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Effect of gap size on tree species diversity of natural regeneration – case study from Masaryk Training Forest Enterprise Křtiny

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Abstract: Forest gaps remain the optimal forest management practice in modern forestry. Upon all the physical properties of forest gaps, the 'gap size' feature stands out as an essential property. The effect of gap size on tree species composition and diversity of natural regeneration in forest gaps of different sizes was investigated. Eight research forest gaps were selected from the Training Forest School Enterprise, also called Masaryk Forest in Křtiny, a temperate mixed forest in the Czech Republic. By given gap sizes, small (< 700 m^2) and large gaps (≥ 700 m^2) were defined. Forty-one (41) regeneration microsites (RSs) of 1 m^2 circular area at 2 m intervals were demarcated within each forest gap. These RSs served as data collection points. From the total of eleven (11) species enumerated, large gaps obtained higher species composition (10) and diversity (Simpson = 0.5 1-*D*; Shannon = 1.0 *H* and Pielou's evenness = 0.5 *J* indices) records, yet, small gaps presented favourable conditions for prolific natural regeneration significantly. Light-adapted species demonstrated no significant difference ($P > 0.05$) between small and large gaps, however, intermediate and shade-tolerant species were significantly higher ($P < 0.05$) in small gaps. There were progressive declines in height growth of natural regeneration from 0–20 cm to 21–50 cm and 51+ cm in small and large gaps at R^2 = 99% and 88%, respectively. The development of herbaceous vegetation in small and large gaps had positive and negative effects on the natural regeneration of *Fagus sylvatica* and *Abies alba* species, respectively.

Keywords: intermediate species; large gaps; light-adapted species; shade-tolerant species; small gaps; species composition and diversity

Forest gaps can be defined as the forest floor areas directly under canopy openings, resulting from one or more displaced trees in the forest stand. Based on Sapkota and Odén (2009) study on forest gaps there exist (*i*) naturally formed forest gaps by single or multiple tree fall(s) through natural disturbances (e.g., windstorms, fires, insect or pest outbreaks etc.) and (*ii*) artificially formed forest gaps resulting from single or group cutting of trees by anthropogenic disturbances (e.g., logging). The creation of forest gaps strongly influences forest regeneration and, at the same time, enhances habitat

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diversity within forest ecosystems by stimulating the coexistence of different tree species (Schnitzer, Carson 2001; Latif, Blackburn 2010). Many papers have reported the relevance of species diversity in relation to forest functioning, including productivity, stability, or provision of ecosystem services (Del Río et al. 2017; Bravo-Oviedo et al. 2018).

Others have also presented empirical evidence on the relevance of species composition for forest dynamics, growth, and yield (Töigo et al. 2015; Pretzsch 2018). Due to the disposition of species composition as the main structural characteristic in temperate mixed-species forests (Bravo-Oviedo et al. 2018), there is a greater demand for knowledge of species composition regarding mixed forest dynamics and management practices (Pretzsch 2018). However, at the forest stand level, both species composition and diversity are very important to characterize the forest structure (Bravo-Oviedo et al. 2018).

Forest gaps are recognized as one of the best silvicultural techniques for ensuring sustainable management of species composition and diversity in most temperate mixed, uneven-aged forests (Dobrowolska 2007; Jaloviar et al. 2020), because they provide conducive growing sites for natural regeneration of different tree species with varying physiological demands and biological traits (Vilhar et al. 2015).

Against this background that gap-based silviculture has become an interesting contemporary key research theme because it represents two very different management practices that are not easy to combine and that potentially act preferentially on different coexistence mechanisms (Cordonnier et al. 2018), hence it is recommended especially when light-adapted or shade-intolerant species (light-demanding species that prefer light for regeneration) or intermediate or mid-tolerant species (species that require either light or shade conditions during a particular growth stage in regeneration) are in competition with shade tolerant species (species that regenerate very well under shade or sheltered conditions for regeneration) (Coates, Burton 1997; Webster, Lorimer 2005).

Gap size is widely thought to be the most crucial feature of forest gaps (Xu et al. 2016; Hammond, Pokorný 2020) because it substantially determines heterogeneity of micro-environmental light and soil (moisture, temperature and nutrients) conditions (Gálhidy et al. 2006; Latif, Blackburn 2010) which are indispensable to the establishment and performance of natural regeneration in forest gaps (Muscolo et al. 2014; Vilhar et al. 2015). Also, to the fact that gap size is a strong predictor of species composition in forest gaps (Čater et al. 2014), it could be used to forecast the success of natural regeneration of different tree species with the varying ecological shade tolerance (*EST*) status.

For instance, large gaps are generally beneficial to the regeneration of light-adapted species (Čater, Diaci 2017; Hammond, Pokorný 2020) whereas small gaps are beneficial to shade-tolerant species (Duke 2001) and generally, forest gaps are favourable spots for intermediate species due to their natural equidistant light-shade tolerance requirements.

In effect, various studies have shown that dynamics and distribution of different tree species regeneration in gaps of different sizes are related to species-specific growth strategies and survival to gap size as well as the type of vegetation under which regeneration occurs (Kern et al. 2013; Wang et al. 2017). Undoubtedly, gap size has a strong influence on tree species regeneration.

