

2  
3 **Comparison of regeneration and recruitment of shade-tolerant and**  
4 **light-demanding tree species in mixed uneven-aged forests:**  
5 **Experiences from the Dinaric region**

6  
7 **Matija Klopčič<sup>1\*</sup>, Tina Simončič<sup>1</sup> and Andrej Bončina<sup>1</sup>**

8 <sup>1</sup>*University of Ljubljana, Biotechnical Faculty, Department of Forestry and Renewable Forest*  
9 *Resource, Večna pot 83, 1000 Ljubljana, Slovenia*

10 \*Corresponding author: Tel: +386 1320 35 51; Fax: +386 1257 11 69; Email: [matija.klopacic@bf.uni-lj.si](mailto:matija.klopacic@bf.uni-lj.si)

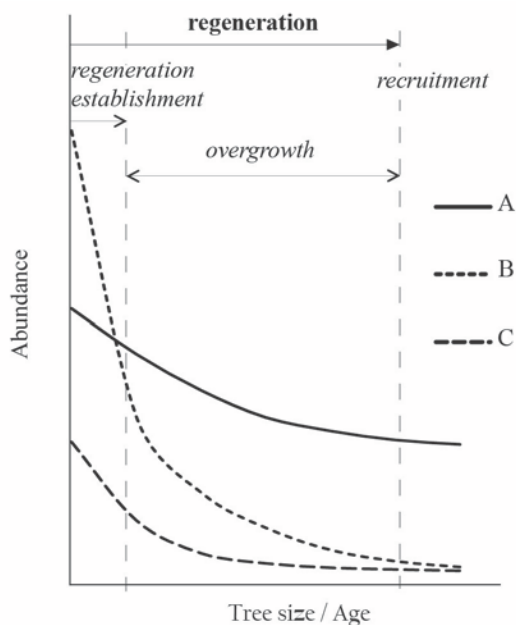
11  
12 Research on the early stages of stand dynamics in uneven-aged forests  
13 often favours regeneration over recruitment of trees into forest stands. We  
14 contrasted both regeneration (i.e. seedlings and saplings existing in a  
15 stand) and recruitment (i.e. the number of trees annually crossing the  
16 threshold of 10 cm dbh) in two main stand types of uneven-aged forests  
17 (plenter and group selection). Data from 1,710 permanent plots across the  
18 Dinaric Mountains in Slovenia were used to study recruitment; on 165 plots  
19 regeneration was additionally analysed. The zero-inflated negative  
20 binomial modelling procedure was applied to identify factors influencing  
21 regeneration and recruitment. Total regeneration (30,212 ha<sup>-1</sup>) and that of  
22 light-demanding species (14,879 ha<sup>-1</sup>) were abundant. The latter  
23 regenerated more successfully in group selection stands compared to  
24 plenter stands. A large reduction in regeneration density was determined  
25 during its growth, which was more dramatic for light-demanding species  
26 (e.g. *Acer pseudoplatanus*) than for shade-tolerant species (e.g. *Fagus*  
27 *sylvatica*, *Abies alba*). The number of recruited trees (5.83 ha<sup>-1</sup> y<sup>-1</sup>) seemed  
28 to be sufficient to maintain the uneven structure but was less promising for  
29 light-demanding species (0.13 ha<sup>-1</sup> y<sup>-1</sup>). However, light-demanding species  
30 have the potential to establish and recruit into uneven-aged stands with a  
31 limited target proportion in the growing stock. Both indicators -  
32 regeneration and recruitment - are indispensable for understanding  
33 patterns of stand dynamics in uneven-aged forests.

## 35 **Introduction**

36 Processes during the early stages of forest stand development substantially affect the structure and  
37 tree species composition of mature forest stands; the most important among them include  
38 regeneration establishment, height and diameter growth of specimens, density reduction, species  
39 replacement, mortality, and recruitment (Schupp, 1995; Oliver and Larson, 1996; Kobe and Coates,  
40 1997; Boyden et al., 2009).

41 Tree regeneration includes establishment of seedlings and their subsequent growth. The density and  
42 composition of established regeneration, defined as the seedlings and saplings existing in a stand  
43 (Helms, 1998), are influenced by several factors, such as site conditions, seed rain and banks, light  
44 conditions, competition by the herbaceous layer, and intra- and interspecies relations (e.g. Schupp,  
45 1995; Oliver and Larson, 1996; Greene et al., 1999). Furthermore, the physical and bio-physical  
46 environment that favours regeneration establishment is a reflection of previous stand development,  
47 formed by natural or human-induced disturbance events. The latter includes different silvicultural  
48 systems which influence the growth conditions for regeneration, such as the availability of light and  
49 other resources (Mathews, 1999). The abundance of regeneration commonly decreases with its age  
50 due to the reduced availability of resources associated with increasing intra- and interspecific  
51 competition and exogenous mortality factors. This relation is often conceptualized with a concave  
52 survivorship curve (Begon et al., 1990; Figure 1), indicating extensive early mortality and  
53 substantially higher survival rate of remaining individuals. Tree species differ significantly in their  
54 regeneration patterns, including the abundance of established regeneration and the intensity of its  
55 reduction (Figure 1), processes that can be defined as their survival strategy. Regeneration patterns  
56 are often streamlined with distinctive types, such as early and late-successional tree species. The  
57 first are usually abundant in the establishment phase, but have a relatively low survival rate,  
58 whereas the second have moderate and periodic establishment, but their survival rate is typically  
59 higher (Kimmins, 2004). The strategy of early-successional species is common for species that need a  
60 large amount of light for their survival and vigorous growth, whereas late-successional species are

61 often shade-tolerant with less abundant regeneration, but with smaller reduction of specimens  
 62 when overgrowing height layers. However, even within the same survival strategy, the survival rate  
 63 of species regeneration may differ due to external factors, a key one often being large ungulates  
 64 (Gill, 1992; Motta, 1996). Moreover, tree species requirements and survival rate may change with  
 65 age (Schupp, 1995), given the specific site conditions (Kobe and Coates, 1997) or if the action of the  
 66 agents of mortality changes (Kimmins, 2004). The unambiguous division of light-demanding and  
 67 shade-tolerant species may therefore be difficult, but it has been useful to describe complex  
 68 patterns in a simplified form.



69  
 70 **Figure 1** Illustration of survivorship curves of tree species with different survival strategies: A) late-successional  
 71 shade-tolerant tree species, B) early-successional shade-mid-tolerant and -intolerant tree species with  
 72 abundant regeneration establishment, C) early-successional shade-intolerant tree species with scarce  
 73 regeneration establishment; additionally, phases of early-stage forest development are defined as  
 74 “regeneration establishment”, regeneration “overgrowth”, and “recruitment”  
 75

76 Recruitment of tree species follows successful regeneration and its vigorous height growth.  
 77 Recruitment is generally defined as the process by which individuals are added to the population. In  
 78 silviculture, recruitment is understood as the process by which trees move from one size class to  
 79 another (Helms, 1998) or by which saplings or young trees overgrow a certain threshold value of

80 height or dbh (Lexerød and Eid, 2005). The latter definition was adopted in our study; accordingly,  
81 this process results in a certain number of individuals crossing the defined threshold value, often  
82 called recruitment rate or simply recruitment. It can be relatively easily and accurately estimated if  
83 suitable data are collected and available from at least two consecutive forest inventories. An  
84 additional parameter indicating recruitment is the number of trees in the smallest inventoried  
85 diameter class (Schütz, 2001), which is typically used in forest inventory data evaluation (Tomppo et  
86 al., 2010). In contrast, a regeneration survey is often excluded from the forest inventory.  
87 Recruitment is strongly conditioned by regeneration patterns. In managed forests, recruitment can  
88 be significantly influenced by pre-commercial silvicultural measures which create canopy structures  
89 favouring certain tree species and hindering others. Other external factors such as the height and  
90 density of forest stands, their tree species composition, or large ungulate damage may also  
91 substantially influence tree species recruitment (e.g. Motta, 2003; Lexerød, 2005; Klopčič et al.,  
92 2012).

93 Information on regeneration and recruitment and their relation is critical to the application of a wide  
94 range of silvicultural systems that are based on natural regeneration, uneven-aged systems being  
95 one of them. Continuous regeneration, sufficient recruitment, and constant replacement of  
96 specimens within different age, height or diameter classes are *conditio sine qua non* for the  
97 application of uneven-aged silvicultural systems. Uneven-aged (Helms, 1998; Matthews, 1999;  
98 Schütz, 2001) or multi-aged (O'Hara, 2014) forests is an umbrella term for different types of forest  
99 stands made up of trees of three or more distinct age classes, either intimately mixed or in small  
100 groups, creating vertically and horizontally uneven structures in a "small forest area".

101 Silvicultural systems influence light conditions within stands by creating horizontal and vertical stand  
102 structure, and thus also the dynamics of tree species in regeneration and recruitment (e.g. Collet et  
103 al., 2001; Stancioiu and O'Hara, 2006; Petritan et al., 2007). Canopy structure substantially modifies  
104 the availability and composition of light reaching the forest floor (e.g. Rozenbergar et al., 2007); both

105 diffuse and direct light intensities increase with increasing canopy gap size. Consequently,  
106 silvicultural systems creating smaller canopy openings perpetuate shade-tolerant tree species,  
107 whereas systems creating larger canopy openings offer greater possibilities for the establishment  
108 and success of mid-shade-tolerant or light-demanding tree species (Mathews, 1999; Schütz, 2001;  
109 Raymond et al., 2009; Klingsporn Poznanovic et al., 2013).

