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Short-Term Effects of Anthropogenic Disturbances on Stand Structure, Soil Properties, and Vegetation Diversity in a Former Virgin Mixed Forest

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Abstract: Despite the sharply growing interest in the disturbances occurring in primary forests, little is known about the response of European virgin forests to anthropogenic disturbance. The present study investigated the effect of the first silvicultural interventions that took place nine years earlier in a former virgin forest (FVF). Changes in the stand structure, environmental characteristics, and diversity of ground vegetation were studied in comparison with a nearby virgin forest (VF), both consisting of a mixture of European beech and silver fir. While the tree density did not differ significantly between the two forests, the number of large trees, the basal area, and the stand volume were significantly reduced in the FVF. The deadwood volume was twice as great in the VF as in the FVF and was found in both forests, particularly from silver fir. Despite significantly better light conditions in the FVF, natural regeneration was not significantly higher than in the VF. However, a slight improvement in the proportion of silver fir and other tree species into total regeneration was reported. The soil temperature was significantly higher in the FVF, independent of the measurement season, while the soil moisture showed a higher value in the VF only in spring. The FVF is characterized by a greater soil CO_2 emission, which is especially significant in summer and fall. The diversity of the ground vegetation did not yet react significantly to the silvicultural intervention. These preliminary findings are important in drawing suitable forest management practices that need to be applied in mixed beech–silver fir stands, especially in terms of maintaining species diversity. However, the short time frame since the intervention obliges further research on this VF–FVF pair over the next 10–20 years, at least regarding silver fir dynamics.

Keywords: former virgin forest; structure; regeneration; deadwood; soil respiration; ground vegetation diversity

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1. Introduction

As a result of intense human exploitation, mainly for the creation of agricultural land or for wood consumption, only a few remnants of virgin forests remain in the contemporary landscape of Europe [1–3]. Furthermore, according to a recent study [4], virgin forests are scarce and continue to disappear. Therefore, one of the most important objectives of the "EU Biodiversity Strategy for 2030" agenda is to define, map, and monitor all of these remnants' forests. Despite the fact that forest covers 35% of Europe's total land area, forest undisturbed by man (i.e., virgin forest) covers only 2.2% of the European forest area. Furthermore, Romania hosts some of the largest remnants of virgin forest in Central Europe, covering about 59,110 ha according to [4] and 71,077 ha according to the last edition of the Romanian virgin forest catalogue [5]. It should be mentioned that the updating of both sources [4,5] is an ongoing process.

These increasingly rare untouched forests have attracted the interest of scientists since the middle of the 19th century, especially after the Second World War at the initiative of the IUFRO forestry section [6,7]. From the point of view of the landscape, this unique and critical forest ecosystem (i.e., primary forest) represents the highest range of naturalness and can be found particularly in the northern and eastern parts of Europe [4,8,9]. Still present in the Carpathian Mountains, such intact ecosystems have a key role in biodiversity conservation [6,10–12], but also in carbon sequestration [13,14], biomass accumulation [15], and riparian functionality [16]. Characterized by high structural complexity driven by natural disturbance processes and natural regeneration dynamics [17,18], virgin forests are an important reference for managed forests, especially for close-to-nature silviculture [19–22], providing a rare opportunity for understanding natural ecosystem processes and functions [11,23].

In the context of climatic change, an increase in the disturbance regime (i.e., in the frequency and severity) has been recorded in the first decade of the current century, with a potential negative impact on the carbon storage capacity of European forests and many implications for other ecosystem services [18,24]. The importance of the disturbance regime in modifying the structure and dynamics of virgin forests has already been shown [7,25]. In addition, the disturbance regime affects forest ecosystems from the functional plant level to the stand level [24,26], as it can change the natural cycle of forest development [7,27]. Forest disturbance can generally be related to natural causes (i.e., windthrow events, insect attacks, drought stress, forest fires) but can also include forest management activities (i.e., silvicultural interventions) with a potential influence on biodiversity maintenance [25,28]. Aside from the devaluation of timber, the consequences of disturbance will amplify the impact of climate change, and forest ecosystem provisioning services (i.e., drinking water) and regulating and supporting services (recreation value, air quality, etc.) will all be seriously affected [18,24]. Therefore, understanding the main effects of the disturbance regime on forest ecosystems constitutes a key challenge for ecological research.

