forests

MDPI

Article

Gap Structure and Regeneration in the Mixed Old-Growth Forests of National Nature Reserve Sitno, Slovakia

Peter Jaloviar, Denisa Sedmáková *, Ján Pittner, Lucia Jarčušková Danková, Stanislav Kucbel, Robert Sedmák and Milan Saniga

Faculty of Forestry, Technical University in Zvolen, T.G. Masaryka 24, 960 01 Zvolen, Slovak Republic; jaloviar@tuzvo.sk (P.J.); pittner@tuzvo.sk (J.P.); dankova.lucia@gmail.com (L.J.D.); kucbel@tuzvo.sk (S.K.); sedmak@tuzvo.sk (R.S.); saniga@tuzvo.sk (M.S.)

* Correspondence: denisa.sedmakova@tuzvo.sk; Tel.: +421-45-5206-246

Received: 1 December 2019; Accepted: 6 January 2020; Published: 9 January 2020

Abstract: Forest management mimicking natural processes represents an approach to maintain mixed, uneven-aged stands at small spatial scales. The reliance on natural processes, especially on natural regeneration leads to the use of gap-based regeneration as a fundamental silvicultural technique. As a baseline for such management, we investigated mixed forest in unmanaged National Nature Reserve Sitno in the Western Carpathians, which harbours extraordinary diversity on a rather small scale. To quantify the impact of gaps on gap-filling processes and to assess the role they play in recently observed changes in tree species composition we established a large (2.5 ha) permanent research plot and surveyed the status of natural regeneration, forest structure, tree species composition, and disturbance regime. Our research highlights the long-term and contemporary difficulties in the establishment of *Quercus petraea* (Matt.) Liebl and *Fagus sylvatica* (L.). Based on the provided evidence, the native tree species diversity in one of the few preserved old-growth multi-species beech-oak forest remnants is not likely to persist, what could have many implications for future ecosystem functioning. Our results suggest that variation in gap size is an important factor contributing to composition of tree species composition of natural regeneration. The recent intermediate-scale disturbance pattern dominating the old-growth beech-oak forest is beneficial to canopy recruitment of species less shade-tolerant than *Fagus sylvatica*, as *Acer pseudoplatanus* (L.), *Acer platanoides* (L.), and *Fraxinus excelsior* (L.). We discuss possible factors behind observed shifts in tree species composition and limitations for application of gap dynamics to forest practice in managed beech-oak forest systems. Overall, results of this study may help to design silvicultural measures promoting mixed-species forests to deliver a range of desired ecosystem services.

Keywords: gap dynamics; regeneration; recruitment; gapmaker; disturbance; European beech; Sessile oak; temperate forests

1. Introduction

Management approaches aiming to preserve tree species diversity in forests are becoming increasingly important. Enhanced diversity stabilises productivity and promotes resilience of forest ecosystems, while diverse forests have higher resistance against various harmful agents and provide more stable wood production under a wide range of environmental conditions [1,2]. One of the key silvicultural practices utilized in such type of management is the natural regeneration of forest stands. The basis for management concepts that stress the importance of spatial partitioning of gap resources in the maintenance of tree species diversity is research on natural disturbance regimes of old-growth forests [3].

Natural disturbance regimes allow various tree species of contrasting life traits to coexist [4,5]. In Central European forests, the main disturbing factor shaping spatial structure and thus affecting the dynamics of the ecosystem is the wind [6]. Wind disturbances create openings in forest canopy, gaps, which is associated with regeneration of various tree species [7]. The process of gap dynamics includes dying of the tree individually or as a group of several trees that are continuously replaced by subsequent natural regeneration without the negative impacts on forest sustainability over the larger forest area [8]. Large gaps created by rarely occurring high severity wind disturbances favour establishment of shade-intolerant, pioneer species. For example, wind disturbance creating a gap (patch) over 0.6 ha resulted in the establishment of *Salix caprea* (L.) in old-growth fir-beech forest in western Carpathians [9]. Single wind-thrown events of moderate severity with estimated occurrence once within the tree's life cycle [10] favour recruitment of intermediate shade-tolerant species, such as oak, in very large gaps (patches) of approximate sizes 0.1–0.4 ha [4,11]. On the other hand, frequent, small gap-scale disturbances benefit recruitment and dominance of shade-tolerant tree species, such as fir or beech [7]. In European temperate forests with *Fagus sylvatica* dominance or co-dominance, distribution of gap sizes exponentially decreases towards large-sized gaps, whereas majority of gaps (above 90%) have size bellow 0.05 ha [12–15].

Applications of gap dynamics to forestry practice is limited [7]. Traditional management systems currently applied in stands where several target tree species with contrasting light requirements coexist may cause difficulties in regeneration and recruitment of some species (Saniga 2019—personal communication). In Slovakia, release thinnings and shelterwood systems utilizing single tree or small group (gap) cuttings are the most frequently used for natural regeneration of forest stands (irrespective their species composition).

In secondary mixed beech forests, utilization of mechanisms of natural regeneration based on tree or small group shelterwood can, paradoxically, lead to decline of biodiversity [16]. Many forest stands affected in this way result in simple undifferentiated structures dominated by single species, even the natural regeneration is successful. As a matter of fact, single tree or small group cuttings best imitate the regeneration processes in natural beech dominated forests [17]. Subsequently, small-scale regeneration methods in mixed stands may hamper the regeneration of other tree species at the favour of beech—a very competitive species and so to alter the composition of forests.

The important role of intermediate and large gaps in the gap dynamics of natural mixed beech forests has been highlighted [15], which agrees with more intensive forest management suggested to increase their species diversity [18]. Findings from other European studies also point to that management of light through sufficient canopy openings in mixed stands of oak and beech is not enough to promote and explain the development of the intermediate shade-tolerant species [19–21]. Other less studied mechanisms than the size of canopy opening are likely to play an important role and influence the final composition of tree species in gap-filling processes [22,23]. The proportion of stand disturbed, frequency of gaps, their temporal dynamics, the duration of periods of release may be more influential to saplings of shade-tolerant species than gap size [22].

The mixed beech-oak old-growth temperate forests can serve as a model base for forest management that aims to maintain high tree species and structural diversity. However, natural old-growth multi-species forests with oak (easily accessible at the coline and submontane climax forests [24]) has remained sparsely distributed in eastern Central Europe [11,19,25–29]. In these forests, under current ecological conditions, *Fagus sylvatica* increases its relative importance at the expense of oak, as mortality increases of both *Fagus sylvatica* and *Quercus petraea*, but higher for *Quercus petraea* [28,30,31].

For the purpose of this study, we selected mixed forest in unmanaged National Nature Reserve Sitno (Slovakia), which harbours extraordinary diversity on a rather small spatial scale and represents one of the best-preserved forest remnants in eastern Central Europe. In the selected forest, we established large (2.5 ha) permanent research plot to survey status of natural regeneration, forest structure, tree species composition and disturbance regime.

Our aim is to test and quantify the effects of gaps and gap-size related partitioning of natural resources (gradients of light, moisture, temperature according to Busing and White [32]), density, and canopy closure of forest stand and the spatial variability of natural conditions in the investigated area on density and tree species composition of natural regeneration.

We aim to answer following groups of mutually related questions:

(i) Are there changes in disturbance regime manifested by differences in the size, distribution or origin of recently created gaps?
(ii) What is the impact of recent disturbance regime, i.e., gap size, and type of its extension on density and species composition of natural regeneration in old-growth beech-oak forest?
(iii) How much variability in abundance of tree species is explainable by the niche environmental gradient formed between gaps and forest stand and how much variability can be attributed to spatial variation of natural conditions on the monitored area?
(iv) What are the practical implications for the management, if we aim the regeneration to preserve the species and structural diversity in beech-oak associations? How to regenerate mature mixed stands with the beech presence to avoid formation of a simple undifferentiated structure dominated by single species?

2. Materials and Methods

2.1. Study Area

The study site (48°23′55″ N; 18°52′54″ E) is located in the National Nature Reserve (NNR) Sitno in the Štiavnicke Mts., which is part of the Western Carpathians (Figure 1). The reserve established in 1951 is located between 770 and 940 m asl with prevailing S and SE exposition. Mean annual precipitation sum is 907 mm. Mean annual temperature is 14 °C. Bedrock consists of volcanic rocks, andesite, and pyroxene. The predominant soil type is eutric cambisol, well aerated, with high share of rocks, and with rapid draining. The mixed beech-oak forests are naturally formed by more than eight tree species: *Acer pseudoplatanus* (L.), *Acer platanoides* (L.), *Fraxinus excelsior (L.), Fagus sylvatica* (L.), *Tilia cordata* (Mill.), *Ulmus scabra* (Huds.), *Carpinus betulus* (L.), and *Quercus petraea* (Matt.) Liebl. The research was conducted on a 2.5 ha (250 × 100 m) permanent research plot (PRP) established in the reserve in 2011 (Figure 1; [33]). The location of the plot was selected in the central core zone of the reserve (800–900 m asl) and corresponds with eumesotrophic site having a moderate-rich amount of dissolved nutrients. Study area comprises two main forest associations, *Querceto-Fagetum tiliosum* and *Tilieto-Aceretum*. *Fagus* and *Quercus* naturally represent this habitat with respective proportion from 30% to 50% and from 5% to 20%, and with higher admixture of above-mentioned broadleaved tree species.

2.2. Field Measurements and Data Analysis

We recorded two types of gaps in accordance with Runkle [5]: open canopy gap and expanded gap. Gaps were defined as openings in the forest canopy >5 m^2 formed due to the mortality of one or more canopy trees with diameter at breast height (dbh) above 25 cm. We considered gaps with the gapmaker (fallen tree causing the canopy opening) presented on the ground. The gap was not recorded and considered to be closed, when the next generation of trees reached the height layer corresponding to one third of upper (dominant) stand height—34.1 m. The positions and crown projections of trees surrounding the canopy gap were gathered, and the gap sizes were calculated using the Field-Map® software package (IFER—Monitoring and Mapping Solutions, Ltd., Jílové u Prahy, Czech Republic).

Location and areas of natural regeneration polygons were initially mapped on the whole PRP by Field-Map (Figure 1). Subsequently, the status of natural regeneration was surveyed on 3.14 m^2 circular plots (i.e., 1 m in radius) established on the grid intersections (n = 216, grid of 10 × 10 m) of the whole PRP. From the 216 plots, 125 plots were placed in expanded gaps and 91 under closed forest canopy. The number of individuals of each species and their height was recorded. The regeneration was classified into two height categories, which include seedlings (≤50 cm of height) and saplings

(>50 cm; dbh ≤ 4 cm). Moreover, the number of young trees with diameter at breast height between 4–8 cm was recorded. In total, three successive developmental cohorts (next tree generation categories) were investigated—seedlings, saplings and young trees.

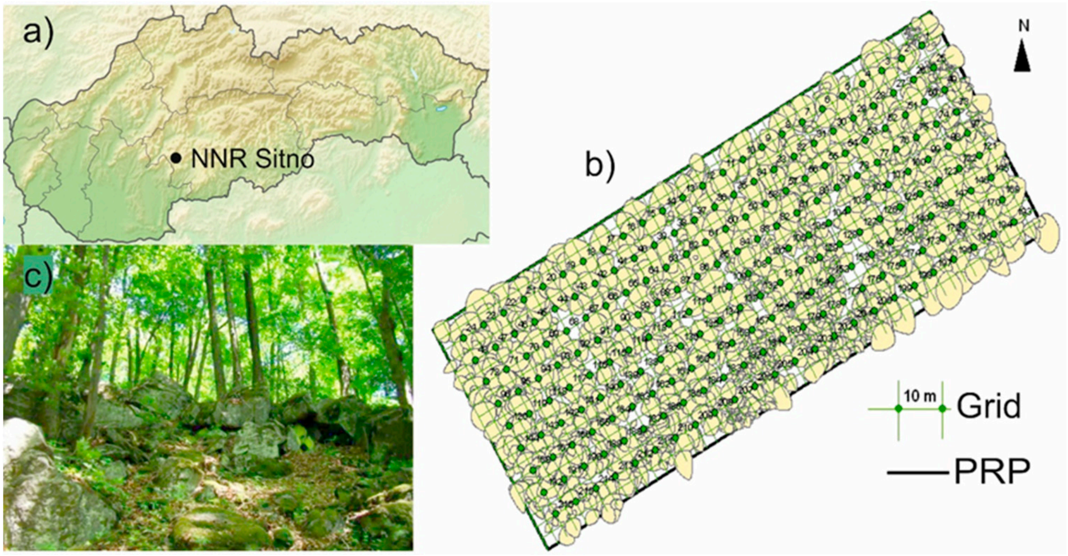

Figure 1. (**a**) Location of the National Nature Reserve (NNR) Sitno in Slovakia; (**b**) permanent research plot (PRP, 250 × 100 m) with horizontal cover of tree crowns and 216 circular research plots (plot size 3.14 m^2, grid intersection 10 × 10 m) established to survey natural regeneration; the longer side of PRP follows the highest counter line; (**c**) intersection of Pannonian and mountain climate together with large stones and stony debris necessitated rich and diversified tree species composition of beech-oak old-growth forests in NNR Sitno.