110 Among uneven-aged systems, the single-tree ('plenter') and group selection systems, and the  
111 irregular shelterwood system, are most commonly applied in Central Europe (Boncina, 2011). The  
112 main desirable species are usually shade-tolerant silver fir (*Abies alba* Mill.), often being the  
113 dominant species, and European beech (*Fagus sylvatica* L.) or mid-shade-tolerant Norway spruce  
114 (*Picea abies* (L.) Karst.) (Schütz, 2001). Tree species of the genus *Acer*, *Fraxinus*, *Sorbus*, *Larix*, *Pinus*,  
115 *Ulmus*, *Taxus* etc. represent a minor but important part of the natural composition of mountain  
116 forest communities (Boncina et al., 2014) since they increase heterogeneity and biodiversity,  
117 improve resilience and adaptive capacity to climate change, and augment ecological, economic, and  
118 social values (Spiecker, 2006; Brang et al., 2014). Most of these species are less shade-tolerant, while  
119 some are shade-tolerant only in the establishment and early regeneration phase, but need more  
120 light for posterior vigorous height growth and successful recruitment into mature stands, sycamore  
121 maple (*Acer pseudoplatanus* L.) being such an example. However, the potential and success of these  
122 species is questionable and may be problematic since uneven-aged silviculture is generally believed  
123 to be less favourable for light-demanding species (O'Hara, 2014). If a high proportion of light-  
124 demanding species is targeted, the application of silvicultural systems creating uneven-aged stands  
125 has been recognized as an ineffective solution (e.g. Schwartz et al., 2005).

126 In contrast to regeneration, which has been frequently examined also in uneven-aged stands (e.g.  
127 Hasenauer and Kindermann, 2002; Stancioiu and O'Hara, 2006; Eerikäinen et al., 2007), recruitment  
128 has been relatively little studied and its importance for monitoring has, at least in Europe, gone  
129 almost unrecognized (e.g. Lexerød, 2005; Klopčič and Boncina, 2012). Studies comparing both

130 processes are even less frequent (e.g. Duc, 1991). Therefore, a question arises which of these  
131 indicators reveals more about stand dynamics and better expresses the potential to promote tree  
132 species in the uneven-aged forests. We contrasted both indicators – regeneration and recruitment –  
133 to study the early stages of stand dynamics and to reveal the potential for managing light-  
134 demanding and shade-tolerant species in mixed mountain uneven-aged forests of the Dinaric region.  
135 In detail, we studied 1) regeneration and recruitment patterns, including density and tree species  
136 composition; 2) the survivorship patterns within the early stages of stand development; and 3) the  
137 main site and stand factors influencing regeneration establishment and recruitment patterns. We  
138 hypothesized that 1) tree species composition significantly differs between regeneration and  
139 recruitment, and 2) light demanding species recruit more successfully in group selection stands than  
140 in plenter stands.

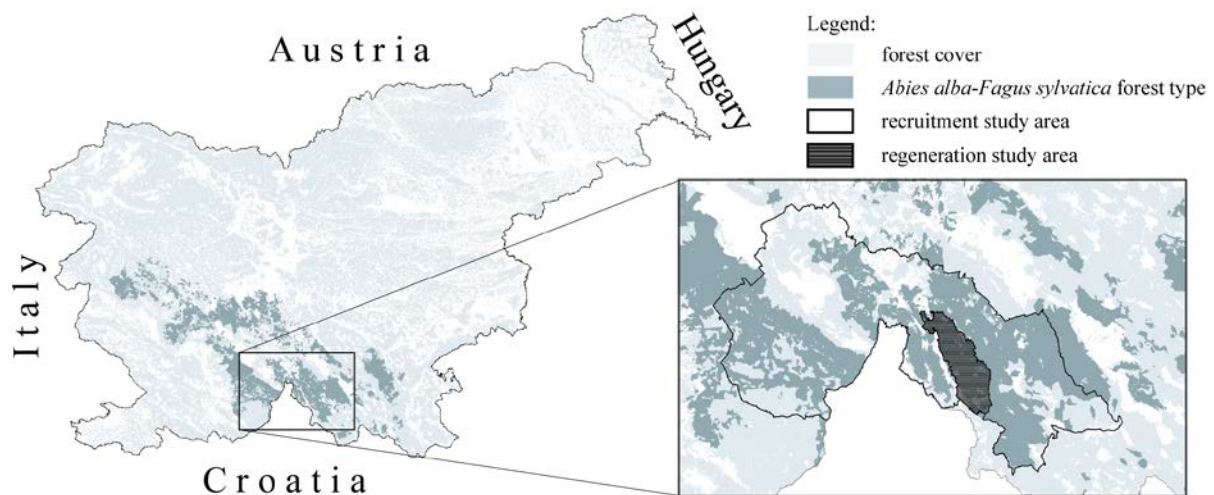
141

## 142 **Methods**

### 143 *Study area*

144 Our study was conducted in mixed uneven-aged forests in the Dinaric Mountains of southern  
145 Slovenia (Figure 2). The region is characterized by a relatively low average annual temperature (6-7  
146 °C) and high annual precipitation (1500-2500 mm). The predominant bedrock is carbonate (i.e.  
147 limestone and dolomite) on which cambisols and leptosols (IUSS Working Group WRB, 2007) of  
148 different depths have developed; if shallow soils are coupled with bedrock that enables rapid  
149 drainage (i.e. limestone and dolomite), sites may be relatively dry despite the high precipitation.  
150 Forests are characterized by a high average growing stock (Table 1) with a mixture of European  
151 beech, silver fir and Norway spruce (hereinafter shade-tolerant species), usually comprising more  
152 than 90 % of stand volume, and less abundant species represented by sycamore maple, wych elm  
153 (*Ulmus glabra* Huds.), small-leaved linden (*Tilia cordata* Mill.), rowan (*Sorbus aucuparia* L.),  
154 whitebeam (*Sorbus aria* (L.) Crantz.), European ash (*Fraxinus excelsior* L.) and wild cherry (*Prunus*

155 *avium* L.) (hereinafter light-demanding species). In addition, some other shade-tolerant (common  
 156 hornbeam *Carpinus betulus* L., hop hornbeam *Ostrya carpinifolia* Scop.) and light-demanding species  
 157 (manna ash *Fraxinus ornus* L., European crab apple *Malus sylvestris* (L.) Mill., European wild pear  
 158 *Pyrus pyraster* (L.) Burgsd., Scots pine *Pinus sylvestris* L.) may individually occur (Puncer, 1980), but  
 159 were not present in the studied plots. The studied uneven-aged forests have been managed  
 160 according to the principles of “close-to-nature” uneven-aged silviculture for the last 50 years, some  
 161 of them even for the last century (Klopčič and Bončina, 2011). In recent decades a combination of  
 162 different silvicultural systems (i.e. plenter, group selection, irregular shelterwood) have been applied  
 163 in order to take advantage of the potential of different stand patches and to take the variety of their  
 164 stand dynamics into consideration (Bončina, 2011).



165  
 166 **Figure 2** Recruitment and regeneration study areas (used to study both indicators, respectively) within mixed  
 167 uneven-aged stands in the Dinaric Mountains, Slovenia

168  
 169 The study was conducted at two spatial levels. Due to data availability, recruitment was studied on a  
 170 broader spatial scale including a large area of mixed uneven-aged stands in the Slovenian Dinaric  
 171 Mountains ( $\approx 400 \text{ km}^2$ ; hereinafter recruitment study area). Natural regeneration was studied on a  
 172 smaller spatial scale comprising an area of  $\approx 30 \text{ km}^2$  (hereinafter regeneration study area). The  
 173 regeneration study area was selected as a good representative of mixed mountain forests in the

174 Dinaric Mountains since stand parameters which were the focus of our research (i.e. tree species  
 175 composition, recruitment) did not differ significantly from the surrounding recruitment study area  
 176 (Table 1).