Thus, gaps of different sizes can belong among the most critical silvicultural mechanisms for the maintenance of tree species diversity and structure in forest management.

The importance of the effect of gap size on plant species diversity and composition in different forest types in temperate (Sapkota et al. 2009; Pourbabaei et al. 2013; Wang et al. 2017) and tropical (Schnitzer et al. 2008; Marra et al. 2014) regions has been validated by several authors.

Therefore, it is an indisputable fact that gap size is a prominent factor in determining tree species composition and diversity in forest gaps. However, there is no information about the effect of gap size on plant species diversity in the temperate mixed-species forest at Křtiny in the Czech Republic.

So, the main objectives of this study were to evaluate the effect of gap size on species composition and diversity of tree species of natural regeneration in gaps of different sizes created by anthropogenic disturbances.

To be specific, we focused our research on: (*i*) the effects of gap size on growth performances of natural regeneration tree species with contradictory shade-tolerance mechanisms in small and large gaps, (*ii*) the effects of gap size on dynamics and distribution of height growth of natural regeneration tree species in small and large gaps, and (*iii*) the role of ground

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herbaceous vegetation in natural regeneration in the above-mentioned gap sizes.

MATERIAL AND METHODS

Study area description. Eight research forest gaps (Table 1) were selected within 13.26 hectares of forest, where anthropogenic disturbances in the form of tree felling had been completed 32 months previously in the Training Forest School Enterprise, also called Masaryk Forest at Krtiny (TFE): teaching, learning and research site of Mendel University in Brno. TFE consists of a temperate mixed forest located in Křtiny, at the Blansko District of the South Moravian Region in the Czech Republic. Geographically, TFE is positioned at latitude 16°15'E and longitude 49°15'N between the altitudes of 210 m and 575 m a.s.l. (Mašínová et al. 2017).

According to the Köppen climate classification, the area is classified as humid continental climate in the temperate climate zone (Deliège, Nicolay 2016) with annual average precipitation and temperature of 610 mm and 7.5 °C, respectively (Mašínová et al. 2017). TFE has rich soil diversity ranging from luvisols, fluvisols to gleysols (Bíšek 2016). European beech (*Fagus sylvatica* L.), sessile oak (*Quercus petraea* /Mattuschka/ Liebl.), Norway spruce (*Picea abies* /L./ Karsten), and larch (*Larix decidua* Mill.) are the widespread tree species in the forest region.

Mild forest management methods such as shelterwood management system and minimum clear-cut policy based on selection principles have been used in the Enterprise since its establishment in 1923, supporting admixed tree species of the natural species composition, especially European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* /L./ Karsten). Notwithstanding, other forest management actions based on forest management guidelines at TFE in compliance with the Forest Stewardship Council (FSC) environmental certificate, such as gap-based silviculture, natural regeneration, preferential selection of the most predominant species, preferential selection of the most competitive species and intermittent planting of weakly competitive species are unreservedly encouraged for the continuous accomplishment of sustainable forest management goals (Anonymous 2013).

Experimental forest gaps, which were numbered from G1 to G8, situated in two mature stands (97 years; average stem diameter at breast height 45 cm; average height 31 m) of different forest types were selected in autumn 2016 (Table 1). We defined "forest gaps" as canopy openings with ≥ 20 m^2 in area (Dobrowolska 2007). By the given gap sizes, for-

Table 1. Necessary information about studied gap plots at TFE

Gap plots	Gap location	Gap size area (m^2)	Gap width (m)	Character number	Forest stand type (species composition %)	Growing stock[a] (m^3·ha^{-1})	Living[a] stock (m^3)
G1	49°19.06768'N, 16°43.66460'E	small size (528)	26	0.7	broadleaved (European beech 90, Norway spruce + European larch 10)	533	7 087
G2	49°19.03118'N, 16°43.66622'E	large size (1291)	41	1.2			
G3	49°19.02657'N, 16°43.62308'E	small size (282)	19	0.5			
G4	49°18.99488'N, 16°43.64303'E	large size (1149)	38	1.1			
G5	49°18.95460'N, 16°43.60152'E	small size (286)	19	0.6	mixed (Norway spruce 50, European beech 30, European silver fir + European larch 20)	533	7 087
G6	49°18.94642'N, 16°43.55067'E	large size (764)	31	1.0			
G7	49°18.89250'N, 16°43.53232'E	large size (904)	34	1.1			
G8	49°18.90320'N, 16°43.50110'E	small size (226)	17	0.6			

[a]data based on forest management guidelines for Training Forest School Enterprise called Masaryk Forest in Křtiny (Anonymous 2013), N – north (longitude), E – east (latitude), character number is the ratio of the average tree height of surrounding parent stand and gap width, and it reflects gap sizes with similar microclimatic conditions

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Table 2. Natural regeneration of tree species in gaps of different sizes