Disturbances are described by the size, distribution, and structure of the resulting canopy gaps. The main natural disturbance regime of European primary forests, especially those consisting of shade-tolerant species [7,29], but not limited to them [27,30,31], is characterized by the frequent occurrence of small canopy gaps (i.e., less than 150 m^2), generated by the mortality of an individual tree or small group of trees and referred to as a low-severity disturbance regime [7]. However, moderate severity disturbance has been found as a key driver of tree species coexistence in primary temperate forests [32]. High-severity stand-replaced disturbances can also occur [7,30], with this type of disturbance being very important in the establishment of light-demanding tree species.

While the study of the natural disturbance regime of virgin forests has been intensified over the last decades [7,27,30,31], there is a lack of information about the short-term impact of first silvicultural interventions on a former virgin forest in Europe. In the Southern Carpathian Mountain range in Romania, in the immediate vicinity of the virgin forest Sinca (a forest included in the UNESCO World Heritage Site of "Primeval Beech Forests of the Carpathians and the Ancient Beech Forests of Germany" in 2017), there is a forest with the same composition and stand characteristics, where the first silvicultural (human) interventions (i.e., group shelterwood system) occurred in 2009. This rare situation gave us the opportunity to study the short-term impacts of the first management interventions on the main traits of the former virgin forest. A better understanding of how forest management (i.e., silvicultural interventions) reshapes the main characteristics of stand diversity is crucial to anticipating forest ecosystem responses to the intensity and frequency of disturbance events [33], and in our case, will contribute to understanding the main consequences of the loss of these unique and diverse forests.

Unlike the few comparative studies that have investigated stand characteristics in virgin and managed forests [6,11,22,34,35], our study provides valuable insights into the changes induced by the anthropic interventions within the first decade. The specific objectives of our study were the following: (i) to assess the short-term effects of silvicultural intervention on the stand structural characteristics, amount of deadwood, and natural regeneration; (ii) to describe the possible consequences of light condition changes on ground vegetation diversity; and (iii) to test whether the soil microclimate and soil respiration are affected by the reduction in stand stocking volume.

2. Materials and Methods

2.1. Study Site

The study area (Figure 1A) is located in the Southern Carpathians, in the northern part of the Fagaras Mountains, in central Romania (45°40′0.420″ N and 25°10′14.359″ E), at an altitude ranging from 850 to 1350 m (a.s.l.). The experimental sites of our study are homogeneous in terms of ecological and vegetation characteristics. They are part of the Pulmonario rubrae-Fagetum (Soo, 1964) association [36] and are in accordance with the Natura 2000 classification of the 91V0 Dacian beech forest (Symphylo-Fagion) [37]. The forest composition is largely dominated by European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) trees in different proportions. The soils are derived from recent moraines of the Weichsel glacial period. The main soil type is Cambisol, developed on a parental material of crystalline schists. The main humus type is mull-moder. According to the Koppen classification, the climate is temperate continental, with a mean annual temperature of 6.1 °C and mean annual precipitation of 1100 mm [38].