177

178 **Table 1** Basic stand and site characteristics of the recruitment and regeneration study areas

	Regeneration study area		Recruitment study area		p *
	mean	sd	mean	sd	
Stand basal area (m <sup>2</sup> ha <sup>-1</sup> )	29.60	10.77	32.58	11.78	0.016
Stand volume (m <sup>3</sup> ha <sup>-1</sup> )	348.0	143.5	417.4	167.0	0.000
Proportion of light-demanding species (% of stand basal area)	4.00	9.34	4.38	9.16	0.178
Quadratic mean dbh (cm)	33.9	7.5	36.1	10.2	0.000
Annual total recruitment (n ha <sup>-1</sup> y <sup>-1</sup> )	5.81	10.45	5.84	10.96	0.366
Annual recruitment of shade-tolerant species (n ha <sup>-1</sup> y <sup>-1</sup> )	5.68	10.40	5.71	10.83	0.381
Annual recruitment of light-demanding species (n ha <sup>-1</sup> y <sup>-1</sup> )	0.12	0.90	0.13	1.15	0.809
Elevation (m)	949	94.9	918	139.0	0.000
Mean annual temperature (°C)	6.8	0.6	6.8	0.7	0.869
Mean annual precipitation (mm)	2062	196.8	1972	239.8	0.000

179 \* p-values obtained by the non-parametric Mann-Whitney test

180

### 181 *Data acquisition*

### 182 *Recruitment*

183 For the purpose of the study, recruitment was defined as the number of trees annually crossing the  
 184 measurement threshold of 10 cm in dbh per hectare per year. Data from several regional forest  
 185 inventories were used to study recruitment (SFS, 2014). In Slovenia, the regional forest inventory is  
 186 based on measurements of trees on permanent sampling plots (hereinafter plots) on a 10-year  
 187 interval. Plots (200 m<sup>2</sup> each) are mainly located on a 250×250 m grid with known longitude and  
 188 latitude coordinates of each plot centre, which is clearly marked in the field. On a plot area, all  
 189 individual trees above the measurement threshold of 10 cm in dbh are surveyed; for every tree,  
 190 exact location is determined by an azimuth and a distance from the plot centre, dbh is measured and



191 tree species with some other tree parameters are visually assessed. The stand type on a plot is  
192 determined; among the uneven-aged stand types, two main sub-types are distinguished: 1) single-  
193 tree selection (plenter) stand type (hereinafter plenter) and 2) group selection and small-scale  
194 irregular shelterwood stand type (hereinafter group selection) (see also Appendix 1). In plenter  
195 stands, stand replacement is carried out on the single tree level (gap diameter  $<1 h_{\max}$  (maximum  
196 stand height)), while in group selection stands of the study area, it is performed on areas exceeding  
197 a diameter of  $1 h_{\max}$  but not exceeding an area of  $2 h_{\max}$  (Boncina, 2011). Mainly based on this  
198 criterion, surveyors determined the stand type on each plot including the surrounding stands (SFS,  
199 2014). A total of 1,710 plots with data from two consecutive inventories were included in the  
200 analysis of tree recruitment; 822 for plenter and 888 for group selection stands.

201

## 202 Regeneration

203 Regeneration was surveyed in 2014 in the regeneration study area on a sub-sample of 165 plots, 88  
204 in plenter and 77 in group selection stands, respectively. On each plot, seedlings ( $<50$  cm in height)  
205 and saplings ( $>50$  cm in height &  $<10$  cm in dbh) were tallied on two  $2 \times 2$  m subplots, located 2 m  
206 from the plot centre in the north and south directions. For every individual specimen, we recorded  
207 tree species and height/dbh class: 1) C1 = 0-19 cm in height; 2) C2 = 20-49 cm; 3) C3 = 50-89 cm; 4)  
208 C4 = 90-129 cm; 5) C5 =  $\geq 130$  cm &  $<5$  cm in dbh; 6) C6 = 5-9 cm in dbh.

209

## 210 *Data processing*

211 Data on regeneration and recruitment were used to develop survivorship curves (Begon et al., 1990)  
212 for shade-tolerant and light-demanding species as well as for individual species with an adequate  
213 number of specimens per height/dbh classes to conduct the calculation. The survivorship curve  
214 shows the mean number of specimens overgrowing each height/dbh class and recruiting to a

215 subsequent class. The curves were determined as the best fitted curve regression considering the R-  
216 square. To test differences in mean density of regeneration in a particular height/dbh class and  
217 recruitment between shade-tolerant and light-demanding species, as well as between individual tree  
218 species, and to compare differences in regeneration and recruitment between plenter and group  
219 selection stand types, the non-parametric Mann-Whitney test was applied. The correlation between  
220 regeneration abundance, recruitment, and stem density in the smallest inventoried dbh class 10-  
221 14.9 cm (DC10) was estimated with the non-parametric Kendall's tau-b correlation; its advantage is  
222 in its sensitivity to all monotonous and not just linear correlations between variables, and it does not  
223 presume a normal distribution of a variable (Hollander and Wolfe, 1999). All described statistical  
224 analyses were performed using the IBM SPSS 21.0 software (IBM Corp. Released, 2012).

225 The zero-inflated negative binomial (ZINB) modelling procedure (Greene, 1994) was applied to  
226 identify the influence of stand type, stand parameters, site conditions, large ungulate density, and  
227 harvesting intensity (Table 2) on the occurrence and the abundance of seedlings and recruitment of  
228 both light-demanding and shade-tolerant tree species. The independent variables were included into  
229 the modelling procedure due to their relevance for regeneration establishment and recruitment (see  
230 Motta, 2003; Lexerød, 2005; Lexerød and Eid, 2005; Eerikäinen et al., 2007; Boyden et al., 2009;  
231 Klopčič and Boncina, 2012; Klopčič et al., 2012). Stand characteristics were derived from surveyed  
232 data on each plot, while most of site conditions were assessed during the forest inventory on a plot;  
233 only site productivity MAI (Kadunc et al., 2013) and modified ungulate density index UDI' (Jerina,  
234 2008) were derived from other data-sources. Harvesting intensity (CUT) was calculated as the basal  
235 area of cut trees on each plot in the inventory period. In addition, other independent variables (e.g.  
236 mean annual temperature and precipitation) were tested, but were not significantly correlated with  
237 the dependent variables and were not included into the models.

238

239 **Table 2** Independent variables included into the zero-inflated negative binomial modelling  
 240 procedure with mean and standard deviation (sd) values for the recruitment and regeneration study  
 241 areas

Variable	Description	Recruitment study area		Regeneration study area	
		mean	sd	mean	sd
ST	Uneven-aged stand type (plenter = 0, group selection = 1)	-	-	-	-
BA	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	30.58	11.93	28.76	11.16
BA <sub>LD</sub>	Basal area of light-demanding tree species (m <sup>2</sup> ha <sup>-1</sup> )	1.22	2.48	0.98	2.07
DBH <sub>BA</sub>	Quadratic mean diameter (cm)	35.8	9.9	33.9	7.5
ELV	Elevation in 100 m belts (= elevation in m a.s.l./100)	9.23	1.34	9.50	0.95
INC	Inclination (°)	16.9	7.5	15.3	7.3
ASP	Aspect (0 =N,NE, E, NW; 1 = SE, S, SW, W, plane)	-	-	-	-
TOP	Topography (0 = plane + foot of the hills, 1 = slope+ridge)	-	-	-	-
MAI	Site productivity – mean annual stand increment (m <sup>3</sup> ha <sup>-1</sup> y <sup>-1</sup> )	8.72	0.84	9.06	0.99
CUT	Basal area of harvested trees (m <sup>2</sup> ha <sup>-1</sup> 10y <sup>-1</sup> )	3.84	5.07	4.58	5.63
UDI'	Modified Ungulate Density Index* (N km <sup>-2</sup> )	14.27	16.10	12.53	11.69

242 \* adapted after Motta (1996): UDI'=red deer density+1/2 fallow deer density+1/4 chamois density+1/4 mouflon  
 243 density+1/5 roe deer density

244  
 245 For modelling purposes, we joined C1 and C2 into C1-2 height/dbh class of regeneration, assuming  
 246 that seedlings are mostly influenced by stand and site conditions and less by other external factors  
 247 such as large ungulates, while (saplings and) recruitment was assumed to be highly influenced by  
 248 external factors (Rooney et al., 2000).

249 The ZINB model is a modified Poission regression model which was designed to deal with an  
 250 overdispersion and excess zeros which may occur in the count data (Greene, 1994), both of which  
 251 were true for our data. There are supposed to be two kinds of zeros, “true zeros” and “excess zeros”.  
 252 The ZINB model estimates two equations, the negative binomial one for the count model and the  
 253 logistic regression (probability) model for the “excess zeros”. The probability function for ZINB is  
 254 expressed as follows (equation 1):

$$255 \quad f(y_i | B_i, G_i, \beta, \gamma, \theta) = \begin{cases} p_i + (1 - p_i)q(0 | \mu_i, \theta) & \text{for } y_i = 0 \\ (1 - p_i)q(y_i | \mu_i, \theta) & \text{for } y_i = 1, 2, \dots \end{cases} \quad (1),$$

256 where

$$257 \quad q(0 | \mu_i, \theta) = \frac{\Gamma(\theta + y_i)}{\Gamma(\theta) \Gamma(y_i + 1)} \left( \frac{\theta}{\theta + \mu_i} \right)^\theta \left( \frac{\mu_i}{\theta + \mu_i} \right)^{y_i} \quad (2),$$

258 
$$\log(\mu_i) = B_{i0} + B_{i1}\beta_1 + \dots + B_{ik_g}\beta_{k_g} = B_i\beta \quad (3),$$

259 
$$\text{logit}(p_i) = \log\frac{p_i}{1-p_i} = G_{i0} + G_{i1}\gamma_1 + \dots + G_{ik_y}\gamma_{k_y} = G_i\gamma \quad (4).$$

260  $B_i$  and  $G_i$  are row vectors comprising covariate values for the  $i^{\text{th}}$  observation for count and zero-  
261 inflated probability models, respectively. From the derived coefficients in the model, the factor  $F$  of  
262 the abundance (count model) or odds (logistic model) change can be calculated as

263 
$$F = \exp(\text{coefficient}), \quad (5)$$

264 giving the expected change for each unit increase in the corresponding predictor while holding all  
265 other predictors constant.