Tree species	Ecological shade tolerance status	Small gaps		Large gaps	
		Reg. d. (trees·ha^{-1})	Rel. d. (%)	Reg. d. (trees·ha^{-1})	Rel. d. (%)
Larix decidua Mill.	light-adapted	101	0.11	1 088	8.05
Pinus sylvestris L.	light-adapted	0	0.00	19	0.14
Populus nigra L.	light-adapted	0	0.00	29	0.21
Salix alba L.	light-adapted	689	0.72	826	6.11
Acer pseudoplatanus L.	intermediate	561	0.59	0	0.00
Fraxinus excelsior L.	intermediate	132	0.14	10	0.07
Picea abies (L.) Karsten	intermediate	59 967	62.66	4 869	36.04
Pseudotsuga menziesii (Mirb.) Franco	intermediate	99	0.10	263	1.95
Abies alba Mill.	shade-tolerant	12 442	13.00	3 642	26.96
Carpinus betulus L.	shade-tolerant	0	0.00	19	0.14
Fagus sylvatica L.	shade-tolerant	21 716	22.69	2 746	20.32
Total		95 707	100	13 511	100

Reg. d. – Regeneration density, Rel. d. – Relative density

est gaps were categorized from small (< 700 m^2) to large gaps (≥ 700 m^2) (Table 1) (Hammond, Pokorný 2020). The shapes of the selected gaps were close to regular circles or slightly elliptical in the cases of both small and large gaps.

Data survey. Within each gap, four transects towards north-south-east-west cardinal directions were laid from the gap centre. Afterward, ten (10) regeneration microsites (RS; 1 m^2 circular subsampling area with radius = 56 cm) each were marked out at 2 m intervals along individual transects including one (1) additional RS at the gap centre. This was repeated for all selected gaps.

For ground herbaceous vegetation data, dominant herb species within the areas of all created RS were first appraised, identified by the species name, counted, and recorded accordingly.

For natural regeneration data, every tree species within the areas of all delineated RS were first identified by the species name and counted. Next, their respective heights were measured with a calibrated gauge pole (in cm). Tree species in three (3) size classes below the height of 350 cm (0–20 cm, 21–50 cm, and 50+ cm) were recorded accordingly. Further, tree species were grouped into three (3) basic (light-adapted, intermediate and shade-tolerant species) *EST* statuses according to tree ecology as described by Úradníček et al. (2010) (Table 2).

Estimation of diversity indices. The widely used Paleontological Statistics and educational software (PAST 3.24 version) by Hammer et al. (2001) was used for the estimation of species diversity in the study area. Four (4) diversity indices (Equations 1–4) and relative density (equation 5) were suitably considered because of their relevance to the study goals.

Firstly, Simpson's index (1-*D*) was used to estimate species dominance.

$$D = \sum(n_i/n)^2 \text{ (Harper 1999)} \quad (1)$$

where:
D – dominance,
n_i – number of individuals of i^{th} taxon,
n – number of individuals.

Followed by the Shannon diversity index (*H*), *H* was used to estimate species diversity.

$$H = -\sum_i \frac{n_i}{n} \ln \frac{n_i}{n} \quad \text{(Harper 1999)} \quad (2)$$

Pielou's evenness (*J*) was used to estimate the even distribution of species within gaps.

$$J = H/\ln(S) \text{ (Harper 1999)} \quad (3)$$

where:
H – Shannon diversity index,
S – number of taxa.

In addition, Sorensen's similarity index (*SSI*) was used to estimate the pairwise comparison of species composition within small and large gaps using this formula:

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$SSI = 2M / (2M + N)$ (Raup et al. 1979) (4)

where:

M – number of species matches within the comparison pair,

N – sum (total) number of species frequencies at forest areas in a column with the presence in just one row of species frequency.

Also, relative density (%) was calculated for each presented tree species (Table 2).

$$\text{Relative density} = \frac{\text{Sum of particular tree species}}{\text{Sum of all presented tree species}} \times 100 \quad (5)$$

Data analysis. All results were analyzed using STATISTICA (Tulsa, Statsoft, USA) data analyzing software (TIBCO software Inc; 13.4.0.14 version; Palo Alto, California, USA). Fisher's multiple comparison test was used to test significant differences in various indices between gap sizes (the mean of 4 gap plots per gap size). Pearson's rank correlation analysis was also applied to examine significant relationships between the ground herbaceous vegetation and the measured natural regeneration variables for determination of correlation coefficient (R). All statistical tests were considered significant at $P < 0.05$ level. Descriptive statistics (frequencies, percentages, proportions) was also carried out on the same software platform.

RESULTS AND DISCUSSION

Species composition and diversity in gaps of different sizes

In the present study, eleven (11) different tree species were enumerated (see Table 2). Four tree species each were recognized as species with light-adapted and intermediate growth strategies, respectively while three tree species were identified as species with shade-tolerant growth strategy. *Abies alba* Mill. (13–27%), *Fagus sylvatica* L. (30 to 23%) and *Picea abies* (L.) Karsten (36–63%) were the most frequently occurring species while *Fraxinus excelsior* L. (0.1%) and *Pseudotsuga menziesii* (Mirb.) Franco (0.1–2.0%) were the scarcely occurring species. Further, out of the eleven encountered species, ten species were enumerated in large gaps while eight species were found in small gaps. Nevertheless, the regeneration of *Carpinus betulus* L., *Pinus sylvestris* L. and *Populus nigra* L. species was typical in large gaps whereas *Acer pseudoplatanus* L. species exclusively occurred in small gaps (see Table 2). Similarly, in Table 3, measured tree species diversity in large gaps (Simpson's (1-D) = 0.7, Shannon diversity (H) = 1.5, Pielou's evenness (J) = 0.7 indices) was significantly higher than that assessed in small gaps (1-D = 0.5, H = 1.0, J = 0.5) across all three estimated diversity indices at $P < 0.001$ significance level.