Gaps' characteristics were described in terms of relative frequencies of gaps of different size classes, proportion of gap area on the study area and the number of gapmakers per gap and the degree of their decomposition according to Albrecht [34]. Gaps were further categorized based on the type of their enlargement (dynamics) into three categories: 1—no enlargement; 2—past enlargement; 3—recent enlargement. Gap openings originating from simultaneous death of one or more gapmakers with the identical degree of decomposition were included in enlargement category one. The second category was represented by gaps comprising two and more gapmakers of varying degree of decomposition, but non-including the first degree of decomposition. The third category represented gaps, in which gapmakers had varying degree of their decomposition including also the first degree.

2.3. Data Analysis

To evaluate the changes in the disturbance regime on the monitored PRP, standard descriptive statistics of species composition, density, basal areas and volume of living trees, deadwood, and natural regeneration (seedlings, saplings, and young trees) were calculated in statistical package Statistica 12.0 [35]. The diameter distributions of individual species in mature stand were obtained by sorting of individual diameters and standard size and variability characteristics were calculated (averages, standard deviations). Similarly, the gap size and gap enlargement frequency distributions and simple descriptive characteristics of gapmakers' features were provided with support of software Statistica 12.0 (StatSoft, Inc., Tulsa, OK, USA).

To analyze the impact of disturbance regime on natural regeneration, the absolute and relative density (abundance) of particular species was evaluated under canopy and in gaps respectively. Differences in absolute numbers (densities) of main species between closed canopy and expanded gaps were tested by Mann–Whitney *U* test separately for each regeneration category (e.g., seedlings, saplings). The effect of gaps on regeneration was also examined by employing ratio calculated as absolute density of species individuals in gap relative to density in the control undisturbed area (under canopy). One-way ANOVA was applied to test if significant differences exist in the absolute density of seedlings, saplings and young tress (separately for dominant species) according to gap enlargement categories (none, recent, past).

To determine how much of variation of tree species abundances on sampling plots can be (uniquely) attributed to (i) variation of environmental gradients formed by gaps and density of forest stand surrounding sampling plots, and (ii) spatial variation of environmental conditions on sampling plots across the PRP, we applied two ordination analyses—detrended correspondence analysis (DCA) and redundancy analysis (RDA). Software package CANOCO 4.5 [36] for ordination analyses and the visualization of the results was used.

Tree species densities of natural regeneration on sampling plots (size 1 m^2, $n = 216$) entered the analyses as dependent variables separately for each species and two regeneration categories—seedlings (Sdl) and saplings (Sap). Values of tree species absolute densities were transformed by decadal logarithm ($\log10\ (n + 1)$) to approach normality assumption. The category of young trees was not considered because dataset was dominated by zero values and only two tree species accounted for reasonable numbers allowing multiple comparisons. The plot–species matrix containing 14 dependent variables in total (abundancies of 7 species × 2 regeneration categories on 216 sampling points) was prepared.

Two sets of explanatory variables were used as independent variables characterizing (i) the stand, gap, and gap-size related partitioning of environmental conditions on environmental gradient between the center of gap and closed stand (environmental variables) and (ii) spatial variation of environmental regeneration conditions among sampling plots within the stand (spatial variables). Environmental variables included: (i) three dummy variables of plot presence or absence in open gap, expanded gap, and close canopy conditions, (ii) size of expanded gaps (gap size), and (iii) sum of basal areas (SumBA) and crown projection areas of trees (SumCro) extracted from the 5 m buffer zone surrounding each circular sampling plot. Set of spatial variables was derived from x and y coordinates (by their multiplication or power transformation) of each sampling plot: x, y, x^2, xy, y^2, x^3, x^2y, xy^2 a y^3 in accordance with the methodology for variation partitioning suggested by Borcard et al. [37]. The plot-environmental matrix consisting of 15 environmental/spatial predictors in total (6 environmental variables + 9 spatial variables on 216 sampling plots) was elaborated.

The variables in plot-environmental matrix entered the RDA as the set of explaining, predictor variables for set of species absolute densities (involved in plot-species matrix) defining abundance and species composition of natural regeneration.

DCA as indirect gradient method had confirmation character and verified the selection of RDA as valid method of linear ordination. Detrended correspondence analysis (DCA) applied on both independent and dependent variable sets revealed the length of the longest ordination axis was 2.789. This fact suggests, the studied environmental gradients are short and as such, it allows to apply linear approximation of species response.

Subsequently, following the methodology of Borcard et al. [37], variance partitioning [37,38] through partial RDA-analyses was used to identify relative proportion of environmental and spatial factors—individually or jointly—on the amount of explained variation of tree species density, separately for seedlings and saplings. For this purpose, forward selection of explanatory variables was employed, only the variables with $p < 0.05$ were selected. Species densities were centred. To test statistical significance of individual variables and models, we used Monte-Carlo test of permutation. As our aim was also to reveal the spatial influences despite the sampling plots were placed in the grid, we used 999 unrestricted permutations [36]. Besides the variation portioning, the RDA allow to reveal the most influential environmental and spatial factors explaining significant amount of variation in dependent set of absolute species densities.

To study the responses of individual species in more detail, we built and tested the general linear models (GLM). GLMs were used to evaluate the relationship between log-transformed density of each tree species in natural regeneration ($\log_{10}(n + 1)$) and set of environmental factors. Main intention was to reveal the differences in sets of environmental variables allowing intentionally supporting the regeneration and survival of some tree species over other ones. Thus, the GLM models can provide useful information applicable for promotion of the species diversity in managed beech-oak stands.

3. Results

3.1. Description of the Stand

Forests with basal area of 39.8 $m^2 ha^{-1}$ and stem density of 603 trees ha^{-1} cover the study site and include the presence of nine tree species (Table 1). The canopy layer is dominated by *A. pseudoplatanus*, *F. sylvatica*, and *F. excelsior.* Together with *A. platanoides* the dominant species attain more than 75% of total tree number. Other more represented tree species are *C. betulus* and *T. cordata*, with relative density of 7.8% and 9%. *Q. petraea* has proportion only 3.5%.

Table 1. Species composition and basic characteristics of living trees (dbh ≥4 cm) on the permanent research plot.

Tree Species	Density		Basal Area	
	$N\ ha^{-1}$	%	$m^2\ ha^{-1}$	%
Acer platanoides	17	2.8	1.8	4.6
Acer pseudoplatanus	210	34.8	7.6	19.1
Fraxinus excelsior	99	16.4	3.2	7.9
Fagus sylvatica	135	22.4	15.3	38.4
Tilia cordata	54	9.0	3.2	8.1
Ulmus scabra	18	2.9	0.7	1.6
Carpinus betulus	47	7.8	3.2	8.1
Quercus petraea	20	3.4	3.6	9.2
Abies alba	3	0.5	1.2	3.0
Total	603	100.0	39.8	100.0

The total deadwood volume represents 115 $m^3 ha^{-1}$ (Table A1). Overall, diameter distribution of living trees on the PRP shows continuous recruitment and resembles J-shape form, indicating continuous establishment of trees (Figure 2a). Diameter distributions of *A. pseudoplatanus* and *F. excelsior* exhibit peaks in the lowest diameter classes (Figure 2b), which indicate their successful contemporary establishment. *F. sylvatica* unlike the *A. pseudoplatanus* and *F. excelsior* shows continuous recruitment with the widest range of diameter classes, but with decreased number of trees in the lowest diameter class, what can be regarded as the early sign of difficulties in establishment. Diameter distribution of *Q. petraea* shows peak in middle classes and the absence of recruitment in low diameter classes indicating inability to establish for a longer time.

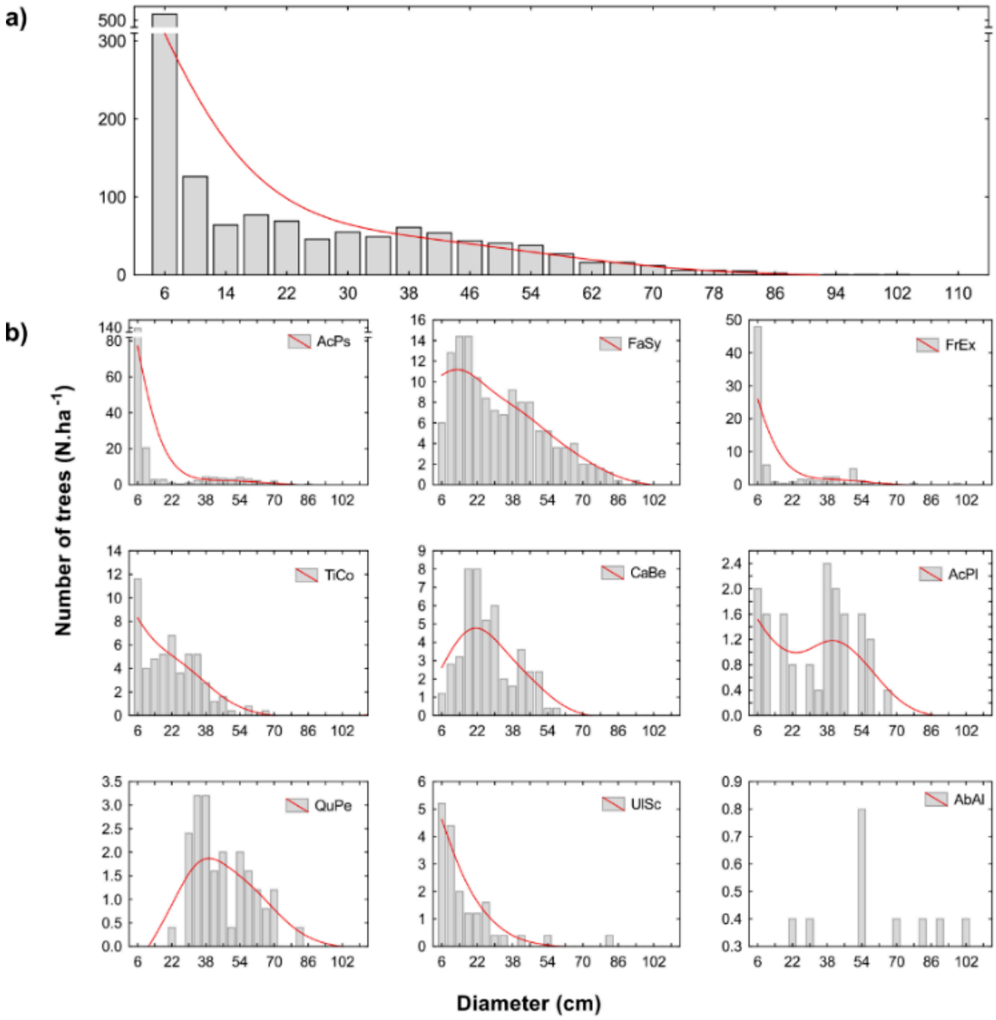

Figure 2. Diameter distributions of (**a**) all and (**b**) individual tree species on the permanent research plot Sitno (trees with dbh >4 cm). AcPs—*A. pseudpolatanus*, AcPl—*A. platanoides*, FrEx—*F. excelsior*, FaSy—*F. sylvatica*, TiCo—*T. cordata*, UlSc—*U. scabra*, CaBe—*C. betulus*, QuPe—*Q. petraea*, AbAl—*A. alba*.