266 Statistical analyses were performed in the free-software R version 3.1.1 (R Core Development Team,  
267 2014). The ZINB model was firstly implemented in the R package “pscl” (‘zeroinfl’ algorithm), and the  
268 obtained model was implemented afterwards into a backward stepwise modelling procedure in the  
269 R package “mpath” (‘be.zeroinfl’ algorithm) with a significance level of 0.05 for a variable to be  
270 retained in the final model. Selection of the final model was based on two measures of the relative  
271 quality of a statistical model, the log-likelihood value and Akaike’s information criterion (AIC).

272

## 273 **Results**

### 274 *Regeneration*

275 On average more than 30,000 individuals  $\text{ha}^{-1}$  in regeneration were found in the analysed forest  
276 stands. Regeneration was absent on 4 % of the plots, while regeneration of the shade-tolerant  
277 species and light-demanding species was absent on 7 % and 23 % of all plots, respectively. The  
278 variability in regeneration abundance was noteworthy; all coefficients of variation were more than

279 1, some even over 10 (Table 3). Shade-tolerant species prevailed in the regeneration, European  
 280 beech being the most abundant. Light-demanding tree species occupied an important part (49.2 %)  
 281 of the total regeneration. Among them, sycamore was the most abundant, followed by wych elm,  
 282 rowan, European ash, and others.

283

284 **Table 3** Tree species composition of regeneration in both stand types

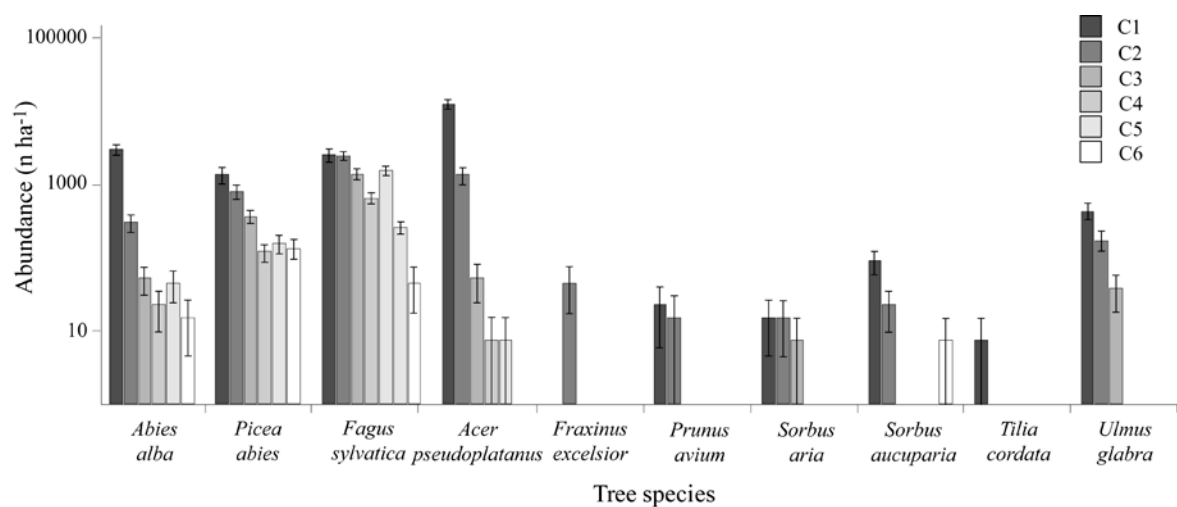
	Total		Plenter stand type		Group selection stand type		p
	n	cv	n	cv	n	cv	
shade-tolerant species	15333	1.08	13821	1.00	17062	1.13	0.547
<i>silver fir</i>	3462	1.66	4588	1.45	2175	1.94	0.000
<i>Norway spruce</i>	2970	2.30	2571	2.29	3425	2.27	0.727
<i>European beech</i>	8902	1.37	6662	1.15	11461	1.36	0.101
light-demanding species	14879	1.70	11733	1.72	18474	1.62	0.205
<i>sycamore maple</i>	13932	1.77	10838	1.78	17468	1.68	0.222
<i>wych elm</i>	652	2.75	724	2.28	568	3.43	0.136
<i>rowan</i>	121	4.30	85	5.35	162	3.61	0.327
<i>European ash</i>	91	7.21	43	6.96	146	6.20	0.538
<i>whitebeam</i>	38	6.74	43	6.96	32	6.16	0.902
<i>wild cherry</i>	38	10.58	0	-	81	7.21	0.129
<i>small-leaved linden</i>	8	12.85	14	9.38	0	-	0.350

285 \*n – number of seedlings and saplings per hectare; cv – coefficient of variation; p – p-value obtained in the Mann-Whitney  
 286 non-parametric statistical test of differences in mean values between plenter and group selection stand types

287

288 There was a decreasing trend in the abundance of all tree species with increasing regeneration  
 289 height/dbh class (Figure 3). In total, light-demanding tree species were much more abundant in the  
 290 shortest height class C1 compared to shade-tolerant species (13,121 ha<sup>-1</sup> and 6,955 ha<sup>-1</sup>,  
 291 respectively), but the difference was insignificant (p=0.199). In contrast, shade-tolerant species were  
 292 significantly more abundant in height classes above 20 cm (3,576 ha<sup>-1</sup> and 1,636 ha<sup>-1</sup> for C2, 98 ha<sup>-1</sup>  
 293 and 1,833 ha<sup>-1</sup> for C3, 8 ha<sup>-1</sup> and 803 ha<sup>-1</sup> for C4, 8 ha<sup>-1</sup> and 1758 ha<sup>-1</sup> for C5, and 8 ha<sup>-1</sup> and 409 ha<sup>-1</sup>  
 294 for C6, respectively; all p<0.001). The number of saplings of light-demanding species represented  
 295 only 0.7 % of the total sapling number.

296 In general, regeneration was more abundant in group selection than in plenter stands, with the  
 297 exception of silver fir as shade-tolerant species, and wych elm, whitebeam, and small-leaved linden  
 298 among the light-demanding species. Silver fir was the only species with significant difference in  
 299 mean abundance between group selection and plenter stands ( $p < 0.001$ ), while the difference in  
 300 abundance of the majority of species was insignificant, indicating high variability of regeneration  
 301 density in both stand types.

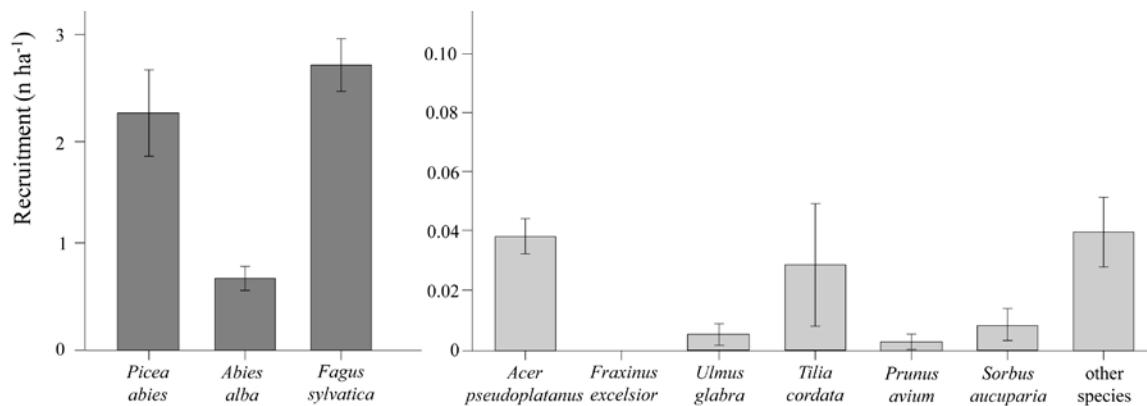


302  
 303 **Figure 3** Height structure of regeneration per tree species (C1 = 0-19 cm in height; C2 = 20-49 cm; C3 = 50-89  
 304 cm; C4 = 90-129 cm; C5 =  $\geq 130$  cm &  $< 5$  cm in dbh; C6 = 5-9 cm in dbh; mean values  $\pm$  standard errors of mean  
 305 are shown)

306  
 307 *Recruitment*

308 The annual recruitment of shade-tolerant species averaged  $5.70 \text{ trees ha}^{-1} \text{ y}^{-1}$ , whereas the  
 309 recruitment of light-demanding species was  $0.13 \text{ trees ha}^{-1} \text{ y}^{-1}$ , representing only 2.2 % of total  
 310 annual recruitment. Recruitment was not registered on 53 % of plots, while recruitment of light-  
 311 demanding species was not present on 98 % of all plots. Variability in recruitment per species was  
 312 very high; the coefficients of variation ranged from 2.00 to 3.88 and 12.28 to 41.69 for shade-  
 313 tolerant and light-demanding tree species, respectively. Shade-tolerant European beech and Norway  
 314 spruce recruited most successfully (Figure 4), while sycamore was the most abundant among light-

315 demanding species (0.04 trees ha<sup>-1</sup> y<sup>-1</sup>), followed by small-leaved linden (0.03 trees ha<sup>-1</sup> y<sup>-1</sup>), rowan  
316 (0.01 trees ha<sup>-1</sup> y<sup>-1</sup>), wych elm (0.01 trees ha<sup>-1</sup> y<sup>-1</sup>), and others.