Table 3. Results of diversity estimation of naturally regenerated tree species in gaps of different sizes

Gaps		Simpson's index (1-D)	Shannon diversity index (H)	Pielou's evenness (J)
Small		0.539[a]	0.984[a]	0.473[a]
	SE	±0.002	±0.003	±0.001
	min	0.536	0.978	0.471
	max	0.542	0.989	0.476
Large		0.746[b]	1.532[b]	0.665[b]
	SE	±0.002	±0.007	±0.003
	min	0.742	1.520	0.660
	max	0.749	1.544	0.671
	df	1	1	1
	F-ratio	6345.5	5256.7	3109.5
	P-value	0.0001	0.0001	0.0001

means (n = 4) with different letters are significantly different at $P < 0.05$ significance level, SE – std. error (±) is standard error

According to Forman and Godron (1986), species composition is the presence of particular species within a specific community. Hence, the total number of different tree species encountered in the composition of natural regeneration within the observed forest gap communities in this study was comparatively higher than the total of tree species (8) identified in natural regeneration under canopy gaps in Danková and Saniga (2013) study conducted in a mixed old-growth forest in Slovakia.

The lower turnout of tree species in the overall species composition of natural regeneration in gaps is a typical feature in the structure and development of natural regeneration under temperate mixed European forests (e.g., Bobiec 2007; Dobrowolska 2007; Slanař et al. 2017; Jaloviar et al. 2020). Generally, tree species diversity in Temperate European forests has been reported to be declining, as fewer common species are being replaced by more widespread species (Staude et al. 2020). Thus, in this study, the vegetation structure and composition of the studied gap stands may have generally

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influenced tree species composition in those assessed forest gaps.

It was no surprise that this finding was reflected in the species similarity test (*SSI*), where the estimated *SSI* value for the pairwise comparison of tree species composition in small and large gaps (*SSI* = 0.78) *SSI* according to Akoto et al. (2015) (*SSI* < 0.5 = different species composition while > 0.5 = similar species composition) indicated similar species composition.

Our results, therefore, support the hypothesis that similar species assemblages give rise to similar patterns of species composition in forests through the employment of the same recruitment mechanisms in regeneration (Wang et al. 2017) but contradicts a statement from Myers et al. (2013) that forest types with similar overall stand structure engage different recruitment mechanisms for their regeneration patterns, therefore yielding different species composition. Notwithstanding, a higher percentage of different tree species was evaluated in large gaps (91%) compared to small gaps (73%) in the present study. This observation contradicts the finding of Bobiec (2007) that gap size has no significant influence on tree species composition in gaps but it rather confirms conclusions of other studies (e.g., Dee, Menges 2014; Jaloviar et al. 2020) that the composition of different natural regeneration tree species in gaps largely depends on the 'gap size' factor.

More so, the 'gap size' factor became an important explanatory factor that significantly brought variations in species diversity between small and large gaps in this study. This result is in agreement with previous studies of Pourbabaei et al. (2013) and Dee and Menges (2014) but it disagrees with a conclusion in the study of Dobrowolska (2007), who found a significant influence of gap creation on species biodiversity rather than the gap size factor. The important effect of gap size on the biodiversity of plant species has been researched widely (e.g. Shabani et al. 2001; Vajari 2018).

This study shows that in spite of compositional similarities in overstorey tree species (see Table 1) of the parent stand composition of gaps, variation in light intensity ensuing from different gap sizes significantly affected the diversity of understorey species. The high species diversity in large gaps was the consequence of the bigger 'gap size' factor which allowed the penetration of higher incidence of light levels into the large gap microclimate, and this corresponds to Bullock (2000) that gap sizes with large areas typically accommodate high light availability.

This amount of light received at the forest floor within large gaps was sufficient to have supplied the wide range of optimal light requirements needed by several cohabiting understories of regenerating tree species (Barbier et al. 2008) for the effective delivery of their individual physiological processes such as seed germination and development (Březina, Dobrovolný 2011) and photosynthesis (Schmid et al. 2005) as light is widely known to be prime to seedling growth and development (Babaei et al. 2017). Clearly, this study has demonstrated that an increase in species diversity beneath gaps is mainly due to larger space and higher light availability (King et al. 2006).

According to Cordonnier et al. (2018), creating larger mean gap sizes favour early successional species, trigger species coexistence through both successional and competition-establishment trade-offs because the ecological processes that evoke species coexistence mechanisms are mechanistically implicated in complementarity effects such as differences between emerging species in light interception, light use efficiency and differences in the exploitation of water and nutrient resources in responses to environmental variations. Several studies have expressed the important relationship between gap size and ecological factors for species diversity in temperate forests (e.g., Bullock 2000; Vajari et al. 2012).