3.2. Description of the Disturbance Regime

Based on the field mapping of the whole area, we identified 25 gaps, representing on average 10 gaps per hectare (Figure 3). Almost 60% of the PRP is covered by gaps (open canopy gaps—22.8%, expanded gaps—59.5%). Small expanded gaps (100–300 m^2) represent 28% of the total number of gaps and 9% of the total area of gaps, large expanded gaps (300–1000 m^2) account for 64% and 62% of the gap area, and very large expanded gaps (>1000 m^2) account for 8% of the number of gaps and 29% of the gap area respectively (Figure A1).

Mean size of open gap is 228 m^2 and ranges from 14–1694 m^2 and mean size of expanded gap is 595 m^2 and ranges from 94 to 3221 m^2. Natural regeneration covers significantly smaller area than open or expanded gaps (18.1%) because some gaps are filled by the next generation of young trees (Figure A3). The smaller than 250 m^2 regeneration polygons prevail (Figure 3).

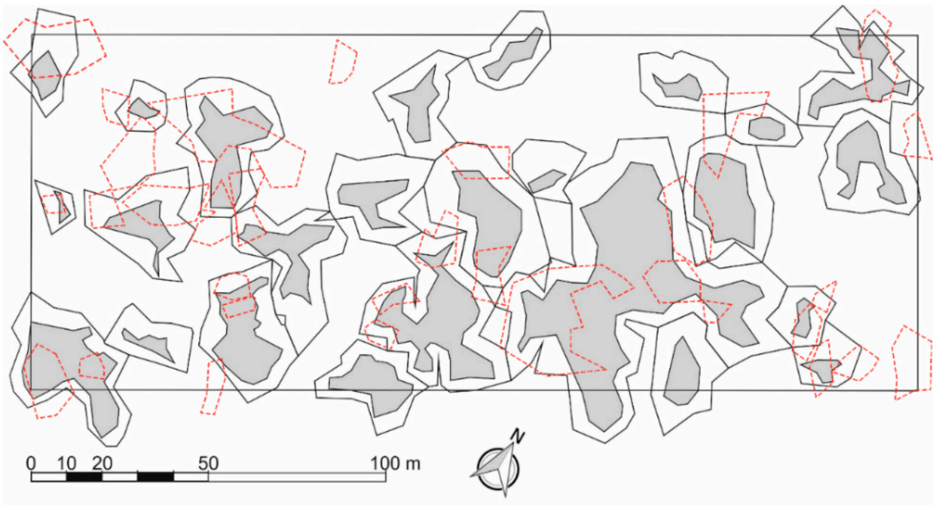

Figure 3. Spatial distribution of open and expanded gaps and of polygons of mapped natural regeneration on the permanent research plot Sitno.

From the total expanded gap area, the largest proportion is represented by the recently enlarged gaps (approximately 50%, Figure 4a). There, within a single gap, the first and some other or all other degrees of decomposition of gapmakers are presented. The median gap size of recently enlarging gaps is higher than the rest of categories, where difference is almost significant (F (2; 22) = 2.94; $p < 0.07$). All of gaps in none enlargement category have been formed in the past. Any gap created solely by gapmakers of 1st degree of decomposition exists. This indicates that all gaps on the PRP have originated in the more distant past, but 50% of them have been expanded recently.

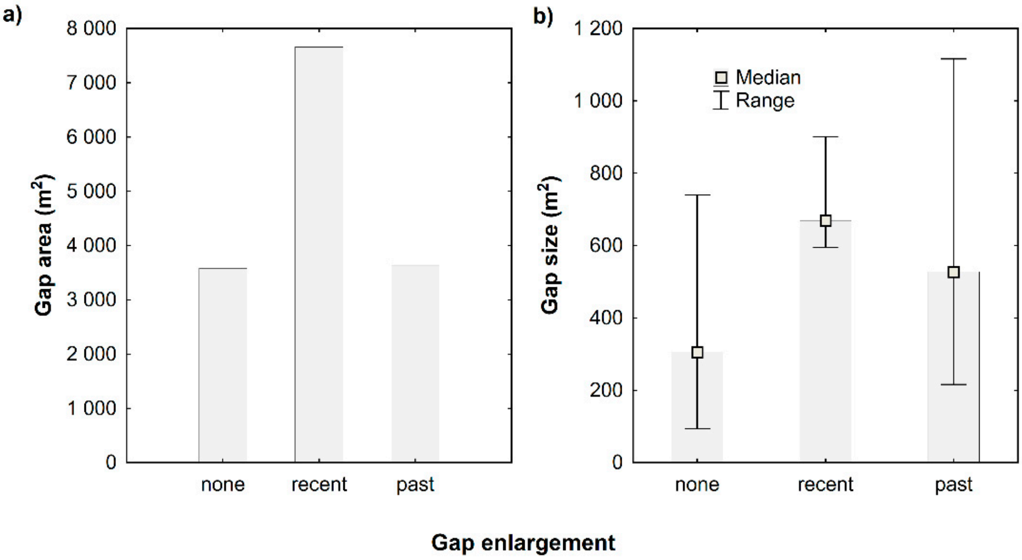

Figure 4. (**a**) Total gap area and (**b**) median size of expanded gaps according to enlargement categories. Range of individual gap sizes is shown without outliers.

Totally, 169 gapmakers are recorded on the sampling plot, 46% and 44% of gapmakers are in the 3rd and the 4th degree of decomposition. Large ratios of gapmakers with high degree of decomposition can be considered as additional evidence that majority of gaps have originated in more distant past.

The most frequent species among gapmakers are *Q. petraea* and *F. sylvatica* (Table 2, Table A1). If we take into account only the numbers of identified gapmakers, proportion of *Q.petraea* in the past species composition is approximately 50% and proportion of *F.sylvatica* is approximately 25%. The number of gapmakers on single gap ranged from 1 to 37, accounting on average for seven gapmakers. Almost

50% of gaps originated from fall of less than five gapmakers, approximately one third of gaps were created either by one or four gapmakers (equally 17%, Figure A2).

Table 2. Species composition of gapmakers according to degree of decomposition.

Tree Species	**Degree of Decomposition**									
	1	**%**	**2**	**%**	**3**	**%**	**4**	**%**	**Total**	**%**
Acer pseudoplatanus	0	0.0	0	0.0	7	9.0	0	0.0	7	4.1
Fagus sylvatica	4	33.3	4	80.0	10	12.8	2	2.7	20	11.8
Quercus petraea	4	33.3	0	0.0	31	39.7	6	8.1	41	24.3
Tilia cordata	1	8.3	0	0.0	0	0.0	0	0.0	1	0.6
Fraxinus excelsior	1	8.3	0	0.0	1	1.3	0	0.0	2	1.2
Carpinus betulus	2	16.7	1	20.0	1	1.3	1	1.4	5	3.0
Abies alba	0	0.0	0	0.0	1	1.3	2	2.7	3	1.8
Undetermined	0	0.0	0	0.0	27	34.6	63	85.1	90	53.3
Total	12	100.0	5	100.0	78	100.0	74	100.0	169	100.0

3.3. Regeneration

Total density of regeneration is 69282 stems ha^{-1}. *A. pseudoplatanus* and *A. platanoides* are the most abundant species in the regeneration layer, with relative density of seedlings between 25%–50% and saplings between 40–50% from the total number of individuals (Table 3). The relative frequency of occurrence on sampling plots for *Acer sp.* is even higher ranging between 35–80%. The *F. excelsior* has relative density 13% in seedlings and saplings, and frequency of occurrence on sampling plots between 35–55%. Proportion sum of all these three species on the tree number of regeneration (near to 95% in the seedling and near to 90% in the sapling category) markedly surpass the proportion sum on tree number of main upper layer, which is 54%.

Table 3. Density of natural regeneration on the permanent research plot Sitno.

Tree Species	**Seedlings (≤50 cm)**			**Saplings (>50 cm)**			**Young Trees (4–8 cm)**	
	Density		**Freq ***	**Density**		**Freq**	**Density**	
	N ha^{-1}	**%**	**%**	**N ha^{-1}**	**%**	**%**	**N ha^{-1}**	**%**
Acer platanoides	12,901	25.9	69.9	5116	26.1	43.1	2.4	1.0
Acer pseudoplatanus	27,925	56.2	77.3	9952	50.9	49.0	149.6	59.5
Fraxinus excelsior	6885	13.8	54.6	2654	13.6	35.6	74.0	29.4
Fagus sylvatica	1032	2.1	17.1	265	1.4	6.5	6.0	2.4
Tilia cordata	605	1.2	6.9	693	3.5	6.9	12.0	4.8
Ulmus scabra	177	0.4	3.7	722	3.7	9.7	5.2	2.1
Carpinus betulus	192	0.4	3.2	147	0.8	4.2	1.2	0.5
Quercus petraea	0	0	0	15	0.1	0.5	0	0.0
Total	49,717	100.0		19,565	100.0		251.6	100.0

* Freq—frequency of occurence.

F. sylvatica, *T. cordata*, *U. scabra*, and *C. betulus* are presented in both seedlings and saplings categories only marginally (0.5–3%), although the frequency of their occurrence is somewhat higher (3–17%). Their proportion sums are 4% in the seedling and 9% in the sapling category. That fact is that in contrast with their proportion on the main tree layer 41%—these species are clearly under-represented in regeneration layer.

None of *Q. petraea* seedlings has been recorded on the sampling plots, and density of saplings is sparse. *Q. petraea* in regeneration is absent although its proportion in the tree number of main layer is still 3.5%. Overall, there is a significant disproportion between the expected tree species composition corresponding to the habitat, the current tree species composition of the main tree layer and the tree species composition of the next generation.

3.4. Impact of Gaps on Density and Species Composition of Regeneration

The absolute density of seedlings in gaps is lower than the density under closed canopy on average by 16% (Table 4). Among the most abundant tree species, *F. excelsior* is the only species, which seedlings significantly profit from growing under canopy (Mann–Whitney *U* test; $p < 0.05$). In later regeneration categories, gaps significantly increase the regeneration density of all saplings by 77% and of young trees by 545%. Differences between densities of *A. pseudoplatanus* and *F. excelsior* saplings in gaps compared to canopy are statistically significant.

Table 4. Tree species density of natural regeneration in expanded gaps and under closed canopy.

Tree Species	Seedlings (≤50 cm)			Saplings (>50 cm)			Young Trees (4–8 cm)		
	Canopy	Gap	Ratio	Canopy	Gap	Ratio	Canopy	Gap	Ratio
	N ha^{-1}	N ha^{-1}	%	N ha^{-1}	N ha^{-1}	%	N ha^{-1}	N ha^{-1}	%
A. platanoides	15,014	11,363	76	4270	5732	134	0.8	1.6	200
A. pseudoplat.	28,522	27,490	96	6264 *	12,637 *	202	6.0	143.6	1396
F. excelsior	8924 *	5401 *	61	1540 *	3465 *	225	20.4	53.6	340
F. sylvatica	1225	892	73	105	382	364	4.0	2.0	50
T. cordata	840	433	52	875	561	64	2.0	10.0	500
U. scabra	210	153	73	455	917	202	0.8	4.4	550
C. betulus	105	255	243	35	229	654	0	1.2	-
Q. petraea	0	0	-	0	25	-	0	0.0	-
Total	54,840	45,987	84	13,544	23,949	177	34	218	645

Tree species with relative density or frequency of occurrence above 10% are marked bold; *—Mann–Whitney *U* test; $p < 0.05$.

Under the canopy, relative densities of tree species more differ among regeneration categories than in gaps (Figure 5a). *A. pseudoplatanus* and *platanoides* show big decrease in relative density of young trees under the canopy. Other less presented species are even absent in the category of young trees under canopy, i.e., they are not able to survive. Oppositely, young trees of *F. excelsior* and *F. sylvatica* show increased densities indicating their better contemporary ability to survive the initial regeneration stages compared to all other species. Two species can grow and survive under canopy for a longer time—*F. excelsior* and *F. sylvatica*—under contemporary natural conditions.

