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ORIGINAL PAPER

Gap regeneration and dynamics: the case study of mixed forests at Křtiny in the Czech Republic

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Abstract
Gap regeneration remains the best silviculture technique for sustainable forest regeneration in mixed forests. The study examined tree species composition, diversity and dynamics of natural regeneration in gaps under three contrasting forest stands at Křtiny in the Czech Republic. In spring 2013, experimental gap design begins, when semi-permanent 1 m^2 circular sub-sampling plots along North-South-East-West transects were delineated under 6 selected natural canopy openings ≤ 20 m^2. In winter 2013/14, these naturally originated openings were artificially enlarged to the current gap sizes ranging between 255 and 1149 m^2 through group felling. Natural regeneration in gaps was measured four times: from the growing season before disturbance (BD) in 2013 to the next three consecutive growing seasons after disturbance in 2014 – 2016, respectively. Seven (7) new species with light demanding growth strategy that were previously not present at mother stands were occurring there during the first growing season after disturbance (FGS), yielding the highest taxa (14 species) and diversity (Shannon diversity index, H = 1.7) while BD attained the lowest (8 species; H = 0.9), respectively. Study site being part of *Fagus sylvatica* vegetation community and providing favorable natural conditions for the optimal growth of *Picea abies* significantly explains the regeneration dominance of these species in gap regeneration from BD until the third growing season after disturbance (TGS), respectively. Small scale gap-disturbance contributed to the higher regeneration densities of all studied species during FGS. However, drought, competition from other life forms, and browsing activities substantially caused a progressive decline in natural regeneration during three consecutive years after disturbance.

Key words: composition; diversity; disturbance; growing season; tree species

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1. Introduction

Gap regeneration is a nature-promoting silviculture technique that champions the quest for sustainable natural forest management. Within the last 30 years, this concept has gained much research attention globally (e.g., Runkle 1990; Bullock 2000; Dusan et al. 2007; Wang et al. 2017b; Hammond & Pokorný 2020a) since its inception in the 20th century (Watt 1947; Runkle 1981) due to its unmatched positive ecological importance on sustainability of mixed-species forests. The recent promotion of mixed stands in sustainable forest management is unquestionably owing to the importance of species diversity (Pretzsch 2009; Hammond et al. 2020) in providing numerous forest functions and services (Del Río et al. 2018). In Central Europe, the rising importance of mixed forests reflects the growing complexity of societal demands for forest ecosystems (Bravo-Oviedo et al. 2014; Sedmákov et al. 2019). Mixed forests are known to be resilient to environmental threats and also possess a more diversified portfolio of environmental benefits (Bravo-Oviedo et al. 2014; Del Río et al. 2016). The "insurance hypothesis" postulates that mixed forests response to disturbance is less intense and their recovery is much quicker than monocultures (Pretzsch 2018). The greater demand for knowledge regarding regeneration and dynamics of mixed forests is the reason behind increasing number of studies focusing on the effect of gap regeneration on forest dynamics, growth and yield in mixed-species stands (Griffiths et al. 2007; Vilhar et al. 2015; Khodaverdi et al. 2019; Hammond & Pokorný 2020b). Recently, many researchers have been focusing on the understanding of appropriate silviculture methods of the underlying mechanisms that control the interactions among species, and also between species and their growing environments in order to more adequately predict the outcomes of forest activities (Bravo-Oviedo et al. 2014).

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Forest management approaches that emphasize wholly on a diverse forests' agenda rely heavily on natural disturbances as key drivers that promote and maintain tree species diversity (Sommerfeld et al. 2018; Jaloviar et al. 2020). In many gap-recruitment studies, small scale gap-disturbance has been identified as influencing the structure and development of natural forests essentially through the emergence and survival of natural regeneration in a variety of conditions within gaps (Hammond & Pokorný 2020b; Jaloviar et al. 2020). The regime of small scale disturbances is characterized by low intensity felling of few individual trees for the forest management purpose of gap creation (Rugani et al. 2013; Hammond & Pokorný 2020b). Mostly, disturbances that initiate gap formation are accompanied by environmental heterogeneity that generate favorable microclimatic light conditions in gaps that offer a broad spectrum of growing niches which enable ecological organization, regeneration and coexistence (Busing & White 1997) of tree species with different life history attributes (Dusan et al. 2007; Kollár 2017; Vacek et al. 2017). Often creating comparable occupancy opportunity for natural regeneration of contrasting light demanding and shade-tolerant species simultaneously in gaps (Sapkota & Odén, 2009; Nagel et al. 2010; Hammond & Pokorný 2020b). In view of this, several studies have found gap regeneration as an appropriate forest management technique for the maintenance of mixed-species stands in many forest types (Sapkota & Odén 2009; Kollár 2017; Hammond et al. 2020).

Natural regeneration is an excellent gap-beneficial tree regeneration option that is ecologically pivotal to mixed forest management. For decades, mixed forests at Křtiny in the Czech Republic have set a long-standing silviculture record of sustainable natural regeneration. However, there has been minimal research on the comprehensive effect of gap regeneration and its accompanying dynamics in the forests. Hence, the main objective of this paper is to examine the dynamics of natural regeneration in gaps, comparing from the growing season before disturbance (BD) to the third consecutive growing season after disturbance (TGS) under mixed forest stands at Křtiny. We, therefore, compared species composition and species diversity of natural regeneration tree species in gaps within four consecutive growing seasons (2013 – 2016) and evaluated the ecological dynamics and distribution of future natural regeneration potential under three different forest stands.

2. Materials and methods

2.1. Study site

The study site (49º 13'– 49º 21'N; 16º 34'– 16º 40'E) on the Mendel University's Training Forest School Enterprise (UFE), is located in Křtiny, North of Brno in the Blansko District of the South Moravian Region in the Czech Republic (Fig. 1). UFE established in 1923, is situated between 210 m to 575 m a.s.l. altitude with prevailing continental temperate humid climate according to Köppen climate classification. The mean annual precipitation sum is 610 mm while mean annual tem-