Many authors believe that gaps with larger areas promote optimal microclimatic conditions like light (Březina, Dobrovolný 2011), temperature and soil water content (Latif, Blackburn 2010) compared to smaller gaps for the initiation and coexistence development of natural regeneration tree species with diverse ecological demands for growth and survival. While others also believe that in situations where stabilizing mechanisms are weak, gap-based silviculture is favourable because it differentiates growth resources in space and time and this perhaps can stimulate species coexistence provided that species vary in their resource requirements and that gap characteristics are adaptable to these requirements (Kern et al. 2017).

Hence, gap size is assumed to have a direct effect on the rate of change in microclimatic and edaphic conditions (Gálhidy et al. 2006; Latif, Blackburn 2010; He et al. 2015; Kučera et al. 2018). In another observation, the effect of abiotic conditions on soil microbial activities has been revealed (Hortal et al. 2015). So, high species diversity in large gaps was

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a result of the increased soil enzymatic activities following from the active role of the soil microbial community (Dick 1994) in the forest soils of the studied stands.

The results of Kučera et al. (2018) that showed increased enzyme activities in forest gap soils of beech and mixed stands (i.e. the same 156A 10 stand) validate our observation. According to Burns et al. (2013), profuse plant growth highly correlates with greater soil enzyme activity, and again, the effect of plant growth on soil enzyme activities is more pronounced. In the same account, Muscolo et al. (2014) and Settineri et al. (2018) described an ecological association between enzyme activities and natural regeneration processes in their studies. Therefore, gap size is a critical factor in determining the relationship between physical and biological components and plant diversity in a forest following disturbance (Vajari et al. 2012).

Ecological shade tolerance status of natural regeneration tree species in gaps of different sizes

The regeneration dynamics of light-adapted, intermediate and shade-tolerant species in small and large gaps is presented in Figure 1 and 2. From Figure 1, it can be seen that intermediate species (63%) in small gaps while shade-tolerant species in large gaps happened to be the most dominant tree species (47%) that topped the natural regeneration composition in those respective gap environments. Yet, regeneration densities of intermediate (60 759 trees·ha^{-1}) and shade-tolerant species in small gaps (34 158 trees·ha^{-1}) were twelve (12) and five (5) times higher than those estimated in large gaps (intermediate species = 5 141 trees, shade-tolerant species 6 407 trees·ha^{-1}).

Meanwhile, the abundance of light-adapted species (15%) in large gaps was relatively higher than that monitored in small gaps. Furthermore, the

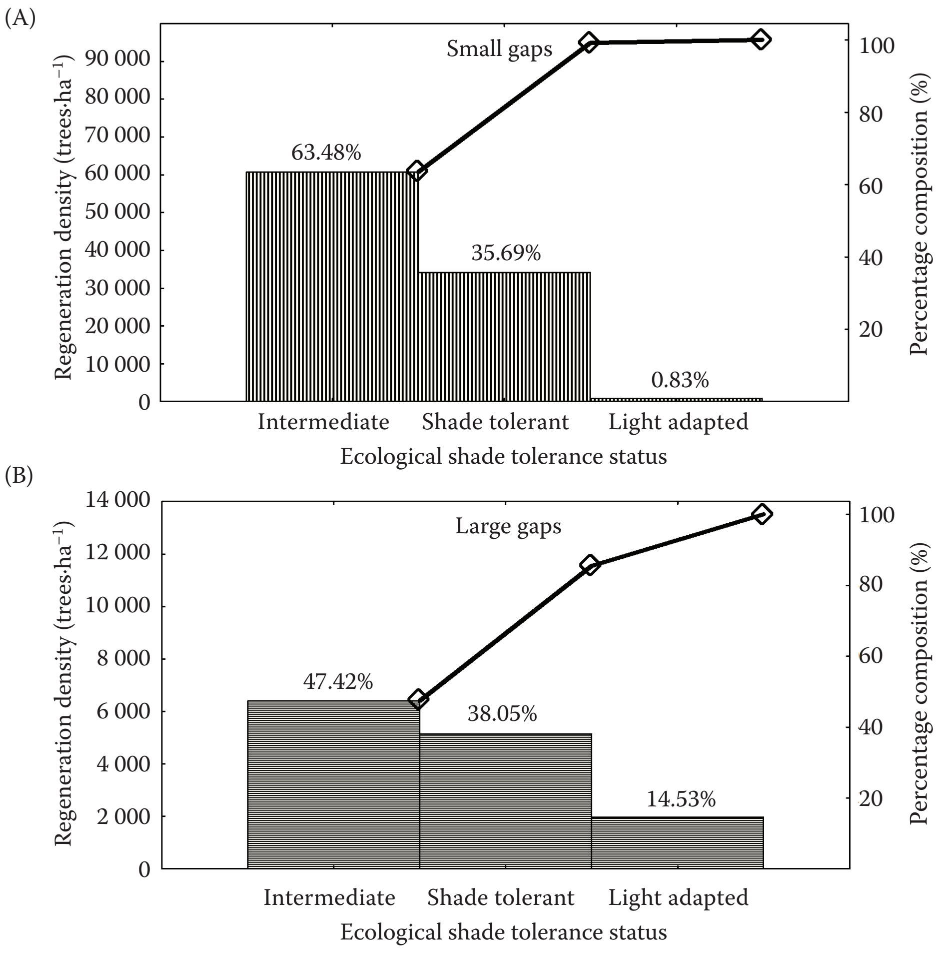

Figure 1. Pareto chart showing representations of naturally regenerated tree species categorized under three ecological shade tolerance (*EST*) statuses indicating their respective regeneration densities (left *y*-axes) and related percentage proportions (right *y*-axes) in small (A) and large (B) gaps