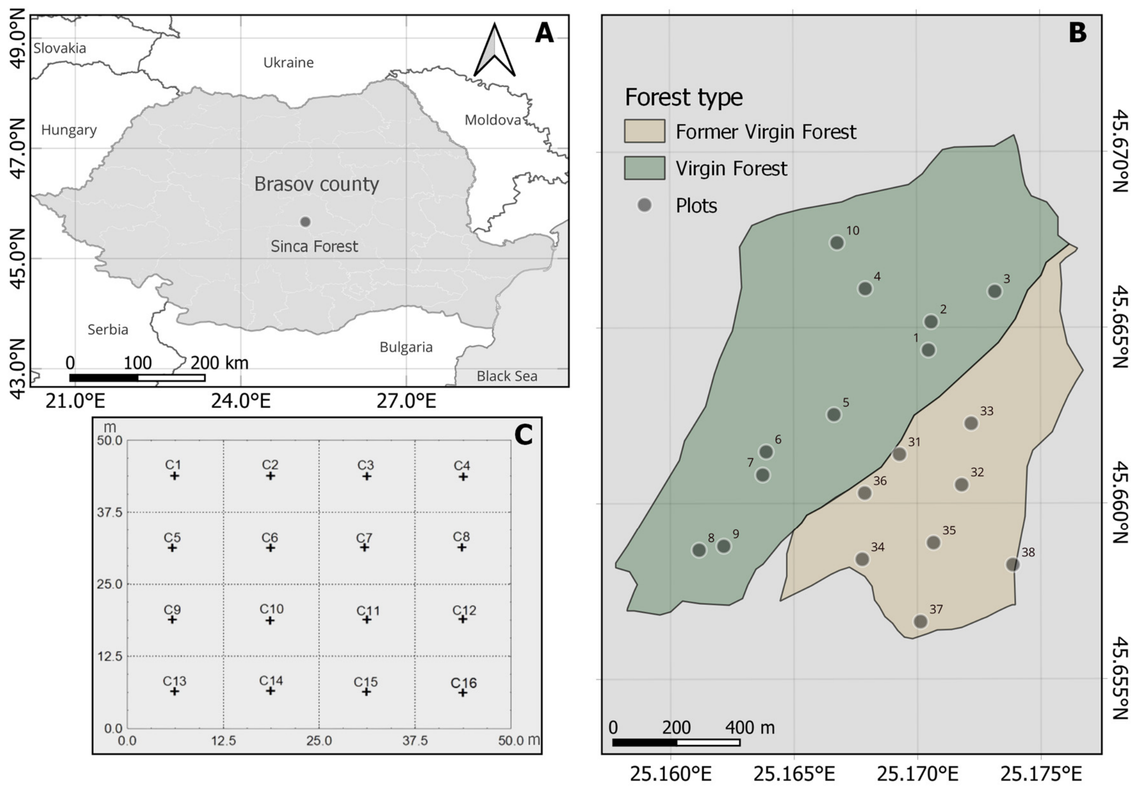

Figure 1. Study area maps: (**A**)—Location of Sinca Forest, (**B**)—Distribution of plots by each forest type (VF and FVF), (**C**)—Experimental design for soil properties and light availability inside of each plot (50 m × 50 m) where C1–C16 represent the center of each subplot.

In the former virgin forest, the initial felling of the group shelterwood system was applied in 2009, with a harvesting intensity of around 30% stand volume. The group shelterwood system is the most widespread management practice applied in Romania, currently used in 81% of Romanian forests [39]. This forest management consists of repeated and successive fellings. The trees are extracted irregularly and concentrated in gaps, their size and distribution of which depends on the species' composition and light requirements, with the goal to firstly provoke natural seedings and to secondly provide enough light to advance growth [40]. Therefore, this kind of silvicultural intervention is formed by three kinds of fellings, starting with gap opening, followed by extending the gaps to provide light conditions for seedlings, and finishing with removing the last old trees. Consequently, a stand with this type of forest management can simultaneously include areas with all of these three felling types with successive stages of regeneration. For shade-tolerant species (i.e., European beech and silver fir), in our case, the gaps were generally small, up to 0.5–0.75 of the mean stand height [40]. Thus, in this beech–silver fir mixed forest, the initial felling could be taken as a uniform intervention (i.e., only thinning around the seed trees). The regeneration period (including all three felling types) for shade-tolerant species is about 30 years.