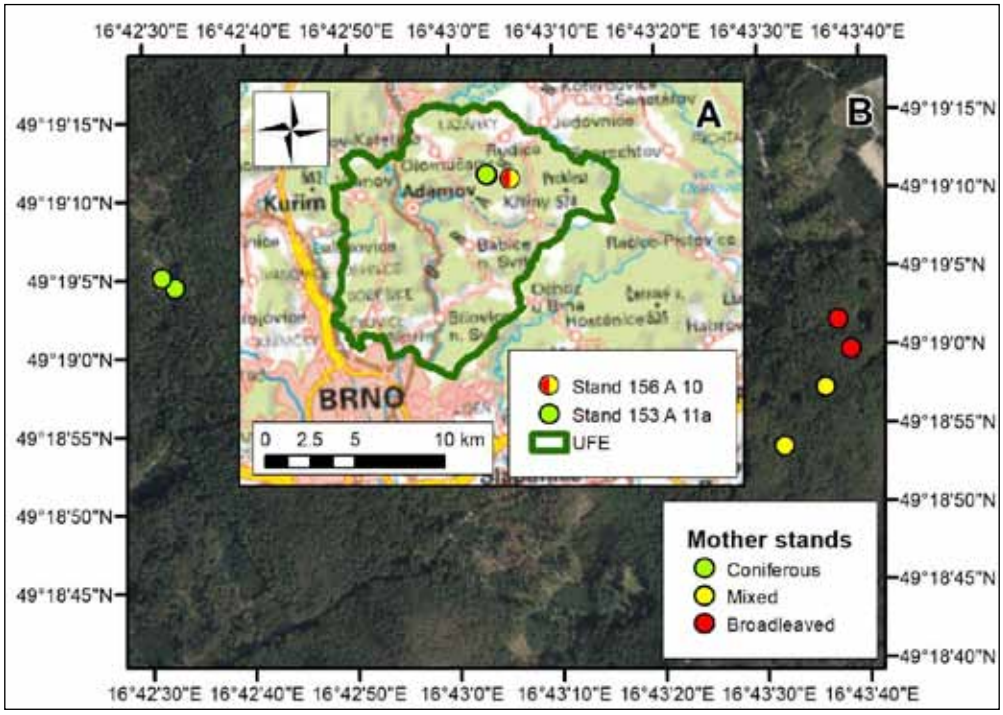

Fig. 1. Geographical positions of six research gaps (B) from three distinct mother stands under two categorized forest management stands (A) within temperate mixed Mendel University's Training Forest School Enterprise (UFE) at Křtiny in the Czech Republic.

perature is 7.5 °C (Hammond et al. 2020). Bedrock varies from granodiorites to culmian grawacks and limestone. The predominant soil types are cambic rendzinas, luvisols, brown earth and mesotrophic cambisols, broadly grouped under the cambisol (kambizem) soil type category based on the Czech taxonomic soil classification system. The UFE region is naturally represented by mixed forests dominated by 54% of broadleaved and 46% coniferous tree species. The whole forest area of UFE covers approximately 10,265 ha under some 116 management units/stands categorized into three forest districts. We selected two mixed forests of management stands 156A 10 and 153A 11a (520 m – 570 m a.s.l.) in the Habrůvka forest district. The forest district where natural regeneration remains the long-lasting preferred tree regeneration method and group selection silviculture system is encouraged to a certain level in forest management.

Six gaps numbered from Gap 1 to Gap 6 under three different mature stands were considered for the study. Gap 1 – 2 under coniferous forest type (100% *Picea abies*) in Forest Management Stand 153A 11a (109 years old) and Gap 3 – 4 under mixed forest type (50% *Picea abies*), and Gaps 5 – 6 under broadleaved forest type (90% *Fagus sylvatica*) in Forest Management Stand 156A 10 (97 years old) situated within two main forest associations, 3S7 medium-nutrient oak-beech – *Querceto-Fagetum mesotrophicum* and 4W1 limestone beech – *Fagetum calcarium* (Anonymous 2013), respectively.

2.2. Gap design and expansion of experimental gaps

In 2013 spring, we purposively selected six(6) naturally occurred gaps with irregular shapes. Gaps were defined as 15 – 20 m^2 forest canopy openings formed through the mortality of one or more canopy trees with diameter at breast height (dbh) above 20 cm due to natural disturbances. Next, four(4) independent transects of 20 m length in the North-South-East-West cardinal directions were demarcated from individual gap center. Then, one(1) semi-permanent 1 m^2 circular sub-sampling plot (i.e., 56 cm in radius) was established first at gap center and then followed by forty(40) additional sub-sampling plots, i.e., ten(10) placed at 2 m intervals along each transect.

In 2013/14 winter, small-scale artificial disturbances (i.e., felling of a few number of trees by man) were carried out within the stands of the three selected forest types. In this regard, a group felling comprising three mature trees ≥ 30 cm dbh minimum were harvested for the gap disturbance procedure. This silviculture procedure resulted in the enlargement of already existing canopy openings. As a result, original gaps were expanded into gaps of different sizes varying from 255 to 1149 m^2 (see Table 1). WinSCANOPY (2012a edition, Regent Instruments Canada Inc.; Quebec Canada) was used to measure both pre-and post-disturbance gap sizes as canopy openings of natural-original and artificial-final gaps using hemispherical photos. The procedure was carried out during winter so as to either minimize or possibly prevent any adverse effects that may accompany disturbances on the gap microsites. For forest management guidelines of mixed forests, Křtiny, usually a natural disturbance regime in the form of small-scale disturbance, is regular and recommended silviculture practice in the forest establishment that warrants sustainable forest development.

2.3. Field measurements

To assess microclimatic light condition, one hemispherical photo was shot at all forty-one (41) sub-sampling circular plots with WinSCANOPY photography accessories; 1.2 m tripod, auto-leveling frame, Sony Nex 10 camera (Sony, Minato, Tokyo, Japan) with an inbuilt automated N90° search engine calibrated fish-eye lens (Nikon, model FC–E8 0.21x, Tokyo, Japan) during the first growing season after disturbance (autumn 2014) within each selected gap. Subsequently, natural regeneration status was surveyed within every delineated circular plot along transects and gap centers in the growing season before disturbance (autumn 2013) and repeatedly in the following three consecutive growing seasons after

Table 1. Basic characteristics of research gaps within the three studied forest types at Mendel University's Training Forest School Enterprise Křtiny.

Gap no.	Gap Area [m^2] Nat – Org/ Art- Exp	Gap size/shape	Aspect[b]	Mother Stand[b]	Forest Management Stand (coverage)[a]	Percentage composition of stand species with their respective dbh, height and tree volume [cm/m/m^3][a]	Growing stock [$m^3\,ha^{-1}$][a]	Living stock [m^3][a]
1	18/255	Small-size/Elliptical	SE	Coniferous	153A 11a (7.4 ha)	61% *Picea abies* (35/31/1.26); 25% *Larix decidua* (43/33/1.99); 6% *Fagus sylvatica* (33/28/1.06); 6% *Pinus sylvestris* (42/31/1.75); 1% *Acer pseudoplatanus* (43/32/2.17) and 1% *Carpinus betulus* (30/26/0.73).	536	4139
2	20/713	Big-size/Circular	SE	Coniferous				
3	20/286	Small-size/Elliptical	W	Mixed	156A 10 (13.3 ha)	70% *Fagus sylvatica* (35/31/1.33); 14% *Picea abies* (39/32/1.58); 6% *Larix decidua* (50/34/2.54); 6% *Abies alba* (37/30/1.53); 2% *Pinus sylvestris* (43/30/1.78); 1% *Quercus petraea* (67/36/4.74) and 1% *Pseudotsuga menziesii* (42/26/1.63).	533	7087
4	20/904	Big-size/Circular	W	Mixed				
5	15/282	Small-size/Elliptical	NW	Broadleaved				
6	20/1149	Big-size/Circular	NW	Broadleaved				

Nat – Org/Art- Exp is Natural – Original/Artificial – Expansion. Data based on guidelines from the forest management plan for Training Forest School Enterprise Křtiny. [a]Anonymous (2013); [b] iitola (2018).

disturbance (i.e. 2014, 2015 and 2016 autumns). Naturally regenerated tree species were firstly identified at the species level (name), assessed morphologically (height growth 0 – 350 cm limit), counted (frequency), and recorded appropriately. Base-line measurement of regeneration was also carried out at the same time. Advance regeneration, new recruits, as well as resprouts with maximum 350 cm height were surveyed. However, one-year-old regeneration (ephemeral tree species that are not a good indicator of light availability) were excluded from the data survey.