317

318 **Figure 4** The average annual recruitment of shade-tolerant (left) and light-demanding tree species (right)  
319 (mean value ± standard error of mean is shown)

320

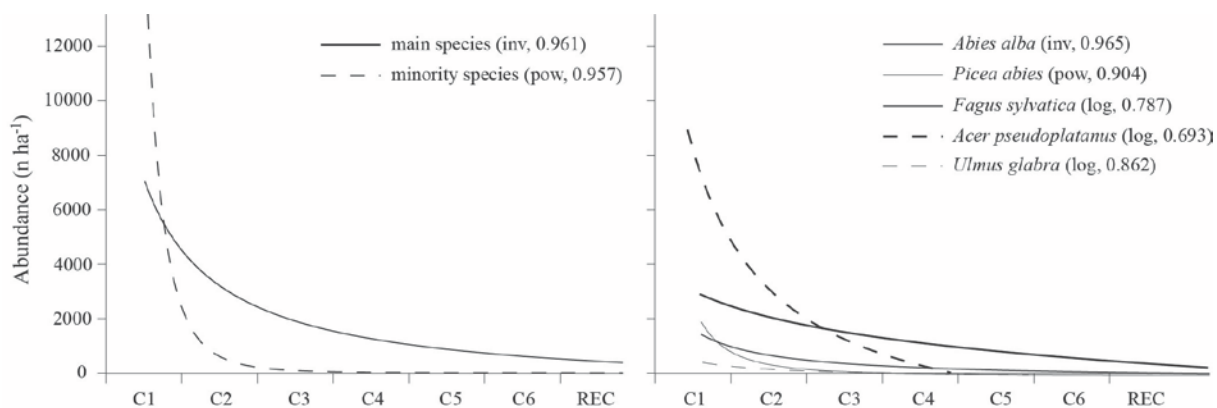
321 In plenter and group selection stands, total recruitment averaged 4.93 and 6.67 trees ha<sup>-1</sup> y<sup>-1</sup>,  
322 respectively, and significantly differed between the two stand types (p<0.001). Compared to the  
323 shade-tolerant species, average annual recruitment of light-demanding species was significantly  
324 lower (p<0.001), amounting to only 0.04 and 0.21 trees ha<sup>-1</sup> y<sup>-1</sup> in plenter and group selection stands,  
325 respectively.

326

### 327 *Regeneration vs. recruitment*

328 For all species, the survival rate of seedlings and saplings decreased with increasing height/dbh  
329 gradient. The survival rate of the regeneration during development until recruitment was noticeably  
330 greater for shade-tolerant species than for light-demanding species (Figure 5), but it also differed  
331 among the two groups of species. Norway spruce and European beech were the most successful  
332 shade-tolerant species in overgrowing the height classes and recruiting over the measurement

333 threshold, whereas sycamore was the most successful among the light-demanding species, with the  
 334 exception of passing the threshold of the C6 class, where only rowan specimens were tallied.



335  
 336 **Figure 5** Survivorship curves of the shade-tolerant and light-demanding tree species in the analysed uneven-  
 337 aged stands (type of the estimated curve (inv – inverse, pow – power, exp – exponential, log – logarithmic) and  
 338 R-square is given in the brackets)

339  
 340 Correlation analysis between regeneration and recruitment abundance and stem density in the  
 341 smallest inventoried dbh class DC10 (Table 4) showed no significant correlation between  
 342 regeneration abundance and the other two variables. However, we found a weak positive  
 343 correlation between regeneration abundance and DC10 for light-demanding species. In contrast, we  
 344 found strong positive correlations between recruitment abundance and DC10 for the total  
 345 regeneration and that of shade-tolerant species, as well as between recruitment and DC10 of light-  
 346 demanding species.

347 **Table 4** Correlations between regeneration (reg), recruitment (rec), and stem density in the smallest  
 348 inventoried diameter class (10-14.9 cm in dbh) (DC10); ST – shade-tolerant species, LD – light  
 349 demanding species

	rec_total	rec_ST	rec_LD	DC10_total	DC10_ST	DC10_LD
reg_total	-0.028	-0.023	-0.034	-0.101	-0.109	0.073
reg_ST	-0.038	-0.037	0.008	-0.095	-0.098	0.008
reg_LD	0.032	0.038	-0.025	-0.029	-0.039	0.114*
rec_total				0.620**	0.630**	-0.003
rec_ST				0.627**	0.641**	-0.020
rec_LD				-0.003	-0.035	0.158**

350 \*\* - statistically significant correlation with a confidence level of 0.05; \* - statistically significant correlation with a confidence level of 0.10



351 *Influential factors of regeneration and recruitment*

352 Several stand and site characteristics were included in the count and zero-inflated models of the  
 353 established seedlings (C1-2) and recruitment (Table 5). Stand characteristics significantly influenced  
 354 the abundance of seedlings, whereas site conditions more greatly influenced the probability of  
 355 absence of seedlings or recruitment (“a certain zero”).

356

357 **Table 5** Influential factors of seedlings and recruitment of light-demanding and shade-tolerant tree  
 358 species (only statistically significant coefficients B or G ( $p < 0.05$ ) with the corresponding factors F are  
 359 shown)  
 360

Variable	Light-demanding tree species				Shade-tolerant tree species			
	seedlings		recruitment		seedlings		recruitment	
<i>Count model</i>								
	B	F	B	F	B	F	B	F
constant	6.1504		2.1003		10.7209		3.5935	
ST							-0.1101	0.896
BA	-0.0393	0.961					-0.0328	0.968
BA <sub>LD</sub>								
DBH <sub>BA</sub>							-0.0068	0.993
INC					-0.0261	0.974	-0.0090	0.991
ELV								
ASP			-0.3987	0.671	-0.3969	0.672		
TOP								
MAI	0.5313	1.701						
CUT	0.0621	1.064					0.0305	1.031
UDI'								
Log(Theta)	-0.1903		1.9761		0.2310		1.0358	
<i>Zero inflation model</i>								
	G	F	G	F	G	F	G	F
constant	-6.9202		-3.5493		-7.1307		-2.3581	
ST								
BA	-0.0746	0.928	0.0757	1.079			0.0427	1.044
BA <sub>LD</sub>			-0.1535	0.858				
DBH <sub>BA</sub>			0.0451	1.046			0.0264	1.027
INC	0.0766	1.080			0.2059	1.229	0.0248	1.025
ELV	0.6197	1.858	0.5387	1.714				
ASP							-0.2601	0.771
TOP					4.0864	59.525	0.5991	1.820
MAI								
CUT							-0.0281	0.972
UDI'	0.0394	1.040						
Theta	0.8267		7.2148		1.2599		2.6322	
logLik	-1313.96		-198.75		-1539.93		-3661.3	
AIC	2647.93		413.50		3093.86		7344.59	

361 The stand type of uneven-aged forests (ST) was the only predictor of the recruitment abundance of  
362 shade-tolerant species; the recruitment was lower by a factor of 0.896 in group selection stands  
363 compared to plenter stands. Stand basal area (BA) decreased the abundance of seedlings of light-  
364 demanding species and recruitment of shade-tolerant species by a factor of 0.961 and 0.968,  
365 respectively. BA also decreased the odds of “a certain zero” in the C1-2 of light-demanding species  
366 by 7.2 % and increased these odds in the recruitment of light-demanding and shade-tolerant species  
367 by 7.9 % and 4.4 %, respectively. Basal area of mature trees of light-demanding species ( $BA_{LD}$ )  
368 influenced only “a certain zero” presence of light-demanding species recruitment, while a quadratic  
369 mean diameter on a plot ( $DBH_{BA}$ ) increased the odds of the absence of light-demanding and shade-  
370 tolerant species in the recruitment and decreased the abundance of shade-tolerant species  
371 recruitment.

372 Site conditions were identified as predictors in all four models. The absence of seedlings of light-  
373 demanding species was more likely to occur on steeper slopes (INC) and at higher elevations (ELV);  
374 also the absence of recruitment of light-demanding species was more likely at higher elevations. In  
375 addition, inclination (INC) increased the odds of “a certain zero” and decreased the abundance of  
376 seedlings and recruitment of shade-tolerant species. The abundance of light-demanding species  
377 recruitment and seedlings of shade-tolerant species was higher on northern aspects (ASP), as was  
378 the probability of the absence of shade-tolerant species recruitment. Seedling abundance of light-  
379 demanding species was higher in sites of high productivity (MAI).

380 Harvesting intensity (CUT) increased the abundance of seedlings of light-demanding species and  
381 recruitment of shade-tolerant species, as well as decreased the odds of the absence of shade-  
382 tolerant species recruitment. Finally, if a large ungulate density index (UDI') increased by 1 per  $km^2$ ,  
383 the odds of light-demanding species seedlings absence increased by a factor of 1.040.