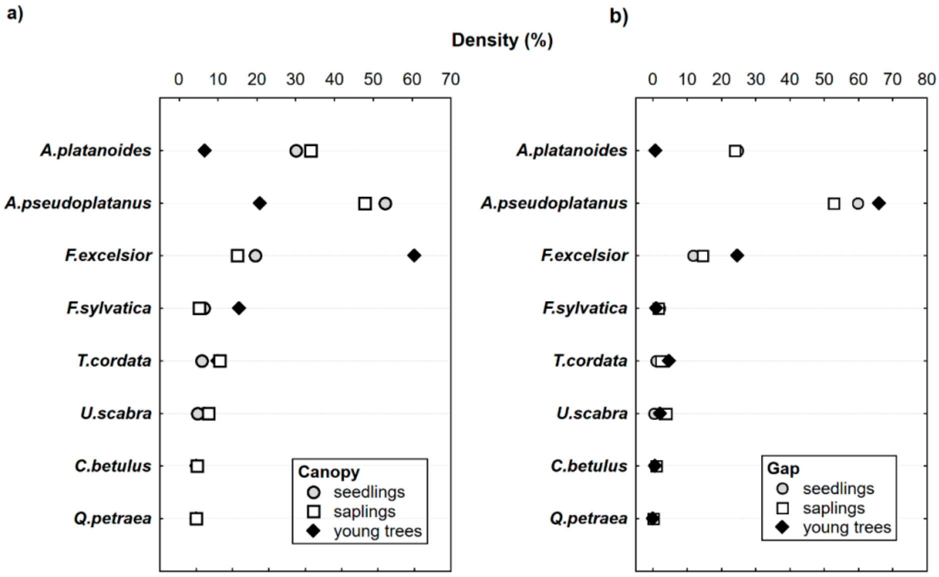

Figure 5. Relative density of seedlings, saplings and young trees under (**a**) closed canopy and (**b**) in expanded gaps.

In expanded gaps, relative densities of tree species remain stable across all regeneration categories, except *A. platanoides* (Figure 5b). The ingrowth into young trees show *A. pseudoplatanus* and *F. excelsior*. Relative densities of other species remain stable in different regeneration categories, i.e., other species sustain their presence reached as seedlings.

In summary, *F. excelsior* and *F. sylvatica* manifest higher absolute and relative regeneration densities and good ability to survive severe competition in initial developmental stages. *A. pseudoplatanus* regenerates in very high density, but successfully survives only in gaps. Similarly, *A. platanoides* regenerates in very high densities, but irrespective whether it grows in gap or under the canopy. The lower competitive ability on the given site severely limits its ingrowth into upper tree layers. Other species show very limited ability to regenerate (low absolute and relative densities) and they grow into the category of young trees only in gaps.

3.5. Impact of Environmental and Spatial Factors on Natural Regeneration

Relationships between environmental factors, spatial variables and tree species densities revealed by linear RDA ordination are provided on Figure 6. The position of environmental variables in ordination space allows to interpret the ordination axis as gradients: (i) horizontal axis X is strongly positively correlated with variable canopy and at the same time strongly negatively with dummy variable open gap that suggest interpretation as light-moisture gradient between the closed canopy and open gap. The increase of x ordination coordinates means decrease of light and increase of moisture *on environmental gradient* formed on open gap—closed canopy link; (ii) vertical axis Y is positively correlated with x and y coordinates of sampling plots. Movement across the PRP in the direction of increasing spatial coordinates x and y means movement along the longer side of the transect (*spatial gradient*). A significant correlations of species densities with second ordination axis means that variation of environmental conditions along longer side of PRP significantly affect the variation of species densities—density can increase or decrease along investigated direction.

On the Figure 6, the arrows of variables depict the magnitude of correlations of individual variables with ordination axis. The close position of different variables in the same sector of ordination space means not only similar relationships with ordination gradients, but also strong mutual correlation.

The seedlings' densities of the most abundant species *Acer* sp., *F. excelsior*, and *F. sylvatica* and sum of crown projections show positive correlation with environmental gradient—the increase of canopy closure and lower distance from closed canopy (source of seeds) support their density in the initial regeneration category. The gap size and sapling density of *A. pseudoplatanus* manifests the negative correlations with environmental gradient and due to close position, they are positively correlated. The decreasing canopy closure and increasing gap size support the survival of *A. pseudoplatanus* saplings. A similar, although weaker trend is characteristic also for saplings of *U. scabra*, *C. betulus*, and *A. platanoides*.

In the same time, the densities of saplings and seedlings of *F. sylvatica* and *Acer* sp. show stronger negative correlation with spatial gradient. That means the densities are decreasing with the increasing distance along longer side of the transect and they are affected by some systematic spatial trends in environmental conditions or stand characteristics on the PRP. *F. excelsior* shows almost no spatial trends, suggesting its ability to regenerate and survive in a wide range of natural conditions. Other less abundant species and saplings of *F. excelsior* depend on environmental and spatial gradients only very marginally. Slight supportive effects of decreasing shading and short distance position on the transect of sapling density of *Ulmus, Carpinus*, and *A. platanoides* is observable.

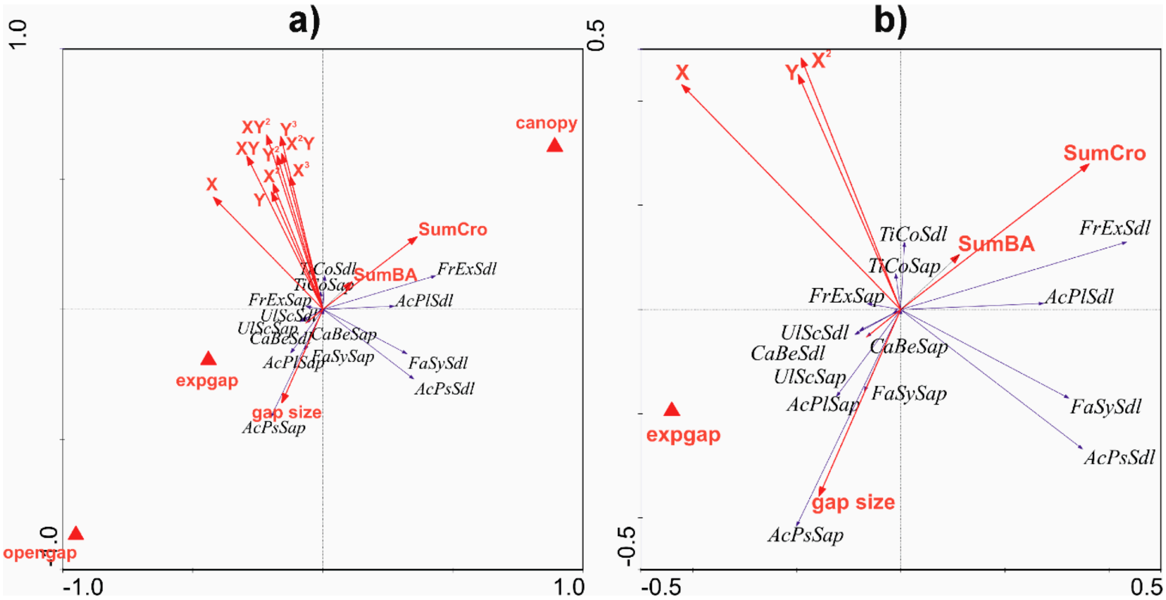

Figure 6. Graphical output of linear direct gradient analysis (redundancy analysis, RDA); (**b**) is extension of view on (**a**). Sdl—seedlings, Sap—saplings, AcPs—*A. pseudpolatanus*, AcPl—*A. platanoides*, FrEx—*F. excelsior*, FaSy—*F. sylvatica*, TiCo—*T. cordata*, UlSc—*U. scabra*, CaBe—*C. betulus*, SumCro—sum of crown projections of trees, SumBa—sum of basal areas of trees, expgap—expanded gap, gap size—size of the expanded gap, X,Y,X^2—coordinates of sampling plots.

The several settings of partial RDA models were explored for partitioning of explained variance of dependent densities according the groups of independent variables (Table 5). List of independent variables selected by forward selection and final partitioning results are summarized in Table 6 and Figure 7.

Total amount of variation in species compositions of natural regeneration (defined as sets of absolute densities on sampling plots) explained by the final RDA models is 18.7% for seedlings ($p < 0.001$) and 17.9% for saplings ($p < 0.001$, Table 5). Spatial characteristics explain more variability in composition of natural regeneration—17.5% in seedlings and 11.4% in saplings (Tables 5 and 6; Figure 7). The proportion that can be uniquely attributed to environmental factors is 1.2% in seedlings and 6.5% in saplings (Table 5, Figure 7)).

The higher importance of spatial variability indicates that spatial distribution of some other parameters as distribution of parent trees, soil characteristics on the study site or other unknown environmental and stand parameters have a stronger impact on natural regeneration than manipulation of the light and moisture conditions by gaps. From environmental factors, the variables related to environmental gradient—gap size and position on gap-canopy gradient—were the most important within the seedling's category. The variables related to density of stand—sum of basal areas and crown projections—in connection with position on gap-canopy gradient were important for saplings.

The growing proportion of explained variability by environmental factors in sapling category may indicate the increasing importance of gap extension in later developmental stages to secure a good survival and ingrowth of natural regeneration.

The common variability explained by both spatial and environmental variables of around 2% (Figure 7) could be attributed to spatial trends of one or more stand or gap characteristics (basal area, crown projections, or number and size of gaps, etc.).

Table 5. Amount of variation of tree species compositions explained by environmental and spatial factors in different RDA variants in the old-growth forest Sitno.

Factors	Covariables	F	*p*	%
Seedlings				
Envir + Spatial	None	5.252	**0.001**	18.7
Envir	None	2.549	**0.018**	3.5
Spatial	None	7.373	**0.001**	17.5
Envir	Spatial	1.009	0.439	1.2
Spatial	Envir	6.409	**0.001**	15.2
Saplings				
Envir + Spatial	None	4.814	**0.001**	17.9
Envir	None	4.754	**0.001**	8.3
Spatial	None	5.425	**0.001**	11.4
Envir	Spatial	4.062	**0.001**	6.5
Spatial	Envir	4.841	**0.001**	9.6

Models comprise all variables (factors) selected by forward selection in RDA separately for *Envir.* and *Spatial* group of variables (see Table 3); F—the value of the test criterion; $p < 0.05$ is marked bold; %—relative proportion of variation explained by the model.

Table 6. The relative amount of varation of tree species composition explained by selected environmental and spatial factors (forward selection) in the RDA analysis in the old-growth forest Sitno.

Group of Factors	**Seedlings**			**Saplings**		
	Variable/Factor	**%**	***p***	**Variable/Factor**	**%**	***p***
Envir.	gap size	2	0.020	SumCro	4	0.001
	Canopy *	1 **	0.018	canopy	2	0.017
				SumBA	2	0.006
Total		**3.5**	**0.018**		**8.3**	**0.001**
Spatial	X	4	0.003	Y^3	3	0.002
	X^2	6	0.001	Y	4	0.001
	X^3	2	0.002	X^2Y	1	0.006
	XY^2	2	0.006	Y^2	2	0.008
	Y^3	2	0.018	X^3	1	0.040
	Y	1	0.010			
Total		**17.5**	**0.001**		**11.4**	**0.001**

(*) as variable *canopy* is one of three categories coding the type of canopy closure, variables *expgap* and *opengap* entered the analysis automatically without further testing. (**) % of explained variability for selected variables (factors) representing conditional effect, i.e., it is the percentage of explained variability for individual variables, when simultaneously used the earlier selected variables as covariables. $p < 0.05$ is marked bold.

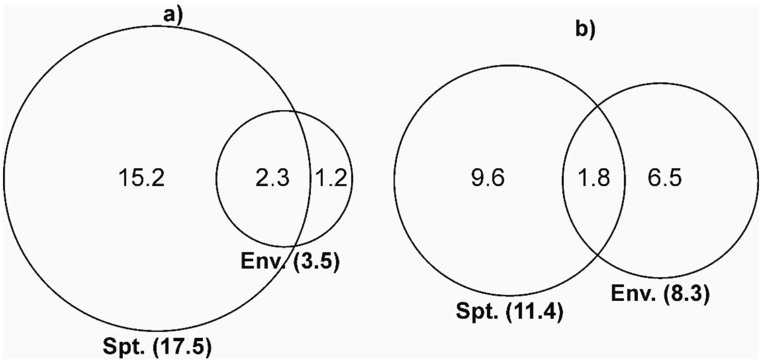

Figure 7. Variation partitioning between environmental (Env.) and spatial factors (Spt.). Venn diagrams display how much tree species variation of (**a**) seedlings and (**b**) saplings can be uniquely attributed to environmental (gap related) factors and how much variation they have in common.