2.4. Data processing and analysis

Regent's WinSCANOPY Technology (2012a edition, Regents Instruments Canada Inc; Quebec, Canada) processed hemispherical gap photos into Total Site Factor (TSF) light condition. TSF light condition is the combination of Direct Site Factor (DSF) and Indirect Site Factor (ISF) (Guay 2012). STATISTICA software (13.4.0.14 edition, TIBCO Corporation Inc; Palo Alto, California, USA) was employed for all data analyses. Prior to analyses of variance (ANOVA) and post hoc Fisher's LSD analyses were computed to obtain the significant difference at $p < 0.05$ significance level, data were checked for normality and variances of homogeneity conditions. Simple linear regression was also performed to determine the significant relationship between TSF light condition and natural regeneration of tree species at $p < 0.05$ significance level for the determination coefficient of the linear regression (r^2). Paleontological Statistics Software (3.24 edition) (Hammer et al. 2001) was used for biodiversity estimation. Four (4) diversity indices [equations 1 – 4] relevant to the study objectives were considered.

Firstly, Shannon diversity index (H) was used to ascertain species diversity in gaps (Harper 1999).

$$H = -\sum_{i} \frac{ni}{n} \ln \frac{ni}{n} \quad [1]$$

where:

ni – number of encountered individuals of ith taxon,

n – the number of all encountered individuals within a particular growing season,

In – logarithm sign.

Secondly, Pielou's Evenness (J) was used to measure species evenness within gaps (Harper 1999).

$$J = \frac{H}{In(S)} \quad [2]$$

where:

H – Shannon diversity index,

S – number of taxa.

Thirdly, Berger-Parker Index (D) simply measured the numerical importance of the most abundant species in gaps (Berger & Parker 1970).

$$D = \frac{N max}{n} \quad [3]$$

where:

Nmax – number of individuals of the most abundant species.

Finally, Sorensen's Coefficient (SC) index measured species similarity of gap regeneration among the three studied growing seasons (Raup & Crick 1979).

$$SC = 2M / (2M+N) \quad [4]$$

where:

M – number of shared similar species of the compared pair,

N – total number of species frequencies of growing seasons in a column with presence in just one row of species frequency.

In addition, relative density (%) was used to calculate abundance proportions of all encountered tree species in natural regeneration.

$$\text{Relative density} = \frac{Total\ number\ of\ a\ specific\ species}{Overall\ total\ of\ all\ presented\ species} \times 100 \quad [5]$$

3. Results

3.1. Description of species composition and diversity in gaps

A total number of fifteen (15) different species belonging to six (6) families identified within four consecutive growing seasons are presented in Table 2. Pinaceae (5 species) had the greatest number of occurrences, whereas Oleaceae (1 species) family had the least. Eleven (11) species out of the overall species presented were found to be possessing non-dominant status in regeneration, while two species each were observed to have exhibited predominant and dominant statuses in regeneration.

Species with light-demanding and intermediary (6 species each) growth strategies topped species composition, while those with shade growth strategy (3 species) attained the least representation in gap regeneration. The lowest species turnout (8 species) was enumerated in BD, while the highest (14 species) was attained in FGS. During BD and SGS, *F. sylvatica* (69.41%; 31.49%) displayed the highest relative densities. Also, *L. decidua* (25.60%) and *P. abies* (68.90%) displayed the highest relative densities in FGS and TGS, respectively. On the other hand, *A. platanoides* (0.33%), *B. pendula* (0.05%), *F. excelsior* (0.07%) and *P. menziesii* (0.07%), and *C. betulus* (0.06%) had the lowest relative densities in BD, FGS, SGS and TGS, respectively. Besides, *F. excelsior, F. sylvatica, P. abies* and *A. alba* were present throughout the four growing seasons while *L. decidua, P. menziesii, P. sylvestris* and *S. alba* were only absent in BD and likewise for *C. betulus* in FGS and *A. pseudoplatanus* in TGS. Natural regeneration of *B. pendula* and *Q. petraea* species were exclusively present in FGS.

The estimation of diversity indices revealed a general higher species diversity in FGS and SGS compared to TGS and BD in Table 3. It is evident that after two

Table 2. Species composition of gap regeneration within four consecutive growing seasons at mixed forests at Křtiny.

Common name	Scientific name	Taxonomic family designate	Regeneration dominance category	Guild	Relative density [%]			
					BD	FGS	SGS	TGS
European beech	*Fagus sylvatica* L.	Fagaceae	Predominant	Shade	69.41	22.39	31.49	13.73
Norway spruce	*Picea abies* (L.) Karst.	Pinaceae	Predominant	Inter	17.93	25.10	23.95	68.90
European larch	*Larix decidua* Mill.	Pinaceae	Dominant	Light	—	25.60	25.16	3.01
European silver fir	*Abies alba* Mill.	Pinaceae	Dominant	Shade	7.40	16.87	14.78	11.35
Black poplar*	*Populus nigra* L.	Salicaceae	Non-dominant	Light	—	0.20	—	0.06
European ash*	*Fraxinus excelsior* L.	Oleaceae	Non-dominant	Inter	0.99	0.15	0.07	0.09
European birch*	*Betula pendula* Roth.	Betulaceae	Non-dominant	Light	—	0.05	—	—
European hornbeam	*Carpinus betulus* L.	Betulaceae	Non-dominant	Shade	0.66	—	0.14	0.03
Douglas fir	*Pseudotsuga menziesii* (Mirb.) Franco	Pinaceae	Non-dominant	Inter	—	1.05	0.07	0.54
Horse chestnut*	*Aesculus hippocastanum* L.	Sapindaceae	Non-dominant	Inter	0.66	0.10	—	—
Norway maple*	*Acer platanoides* L.	Sapindaceae	Non-dominant	Inter	0.33	0.10	—	0.31
Scots pine	*Pinus sylvestris* L.	Pinaceae	Non-dominant	Light	—	0.35	0.35	0.11
Sessile oak	*Quercus petraea* (Matt.) Liebl.	Fagaceae	Non-dominant	Light	—	0.15	—	—
Sycamore maple	*Acer pseudoplatanus* L.	Sapindaceae	Non-dominant	Inter	2.63	0.65	0.21	—
Willow*	*Salix alba* L.	Salicaceae	Non-dominant	Light	—	7.23	3.77	1.87
Total					100	100	100	100

