely  
517 independent from irradiance (light was absent even from the partial model). The observed  
518 shade-tolerance of beech is in accordance with many previous studies (Emborg 1998, Modrý  
519 2004, Schnitzler and Closset 2003, Ligot et al. 2013).

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

526

#### 527 *4.2. Implications for conservation and management*

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

541 With some amount of extra effort, high tree species diversity can be maintained in the course  
542 of the shelterwood forestry system. However, most of the listed aims (heterogeneous tree size  
543 distribution, large trees, various light conditions) are much better achieved by continuous  
544 cover forestry. This management system is traditionally applied in the region (in the form of

545 spontaneous selection), but from a conservational aspect, the increase of its ratio would be  
546 desirable, in the form of standardized selective cutting, which adapts knowledge from  
547 spontaneous selection into the planning process.

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

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

558

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566

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