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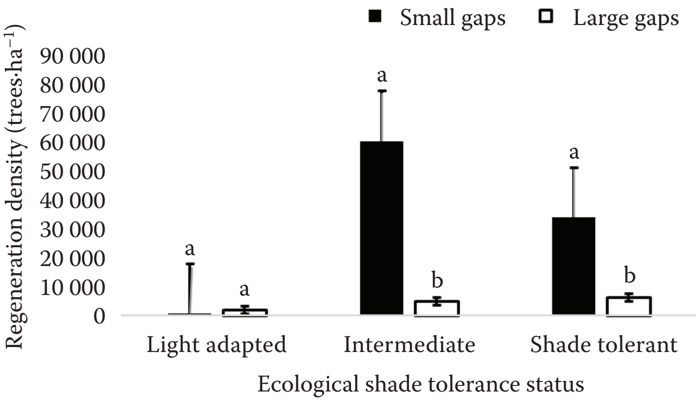

Figure 2. Comparative analysis of light-adapted, intermediate and shade-tolerant naturally regenerated tree species within gaps of different sizes (overlapping bars with the same letters denote homogeneous groups statistically at $P < 0.05$ significance level)

gap size variable could not explain the variation in the regeneration of light-adapted species between small and large gaps in Figure 2. By contrast, there was a significant difference ($P < 0.05$) in the regeneration of shade-tolerant species between small and large gaps, and likewise for intermediate species in Figure 2.

Forest gaps as desirable growing sites for natural regeneration tree species with different *EST* status (Coates, Burton 1997; Schnitzer, Carson 2001; Webster, Lorimer 2005; Vilhar et al. 2015) have also been proved in this study. The ecological stability of the microclimates (Brunet et al. 2010) within large gaps helped to maintain a balanced regeneration ratio between shade-tolerant, intermediate, and light-adapted species (3:3:1) in such by offering equal-level growth chances within gap microsites for the competitive regeneration performances of different tree species. The equitability in organization and distribution of tree species with the varying *EST* status in large gaps was mainly due to reduced seedling competition for light, water, and nutrients in comparison with small gaps (Bullock 2000; Muscolo et al. 2014).

Apart from this, it was also observed that light-adapted species found large gaps as conducive regeneration niches for their higher proliferation. In contrast, shade-tolerant species found theirs within small gaps for their best regeneration and abundance performances, respectively. Patterns of regeneration and recruitment of light-adapted and shade-tolerant tree species in temperate mixed uneven-aged forests in this study are consistent with Klopčič et al. (2015) and at the same time, they support a widely held hypothesis that light-demanding tree species germinate and grow best under canopy openings while shade-tolerant tree species require closed canopy for the same physiological functions (Kern et al. 2013; Muscolo et al. 2014; Wang et al. 2017). Furthermore, the contradictory statement of Schulz (1960) that the larger the gap in the forest canopy, the more light that reaches the undergrowth, and the possibility of more intense competition could probably explain the observation of lower regeneration densities of natural regeneration tree species in large gaps.

By contrast, the comparatively higher number of the total regeneration density of natural regeneration tree species in small gaps (95 708 trees·ha^{-1}) was the outcome of the predominance contribution of *Fagus sylvatica* L. and *Picea abies* (L.) Karsten species in natural regeneration originating from the copious supply of seeds from both nearby and in-stand parent trees, coupled with the ecological shade-tolerant ability of the former species and ecological shade-light intermediary ability of the latter species which significantly influenced their prolific natural regeneration under small canopy gaps: regeneration sites with limited supply of light.

The underlying explanation for small gaps as favourable growing spaces for buoyant natural regeneration performances in our study is fewer evaporation events which facilitated sequestration of soil water resources and this corroborates a statement from Fanta (1995) that success of establishment depends much more on soil moisture than on light conditions. On the other hand, the lower level of light in small gaps led to a strong competition among understorey tree species (Bullock 2000). It was fatal for species with uncompromising greater

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light demands, hence recounting higher incidence of seedling mortality among light-adapted species (Figure 1).

Besides, a completely different finding was made about natural regeneration of intermediate species in gaps. These species maintained impressive regeneration performances in both small and large gaps. This outstanding record of intermediate species in gaps could be attributed to their dynamic nature of their utilization of light changes during growth and development in the natural regeneration process (Uradníček et al. 2010). This observation substantiates an opinion that the most successful species in gap-based forest management are those that can respond rapidly to light throughout all growth stages favoured by canopy openings (Schulz 1960; Webster, Lorimer 2005). In brief, our findings illustrate that the variation in gap composition is accompanied by differences in species functional traits (Figure 1). Species with smaller seeds, lower shade tolerance, later bloom time, shorter stature and longer leaves were associated with higher light and larger gap sizes while generally, species which were associated with low to high light differentiation related to small to large gap sizes, respectively.. The shifts in functional trait distribution suggest that variations in gap size provided contrasting gap environments in which certain traits were differentially advantageous (Kern et al. 2013).