BD – The growing season before forest disturbance, FSG – First growing season after forest disturbance, SGS – Second growing season after forest disturbance and TGS – Third growing season after forest disturbance. Shade – shade tolerant, Inter – intermediate and Light – light demanding species. Absence of species indicated by (—). Tree species with indicated (*) are not present in mother stands but presumably from the nearest seed trees of those species: *Populus nigra* (9500 m), *Fraxinus excelsior* (400 m), *Betula pendula* (280 m), *Aesculus hippocastanum* (3000 m), *Acer platanoides* (350 m) and *Salix alba* (2000 m) with distance in parentheses.

growing seasons after forest disturbance, all the indices reached the same values as BD. When subjected to an analysis of variance test, the mean values of the indices for the four growing seasons revealed a significant difference ($p < 0.001$) among growing seasons in each case. Mean Shannon diversity index values of H = 1.67, H = 1.51, H = 1.02 and H = 0.98 were recorded for FGS, SGS, TGS, and BD, respectively. However, measured species evenness in SGS (J = 0.66) was significantly higher than indices attained in FGS (J = 0.63), BD (J = 0.47) and TGS (J = 0.43), respectively. Furthermore, BD and TGS showed no significant difference for Berger-Parker index estimation, but FGS and SGS showed significant difference. This clearly showed the significant influence of species dominance in species diversity.

Table 3. Species diversity of gap regeneration within four consecutive growing seasons.

Growing seasons		Shannon diversity index (H)	Pielou's Evenness (J)	Berger-Parker Index
BD	Mean	0.98 a	0.47 b	0.69 c
	Std. dev.	±0.02	±0.01	± 0.01
	Minimum	0.97	0.46	0.69
	Maximum	1.00	0.48	0.70
FGS	Mean	1.67 d	0.63 c	0.26 a
	Std. dev.	± 0.01	± 0.00	±0.00
	Minimum	1.67	0.63	0.25
	Maximum	1.68	0.64	0.26
SGS	Mean	1.51 c	0.66 d	0.31 b
	Std. dev.	± 0.01	± 0.00	± 0.00
	Minimum	1.51	0.65	0.31
	Maximum	1.52	0.66	0.32
TGS	Mean	1.02 b	0.43 a	0.69 c
	Std. dev.	± 0.04	± 0.01	± 0.2
	Minimum	0.99	0.41	0.67
	Maximum	1.06	0.44	0.70
	P value	***	***	***

Means presented with the same letters in a column represent homogenous groups with statistically insignificant difference at p = 0.05 level. Estimated p values at 0.001 significance level indicated as (***). BD – The growing season before forest disturbance, FSG – First growing season after forest disturbance, SGS – Second growing season after forest disturbance and TGS – Third growing season after forest disturbance.

The SC values of 0.86, 0.75 and 0.64 for SGS × TGS, FGS × SGS and BD × FGS combinations, respectively indicate that despite the differences in the species diversity observed among the four growing seasons, there was, however, a contradictory high level of species similarity among growing seasons (see Tables 3 and 4).

Table 4. Sorenson's coefficient index of species composition of natural regeneration in gaps within four consecutive growing seasons.

Comparing seasons	Comparing species		Sorenson's coefficient
	Shared species	Unique species	
BD × FGS	7	8	0.64
FGS × SGS	9	6	0.75
SGS × TGS	9	3	0.86

BD – The growing season before forest disturbance, FSG – First growing season after forest disturbance, SGS – Second growing season after forest disturbance and TGS – Third growing season after forest disturbance.

3.2. Effects of disturbances on dynamics of natural regeneration of tree species with different growth strategies

Three categories of tree species with different growth strategies in gaps depending on their physiological light preferences are presented in Fig. 2. FGS was the best performing growing season (mean regeneration density = 70,662 trees ha^{-1}) as higher regeneration yields were attained for all three studied growth strategies (Shade = 26,695 trees ha^{-1}, Inter 23,523 trees ha^{-1} and Light = 20,444 trees ha^{-1}) of tree species. Followed by SGS (53,910 trees ha^{-1}) and BD (26,436 trees ha^{-1}), while TGS (12,467 trees ha^{-1}) stood as the poor performing growing season for species performances. Apart from BD, when light strategy species were absolutely absent, all the other growing seasons showcased every considered growth strategy of species within gaps. Notwithstanding, both FGS and SGS presented a balanced proportion of Light: Inter: Shade (1:1:1) species in gaps, while TGS showed an imbalanced proportion among species under various categories of growth strategy.

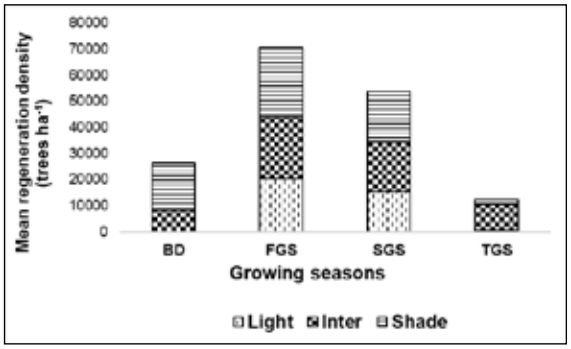

Fig. 2. Dynamics of natural regeneration tree species with light demanding (Light), intermediate (Inter) and shade tolerant (Shade) growth strategies in gaps during four consecutive growing seasons in mixed-species forest. BD – the growing season before forest disturbance, FSG – First growing season after forest disturbance, SGS – Second growing season after forest disturbance and TGS – Third growing season after forest disturbance.

3.3. Effects of parent stand on dynamics of natural regeneration of tree species in gaps

According to Bonham (2013), density is the number of individuals within a defined area, while De Rio et al. (2018) defined density as the abundance of an organism per unit area. From the presented results in Fig. 3, it can be seen that *P. abies* (BD = 18,339 trees ha^{-1}; FGS = 49, 617 trees ha^{-1}) was abundant under coniferous forest stands while *F. sylvatica* (BD = 24,824 trees ha^{-1}; FGS = 14,683 trees ha^{-1}) was highly abundant under broadleaved forest stands in the two assessed growing seasons. Meanwhile, *A. alba* and *L. decidua* grew abundantly in gaps during FGS, however, the abundance of *A. alba* (26,219 trees ha^{-1}) was detected under mixed forest stand while that of *L. decidua* was noticed under coniferous (31,108 trees ha^{-1}) and broadleaved (16,280 trees ha^{-1}) forest stands. On the other hand, *A. alba* and *L. decidua* showed poor regeneration performances in gaps with zero regeneration occurrence under coniferous and broadleaved forest stands during BD and again for only *A. alba* under coniferous forest stand during FGS. Looking at presented mean regeneration densi-