2.2. Field Sampling

During the year 2017, eighteen permanent, randomly distributed 50 m $\times$ 50 m (2500 m^2) sample plots, ten in the virgin forest (VF) and eight in the former virgin forest (FVF), were established (Figure 1B). In each plot, the standing trees with a diameter at breast height (dbh) greater than 6 cm were recorded by their species and vitality attributes (live/dead). Their dbh and total height (H) were measured using tape and a Vertex IV Hypsometer (Haglof, Sweden), respectively. For the broken standing trees, the diameter at the breakage point was measured with an optical caliper. All lying deadwood pieces with a length $\geq$ 3 m and thick-end diameter $\geq$ 15 cm were registered with species, and their diameter at both ends and the total length within the plot were measured. According to Keller [41], each piece of deadwood (standing and lying) was classified within one of the five decay classes, namely, fresh (A), hard (B), rotten (C), moldering (D), or mull (E) wood. For the FVF site, we noted if the deadwood was caused by silvicultural intervention or natural disturbance. Following the methodology described by Petritan et al. [42], the natural regeneration (all samplings taller than 10 cm and smaller than 6 cm in dbh) was sampled in four circular subplots, the centers of which were located 17.68 m apart from each corner on the diagonals of the plot. Each subplot included three concentric circles: a 5 m^2 circle (RC1) for saplings between 10 and 39.9 cm tall, a 10 m^2 circle (RC2) for saplings between 40 and 129.9 cm height, and a 20 m^2 circle (RC3) for saplings with a height $\geq$1.3 m and dbh <6 cm. Saplings smaller than 130 cm were evaluated for ungulate browsing to the leading shoot. The ground vegetation composition was determined through phytosociological relevés conducted in each plot. The cover of each vascular plant species was estimated using the Braun-Blanquet scale [43]. For data analysis, scale values were transformed into percentage values as follows: r = 0.1; + = 0.5; 1 = 2.5; 2m = 5; 2a = 10; 2b = 20; 3 = 37.5; 4 = 62.5; 5 = 87.5 [44]. Twelve of the eighteen permanent sample plots were randomly selected, with six in each forest, to study the environmental conditions. These plots were divided into sixteen equal subplots of 12.5 m $\times$ 12.5 m (Figure 1C). Light availability, microclimate, and soil respiration were determined at the center of each subplot, i.e., at 96 points in each forest. In summer, a hemispherical photograph was taken of the center of each square using a digital camera coupled with a fisheye lens. The light availability conditions, expressed by diffuse light (indirect site factor (ISF)) and direct light (direct site factor (DSF)), as a percentage of the full light, were determined for each photo using the WinScanopy Pro B software 2012 (Regent Instruments Inc., Quebec City, QC, Canada). The soil temperature (Ts) was measured using a soil temperature sensor (STP; PP Systems) that was inserted at a depth of 5 cm into the soil, and the soil moisture (Us) was measured at a depth of 14 cm into the soil using a Trime Pico 64 sensor coupled with an HD2 data logger (IMKO GmbH, Germany). Two weeks prior to the start of soil respiration (Rs) measurements, at the center of each subplot, a PVC collar (10 cm in diameter and 8 cm in height) was inserted into the soil at approximatively 3 cm, as recommended by Curiel Yuste et al. [45]. A portable infrared gas analyzer (IRGA) connected to a soil respiration chamber (EGM-4 and SRC-1; PP Systems, USA) was used to carry out the soil respiration measurements. The volume of the collars above the soil was added to the chamber volume. The duration of each measurement was 2 min. Soil respiration measurements were taken between 9 a.m. and 18 a.m. (1–2 days), at least two days after a rainy day. The soil measurements were carried out in three different seasons (spring, summer, and fall).

2.3. Data Analysis

The height and diameter of the dominant trees (h_{dom} and d_{dom}), defined as the mean diameter/height of the 100 largest trees per ha [6], were calculated for each species (beech and silver fir). The volume (V) of living and standing dead trees was determined by applying a double-logarithmic regression:

$$log(v) = a_0 + a_1 \times log(d) + a_2 \times log^2(d) + a_3 \times log(h) + a_4 \times log^2(h)$$