384

## 385 Discussion

### 386 *Regeneration vs. recruitment*

387 Focusing on both recruitment and regeneration provides much more comprehensive information on  
388 the dynamics and potential of tree species in mixed uneven-aged forests than regeneration or  
389 recruitment alone since dramatic changes in both abundance and composition occur in the early  
390 stages of stand dynamics. Although the abundance in the regeneration “establishment” phase may  
391 indicate the potential for tree species to thrive in forest stands, the results of our study showed that  
392 this may be misleading; the “overgrowth” and “recruitment” phases predicted different conclusions.

393 Over 30,000 specimens ha<sup>-1</sup> were registered in the regeneration, which can be considered sufficient  
394 (*sensu* Duc, 1991) to maintain uneven structure in the studied forests. Differences in abundance and  
395 survival rate between tree species were identified, indicating various survivorship strategies of  
396 species. The shade-tolerant species germinated relatively less abundantly, but continued with a  
397 relatively high survival rate through the “overgrowth” and tree “recruitment” phases (curve A in  
398 Figure 1). The mortality of seedlings in their “establishment” phase was much greater for light-  
399 demanding species, especially for sycamore; its development is typical for species illustrated by  
400 curve B in Figure 1. Sycamore seems to be highly representative of a seed-seedling conflict (Schupp,  
401 1995), clearly exhibiting that environmental conditions promoting seed rain and seedling  
402 establishment are not always the most favourable for their survival and vigorous growth.

403 In our study, a dramatic 48-fold reduction in the number of specimens between the established  
404 regeneration and the tallest regeneration class was observed. This huge drop was especially evident  
405 for light-demanding species; the number of specimens of light-demanding species in the established  
406 regeneration and in the tallest regeneration class C6 declined from 13,121 ha<sup>-1</sup> to 8 ha<sup>-1</sup>. The  
407 decrease itself was not surprising, but the number of saplings in the tallest class and among  
408 recruited trees was critically low. The recruitment of light-demanding species was much lower than

409 that of shade-tolerant species, amounting to only 0.13 trees ha<sup>-1</sup> y<sup>-1</sup> (only 2.2 % of total recruited  
410 trees) or 44-times less than shade-tolerant species. The low light availability in uneven-aged stands  
411 seems to be sufficient for the establishment of light-demanding species regeneration, but it hinders  
412 their height growth and increases their mortality rate (Kobe and Coates, 1997; Stancioiu and O'Hara,  
413 2006; Petritan et al., 2007).

414 The abundance, structure and composition of regeneration demonstrated the potential for  
415 promotion of tree species that forest managers can consider when planning the target tree species  
416 composition and selecting the type of regeneration cut. However, comparison of both regeneration  
417 and recruitment is needed to understand the dynamics of tree replacement between age, height or  
418 diameter classes. In addition, both indicators can be used as indicators of probable structural and  
419 compositional changes when long-term stand dynamics is studied (e.g. Yoshida et al., 2006; Klopčič  
420 and Boncina, 2011).

421 Our correlation analysis showed that the number of trees in the smallest inventoried diameter class  
422 could be a useful indicator for assessing the recruitment process. It is simply derived from the  
423 diameter structure of forest stands and is thus also applicable where only data from one forest  
424 inventory are available. However, this indicator gives limited insight into stand dynamics since a high  
425 number of trees in the smallest diameter class can be a consequence of either a high recruitment  
426 rate or very slow growth of small trees under the canopy remaining in the smallest diameter class  
427 for decades (Ferlin, 2002), barely alive and unable to respond if better light conditions appear. In  
428 contrast, recruitment better describes the dynamics of specimens from the regeneration crossing  
429 the threshold dimension.

430

431 *Influential factors*

432 According to evidence from case study research (e.g. Jarni et al., 2004; Klopčič et al., 2010) and  
433 personal communication with local foresters, the impact of large ungulates is the key external factor  
434 influencing the overgrowing of regeneration in the studied forests. A number of light-demanding  
435 species are high on the list of the most palatable tree species (Gill, 1992), and relatively high large  
436 ungulate densities in the study area may substantially reduce the survival rate and recruitment  
437 success of light-demanding species as well as silver fir (Motta, 1996, 2003; Klopčič et al., 2010). Our  
438 field observations indicated that large ungulates substantially impacted the regeneration. Browsing  
439 resulted in damage to 45 % of the regeneration of light-demanding species (results not shown);  
440 while only 29 % of seedlings up to 20 cm in height were damaged, this share amounted to 44 % in  
441 seedlings of 20-49 cm in height, and reached 56 % in saplings. As found for eastern hemlock in the  
442 Upper Great Lakes, USA (Rooney et al., 2000), the impact of large ungulates seems to be greater on  
443 individuals above 20 cm in height and lasts until they surpass the browse height limit. Comparative  
444 studies of regeneration in fenced and unfenced areas of the same forest type (Jarni et al., 2004;  
445 Klopčič et al., 2010) showed that light-demanding species, especially sycamore and wych elm,  
446 regenerated and recruited abundantly in the fenced areas, but were practically non-existent outside;  
447 similar findings were reported by Ammer (1996) and Motta (2003). However, in our study we did not  
448 find that large ungulates significantly hindered regeneration success. This is likely due to the limited  
449 performance of UDI' for our study data. Firstly, it was adapted to the plot level from a larger spatial  
450 scale, possibly causing some discrepancies with the dependent variables, and secondly, this index is  
451 more appropriate for regional or larger spatial scales since it may not effectively identify (small)  
452 differences in densities of large ungulates at the landscape or stand scale.

453 Stand type was expected to be an important factor related to regeneration and recruitment of both  
454 light-demanding and shade-tolerant tree species. Although the total number of light-demanding  
455 regeneration was higher in group selection than in plenter stands, no statistically significant  
456 differences were found. This was also evident from the models in which stand type (ST) was

457 identified as a predictor only in the model of recruitment of shade-tolerant species. The differences  
458 in stand characteristics between the studied stand types seem to be too small to actually influence  
459 the potential and success of both light-demanding and shade-tolerant species. In contrast, Klopčič  
460 and Boncina (2012) determined stand type as one of the most important predictors in the  
461 recruitment models of shade-tolerant silver fir and European beech as well as light-demanding  
462 sycamore. However, the study encompassed a broader area of uneven-aged stands, including large-  
463 scale irregular shelterwood stands (not included in this study) that differ significantly in stand  
464 characteristics compared to plenter and group selection stands.

465 Some other stand characteristics significantly influenced regeneration and recruitment. Stand basal  
466 area is closely related to the growing space of an individual tree and availability of (light) resources  
467 for trees. Higher stand density leads to increased competition and higher mortality among  
468 regeneration and trees, especially for those growing in the understory (Monserud and Sterba, 1999).  
469 Tree species composition of the mature stand may also influence the composition of regeneration  
470 and recruitment. Although the small size of plots was not perfect to study these relations, we found  
471 that the proportion of light-demanding species had only a minor influence on their recruitment;  
472 however, for some species their proportion in forest stands may be highly significant due to limited  
473 seed rain and seed banks or seed dispersal (e.g. European beech; Sagnard et al., 2007). The small  
474 influence of the proportion of light-demanding species on their regeneration and recruitment is  
475 likely due to the fact that their seed rain and seed dispersal is generally not problematic since they  
476 have relatively light seed which is wind- or animal- dispersed (Hein et al., 2009; Dobrowolska et al.,  
477 2011). Instead, we assume that site conditions may often limit the presence and abundance of at  
478 least certain light-demanding species (Kobe and Coates, 1997).

479 Site conditions vary substantially within the analysed forest type (Puncer, 1980). Five site variables  
480 (i.e. elevation, inclination, aspect, topography and site productivity) have been included in at least  
481 one of the four developed models explaining the occurrence and abundance of shade-tolerant and

482 light-demanding species regeneration and recruitment. Light-demanding tree species can be more  
483 competitive in some specific (micro)site conditions within mixed mountain forests (Puncer, 1980);  
484 for example, sites with nutrient-rich soils and high water content are preferred by sycamore,  
485 European ash and small-leaved linden (e.g. Dobrovolska et al., 2011). Our results confirmed that the  
486 regeneration of light-demanding species was more abundant in sites of higher productivity. The  
487 results also indicated higher probability of light-demanding species establishment and success on  
488 lower elevations which is expectedly in accordance with findings on decreasing species diversity  
489 along the elevation gradient (Kimmins, 2004). However, detailed analysis of the influence of  
490 potentially important site variables, such as soil characteristics (e.g. Kobe and Coates, 1997;  
491 Hasenauer and Kindermann, 2002), was not the main focus of our research, especially given the lack  
492 of reliable data. In addition, the influence of certain independent variables (e.g. aspect) was not  
493 unambiguously indicated, imposing the necessity for further detailed research.

494

#### 495 *Management implications for promotion of light-demanding tree species*

496 In mixed mountain forests, there are fewer possibilities for promotion of light-demanding tree  
497 species compared to lower altitudinal forests in the planar, coline or submontane vegetation belt  
498 due to the more extreme site conditions. Still, our study has shown that light-demanding species can  
499 also be promoted in a low proportion in mountain forests. According to forest management plans in  
500 the study area, the target proportion of sycamore and other light-demanding species was 5-10 % of  
501 stand volume in the plenter stands and 10-15 % in the irregular shelterwood stands, while target  
502 values can be even higher (>15 %) in some specific sites where these species are more competitive.  
503 In the Rajhenav old-growth forest of the same forest type, their proportion was less than 0.5 %  
504 (Boncina, 2000).