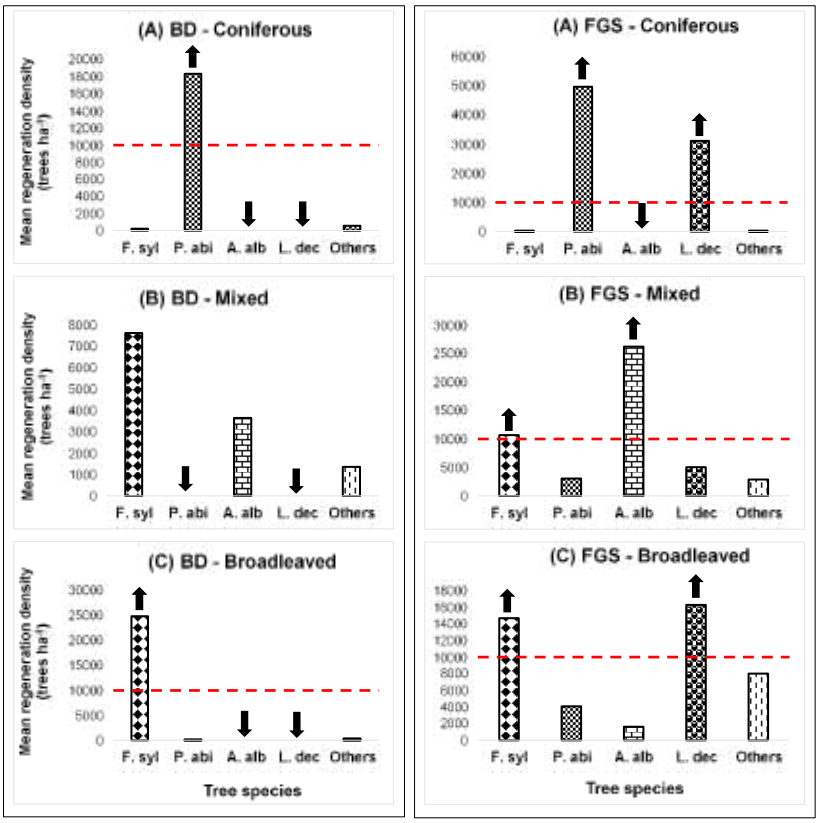

Fig. 3. Comparative assessment of different natural regeneration tree species under three distinct parent stands between the growing season before forest disturbance (BD) (left) and First growing season after forest disturbance (FGS) (right). The dashed lines denote the regeneration threshold (10,000 trees ha^{-1}) for various species to demonstrating high potential for establishment and recruitment prospects presently at stand-level and in the future at forest-level. Upward arrows represent leading species with great natural regeneration prospects while downward arrows represent poor performing species with zero records of natural regeneration. *A. alb* – *Abies alba*, F. syl – *Fagus sylvatica*, L. dec – *Larix decidua, P. abi* – *Picea abies* and Others – the remaining encountered tree species.

ties of species (> 10,000 trees ha^{-1}), it is presumed that at every 1 m^2 area of forest floors under gaps, at least one seedling each would be encountered as *P. abies* species under coniferous forest stand, *F. sylvatica* species under broadleaved forest stand, *A. alba* species under mixed forest stand and *L. decidua* species under coniferous and broadleaved forest stands. Hence, showing great establishment, recruitment and survival potentials of natural regeneration of these tree species under the predicted forgoing associated forest stands, respectively. From results, mirroring overstory tree species composition, *P. abies* would likely be the most prolific understory species under coniferous forest stand and similarly for *F. sylvatica* seedlings underneath broadleaved forest stand. The result in Fig. 2 describes the stimulating effect of forest stand on the distribution, proportions, and dynamics of natural regeneration tree species in gaps.

Furthermore, the simple linear regression results showed that measured TSF light condition significantly influenced natural regeneration of *F. sylvatica* (r_{TSF} = −0.58 at p = 0.012) and *L. decidua* (r_{TSF} = 0.62 at p = 0.006) in gaps during FGS in opposite ways (i.e., in a negative way for *F. sylvatica* and positive for *L. decidua*). On the contrary, the natural regeneration of other tree species was not significantly influenced by this light condition factor at the p < 0.05 significant level.

3.4. Effects of parent stand on dynamics of overall natural regeneration in gaps

Fig. 4 presents a forest undergoing natural regeneration processes and development in gaps under three distinct parent stands following small scale gap-disturbance. It was observed that during both FGS (16,197 trees ha^{-1}) and SGS (15,660 trees ha^{-1}), coniferous stand recorded the highest mean natural regeneration densities. In contrast, during TGS, the lowest comparable mean natural regeneration densities were found in gaps under mixed (623 trees ha^{-1}) and broadleaved (371 trees ha^{-1}) stands. Overall, natural regeneration in gaps declined from FGS to TGS in coniferous, mixed, and broadleaved stands at rates of 78%, 86% and 90%, respectively (see Fig. 4), demonstrating the ecological dynamics of natural regeneration in gaps after disturbance.

3.5. Effects of parent stand on dynamics of natural regeneration tree species in gaps

Dynamics and distribution of *F. sylvatica* and *P. abies, L. decidua* and *A. alba* including "Others" (any other participatory tree species) natural regeneration in gaps under three distinct parent stands within three consecutive growing seasons after small scale gap-disturbance

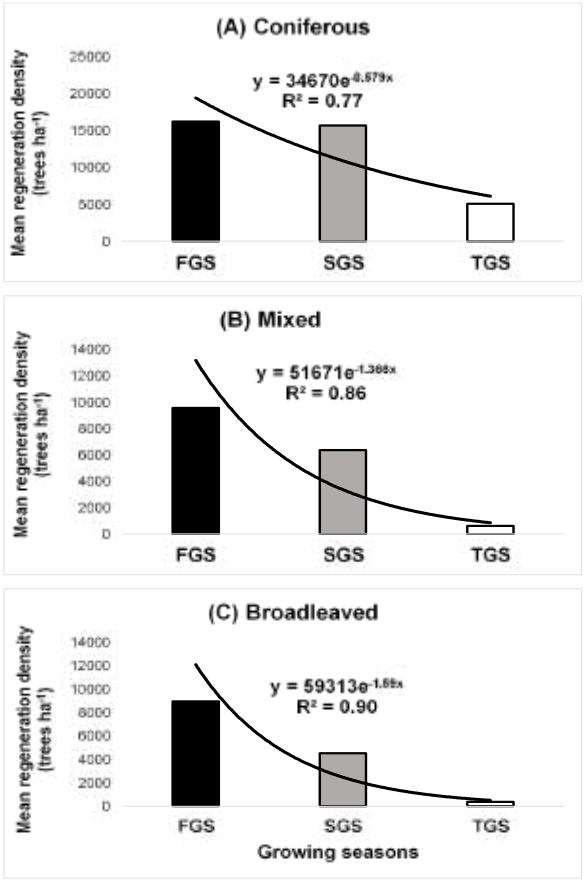

Fig. 4. Dynamics of gap regeneration under three distinct parent stands within three consecutive growing seasons after forest disturbance. FSG – First growing season after forest disturbance, SGS – Second growing season after forest disturbance and TGS – Third growing season after forest disturbance.

are presented in Fig. 5. In the coniferous stand, the mean regeneration densities of *P. abies* and *L. decidua* during FGS and SGS were significantly higher (p < 0.05) than those recorded in TGS. However, no significant difference (p >0.05) was found for *A. alba* and "Others" regeneration in the various growing seasons. Also, natural regeneration of *F. sylvatica* was totally absent during SGS and TGS while *A. alba* was only missing during FGS in gaps under the coniferous stand. Under the mixed stand, there were no significant observable differences (p >0.05) among FGS, SGS and TGS for *P. abies, L. decidua* and Others regenerations. By contrast, significant differences (p < 0.05) were observed among the various growing seasons for *F. sylvatica* and *A. alba* regeneration under mixed stand. Beneath the broadleaved stand, all species except *A. alba* showed significant differences (p < 0.05) among the three growing seasons for their respective natural regeneration.