To assess the influence of environmental variables on natural regeneration in more detail, multiple linear regressions of log-transformed densities are tested separately for each tree species (Table 7).

Table 7. Regresion β-coefficients obtained from general linear models for each individual tree species and height growth category of natural regeneration in relation to independent environmental factors, displayed are R-squares of the whole models and their *p*-values.

Tree Species	Gap Size	SumCro	SumBA	Plot Position		R^2 (%)	*p*
				Canopy	Exp. Gap		
			Seedlings				
A. pseudoplatanus	0.12	0.16	−0.09	0.14	-	3.08	0.254
A. platanoides	**0.17**	0.17	−0.15	**0.23**	-	**5.22**	**0.046**
F. excelsior	**−0.23**	0.03	−0.03	0.04	-	**6.74**	**0.012**
F. sylvatica	0.14	0.12	−0.16	0.13	-	3.13	0.245
T. cordata	0.00	0.16	−0.08	-	0.06	1.90	0.545
U. scabra	0.11	−0.10	0.08	0.14	-	2.01	0.509
C. betulus	−0.03	−0.10	−0.09	-	0.14	4.75	0.069
			Saplings				
A. pseudoplatanus	0.08	**−0.43**	**0.31**	**−0.18**	-	**14.08**	**0.000**
A. platanoides	0.05	**−0.22**	0.07	0.04	-	3.14	0.243
F. excelsior	**−0.21**	**−0.24**	0.15	**−0.29**	-	**9.83**	**0.001**
F. sylvatica	**0.25**	−0.06	0.02	0.07	-	4.75	0.069
T. cordata	−0.11	0.20	−0.08	−0.14	-	3.76	0.153
U. scabra	0.07	−0.14	−0.10	−0.01	-	**6.37**	**0.017**
C. betulus	−0.14	−0.12	−0.01	**−0.19**	-	4.63	0.076

R^2 (%) = R-square × 100; $p < 0.05$ is marked bold.

Results confirm and underline several facts revealed by RDA ordination and by variance partitioning:

(i) environmental factors have greater impact on the density of saplings compared to seedlings—documented by higher percentage of explained variability and higher statistical significances of individual GLM models in the sapling category,

(ii) in the category of seedlings, the gap size and under canopy position (as revealed in the RDA) have a predominant effect, which is also approached by the sum of crown projections for the prevailing tree species *Acer* sp., *F. excelsior*, *F. sylvatica*—documented by higher absolute values of standardized beta coefficients,

(iii) in the category of saplings, the amount of crown projections and under canopy position—again documented by the higher absolute values of the standardized beta coefficients—have a predominant effect (in accordance with the RDA).

However, unlike the RDA, GLM models also allow evaluation of the nature of linear impact and allow the development of individual tree profiles.

From this perspective, it is important in seedlings' categories that:

(i) signs of beta coefficients of canopy position, gap size and sum of crown projections are predominantly positive—under canopy position, increasing gap size and sum of crown projections have positive influence on species densities;

(ii) The previous statement fully applies to *Acer sp.* and *F. sylvatica*, but not for *F. excelsior*. Here, the presence or absence of under canopy position and sum of crown projections loses its influence and, in addition, the gap size has a negative effect—the larger the gap area, the lower the density of the natural regeneration of *F. excelsior*.

In saplings' category GLM indicate that:

(i) under canopy position and increasing sum of crown projections reduce the density of regeneration (*F. excelsior* is also negatively affected by the increasing size of gaps)

(ii) the previous statement fully applies to *A. pseudoplatanus* and *F. excelsior* and partly also to *A. platanoides*, but not to *F. sylvatica*. The only significant environmental variable for *Fagus*, is the gap size. As a result, the larger the gap area, the better survival of *Fagus* seedlings.

4. Discussion

4.1. Natural Regeneration

Small-scale disturbances maintain the old-growth forest structure mainly through the emergence and survival of natural regeneration in the variety of conditions in canopy openings. Total density as well as tree species composition of natural regeneration in species-rich old-growth forest in NNR Sitno corresponds well with the abundance found in other broadleaved-dominated, mixed old-growth forests of the Western Carpathians (e.g., [39]). In tree species composition, *Acer* species (*A. pseudoplatanus* and *A. platanoides*) are the most abundant except the category of young trees under the canopy. *Acer* sp. achieve a high density of regeneration in the positions under the canopy near larger gaps and for survival they need decreased shading achieved mainly through the lower sum of crown projections. *A. pseudoplatanus*, however, unlike *A. platanoides* clearly survives well in open gaps. *F. excelsior* has the highest relative share in the category of young trees under the canopy and the second highest in the same category in gaps. *F. excelsior* regenerates and survives well especially in smaller gaps, although in later ages it demands lower sum of crown projections and prefer expanded or even open gap position.

Considering the density of (potentially) seed-producing *F. excelsior* stems, i.e., the canopy trees with dbh over 20 cm comprising about 10%, the abundance of *F. excelsior* seedlings and saplings is over-proportionately high. *F. sylvatica* regenerates especially under the cover of the mature stand near larger gaps, but in a later developmental stage of saplings it may survive better in larger gaps. *T. cordata*, *U. scabra*, and *C. betulus* reveal less clear pattern. These species show the very limited ability to regenerate (low absolute and relative densities) and they ingrow into upper stand layers only in gaps. The higher number of tree species is able to survive initial regeneration stages and ingrowth into the category of young trees in gaps.

Natural regeneration of *Q. petraea* is scarce in the long-term. Saniga et al. [40] have reported the lack of *Q. petraea* individuals above the height of 80 cm on all permanent research plots established in NNR Sitno, with the maximum density of natural regeneration 667 individuals per hectare since the late 80-ties of the previous century. Species composition as well as abundance and height structure of natural regeneration are affected not only by gap properties, but also by other factors that are relevant for the survival and height growth of seedlings and saplings. The influence of herbivory may limit the competitive strength of particular species and possibly to change tree species composition [41–43]. Therefore, we assume that especially regeneration of light-demanding oak suffers under repeated browsing and is unable to grow out of its competitors.

4.2. Disturbance Regime

Many studies are devoted to gap dynamics and to the undoubted effect, which canopy gaps have on regeneration density [44]. Forest management aimed at the importance of diverse forests relies on that natural disturbances are key drivers of promoting and maintaining tree species diversity [45]. Gap dynamics of mixed beech-oak old-growth forests characterized by diverse composition of canopy layer are less frequently studied in Central Europe [11,31,46,47] and provide fragmented base of scientific information. Canopy layer of investigated preserved forest remnant consists of nine tree species with contrasting light requirements (*F. sylvatica*, *A. pseudoplatanus*, *Q. petraea*, *F. excelsior*, *T. cordata*, *A. platanoides*, *A. alba*, *C. betulus*, and *U. scabra*) and possess relatively higher basal area (39.8 m^2 ha^{-1}) and stem density of trees (603 trees ha^{-1}). In the investigated forest, mid-scale disturbances (16 expanded gaps >300 m^2) prevail with a low occurrence of disturbances corresponding with very large gaps (two expanded gaps >1000 m^2). Disturbance regime and to this related light availability may thus favour tree species of less shade (as *A. pseudoplatanus* or *F. excelsior*) and intermediate shade tolerant species (*Q. petraea*) to regenerate, establish, grow, and recruit into the forest canopy [7,23,48].

Large proportion of stand area (up to 60%) is under gaps created by the mortality of canopy trees. The mortality of both *Q. petraea* and *F. sylvatica* drives the disturbance regime of NNR Sitno, which are the main gapmakers and represent the highest density and basal area among dead trees.

Our results clearly indicate the significant shift in species composition over the time. The Quercus has declined in the recent period. Additionally, massive spread of *F. excelsior* and associated decrease of *F. sylvatica* dominance is registered. Results point to significant disproportion between the expected tree species composition corresponding to the habitat, the current tree species composition of the main tree layer and the tree species composition of the next generation.

In the long-term (over 30 years of inventory) the relative density of adult living trees in tree species composition decreases for both *Q. petraea* and *F. sylvatica*, but more rapidly for *Q. petraea* [40]. This agrees with the study showing increased mortality during 50 years of natural forest development for both *Q. petraea* and *F. sylvatica*, but stronger for *Q. petraea* in Swiss lowlands [30]. The study from Romanian oak-beech forests also support our results declaring disturbance regime is primarily driven by the mortality of *Q. petraea*, showing the absence of this species in the process of tree recruitment [31].

The largest number of gapmakers is represented by lying deadwood in advanced stage of decomposition (89%), while recently dead trees represent only 7%. Wind has an important role in creating gaps by single or by consecutive disturbance events (only 17% trees died standing). The group mortality prevails in the process of gap formation.

Progressive mortality of trees in separate canopy gaps is the typical feature. Successive extensions of more than a half of gaps resulted in formation of large and very large gaps, which is in agreement with reports from mixed beech forests [49]. Higher proportion of progressively enlarged gaps (above 2/3) is reported in mixed old-growth oak forests of NNR Kašívárová [47]. Differences in gap dynamics of beech-oak forest in NNR Sitno (lower frequency of small gaps, absence of very large gaps, and lower proportion of stand area under gaps) in comparison to mixed oak old-growth forest Kašivárová could be attributed to the fact that trees in NNR Sitno grow on less productive volcanic site with high share of rocks. Interestingly, distribution of expanded gaps in NNR Sitno does not follow negative exponential form described in other temperate oak and beech forests [13,15,31,47], probably due to the recent lack of small gap-scale disturbances. No single gap without extension has been formed recently, suggesting recent changes in disturbance regime.

4.3. *Gap Partitioning*

The distribution of natural regeneration corresponds with the distribution of gaps, which agrees with gap-recruitment studies [44]. Our results suggest that wind disturbances creating successively expanding large gaps do allow maintaining of mid- and late-successional tree species and do not allow early-successional ones and ground vegetation to hamper the regeneration process. Originally, gap partitioning hypothesis assumes that the variety of micro environmental conditions along the gradient shaded understorey—canopy gap enable co-existence of several tree species partly because of higher stem density in gaps [48]. Different tree species supposedly have different probability of establishing seedlings in particular range of gap sizes [48].

However, as shown in several studies, gaps not necessarily provide primary environment for regeneration e.g., [32,50]. Our results, the higher regeneration density of seedlings observed under the forest canopy compared to gaps, the continuous recruitment, and narrow and linear ordination gradient confirmed by DCA, which suggests relatively homogenous tree species composition on the most plots, confirm these later studies.

The influence of environmental gradient between closed canopy and gap (denoted also as gap-partitioning) in seedling category is not evident for any of the investigated tree species.

The variability that can be uniquely attributed to gap and stand related environmental factors is very low. The species composition under the canopy and gaps is very similar—all species can establish also under canopy, even in higher densities due to the proximity of seed trees. At seedling stage (≤50 cm), species relationships and abiotic soil related factors have probably the higher importance than distribution of environmental conditions along stand-gap gradient [51].

On the other hand, the relative importance of tree species interactions changes with regeneration developmental category [51]. Our results suggest that environmental gradient is manifested through differential survival rate of different species in saplings and young trees phase. The position under canopy and increasing sum of crown projections reduce the density of saplings. The environment within the gap has significant impact on the tree species composition and positively influences four out of eight studied tree species in sapling category (>50 cm), in agreement with original gap-partitioning theory [48].

Under the assumption that fluctuations in light/moisture availability and spatial variation in disturbance allow limited number of tree species to coexists [23], the two most successful gap fillers *A. pseudoplatanus* and *F. excelsior* and recent shifts in disturbance regime suggest future changes in tree species composition in the investigated nature reserve.

The probability of establishment of *intermediate* shade tolerant tree species increases with increasing of gap size [37]. The presence of two very large gaps (above 1000 m^2) does not create sufficient conditions for *Q. petraea* regeneration. Complete lack of regeneration along with the high mortality of old-grown *Q. petraea* trees underlines *its* decline in NNR Sitno. *Quercus* can successfully establish in gaps of sizes between 300–500 m^2, however for further successful growth, saplings require gaps of approximately 1000 m^2 [11] or even more than 2000 m^2 [52].