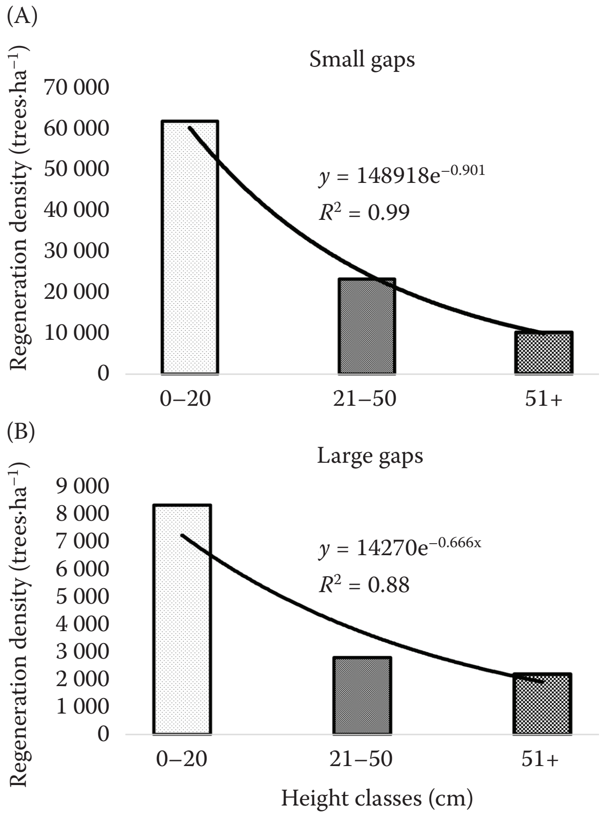

Figure 3. Height classes of natural regeneration in gaps of different sizes – small (A), large (B)

In addition, shade-tolerant tree species being significantly higher in small gaps (Figure 2) were the result of the competitive dominance and robust exploitation behaviour of *Abies alba* Mill. and *Fagus sylvatica* L. (Cordonnier et al. 2018) species in natural regeneration under temperate mixed-species forests aside the relatively smaller area of studied gaps (0.02–0.05 ha) that encouraged their profuse growth. A comparable observation was earlier communicated in mountainous mixed-species *Abies alba-Fagus sylvatica* forests in the Dinaric region (Čater et al. 2014).

Generally, our results were contrary to studies of Dobrowolska (2007), who found no significant effect of gap size on the quantity of natural regeneration tree species in gaps.

Distribution pattern of different height growth classes of natural regeneration of tree species in small and large gaps

In Figure 3, three varying height classes (0–20 cm, 21–50 cm, 51+ cm) of natural regeneration of tree species enumerated within small and large gaps are presented. In both gap sizes, regeneration densities of 0–20 cm (small = 62 161 trees·ha^{-1}; large = 8 444 trees·ha^{-1}) height class were comparatively higher than those accounted for 21–50 cm (small = 23 286 trees·ha^{-1}; large = 2 839 trees·ha^{-1}) and 51+ cm (small = 10 260 trees·ha^{-1}; large = 2 228 trees·ha^{-1}) height classes. Thus, the results further revealed that progression of tree species from 0–20 cm to 21–50 cm and 51+ cm height growth was reduced at exponential rates of –0.901 and –0.666, respectively, in small gaps at 99% and large gaps at 88%.

This observation supports the widely held view that gaps are conducive growing grounds for the emergence of natural regeneration largely due to the availability of preferable light conditions for seedling growth (Čater, Diaci 2017); however, it strongly disagrees with the notion that gaps do not necessarily provide an ideal environment for regeneration (Busing, White 1997; Jaloviar et al. 2020). The height class of 0–20 cm presenting the most aggressive distribution was favoured simultaneously in both small and large gaps, compared with an opposing trend of the declining spatial distribution of 21–50 cm and

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51+ cm height classes, also with no clear indication of the favoured gap size, which substantiates that the variability of height growths of natural regeneration in gaps is along the gradient of environmental conditions at the growing site including browsing (Mihók et al. 2007) rather than the gap size factor only (Hammond, Pokorný 2020). This finding corroborates a statement in Jaloviar et al. (2020) studies that environmental factors have a greater impact on regeneration density of saplings (≤ 50 cm) compared to seedlings (> 50 cm) of natural regeneration in gaps. So, it is likely that the patterns of tree regeneration in gaps result from a wide range of factors, but as this study and many others (e.g., Hammond, Pokorný 2020) suggest, the spatial and temporal variation in natural regeneration establishment is greatly related to the ecology of gaps which enormously depends on site conditions, silvicultural or forest management system, especially in changing environmental conditions.