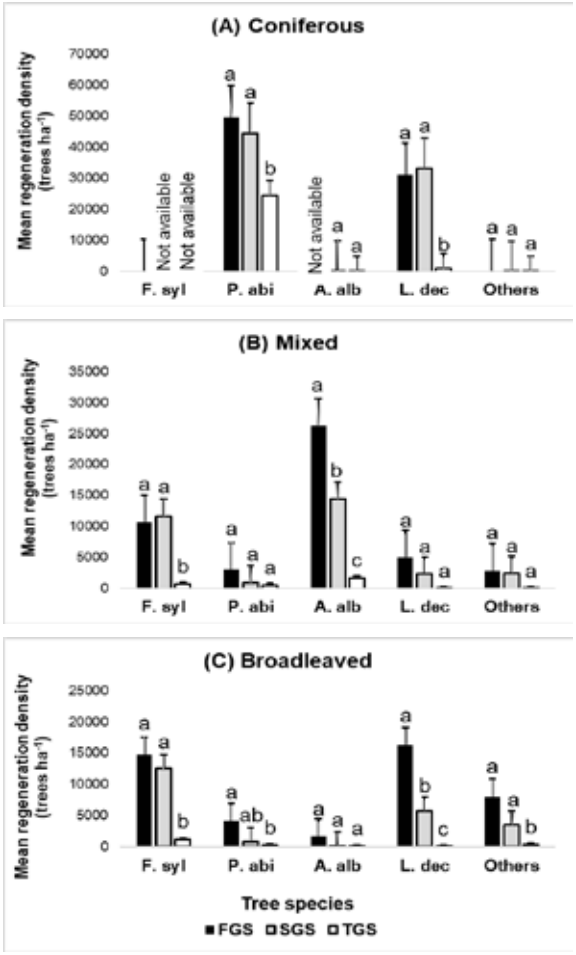

Fig. 5. Dynamics of natural regeneration tree species in gaps during three consecutive growing seasons in mixed-species forest. FSG – First growing season after forest disturbance, SGS – Second growing season after forest disturbance and TGS – Third growing season after forest disturbance. Not available signifies represent zero regeneration records. Bars with the same letters show homogenous group statistically ($p > 0.05$). *A. alb* – *Abies alba*, F. syl – *Fagus sylvatica*, L. dec – *Larix decidua, P. abi* – *Picea abies* and Others – the remaining encountered tree species.

4. Discussion

4.1. Impacts of gaps on species diversity and composition

Species composition is a fundamental structural characteristic in mixed-species stands. By definition, a mixed-species stand is a stand with at least two species (Del Río et al. 2018; Khodaverdi et al. 2019). In this study, we report the relevance of species diversity on forest functioning including: establishment, biodiversity preservation and stability through gap-based regeneration that safeguards sustainable forest development. We considered both species diversity and species composition to give a more detailed description of diversified tree species undergoing natural regeneration in gaps and simultaneously to accurately characterize future species composition and structure at the stand level of mixed forests dominated by small scale gap-disturbance regimes. From our results, we determined that, species diversity increased significantly after the small-scale gap dynamics treatment (see Table 3). Small-scale disturbances have been found to enhance species diversity in forests (Busing & White 1997). Our findings, therefore, support the studies of Dobrowolska (2007) and Khodaverdi et al. (2019) but disagrees with Griffiths et al. (2007). Several researchers have also stressed the role of gap disturbance on species diversity (e.g., Busing & White 1997; Dobrowolska 2007; Khodaverdi et al. 2019) via the subsequent creation of favorable conditions at growing sites especially increasing light condition (Bullock 2000; Dusan et al. 2007; Vilhar 2015) and explaining the mechanisms of species coexistence in gaps (Pacala & Levin1997; Wang et al. 2017b).

Contrary to our findings, Bullock (2000) claimed that gaps always allow increased light intensities, which often raise soil temperature and deplete soil water resources, weakening the vigor of regenerating species, thus accelerating mortality and eventually reducing species diversity in gaps. Other studies emphasize functional diversity more than species diversity (e.g., Hammond & Pokorný 2020a), because they believe that species with similar functional traits tend to occupy the same niche and therefore show similar behavior in growth pattern (de Bello et al. 2007) following openings in the canopies of forests. The regeneration dominance of *F. sylvatica* (69.4%) during BD and *P. abies* (68.9%) during TGS substantially influenced species diversity and this could also be explained for the similar estimated Pielou's Evenness (BD = 0.47 J, TGS = 0.43 J) and Berger-Parker index (BD = 0.69 D, TGS = 0.69 D) values attained for the two growing seasons. Besides, the similar relative densities of natural regeneration of *F. sylvatica* and *P. abies* during BD and TGS suggest that they were the most successful gap fillers under recent forest management (small-scale disturbance regime) during the study period. The same observation has been made elsewhere (Vilhar et al. 2015). In other observations, Rugani et al. (2013) described F. *sylvatica* as autochthonic dominant tree species in Central Europe, which has a typically competitive advantage over other tree species in various mixed-species forests under ecologically-based forest management. Grassi et al. (2004) observed that *P. abies* was one of the best performing tree species in natural regeneration under proper silvicultural practices and favorable conditions for the temporal and spatial continuity of the regeneration process.

Nonetheless, no absolute species dominance was found during FGS and SGS, but rather higher species diversity of the population and a significant balanced proportion between various natural regeneration tree species of different regeneration dominance categories in

gaps were observed. Hence, indicating that gap-oriented silviculture procedure in winter 2013/2014 hastened the processes of forest restoration and dynamics through gap regeneration. Even though other studies have stated that gaps do not necessarily provide the ideal environment for regeneration (e.g., Busing & White 1997; Jaloviar et al. 2020). Our study confirmed a higher gradient of species composition observed during FGS in enlarged gaps from enhanced growing conditions to the improved establishment of advance regeneration and greater regeneration through buoyant recruitment mechanism.

Moreover, similar species composition observed across all four growing seasons suggests homogenous tree species composition at the stand level. Our results do support the hypothesis that similar species assemblages result in similar species composition (e.g., Wang et al. 2017b), but contradict a statement from Myers et al. (2013) that forests with similar overall structure vary in recruitment mechanisms, demonstrating divergent forest types through a shift in the emergent patterns relative to the community assembly mechanisms. Also, Bravo-Oviedo et al. (2014) categorically stated that under analogous forest where similar species, objectives and site conditions exist, for example, in the case of mixed forests, adoption of successful management guidelines may not be straightforward as similarity among species mixtures is not easy to be achieved. Our observation was completely different from this statement.