To emphasize the contrasting light requirements of oak in comparison to more shade tolerant species, dendroecological study from oak-beech old-growth forest in Romania demonstrates that the oak successfully establishes after stand replacing disturbance [29]. This is analogous with establishment of other intermediate shade-tolerant species as *M. obovata* in mixed beech forest in western Japan showing patterns suggesting the ability to establish following the large-scale catastrophic disturbance [53]. In the process of recruitment into the canopy, oak unlike beech is less able to respond with multiple releases to repeating canopy openings. In addition, regeneration of oak is not able to recover once the light conditions in canopy improve.

Therefore, match in the masting of parent oak trees and canopy disturbance events is needed or release of oak saplings at their very young life stage [4]. It is worth of mentioning that another intermediate shade-tolerant tree species, *T. cordata*, responds to disturbance regime in greater densities and shows some potential for continuous recruitment. The recent expansion of *T. cordata*, *C. betulus*, and *A. pseudoplatanus* has been observed in the Bialowieža Primeval Forest in Poland [19].

Among *less shade* tolerant tree species, *F. excelsior* greatly benefits from the presence in small gaps. Due to its sensitivity to late spring frost, it avoids exposed sites in the centre of large gaps and regenerates in greater densities in small gaps and under the closed canopy possibly in surroundings of gap edges [54]. To gap extension, it responds with increased growth succeeding in gap capturing over the *F. sylvatica* [55,56].

The highest frequency of large expanded gaps (300–1000 m^2) allowed recruitment of less shade tolerant *F. excelsior*, *A. pseudoplatanus*, and *A. platanoides*, which agrees with findings demonstrating that intermediate severity wind disturbances create conditions beneficial for recruitment of less shade tolerant species [57]. The high densities of natural regeneration of *F. excelsior* and *A. pseudoplatanus* and patterns of diameter distributions indicating their contemporary establishment suggest that under recent disturbance regime they are the most successful gap fillers. Spatially clumped exclusively in the gap centres, young trees of *A. pseudoplatanus* display clear pattern of gap-size partitioning i.e., dependency on environmental gradient. Seedlings regenerate in higher densities in large expanded gaps and oppositely, saplings and young trees are completely absent in small gaps and under closed forest canopy.

Similar to our findings, *A. pseudoplatanus* shows evident gap-size partitioning in beech-fir forest reserve in the Dinaric Mountains [58]. Along with the *A. pseudoplatanus*, *A. platanoides* is the second most abundant regenerating tree species. Due to its weak competitive ability [59] it recruits in very low density and frequency of young trees, even lower than for example *U. scabra*. Spatio-temporal changes in disturbance regime could have distinct consequences for gap replacement patterns.

Decreases in growth performance of drought-sensitive *F. sylvatica* [60,61] and recent lack of small gaps may hamper regeneration of *shade tolerant* tree species *F. sylvatica* on low water retention site. The importance of small gaps illustrates the fact that *F. sylvatica* is the only species, whose young trees responded to gaps by 50% decrease relative to forest canopy. This agrees with low (below 10%) relative density and frequency of *F. sylvatica* seedlings and saplings and with indicated contemporary difficulties in establishment based on the diameter distribution of trees. Young trees of *F. sylvatica* establish under close canopy, prior to gap formation. Based on our results, shade tolerant *F. sylvatica* reveals no clear gap partitioning similar to reports for old-growth beech-oak forests in Northern Spain [62] or beech-fir forests in the Dinaric Mountains [58]. Analogous patterns of *F. sylvatica* establishment—understorey regeneration with successive releases of trees—reports study from the oak-beech forest in Romania [29].

Our findings confirm that in mixed forests with oak, the more shade tolerant tree species than oak have competitive advantage in recruitment [31,63,64]. Under the canopy and to this related low light availability, *F. sylvatica* shows the highest survival, *A. psedoplatanus* the lowest and *F. excelsior* in between these two species [65]. In expanded gaps with higher light availability, *A. pseudoplatanus* and *F. excelsior* show higher height growth rates and allocate more biomass to their stems than *F. sylvatica*, which allocates more biomass to branches [66]. Different growth strategy points to the ability of *F. sylvatica* adults to expand and close small canopy gaps by lateral growth of branches [67], but saplings and young trees to lose with *Acer* sp., which growth rates can be twofold higher than those of *Fagus* even in small gaps [22,48].

Quantification of relationship between the various gap sizes and the related environment along with the spatial arrangement and the species composition of natural regeneration seems not to be simple. Low amount of extracted variability in our study suggests that a regeneration process is influenced by other factors. Beyond the gap size, many factors and gap-related processes generate the mosaic spatial structure of the regeneration and recruitment in mixed forest stands. Differentiation in the regeneration niche (production of seeds—mast seeding, seed dispersal, germination, and establishment of seedlings [68]), presence, location and abundance of parent trees and seed dispersers, degree of exposed mineral soil and amount of wood debris [69], micro-environmental factors, including position within gaps [48], advance regeneration [70], different life strategies of tree species in accessing the canopy [22], degree of browsing pressure [71] above- and below-ground competition among tree species, and climate change [72], consequently creating new disturbance regimes [73] can be mentioned.

The composition of natural regeneration, its life stage and spatial structure and distribution of gaps might reveal more clear relationships and allow for quantification of higher amount of variability if initial gap size and time since gap formation is related to density of young trees capturing gap. This highlights the future research to concentrate on repeated gap survey studies [67] or to combine the retrospective dendroecological approach and static survey. The studies of disturbance regime in various spatiotemporal scales [6,74] can allow to more accurately predict recruitment of tree species for forest management purposes.

4.4. Implication to Forest Practice

In close-to-nature forest management, the emphasis on stability and continuity of forest ecosystem results in an effort to retain their structural diversity at small spatial scales. The reliance on natural processes, especially the natural regeneration leads to the use of gap-based regeneration as a fundamental silvicultural technique [75]. Small-area shelterwood system successfully uses harvest-created gaps to initiate natural regeneration of shade-tolerant species in mixed forest stands. The negative side of this approach is that size-asymmetric competition eliminates light-demanding or slow-growing species during the regeneration phase entirely [76]. According to tree species composition and gap size distribution found in our study, regeneration in gaps is dominated by shade-tolerant or intermediate species while light-demanding *Q. petraea* is rare.

The most common silvicultural practice, to establish and maintain the light-demanding oak recruitment is the regular shelterwood system with short duration of regeneration period. However, recent efforts for minimization of the canopy layer disruption lead to employment of regeneration techniques based on small gaps and complicate thus the oak regeneration considerably [64]. Moreover, advanced regeneration of shade-tolerant *Acer* sp. and *F. excelsior* reduces the potential of larger gaps for establishment of *Q. petraea* regeneration. Therefore, regeneration requirements of all tree species are often not met with harvest-created gaps alone [77].

If light-demanding species should be regenerated, while the mixed ecosystem should be established and maintained, lags in regeneration of shade tolerant species following creation of large gaps (at least 0.2 ha) would create better situation for light-demanding *Q. petraea*. The selection of shade-tolerant *A. pseudoplatanus* and *platanoides* in the first (seed) cutting contribute to reducing their seed bank in favour of oak. After oak is successfully established, its overtopping should be prevented by combination of fast progressing of gaps enlargement and subsequent control of fast-growing *Acer* sp., *Fagus* and *Fraxinus* recruitment.

The results of our study confirm that to regenerate the mixtures of *Acer*, *Fagus* and *Fraxinus* does not represent a complicated task. Subsequent changes in the proportions of separate tree species in the thicket stage (i.e., saplings and young trees in our study) are dependent on the decision of the forest manager, with the possible modifications caused by the other factors, especially by the selective damage. On the other hand, the maintenance of *Quercus* must be thoroughly planned in advance—already at the identification of suitable conditions for location of the gaps, the determination of their size and the realization of seed cutting therein. The duration of regeneration period should by last 40 years, whereby the duration of regeneration periods within groups should be differentiated: 15 years for *Q. petraea* and 25 years period for *Acer*, *Fagus* and *Fraxinus*.

5. Conclusions

The multiple-species old-growth forest in NNR Sitno shows stable and sustainable regeneration and recruitment of native tree species. Currently, small-scale wind disturbances, which create progressively enlarged gaps of mainly 300–1000 m^2, promote regeneration of four out of nine studied tree species. The current disturbance regime negatively affects regeneration of formerly dominant *F. sylvatica* and seems less suitable for light demanding species as well. The significant shift in species composition over the time is clearly visible. *Q. petraea* has declined in the recent period, also massive spread of *F. excelsior* and associated decrease of *F. sylvatica* is registered. There is a significant disproportion between the expected tree species composition corresponding to the habitat, the current tree species composition of the main tree layer and the tree species composition of the next generation.

Gap size, type of its extension and spatial distribution and gap related stand characteristics have relatively small, but significant impact on natural regeneration. Total explained amount of variation in species composition of natural regeneration (defined as sets of absolute densities on sampling plots) is 18.7% for seedlings ($p < 0.001$) and 17.9% for saplings ($p < 0.001$). Spatial factors have greater influence than gap related factors. The influence of environmental gradient between closed canopy and gap (gap-partitioning) in seedling category is not evident for any of the investigated tree species, but it is manifested in saplings and young trees phase through differential survival rate of different species. The current size and spatial distribution of gaps promote two light less shade tolerant tree species—*A. pseudoplatanus* and *F. excelsior*—that recruit into the canopy with the highest relative densities.

The observed development of beech-oak association provides outstanding information about natural processes ongoing on species rich habitats under current environmental change. The gained knowledge can serve as a baseline for design of silvicultural systems aimed to preserve diverse forest structures by mimicking natural disturbance dynamics in managed mixed stands growing on similar sites. In this regard, if intermediate light-demanding species should be regenerated to preserve species richness and diversity, the use of more variable (mosaic) shelterwood systems in comparison to contemporary practice must be employed. In seed years of light demanding species, some parts of stand canopy must be disturbed by larger gaps (over 0.2 ha) to form wider environmental gradient and to achieve lag in regeneration of shade tolerant species. The removal of less shade-tolerant (e.g., *Acer* sp., *F. excelsior*) in the first (seed) cutting contribute to reducing their seed bank in favour of intermediate light-demanding less abundant species (e.g., *Q. petraea*). Rapid enlargement of older small gaps with the presence of light more demanding species and/or *F. sylvatica* would be beneficial, whereas the reduction of favourable conditions for *F. excelsior* is likely. Supplementary investment inputs, such as competition control from early growth stages, protection against browsing, game control, etc. are required.

Author Contributions: M.S. designed the research; J.P. and L.J.D. collected the data; D.S., L.J.D., and J.P. performed the data analysis and figure plotting; P.J., D.S., and M.S. wrote the first draft of the manuscript and J.P., S.K., and R.S. contributed substantially to revisions; M.S., P.J., and S.K. acquired the funding and were responsible for administration of research projects. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by "The Slovak Research and Development Agency", grant number APVV-14-0014 and "The Ministry of Education, Science, Research and Sport", grant numbers VEGA 1/0021/18 and VEGA-1/0492/17. Authors are very grateful to two anonymous reviewers for valuable comments provided.

Conflicts of Interest: The authors declare no competing interests.

Appendix A

Table A1. Species composition and basic characteristics of deadwood on the permanent research plot.

Table	Density		Basal Area		Volume	
	N ha^{-1}	%	m^2·ha^{-1}	%	m^3·ha^{-1}	%
Acer platanoides	0	0.0	0.00	0.0	0.0	0.0
Acer pseudoplatanus	5	4.4	0.30	3.9	5.2	4.5
Fraxinus excelsior	2	1.7	0.07	1.0	1.2	1.0
Fagus sylvatica	16	13.9	1.32	17.4	20.0	17.4
Tilia cordata	8	7.1	0.42	5.5	5.8	5.1
Ulmus scabra	1	1.0	0.04	0.5	0.0	0.0
Carpinus betulus	4	3.1	0.08	1.1	1.0	0.9
Quercus petraea	21	17.7	1.59	20.9	24.1	21.0
Abies alba	2	1.7	0.23	3.1	1.5	1.3
Undetermined	58	49.3	3.55	46.7	56.0	48.8
Total	118	100.0	7.60	100.0	114.8	100.0

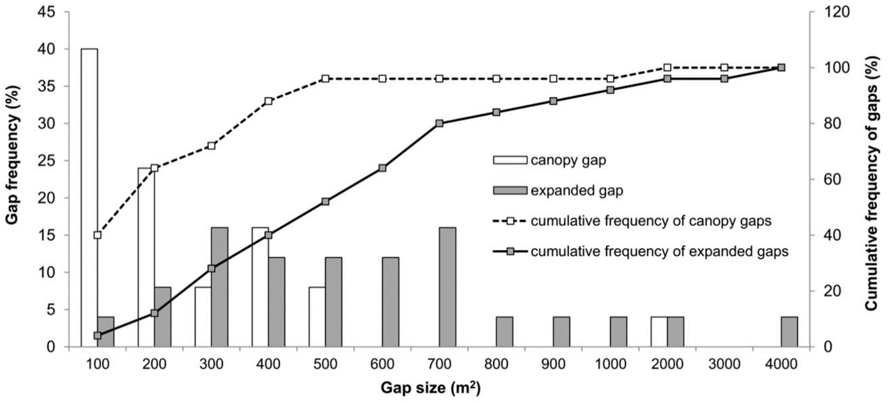

Figure A1. Frequency of canopy gaps (light bars) and expanded gap (dark bars) according to gap size classes (calculated as number of gaps in gap size category per total number of gaps).