505 Despite the common assumption that only shade-tolerant species can successfully regenerate and  
506 grow at the low light levels encountered in selection forests, there may be species that can establish  
507 under the canopy, but need light to recruit into stands. According to our study, sycamore abundantly  
508 regenerates in the shade, but shading becomes an important mortality factor in the “overgrowth”  
509 and “recruitment” phases. In European mountain forests, sycamore commonly mixes with European  
510 beech and silver fir (Hein et al., 2009). All of these species are shade-tolerant in the early  
511 regeneration phase, but throughout its growth sycamore needs more light or its mortality rate  
512 increases (Petritan et al., 2007). However, if light conditions improve, it responds rapidly and  
513 strongly; on good quality sites it can even suppress shade-tolerant and slower-growing species,  
514 though they can catch up some decades later (Hein et al., 2009).

515 Silvicultural systems differ in the size of regeneration gaps, and the promotion of light-demanding  
516 species largely depends on the type of regeneration harvesting. In the Appalachian hardwoods of  
517 the USA, canopy openings of 0.2 ha (0.5 acre) provided suitable light conditions for all species,  
518 including shade-intolerant species (Miller and Kochenderfer, 1998). In Britain, Malcolm et al. (2001)  
519 suggested creation of canopy gaps >0.2 ha for the establishment of light-demanding coniferous  
520 species, 0.05-0.2 ha for intermediate species, and <0.05 ha for shade-tolerant species. In contrast,  
521 for the northern hardwoods in Wisconsin, USA, Kern et al. (2013) ascertained that an optimum gap  
522 size does not exist and asserted that microsite specifics have to be strongly considered when  
523 regenerating stands with the aim of a particular species composition. In the mixed mountain forest  
524 in the Dinaric Mountains, silvicultural systems promoting large canopy openings and even-aged  
525 stands have been rarely applied due to the high sensitivity of sites to degradation and karstification  
526 (Boncina, 2011). In the last decades a free-style silviculture has been applied in these forests (*ibid.*),  
527 characterized by a combination of silvicultural systems on the stand, landscape or regional spatial  
528 scales that is able to target for a larger proportion of light demanding species in certain forest  
529 stands. Applying the group selection and irregular shelterwood systems and modifying the size and



530 arrangement of group cuts would create a wider range of environments and provide beneficial  
531 conditions for a variety of species. Such an approach would perpetuate shade-tolerant species, while  
532 providing the opportunity to promote light-demanding species if the potential exists. In addition,  
533 decreasing browsing pressure is needed to enable palatable light-demanding species overgrowing  
534 into the upper layers of forest stands.

535

## 536 **Conclusion**

537 The study revealed significant differences between regeneration and recruitment in uneven-aged  
538 stands, indicating the importance of understanding both indicators when studying the dynamics of  
539 uneven-aged forests. Comparison of regeneration and recruitment reveals the dynamic processes  
540 during the young stages of uneven-aged forest development and helps in selecting the appropriate  
541 silvicultural system for promoting the target tree species.

542 Although the competitiveness of less shade-tolerant species in uneven-aged stands is limited, they  
543 can establish and succeed, albeit with a low proportion in the growing stock. By applying the  
544 “freestyle silviculture”, a mosaic of irregular sized patches of uneven-aged and partly even-aged  
545 structure is created on a landscape spatial scale, which enables existence of both the dominant  
546 shade tolerant and in some locations also light-demanding minority tree species. The mixture of  
547 both shade-tolerant and light-demanding species increases tree species diversity of forests and  
548 contribute to their higher resilience and adaptive capacity to changing environmental conditions.

549

## 550 **Funding**

551 This work was financially supported by the European research project “Advanced multifunctional  
552 forest management in European mountain ranges” (ARANGE, n° 289437) and a grant from the  
553 Pahernik Foundation.

554

555 **Acknowledgements**

556 We are grateful to the Slovenia Forest Service, especially Dragan Matijašić and Aleš Poljanec, for  
557 providing access to the forest inventory databases, which made our study feasible. The authors are  
558 also grateful to colleagues who helped with the regeneration inventory: Živa Bončina, Andrej Ficko,  
559 Blanka Malus, Aleš Poljanec and Jörg Rössiger. The comments of the anonymous reviewers and the  
560 Editor significantly improved the earlier version of the manuscript.

561

562 **Conflict of interest statement**

563 None declared.

564

565 **References**

- 566 Ammer, C. 1996 Impact of ungulates on structure and dynamics of natural regeneration of mixed  
567 mountain forests in the Bavarian Alps. *For. Ecol. Manag.* **88**(1-2), 43-53.
- 568 Begon, M., Harper, J.L. and Townsend, C.R. 1990 *Ecology. Individuals, Populations and Communities*.  
569 Blackwell Scientific Publications, 945 p.
- 570 Boncina, A. 2000 Comparison of structure and biodiversity in the Rajhenav virgin forest remnant and  
571 managed forest in the Dinaric region of Slovenia. *Global Ecol. Biogeogr.* **9**, 201-211.
- 572 Boncina, A. 2011 History, current status and future prospects of uneven-aged forest management in  
573 the Dinaric region: an overview. *Forestry* **84**(5), 467-478.
- 574 Boncina, A., Cavlovic, J., Curovic, M., Govedar, Z., Klopčic, M. and Medarevic, M. 2014 A comparative  
575 analysis of recent changes in Dinaric uneven-aged forests of the NW Balkans. *Forestry* **87**(1), 71-84.
- 576 Boyden, S.B., Reich, P.B., Puettmann, K.J. and Baker, T.R. 2009 Effects of density and ontogeny on  
577 size and growth ranks of three competing tree species. *J. Ecol.* **97**, 277-288.
- 578 Brang, P., Spathelf, P., Larsen, J.B., Bauhus, J., Bončina, A., Chauvin, C. et al. 2014 Suitability of close-  
579 to-nature silviculture for adapting temperate European forests to climate change. *Forestry* **87**(4),  
580 492-503.
- 581 Collet, C., Lanter, O. and Pardos, M. 2001 Effects of canopy opening on height and diameter growth  
582 in naturally regenerated beech seedlings. *Ann. For. Sci.* **58**(2), 127-134.
- 583 Dobrowolska, D., Hein, S., Oosterbaan, A., Wagner, S., Clark, J. and Skovsgaard, J.P. 2011 A review of  
584 European ash (*Fraxinus excelsior* L.): implications for silviculture. *Forestry* **84**(2), 133-148.
- 585 Duc, P. 1991 Untersuchungen zur Dynamik des Nachwuchses im Plenterwald. *Schweiz. Z.*  
586 *Forstwesen* **142**(4), 299-319.

587 Eerikäinen, K., Miina, J. and Valkonen, S. 2007 Models for the regeneration establishment and the  
588 development of established seedlings in uneven-aged, Norway spruce dominated forest stands of  
589 southern Finland. *For. Ecol. Manag.* **242**(2-3), 444-461.

590 Ferlin, F. 2002 The growth potential of understorey silver fir and Norway spruce for uneven-aged  
591 forest management in Slovenia. *Forestry* **75**(4), 375-383.

592 Gill, R.M.A. 1992 A review of damage by mammals in north temperate forests .1. Deer. *Forestry*  
593 **65**(2), 145-169.

594 Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I. et al. 1999 A review of the  
595 regeneration dynamics of North American boreal forest tree species. *Can. J. For. Res.* **29**(6), 824-839.

596 Greene, W.H. 1994 *Accounting for Excess Zeros and Sample Selection in Poisson and Negative*  
597 *Binomial Regression Models (March 1994). NYU Working Paper No. EC-94-10.*  
598 <http://ssrn.com/abstract=1293115> (accessed on 10 December 2014).

599 Hasenauer, H. and Kindermann, G. 2002 Methods for assessing regeneration establishment and  
600 height growth in uneven-aged mixed species stands. *Forestry* **75**(4), 385-394.

601 Hein, S., Collet, C., Ammer, C., Goff, N.L., Skovsgaard, J.P. and Savill, P. 2009 A review of growth and  
602 stand dynamics of *Acer pseudoplatanus* L. in Europe: implications for silviculture. *Forestry* **82**(4), 361-  
603 385.

604 Helms, J.A. 1998 *The Dictionary of Forestry*. The Society of American Foresters, 210 p.

605 Hollander, M. and Wolfe, D.A. 1999 *Non-Parametric Statistical Methods*. 2<sup>nd</sup> Edition. Wiley, New  
606 York.

607 IBM Corp. Released 2012 IBM SPSS Statistics for Windows, Version 21.0. IBM Corporation, Armonk,  
608 NY.

609 IUSS Working Group WRB 2007 World Reference Base for Soil Resources 2006, first update 2007.  
610 World Soil Resources Reports No. 103. FAO, Rome.