Furthermore, the regime of small scale gap-disturbance to light availability favored light-demanding species (*B. pendula, L. decidua, P. sylvestris, P. nigra, Q. petraea* and *S. alba*) and intermediate species (*P. menziesii,*) to regenerate, establish, grow, and recruit in large gaps (Qu et al. 2004; Hammond et al. 2020), while shade tolerant species (*C. betulus* and *F. sylvatica*) preferred the original small-sized naturally occurring gaps for enhanced natural regeneration processes, optimum growth and survival (Nagel et al. 2010; Feldmann et al. 2020). The ecological relationship between gaps (formation or size) and tree species with different growth behaviors (Hammond & Pokorný 2020a) was confirmed in our study. Also, it should be taken into consideration that SGS was an extremely dry year, thus light demanding species could disappear due to shade tolerant species, but both tree species could be diminished due to drought in TGS. Therefore, presumably, intermediate species could be less susceptible to drought and light changes.

4.2. The ecological contribution of parent stands towards growth potential of natural regeneration of different tree species in gaps

The results showing a higher proliferation (> 10,000 trees ha^{-1}) of predominant *F. sylvatica* and *P. abies* species in gaps under broadleaved and coniferous stands, respectively in both BD and FGS, tells the importance of species identities or species composition (Töigo et al. 2015) on future stand composition and structure through natural regeneration. In contrast to our findings, Vacek et al. (2017) observed that stand canopy had a negative effect on regeneration density of *F. sylvatica* natural regeneration in gaps under broadleaved forests. In another observation, Hammond and Pokorný (2020c) also saw a reduced growth dynamics of *P. abies* in gaps under *P. abies* dominated mixed stand. In this presented study, *F. sylvatica* and *P. abies* demonstrated a considerable advantage over the other species in gap regeneration. The basic characteristics (i.e., the widespread species composition in stand) of forest stand type strongly associated with this finding. This is because both broadleaved and coniferous stands retained the heavy presence of parent trees. The proximity of seed trees facilitated the regular supply of seeds for regeneration processes, seed establishment, and seedlings recruitment. This finding shows the important role of constant seed supply, the quantity of seed supply and reliable seed source for a successful gap regeneration.

The observed favorable regeneration densities of *F. sylvatica* and *A. alba* species in gaps under mixed canopies during FGS is consistent with Čater et al. (2014) hypothesis, which states that the growth behaviors of mentioned species under gap regeneration is mostly influenced by the ability to outcompete their neighbors under favorable light conditions through a fine adjustment of light permeability and improving conditions for their growth and development. However, the higher comparative regeneration density of *A. alba* confirms earlier findings in Slovenia that among variuos tree species in gap recruitment under mixed-species stands, *A. alba* always has a competitive advantage in regeneration (Čater et al. 2014). In order to favor *A. alba* regeneration, gap expansion is an essential silviculture practice (Čater et al. 2014).

Not with standing, the observed higher regeneration densities of *L. decidua* under broadleaved and coniferous stands in FGS could be attributed to the regime of small scale gap-disturbance, which mimicked the natural disturbances that favored the species. Another explanation was the accompanied improved light factor following disturbance and resultant gap expansion state favored the biological light demanding trait of *L. decidua* species causing profuse regeneration under broadleaved and coniferous stands in FGS. This evidently validates other research that found *L. decidua* to be sun-loving species (Qu et al. 2004; Matras & Pâques 2008) that grows best after forest disturbance (Wang et al. 2017a). Many gap-related processes and factors produce the mosaic spatial structure of the gap regeneration and recruitment in mixed forest stands. Our study shows that differentiation in the regeneration niche (Pretzsch 2009) including production of seeds–mast seeding, seed dispersal, germination, and establishment of seedlings (Grubb 1977), presence, location and abundance of parent trees and

seed dispersers, advance regeneration (Yan et al. 2015; Wang et al. 2017a) as well as different life strategies of tree species in accessing the gap space (Bullock 2000), consequently create new disturbance regimes (Sommerfeld et al. 2018) that have significant influence on gap regeneration and dynamics.

The significantly higher mean regeneration densities of *F. sylvatica, P. abies*, *A. alba* and *L. decidua* species in stands give a good prediction that their proportions are expected to rise significantly in the future, since they were the most prevalent species in the natural regeneration layer (5 – 350 cm) of mixed forests at Křtiny (Hammond et al. 2020). Also, because their population, in terms of diameter structure and distribution, is substantially younger than populations of other species on sites where all species cohabit. We hypothesize that species with 10,000 trees ha^{-1} or more density records would have better forest restoration strategies after a small scale gap-disturbance regime and would tend to exhibit greater growth abundances in gap-based regeneration than those observed with less regeneration density (< 10,000 trees ha^{-1}) in gaps. Therefore, requiring different gap sizes, *F. sylvatica, P. abies*, *A. alba* and *L. decidua* may have greater prospects in future forest stand structure in mixed forests Křtiny than any other encountered species in gaps. This knowledge can be a helpful reference for designing silvicultural systems that aim to conserve diverse forest structures by mimicking natural disturbance dynamics in managed mixed-species stands growing on similar sites (Jaloviar et al. 2020).

4.3. Dynamics of natural regeneration in gaps under three distinct parent stands

Our result clearly indicates the significant decrease in natural regeneration densities in gaps within a short-term (over three years) after a small scale gap-disturbance regime. The mixed-species Křtiny forests showed declining and unsustainable regeneration and recruitment of tree species in gaps from FGS to TGS after small scale gap-disturbance. Although the primary objective of small scale gap-disturbance was to enlarge gaps for the promotion of natural regeneration and gap-recruitment and improvement of diversified tree species. Contrary to our findings, Jaloviar et al. (2020) stated that small scale gap-disturbance primarily maintains forest structure through the emergence and survival of natural regeneration upon canopy openings in a variety of conditions and that canopy gaps increase regeneration densities. Progressive mortality of natural regeneration tree species in gaps under mother stands was the typical feature. A significantly similar response of overall natural regeneration between different mother stands during FGS, SGS and TGS periods was observed. Quantification of ecological relationship between the various mother stands and related environment along with the trend of natural regeneration prediction over a period of time is not straightforward. Distribution of the site environmental conditions along stand level-gap gradient (Yan et al. 2015) is probably of higher importance than species relationships and gap environmental conditions. The low amount of extracted variability in natural regeneration dynamics in gaps under coniferous, mixed and broadleaved stands found in our study suggests that a regeneration process is more likely influenced by other factors rather than the general "gap characteristics (size, shape, geographical exposition)" factor of gaps under mixed forests. For instance, during FGS, natural regeneration was seriously compromised by competition from other life forms, to name a few; *Asperula* spp., *Cardamine* spp., *Carex* spp., *Dentaria* spp., *Luzula* spp., *Oxalis* spp., *Urtica* spp. etc. which grew more rapidly, intensely and finally, became more resilient in growth immediately after the completion of small scale gap-disturbance activity in winter 2013/14 for the reason of favorable growing sites conditions (Hammond et al. 2020). Likewise, Vacek et al. (2017) observed similar circumstances at the Krkonoše National Park where seedlings from natural regeneration received keen competition from *Calamagrostis villosa* and *Avenella flexuosa* grasses in mountainous European beech forests.