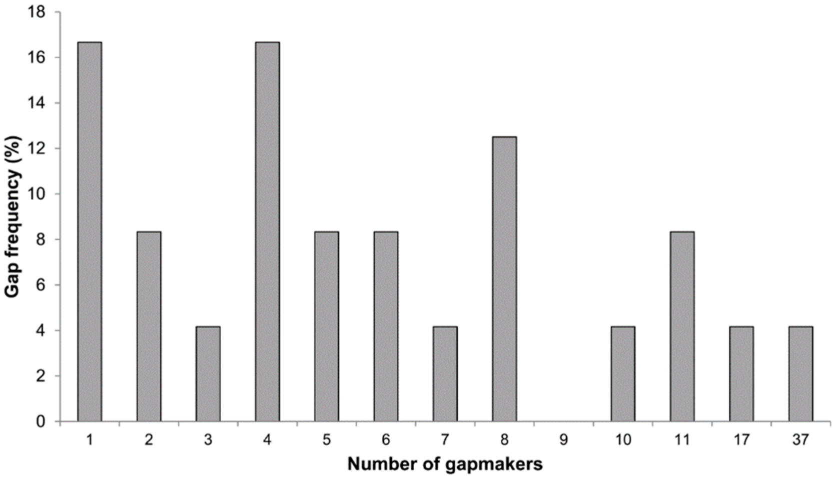

Figure A2. Gap frequency according to number of gapmakers.

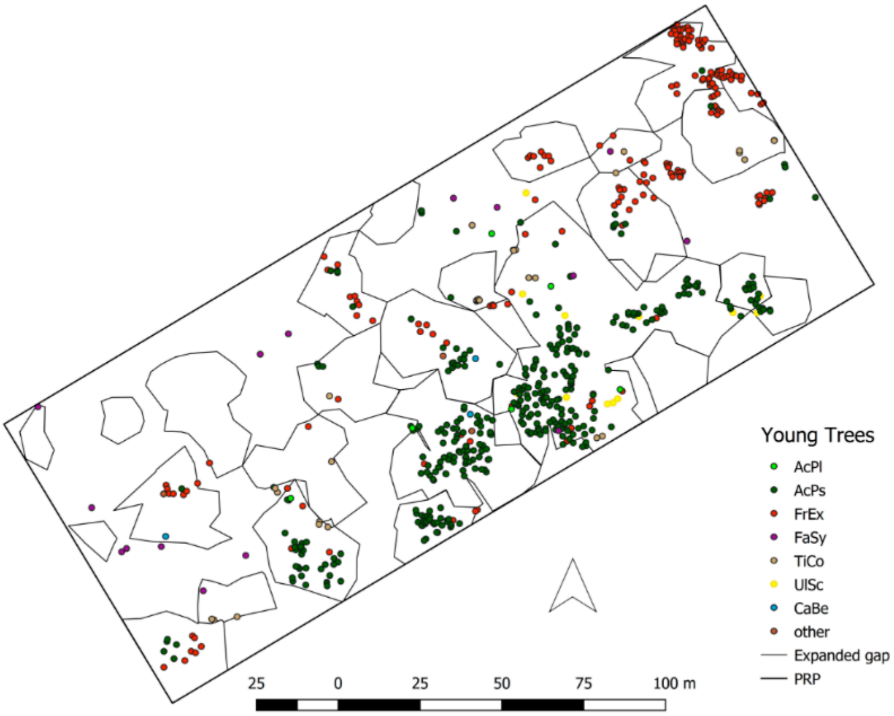

Figure A3. Young trees (dbh 4–8 cm, about to recruit into the middle stand height layer) of *A. pseudoplatanus* and *F. excelsior* dominate canopy openings. *A. pseudoplatanus* is almost absent in the closed canopy, while young trees of *F. sylvatica* grow mainly under closed canopy.

References

1. Ford, S.E.; Keeton, W.S. Enhanced carbon storage through management for old-growth characteristics in northern hardwood-conifer forests. *Ecosphere* **2017**, *8*, e01721. [CrossRef]
2. Jucker, T.; Bouriaud, O.; Avacaritei, D.; Coomes, D.A. Stabilizing effects of diversity on aboveground wood production in forest ecosystems: Linking patterns and processes. *Ecol. Lett.* **2014**, *17*, 1560–1569. [CrossRef] [PubMed]
3. Nagel, L.M.; Palik, B.J.; Battaglia, M.A.; D´Amato, A.W.; Guldin, J.M.; Swanston, C.W.; Janowiak, M.K.; Powers, M.P.; Joyce, L.A.; Millar, C.I.; et al. Adaptive silviculture for climate change: A national experiment in manager-scientist partnerships to apply an adaptation framework. *J. For.* **2017**, *115*, 167–178. [CrossRef]
4. Schütz, J.P.; Saniga, M.; Diaci, J.; Vrška, T. Comparing close-to-nature silviculture with processes in pristine forests: Lessons from Central Europe. *Ann. For. Sci.* **2016**, *73*, 911–921. [CrossRef]

5. Runkle, J.R. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* **1982**, *63*, 1533–1546. [CrossRef]
6. Splechtna, B.; Gratzer, G.; Black, B.A. Disturbance history of a European old-growth mixed-species forest—A spatial dendro-ecological analysis. *J. Veg. Sci.* **2005**, *16*, 511–522.
7. Yamamoto, S.-I. Forest gap dynamics and tree regeneration. *J. For. Res.* **2000**, *5*, 223–229. [CrossRef]
8. McCarthy, J. Gap dynamics of forest trees: A review with particular attention to boreal forests. *Environ. Rev.* **2001**, *9*, 1–59. [CrossRef]
9. Jaloviar, P.; Saniga, M.; Kucbel, S.; Pittner, J.; Vencurik, J.; Dovciak, M. Seven decades of change in a European old-growth forest following a stand-replacing wind disturbance: A long-term case study. *For. Ecol. Manag.* **2017**, *399*, 197–205. [CrossRef]
10. Nagel, T.A.; Svoboda, M.; Kobal, M. Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. *Ecol. Appl.* **2014**, *24*, 663–679. [CrossRef]
11. Diaci, J.; Gyoerek, N.; Gliha, J.; Nagel, T.A. Response of *Quercus robur* L. seedlings to north-south asymmetry of light within gaps in floodplain forests of Slovenia. *Ann. For. Sci.* **2008**, *65*, 105. [CrossRef]
12. Drössler, L.; von Lüpke, B. Canopy gaps in two virgin beech forest reserves in Slovakia. *J. For. Sci.* **2005**, *10*, 446–457. [CrossRef]
13. Zeibig, A.; Diaci, J.; Wagner, S. Gap disturbance patterns of a *Fagus sylvatica* virgin forest remnant in the mountain vegetation belt of Slovenia. *For. Snow Landsc. Res.* **2005**, *79*, 69–80.
14. Nagel, T.A.; Svoboda, M. Gap disturbance regime in an old-growth *Fagus–Abies* forest in the Dinaric Mountains, Bosnia- Herzegovina. *Can. J. For. Res.* **2008**, *38*, 2728–2737. [CrossRef]
15. Kucbel, S.; Jaloviar, P.; Saniga, M.; Vencurik, J.; Klimaš, V. Canopy gaps in an old-growth fir-beech forest remnant of Western Carpathians. *Eur. J. For. Res.* **2010**, *129*, 249–259. [CrossRef]
16. Schall, P.; Gossner, M.M.; Heinrichs, S.; Fischer, M.; Boch, S.; Prati, D.; Jung, K.; Baumgartner, V.; Blaser, S.; Böhm, S.; et al. The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *J. Appl. Ecol.* **2017**, *55*, 267–278. [CrossRef]
17. Commarmot, B.; Bachofen, H.; Bundziak, Y.; Bürgi, A.; Shparyk, Y.; Sukhariuk, D.; Viter, R.; Zingg, A. Structures of virgin and managed beech forests in Uholka (Ukraine) and Sihlwald (Switzerland): A comparative study. *For. Snow Landsc. Res.* **2005**, *79*, 45–56.
18. Barna, M.; Bosela, M. Tree species diversity change in natural regeneration of a beech forest under different management. *For. Ecol. Manag.* **2015**, *342*, 93–102. [CrossRef]
19. Bobiec, A. The influence of gaps on tree regeneration: A case study of the mixed lime-hornbeam (*Tilio-Carpinetum* Tracz. 1962) communities in the Białowieża primeval forest. *Pol. J. Ecol.* **2007**, *55*, 441–455.
20. Ligot, G.; Balandier, P.; Fayolle, A.; Lejeune, P.; Claessens, H. Height competition between *Quercus petraea* and Fagus sylvatica natural regeneration in mixed and uneven-aged stands. *For. Ecol. Manag.* **2013**, *304*, 391–398. [CrossRef]
21. Ligot, G.; Balandier, P.; Courbaud, B.; Jonard, M.; Kneeshaw, D.; Claessens, H. Controlling light exposure to enable shade- and semi shade-tolerant species to coexist in mixed forest regeneration (in French). *Rev. For. Fr.* **2015**, *LXVII*, 195–211. [CrossRef]
22. Canham, C.D. Different respones to gaps among shade-tollerant tree species. *Ecology* **1989**, *70*, 548–550. [CrossRef]
23. Gravel, D.; Canham, C.D.; Beaudet, M.; Messier, C. Shade tolerance, canopy gaps and mechanisms of coexistence of forest trees. *Oikos* **2010**, *119*, 475–484. [CrossRef]
24. Leuschner, C.; Ellenberg, H. *Ecology of Central European Forests. Vegetation Ecology of Central Europe*; Springer International Publishing: Berlin/Heidelberg, Germany, 2017; Volume I.
25. KorpeĹ, Š. *Die Urwälder der Westkarpaten*; Gustav Fischer Verlag: Stuttgart, Germany; Jena, Germany; New York, NY, USA, 1995.
26. Vrška, T.; Adam, D.; Hort, L.; Odehnalová, P.; Horal, D.; Král, K. *Developmental dynamics of virgin forest reserves in the Czech Republic. Volume II, Floodplain forests—Cahnov-Soutok, Ranšpurk, Jiřina*; Academia: Praha, Czech Republic, 2006. (In Czech)
27. Vacik, H.; Rahman, M.M.; Ruprecht, H.; Frank, G. Dynamics and structural changes of an oak dominated Natural Forest Reserve in Austria. *Bot. Helv.* **2009**, *119*, 23–29. [CrossRef]