611 Jarni, K., Robic, D. and Boncina, A. 2004 Analysis of the influence of ungulates on the regeneration of  
612 Dinaric fir-beech forests in the research site Trnovec in the Kocevje forest management region.  
613 *Zbornik gozdarstva in lesarstva* **74**, 141-164.

614 Jerina, K. 2008 *Velika rastlinojeda divjad in razvojna dinamika gozdnih ekosistemov: proučevanje*  
615 *vplivov izbranih okoljskih in populacijskih parametrov ter gozdno-gojitvenih sistemov na zmožnosti*  
616 *naravne obnove: zaključno poročilo o rezultatih opravljenega raziskovalnega dela na projektu v*  
617 *okviru ciljnega raziskovalnega projekta (CRP) "Konkurenčnost Slovenije 2006-2013": research report*  
618 *(in Slovene)*. University of Ljubljana, Biotechnical Faculty, Department for Forestry and Renewable  
619 Forest Resources.

620 Kadunc, A., Poljanec, A., Dakskobler, I., Rozman, A. and Bončina, A. 2013 *Ugotavljanje proizvodne*  
621 *sposobnosti gozdnih rastišč v Sloveniji: poročilo o realizaciji projekta. Research report* (in Slovene).  
622 University of Ljubljana, Biotechnical Faculty, Department for Forestry and Renewable Forest  
623 Resources, 42 p.

624 Kern, C.C., D'Arnato, A.W. and Strong, T.F. 2013 Diversifying the composition and structure of  
625 managed, late-successional forests with harvest gaps: What is the optimal gap size? *For. Ecol.*  
626 *Manag.* **304**, 110-120.

627 Kimmins, J.P. 2004 *Forest Ecology. A Foundation for Sustainable Forest Management and*  
628 *Environmental Ethics in Forestry. Third Edition.* Prentice Hall, 611 p.

629 Klingsporn Poznanovic, S., Webster, C.R. and Bump, J.K. 2013 Maintaining mid-tolerant tree species  
630 with uneven-aged forest management: 9-year results from a novel group-selection experiment.  
631 *Forestry* **86**(5), 555-567.

632 Klopčič, M. and Bončina, A. 2011 Stand dynamics of silver fir (*Abies alba* Mill.)-European beech  
633 (*Fagus sylvatica* L.) forests during the past century: a decline of silver fir? *Forestry* **84**(3), 259-271.

634 Klopčič, M. and Bončina, A. 2012 Recruitment of tree species in mixed selection and irregular  
635 shelterwood forest stands. *Ann. For. Sci.* **69**(8), 915-925.

636 Klopčič, M., Jerina, K. and Bončina, A. 2010 Long-term changes of structure and tree species  
637 composition in Dinaric uneven-aged forests: are red deer an important factor? *Eur. J. For. Res.*  
638 **129**(3), 277-288.

639 Klopčič, M., Poljanec, A. and Bončina, A. 2012 Modelling natural recruitment of European beech  
640 (*Fagus sylvatica* L.). *For. Ecol. Manag.* **284**, 142-151.

641 Kobe, R.K. and Coates, K.D. 1997 Models of sapling mortality as a function of growth to characterize  
642 interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. *Can.*  
643 *J. For. Res.* **27**, 227-236.

644 Lexerød, N. and Eid, T. 2005 Recruitment models for Norway spruce, Scots pine, birch and other  
645 broadleaves in young growth forests in Norway. *Silva Fenn.* **39**(3), 391-406.

646 Lexerød, N.L. 2005 Recruitment models for different tree species in Norway. *For. Ecol. Manag.*  
647 **206**(1-3), 91-108.

648 Malcolm, D.C., Mason, W.L. and Clarke, G.C. 2001 The transformation of conifer forests in Britain -  
649 regeneration, gap size and silvicultural systems. *For. Ecol. Manag.* **151**(1-3), 7-23.

650 Mathews, J.D. 1999 *Silvicultural systems.* Oxford University Press Inc., 284 p.

651 Miller, G.W. and Kochenderfer, J.M. 1998 Maintaining species diversity in the central Appalachians.  
652 *J. For.* **96**(7), 28-33.

653 Monserud, R.A. and Sterba, H. 1999 Modeling individual tree mortality for Austrian forest species.  
654 *For. Ecol. Manag.* **113**(2-3), 109-123.

655 Motta, R. 1996 Impact of wild ungulates on forest regeneration and tree composition of mountain  
656 forests in the Western Italian Alps. *For. Ecol. Manag.* **88**(1-2), 93-98.

657 Motta, R. 2003 Ungulate impact on rowan (*Sorbus aucuparia* L.) and Norway spruce (*Picea abies* (L.)  
658 Karst.) height structure in mountain forests in the eastern Italian Alps. *For. Ecol. Manag.* **181**(1-2),  
659 139-150.

660 O'Hara, K.L. 2014 *Multiaged Silviculture: Managing for Complex Forest Stand Structures*. Oxford  
661 University Press.

662 Oliver, C.D. and Larson, B.C. 1996 *Forest Stand Dynamics*. Wiley, 520 p.

663 Petritan, A.M., von Lüpke, B. and Petritan, I.C. 2007 Effects of shade on growth and mortality of  
664 maple (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*) saplings. *Forestry*  
665 **80**(4), 397-412.

666 Puncer, I. 1980 *Dinarski jelovo bukovi gozdovi na Kočevskem (in Slovene)*. Slovenska akademija  
667 znanosti in umetnosti, 161 p.

668 R Core Development Team. 2014 *R: A language and environment for statistical computing*. R  
669 Foundation for Statistical Computing. ISBN 3-900051-07-0, <http://www.R-project.org>.

670 Raymond, P., Bedard, S., Roy, V., Larouche, C. and Tremblay, S. 2009 The irregular shelterwood  
671 system: review, classification, and potential application to forests affected by partial disturbances. *J.*  
672 *For.* **107**(8), 405-413.

673 Rooney, T.P., McCormick, R.J., Solheim, S.L. and Waller, D.M. 2000 Regional variation in recruitment  
674 of hemlock seedlings and saplings in the Upper Great Lakes, USA. *Ecol. Appl.* **10**(4), 1119-1132.

675 Rozenbergar, D., Mikac, S., Anic, I. and Diaci, J. 2007 Gap regeneration patterns in relationship to  
676 light heterogeneity in two old-growth beech-fir forest reserves in South East Europe. *Forestry* **80**(4),  
677 431-443.

678 Sagnard, F., Pichot, C., Dreyfus, P., Jordano, P. and Fady, B. 2007 Modelling seed dispersal to predict  
679 seedling recruitment: recolonization dynamics in a plantation forest. *Ecol. Model.* **203**, 464-474.

680 Schupp, E.W. 1995 Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *Am. J.*  
681 *Bot.* **82**(3), 399-409.

682 Schütz, J.-P. 2001 *Der Plenterwald und weitere Formen strukturierter und gemischter Wälder*. Parey,  
683 207 p.

684 Schwartz, J.W., Nagel, L.M. and Webster, C.R. 2005 Effects of uneven-aged management on  
685 diameter distribution and species composition of northern hardwoods in Upper Michigan. *For. Ecol.*  
686 *Manag.* **211**(3), 356-370.

687 SFS 2014 *Forest Inventory Database*. Slovenian Forest Service, Ljubljana, Slovenia.

688 Spiecker, H. 2006. Minority species – a challenge for multi-purpose forestry. In: Diaci, J. (ed), Nature-  
689 based Forestry in Central Europe. Alternatives to Industrial Forestry and Strict Preservation.  
690 Biotechnical Faculty, Department of Forestry and Renewable Forest Resources.

691 Stancioiu, P.T. and O'Hara, K.L. 2006 Regeneration growth in different light environments of mixed  
692 species, multiaged, mountainous forests of Romania. *Eur. J. For. Res.* **125**(2), 151-162.

693 Tomppo, E., Gschwantner, T., Lawrence, M. and McRoberts, R.E. 2010 *National Forest Inventories.*  
694 *Pathways for Common Reporting*. Springer, 612 p.

695 Yoshida, T., Noguchi, M., Akibayashi, Y., Noda, M., Kadomatsu, M. and Sasa, K. 2006 Twenty years of  
696 community dynamics in a mixed conifer - broad-leaved forest under a selection system in northern  
697 Japan. *Can. J. For. Res.* **36**(6), 1363-1375.

698

699

700

701 **Appendix 1** Information about forest management in the study area

	Plenter stands		Group selection stands	
	mean	sd	Mean	sd
Cutting intensity ( $\text{m}^2 \text{ha}^{-1} 10\text{y}^{-1}$ )	4.00	5.02	3.90	5.28
Cutting intensity (% of stand basal area)	16.1	53.0	17.6	33.4
Diameter of canopy openings	<1 $h_{\text{max}}$		1-2 $h_{\text{max}}$	
Intervention period (y)	10		10	
Rotation period (y)	-		120-140	
Soil disturbance	absent		minimal	
Natural mortality ( $\text{m}^2 \text{ha}^{-1} 10\text{y}^{-1}$ )	0.25	1.04	0.23	0.93
Natural mortality (% of stand basal area)	0.90	3.79	0.93	4.75

702 \*  $h_{\text{max}}$  - maximum stand height