Ecological relationship between ground herbaceous vegetation and natural regeneration in gaps of different sizes

A total number of fifty-two (52) strongly competitive (dominant) herb species from nineteen (19) genera was encountered in the eight studied gaps (see Table 4). Forty-five (45) species were encountered in small gaps while fifty-one (51) species in large gaps. Regeneration density of *Fagus sylvatica* L. strongly correlated with herb layer density (R^2 = 96 %) in a positive manner (r = 0.96, p = 0.0381) in small gaps while that of *Abies alba* Mill. significantly correlated with herb layer density (R^2 = 99 %) in a negative manner (r = –0.99, p = 0.0013) in large gaps. By contrast, *Larix decidua* Mill., *Picea abies* (L.) Karsten and other thriving tree species showed no correlation with the herb presence at forest floors of varying gap sizes at $p < 0.05$ significance level.

Table 4. Herb layer species within gaps of different sizes in a temperate mixed central European forest

Herb layer species	Small gaps	Large gaps	Herb layer species	Small gaps	Large gaps
Asperula cynanchica L.	+	+	*Impatiens parviflora* DC.	+	+
Cardamine flexuosa With.	+	+	*Juncus conglomeratus* L.	*	+
Cardamine hirsute L.	+	+	*Juncus effuses* L.	*	+
Cardamine impatiens L.	+	+	*Juncus tenuis* Willd.	*	+
Carex digitate L.	+	+	*Lactuca serriola* L.	+	*
Carex hirta L.	+	+	*Lathyrus vernus* (L.) Bernh.	+	+
Carex leporine L.	+	+	*Luzula campestris* (L.) DC.	+	+
Carex muricata L.	+	+	*Luzula luzuloides* (Lam.) Dandy & Wilmott	+	+
Carex pallescens L.	+	+	*Luzula multiflora* (Ehrh.) Lej.	+	+
Carex pilosa Scop.	+	+	*Luzula pallidula* Kirschner	+	+
Carex pilulifera L.	+	+	*Luzula pilosa* (L.) Willd.	+	+
Carex remota L.	+	+	*Melica nutans* Lam.	*	+
Carex spicata Lam.	+	+	*Melica uniflora* Retz.	*	+
Carex sylvatica Dewey	+	+	*Oxalis acetosella* L.	+	+
Dentaria bulbifera L.	*	+	*Rubus idaeus* Blanco	+	+
Dryopteris carthusiana (Vill.) H.P. Fuchs	+	+	*Rubus hirtus* Hegetschw.	+	+
Dryopteris dilatata (Hoffm.) A. Gray	+	+	*Rumex obtusifolius* L.	*	+
Dryopteris filix-mas (L.) Schott	+	+	*Urtica dioica* L.	+	+
Galium album Mill.	+	+	*Veronica beccabunga* L.	+	+
Galium aparine L.	+	+	*Veronica chamaedrys* L.	+	+
Galium odoratum (L.) Scop.	+	+	*Veronica montana* L.	+	+
Galium palustre L.	+	+	*Veronica officinalis* L.	+	+
Galium rotundifolium L.	+	+	*Veronica serpyllifolia* L.	+	+
Galium sylvaticum Besser	+	+	*Viola arvensis* Murray	+	+
Geranium robertianum L.	+	+	*Viola reichenbachiana* Jord. ex Boreau	+	+
Impatiens noli-tangere L.	+	+	*Viola riviniana* Rchb.	+	+

species presence (+) and absence (*), gray colour highlighted differences between gaps in individual herb species

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The total count of herbs in this study is lower than that enumerated in Mihók et al. (2007) (57 species) but it is higher than that reported in Vajari et al. (2012) (33 species). Our study showed that the herb species increased with the gap area, and this is consistent with findings of Gálhidy et al. (2006). The presence of herbs in small gaps created a form of shield against light and browsers and this was favourable to *Fagus sylvatica* regeneration performances. Contrarily, the heavy presence of the herb layer in large gaps became hindrance to *Abies alba* growth and survival. In similar observations, Mihók et al. (2007) recounted how *Urtica dioica* L. caused a negative effect on natural regeneration in gaps. Likewise, Vacek et al. (2017) also observed a negative influence of severe competition of expansive, strongly competitive *Calamagrostis villosa* (Chaix) J. F. Gmel. and *Avenella flexuosa* (L.) Drejer grasses on natural regeneration in their studies.

CONCLUSION

Forest gaps remain the optimal forest management practice in modern forestry. This study has shown that gap-based silviculture has a key role to play in the long-term dynamics of mixed forests by promoting ecological species assemblage mechanisms that facilitate species coexistence which is hugely relatable to the positive effects of species diversity on forest ecosystem stability and functions. Further, the study revealed that the 'gap size' property has a significant influence on naturally regenerated tree and herb species composition and diversity. Though species diversity in large gaps (i.e. with mean ± SE size of 1 027 ± 117 m^2, character no. above 1) was significantly higher, small gaps (i.e. with mean ± SE size of 331 ± 67 m^2, character no. below 1) shared similar species composition with large gaps. Gap size significantly determined the quantities of intermediate and shade-tolerant tree species in gaps. Yet, large gaps were favourable regeneration spots for ligh-adapted species. Intermediate species were the best variant for gap regeneration. Also, the growth of natural regeneration from seedling (≤ 50 cm) to sapling (> 50 cm) stage was hampered by physical conditions at the growing site particularly browsing. The development of herbaceous vegetation in small and large gaps had consequential positive and negative effects on natural regeneration of *Fagus sylvatica* and *Abies alba*, respectively.

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