Nevertheless, the unexpected abiotic drought conditions in 2015 (i.e., expected annual mean precipitation (EMP)/real annual mean precipitation (RMP): 610/430 mm) through to 2016 (i.e., EMP/RMP: 610/533 mm) calendar years (CHMI 2020) and the high air temperature events (2015 EMT/RMT: 7.5/10.4 °C; 2016 EMP/RMP: 7.5/9.7 °C) coupled with the climatic history of very low air humidity in the region resulted in extreme evaporative conditions for regenerating species during vegetation period alongside the extreme browsing activities at the study site (Hammond & Pokorný 2020c) significantly influenced the high mortality among various natural regeneration tree species in gaps. Similar to our findings, many authors have cited the significant effects of browsing pressure (Dusan et al. 2007; Vilhar et al. 2015; Kupferschmid et al. 2019) and drought conditions (Anderegg et al. 2013; Sedmáková et al. 2019) as major sources of tree mortality among species undergoing regeneration at temperate forests in East-Central Europe. Overall, our results also support the contention that natural beech forests in Central Europe are characterized by local biotic and abiotic events (Feldmann et al. 2020).

At the individual species level, poor regeneration performances of *F. sylvatica* in gaps under coniferous stand in this study agrees with Dobrovolný and Cháb (2013) but disputes Sterba and Eckmüllner (2008), who stated that the rate of invasion potential for *F. sylvatica* to occupy an area within a pure conifers forest in central European forests is unmatched. However, the comparably good regeneration densities of *F. sylvatica* during FGS and SGS in gaps under mixed and broad-

leaved stands, respectively, demonstrate the resilience of *F. sylvatica* species to light-exposed environments (Čater et al. 2014) and browsing damage (Vilhar et al. 2015). Further, our study result revealing the excellent regeneration of *P. abies* in gaps from FGS to SGS under a coniferous overstorey is consistent with Dobrovolný & Cháb (2013), who also reported the same observation. On the other hand, the evidenced low yield shift of *P. abies* and *A. alba* species in gaps under broadleaved canopies indicates the significant relationship between cohabiting species at the understory. Although regeneration of *L. decidua* in gaps following disturbance was expected to be profuse across all forest types due to its fast-growing pioneer behavior in gaps (Matras & Pâques 2008). Species competition especially from *F. sylvatica* and lack of silviculture interventions such as thinning, weed control, protection against browsers etc. and other special management activities could explain the relatively limited growth of *L. decidua* in gaps.

The higher regeneration densities of all studied species during FGS illustrate the relevance of the current canopy removal management guidelines at mixed forests, Křtiny, towards the sustainability of natural regeneration. The outcome of gap-disturbance in the preceding growing season (BD) where disturbance regime characterized by small-scale and low-intensity disturbances that were variable in space resulted in favorable light conditions for the successful seedling recruitment in FGS (Rugani et al. 2013). However, under the same intensity of canopy removal management guidelines in Romania, our results of *F. sylvatica*, *P. abies* and *A. alba* natural regeneration in the three mother stands are directly opposite to the results of Stancioiu and O'Hara (2006) studies where gap-disturbance promoted vigorous growth at similar rates for all three species.

Apart from this, our results revealed that TSF light condition established negative and positive significant effects on gap regeneration of *F. sylvatica* ($r^2 = 0.34$) and *L. decidua* ($r^2 = 0.39$), respectively, during FGS. The positive significant linear relationship between abiotic TSF and biotic *L. decidua* in gaps has been mentioned already in a different study conducted at Sessile-Oak-Hornbeam and Turkey Oak Forests in western Hungary (Kollár 2017). Apparently, in another recent research under predominantly *P. abies* mixed stands, *P. abies* was the only natural regeneration tree species that established a significant negative linear relationship with TSF light condition ($r^2_{TSF} = 0.97$ at $p = 0.015$) in gaps (Hammond & Pokorný 2020c). The quantified TSF light condition in Hammond and Pokorný (2020c) ranged between 13.3 – 25.5%, while we estimated comparatively lower minimum and higher maximum values (10.6 – 28.4%) for the same gap-light condition. Generally, our finding projects the integral role of a light factor on the growth of tree regeneration and at the same time, portrays the potent ecological relationship between a particular light condition and specific species with different biological life-history attributes.

5. Conclusions

In contemporary forest management, gap regeneration is an appropriate silviculture technique for sustainable forest management in mixed stands. Our conclusions highlight the potential effect of gaps following disturbance, comparatively smaller in sizes (0.03 – 0.11 ha) but contributing significantly to increasing species composition and species diversity in mixed-species Křtiny forests. Seven (7) new species with light-demanding growth strategy (*Betula pendula, Larix decidua, Pinus sylvestris, Picea abies, Populus nigra, Quercus petraea* and *Salix alba*) that were not present in gaps in the growing season prior to disturbance in 2013 were added to species composition in the first growing season after disturbance (FGS) increased species diversity in the growing seasons after disturbance (2014 – 2016). However, all four studied growing seasons shared similar tree species in gap regeneration. *Fagus sylvatica* and *Picea abies* dominating regeneration, not surprising given the former's roles as climax species on study site and the latter's prominence in the overstorey as a planted species. Besides, stand type could probably be attributed to the prolific regeneration of *Fagus sylvatica* and *Picea abies* under broadleaved and coniferous stands while biological light demanding traits of *L. decidua* could significantly be explained for the excellent performances in gaps during the first two years after small-scale disturbance.

Generally, the micro-growing sites of gaps alone could not be associated to the dynamics and distribution of overall natural regeneration in gaps under various mother stands because the variability that can distinctively be attributed to gap and stand-level related environmental factors seems very high. Progressive decline in regeneration densities of gap regeneration was common from FGS to TGS. To a large extent, extrinsic factor like drought condition in 2015 and intrinsic factors like competition from other life forms and increasing browsing activities (unfortunately not avoided by fencing) were the explanatory factors for the observed natural regeneration dynamics in mother stands. However, at species level, inherent tolerability to light and browsing damage conditions significantly explained variations of *F. sylvatica* regeneration in gaps under coniferous, mixed and broadleaved stands from FGS to SGS, whereas growth of *P. abies* and *A. alba* were greatly hindered by the competitive presence of *F. sylvatica* under broadleaved stand. Nevertheless, lack of silviculture interventions could be explained for the growth variations of *L. decidua* in gaps under the three mother stands. The current management guidelines for small scale gap-disturbance regimes at mixed forests, Křtiny significantly influenced the higher regeneration densities of all studied species during FGS.

It is self-evident that gaps are preferential growing habitats for natural regeneration tree species with different growth strategies under mixed forests, however further management and silviculture protocols like thin-

ning (to enhance light), vegetation control and protection against browsers etc. including climate-change tolerability strategies should be pursued for the sustainable development of natural regeneration of different tree species.

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