28. Saniga, M.; Balanda, M.; Kucbel, S.; Pittner, J. Four decades of forest succession in the oak-dominated forest reserves in Slovakia. *iForest* **2014**, *7*, 324–332. [CrossRef]
29. Petritan, A.M.; Bouriaud, O.; Frank, D.C.; Petritan, I.C. Dendroecological reconstruction of disturbance history of an old-growth mixed sessile oak–beech forest. *J. Veg. Sci.* **2017**, *28*, 117–127. [CrossRef]
30. Rohner, B.; Bigler, C.; Wunder, J.; Brang, P.; Bugmann, H. Fifty years of natural succession in Swiss forest reserves: Changes in stand structure and mortality rates of oak and beech. *J. Veg. Sci.* **2012**, *23*, 892–905. [CrossRef]
31. Petritan, A.M.; Nuske, R.S.; Petritan, I.C.; Tudose, N.C. Gap disturbance patterns in an old-growth sessile oak (*Quercus petraea* L.)– European beech (*Fagus sylvatica* L.) forest remnant in the Carpathian Mountains, Romania. *For. Ecol. Manag.* **2013**, *308*, 67–75. [CrossRef]
32. Busing, R.T.; White, P.S. Species diversity and small-scale disturbance in an old-growth temperate forest: A consideration of gap partitioning concepts. *Oikos* **1997**, *78*, 562–568. [CrossRef]
33. Danková, L.; Saniga, M. Canopy gaps and tree regeneration patterns in multi-species unmanaged natural forest Sitno (preliminary results). *Beskydy* **2013**, *6*, 17–26. [CrossRef]
34. Albrecht, L. *Grundlagen, Ziele und Methodik der waldökologischen Forschung in Naturwaldreservaten. Naturwaldreservate in Bayern*; Schriftenreihe des Bayerischen Staatsministeriums für Ernährung, Landwirtschaft und Forsten gemeinsam mit dem Lehrstuhl für Landschaftstechnik: München, Germany, 1990; Volume 1.
35. StatSoft, I. *STATISTICA (Data Analysis Software System)*; Version 12; StatSoft: Tulsa, OK, USA, 2013.
36. Ter Braak, C.J.F.; Smilauer, P. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5). 2002. Available online: www.canoco.com (accessed on 1 April 2013).
37. Borcard, D.; Legendre, P.; Drapeau, P. Partialling out the spatial component of ecological variation. *Ecology* **1992**, *73*, 1045–1055. [CrossRef]
38. Legendre, P.; Legendre, L. *Numerical Ecology*, 3rd ed.; Elsevier: Amsterdam, The Netherlands, 2012.
39. Saniga, M.; Balanda, M.; Kucbel, S.; Jaloviar, P. Cyclic changes in tree species composition of mixed-species forest in the Western Carpathians: Role of disturbance and tree regeneration. *Pol. J. Ecol.* **2011**, *59*, 699–708.
40. Saniga, M.; Danková, L.; Pittner, J.; Jaloviar, P.; Kucbel, S.; Balanda, M. *Structure of Bio- and Necromass, Disturbance Regime, Light Conditions and Regeneration Processes of the Natural Forest in the National Nature Reserve Sitno*; TU Zvolen: Zvolen, Slovakia, 2014. (In Slovak)
41. Ammer, C.; Vor, T.; Knoke, T.; Wagner, S. Der Wald-Wild-Konflikt Analyse und Lösungsansätze vor dem Hintergrund rechtlicher, ökologischer und ökonomischer Zusammenhänge. *Göttinger Forstwiss.* **2010**, *5*, 1–202.
42. Kern, C.C.; D´Amato, A.W.; Strong, T.F. Diversifying the composition and structure of managed, late-successional forests with harvest gaps: What is the optimal gap size? *For. Ecol. Manag.* **2013**, *304*, 110–120. [CrossRef]
43. Kýpeťová, M.; Walas, Ł.; Jaloviar, P.; Iszkuło, G. Influence of herbivory pressure on the growth rate and needle morphology of *Taxus baccata* L. juveniles. *Dendrobiology* **2018**, *79*, 10–19. [CrossRef]
44. Zhu, J.; Lu, D.; Zhang, W. Effects of gaps on regeneration of woody plants: A meta-analysis. *J. For. Res.* **2014**, *25*, 501–510. [CrossRef]
45. Webster, C.R.; Dickinson, Y.; Burton, J.I.; Frelich, L.E.; Jenkins, M.A.; Kern, C.C.; Raymond, P.; Saunders, M.R.; Walters, M.B.; Willis, J.L. Promoting and maintaining diversity in contemporary hardwood forests: Confronting contemporary drivers of change and the loss of ecological memory. *For. Ecol. Manag.* **2018**, *421*, 98–108. [CrossRef]
46. Emborg, J.; Christensen, M.; Heilmann-Clausen, J. The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. *For. Ecol. Manag.* **2000**, *126*, 173–189. [CrossRef]
47. Saniga, M.; Klimáš, V.; Pittner, J.; Kucbel, S. *Structure, Texture, Regeneration Processes and Disturbance Regime in the Natural Nature Reserve Kašivárová*; TU Zvolen: Zvolen, Slovakia, 2015. (In Slovak)
48. Denslow, J.S. Gap partitioning among tropical rainforest trees. *Biotropica* **1980**, *12*, 47–55. [CrossRef]
49. Vilhar, U.; Roženbergar, D.; Simončič, P.; Diaci, J. Variation in irradiance, soil features and regeneration patterns in experimental forest canopy gaps. *Ann. For. Sci.* **2015**, *72*, 253–266. [CrossRef]
50. Denslow, J.S. Disturbance and diversity in tropical rain forests: The density effect. *Ecol. Appl.* **1995**, *5*, 962–968. [CrossRef]

51. Yan, Y.; Zhang, C.; Wang, Y.; Zhao, X.; von Gadow, K. Drivers of seedling survival in a temperate forest and their relative importance at three stages of succession. *Ecol. Evol.* **2015**, *5*, 4287–4299. [CrossRef] [PubMed]
52. Lüpke, B. von Silvicultural methods of oak regeneration with special respect to shade tolerant mixed species. *For. Ecol. Manag.* **1998**, *106*, 19–26. [CrossRef]
53. Ariya, U.; Hamano, K.; Makimoto, T.; Kinoshita, S.; Akaji, Y.; Miyazaki, Y.; Hirobe, M.; Sakamoto, K. Temporal and spatial dynamics of an old-growth beech forest in western Japan. *J. For. Res.* **2016**, *21*, 73–83. [CrossRef]
54. Couwenberghe, R.V.; Collet, C.; Lacombe, E.; Pierrat, J.-C.; Gégout, J.-C. Gap partitioning among temperate tree species across a regional soil gradient in windstorm-disturbed forests. *For. Ecol. Manag.* **2010**, *260*, 146–154. [CrossRef]
55. Hofmeister, J.; Mihaljevič, M.; Hošek, J. The spread of ash (*Fraxinus excelsior*) in some European oak forests: An effect of nitrogen deposition or successional change? *For. Ecol. Manag.* **2004**, *203*, 35–47. [CrossRef]
56. Dobrowolska, D.; Hein, S.; Oosterbaan, A.; Wagner, S.; Clark, J.O.; Skovsgaard, J.P. A review of European ash (*Fraxinus excelsior* L.): Implications for silviculture. *Forestry* **2011**, *84*, 133–148. [CrossRef]
57. Firm, D.; Nagel, T.A.; Diaci, J. Disturbance history and dynamics of an old-growth mixed species mountain forest in the Slovenian Alps. *For. Ecol. Manag.* **2009**, *257*, 1893–1901. [CrossRef]
58. Nagel, T.A.; Svoboda, M.; Rugani, T.; Diaci, J. Gap regeneration and replacement patterns in an old-growth *Fagus–Abies* forest of Bosnia–Herzegovina. *Plant Ecol.* **2010**, *208*, 307–318. [CrossRef]
59. Carón, M.M.; De Frenne, P.; Brunet, J.; Chabrerie, O.; Cousins, S.A.O.; Decocq, G.; Diekmann, M.; Graae, B.J.; Heinken, T.; Kolb, A.; et al. Divergent regeneration responses of two closely related tree species to direct abiotic and indirect biotic effects of climate change. *For. Ecol. Manag.* **2015**, *342*, 21–29. [CrossRef]
60. Anderegg, W.R.L.; Kane, J.M.; Anderegg, L.D.L. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat. Clim. Chang.* **2013**, *3*, 30–36. [CrossRef]
61. Sedmáková, D.; Sedmák, R.; Bosela, M.; Ježík, M.; Blaženec, M.; Hlásny, T.; Marušák, R. Growth-climate responses indicate shifts in the competitive ability of European beech and Norway spruce under recent climate warming in East-Central Europe. *Dendrochronologia* **2019**, *54*, 37–48. [CrossRef]
62. Rozas, V. Regeneration patterns, dendroecology, and forest-use history in an old-growth beech–oak lowland forest in Northern Spain. *For. Ecol. Manag.* **2003**, *182*, 175–194. [CrossRef]
63. Annighöfer, P.; Beckschäfer, P.; Vor, T.; Ammer, C. Regeneration patterns of European oak species (*Quercus petraea* (Matt.) Liebl., *Quercus robur* L.) in dependence of environment and neighborhood. *PLoS ONE* **2015**, *10*, e0134935. [CrossRef]
64. Mölder, A.; Meyer, P.; Nagel, R.-V. Integrative management to sustain biodiversity and ecological continuity in Central European temperate oak (*Quercus robur*, *Q. petraea*) forests: An overview. *For. Ecol. Manag.* **2019**, *437*, 324–339. [CrossRef]
65. Petritan, A.N.Y.M.; Lüpke, B.V.O.N. Effects of shade on growth and mortality of maple (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*) saplings. *Forestry* **2007**, *80*, 397–412. [CrossRef]
66. Annighöfer, P.; Petritan, A.M.; Petritan, I.C.; Ammer, C. Disentangling juvenile growth strategies of three shade-tolerant temperate forest tree species responding to a light gradient. *For. Ecol. Manag.* **2017**, *391*, 115–126. [CrossRef]
67. Feldmann, E.; Drößler, L.; Hauck, M.; Kucbel, S.; Pichler, V.; Leuschner, C. Canopy gap dynamics and tree understory release in a virgin beech forest, Slovakian Carpathians. *For. Ecol. Manag.* **2018**, *415–416*, 38–46. [CrossRef]
68. Grubb, P.J. The maintenance of species-richness in plant communities: The importance of the regeneration niche. *Biol. Rev.* **1977**, *52*, 107–145. [CrossRef]
69. Marx, L.; Walters, M.B. Survival of tree seedlings on different species of decaying wood maintains tree distribution in Michigan hemlock–hardwood forests. *J. Ecol.* **2008**, *96*, 505–513. [CrossRef]
70. Collet, C.; Piboule, A.; Leroy, O.; Frochot, H. Advance *Fagus sylvatica* and *Acer pseudoplatanus* seedlings dominate tree regeneration in a mixed broadleaved former coppice-with-standards forest. *Forestry* **2008**, *81*, 135–150. [CrossRef]
71. Kupferschmid, A.D.; Bütikofer, L.; Hothorn, T.; Schwyzer, A.; Brang, P. Quantifying the relative influence of terminal shoot browsing by ungulates on tree regeneration. *For. Ecol. Manag.* **2019**, *446*, 331–344. [CrossRef]
72. Saxe, H.; Kerstiens, G. Climate change reverses the competitive balance of ash and beech seedlings under simulated forest conditions. *Plant Biol.* **2005**, *7*, 375–386. [CrossRef] [PubMed]

73. Sommerfeld, A.; Senf, C.; Buma, B.; D´Amato, A.W.; Després, T.; Díaz-Hormazábal, I.; Fraver, S.; Frelich, L.E.; Gutiérrez, Á.G.; Hart, S.J.; et al. Patterns and drivers of recent disturbances across the temperate forest biome. *Nat. Commun.* **2018**, *9*, 4355. [CrossRef]
74. Webster, C.R.; Lorimer, C.G. Minimum opening sizes for canopy recruitment of midtolerant tree species: A retrospective approach. *Ecol. Appl.* **2005**, *15*, 1245–1262. [CrossRef]
75. Bauhus, J.; Puettmann, K.J.; Kühne, C. Is close-to-nature forest management in Europe compatible with managing forests as complex adaptive forest ecosystems. In *Managing Forests as Complex Adaptive Systems: Building Resilience to the Challenge of Global Change*; Messier, C., Puettmann, K.J., Coates, K.D., Eds.; The Earthscan Forest Library; Routledge: Abingdon upon Thames, UK, 2013; pp. 337–354.
76. Vanselow, K. *Natürliche Verjüngung im Wirtschaftswald*; Verlag von J. Neumann-Neudamm: Berlin, Germany, 1931.
77. Kern, C.C.; Burton, J.I.; Raymond, P.; Amato, A.W.; Keeton, W.S.; Royo, A.A.; Walters, M.B.; Webster, C.R.; Willis, J.L. Challenges facing gap-based silviculture and possible solutions for mesic northern forests in North America. *Forestry* **2017**, *90*, 4–17. [CrossRef]