where a_0, a_1, a_2, a_3, and a_4 are species-specific regression coefficients [46]. The volume of broken standing trees and lying deadwood was calculated using the volume formula of a truncated cone, considering only the portion lying within the plot boundaries [37]. The vertical structure of the two forests was described by the A index proposed in [47], which combines the Shannon indices after tree stratification into three height layers (>2/3 top height, 1/3–2/3 top height, and <1/3 top height), where the top height is the average height of the 20% largest trees per sample plot (for more details, please see [48]). All ground vegetation indices were calculated using PAST 4.12 [49]. The Renyi diversity profiles of each sample plot of both forest types were calculated using PAST 4.12 [49]. Renyi curves enable the comparison of different diversity indices (each alpha value on the *y*-axis corresponds to a different diversity index) [49–51]. Low evenness is reflected by an abrupt decrease along the vertical axis, while high evenness is represented by a smooth line [51]. To assess the statistical significance of differences between the two forests regarding the studied traits and ground vegetation diversity indices, we applied an analysis of variance. The differences between mean values were tested by Tukey's HSD for an unequal N' post hoc test. The normality of residuals was tested with the Kolmogorov–Smirnov test and homoscedasticity, with Levene's test. If the assumption necessary to apply ANOVA was not fulfilled, a non-parametric Mann–Whitney U-test was applied. The analyses were achieved using Statistica 12 [52].

3. Results

3.1. Structural Characteristics

Eight years after the first silvicultural intervention (i.e., 2009, group shelterwood system, first cutting to promote seeding), the mean density of living trees per hectare was greater in the VF (650 ± 46.2) than in the FVF (507 ± 53.0), but without a significant difference (Table 1). As we expected, significant differences between the two forests were found in the basal area and stand volume: the basal area was 36% smaller in the former virgin forest compared to the virgin forest, while the volume in the FVF represented 57% of that found in the VF (Table 1). The silvicultural interventions led to significantly smaller d_{dom} and h_{dom} values (Table 1) and a lower number of trees with larger dimensions. The average number of trees with dbh ≥ 80 cm per hectare was more than double in the virgin than in the former virgin forest (28 vs. 11, respectively), but the number of trees taller than 40 m was quite similar between the two forests (Table 1). The main species of both stands were beech and silver fir, with a very rare presence of spruce (<1% in both forest stands). The participation of the two tree species was different between the two forests when the tree number was considered (greater percentage of beech in the FVF of 71% than in the virgin forest of 57%), but more similar (about 50% for each species) when the basal area or volume was considered. The vertical diversity of the former virgin forest was similar to that of the virgin forest (Table 1).

Table 1. Basic statistical parameters for the stand characteristics of the investigated VF and FVF silver fir–beech forests. Abbreviations used: h_{dom} = top height of 100 tallest trees, d_{dom} = mean diameter of 100 thickest trees, CV = coefficient of variation. Different letters represent the significant differences between the means of stand characteristics using ANOVA–Tukey's test.

Stand Characteristics/ Statistical Parameters	Virgin Forest		Former Virgin Forest	
	Mean ± Std. Error (Min–Max)	**CV%**	**Mean ± Std. Error (Min–Max)**	**CV%**
No. of trees per ha	650 ± 46.2 [a] (492–932)	22	507 ± 53.0 [a] (320–776)	29
No. of trees per ha with dbh ≥ 80 cm	28.4 ± 4.6 [a] (12–48)	52	11 ± 1.8 [b] (4–16)	46
No. of trees per ha with height ≥ 40 m	14.8 ± 4.0 [a] (0–40)	85	15.5 ± 3.7 [a] (4–36)	68
Basal area (m^2 ha^{-1})	54.5 ± 3.2 [a] (44.7–77.3)	18	35.0 ± 3.6 [b] (16.6–48.8)	28
Volume (m^3 ha^{-1})	893.1 ± 55.7 [a] (655.2–1236.6)	19	510.0 ± 60.2 [b] (209.7–725.7)	33
h_{dom} (m)	38.4 ± 0.9 [a] (35.4–43.1)	7	32.4 ± 1.7 [b] (24.3–36.1)	11
d_{dom} (cm)	75.9 ± 2.9 [a] (67.6–90.4)	9	54.2 ± 3.8 [b] (37.2–66.3	18
A index	1.53 ± 0.04 [a] (1.25–1.66)	9	1.58 ± 0.04 [a] (1.36–1.71)	8

The largest difference between tree distribution along the diameter gradient was found for the smallest diameter classes, in which the number of silver firs in the FVF was significantly lower (lower than half) than in the VF. In the FVF, the largest trees (dbh > 104 cm) were missing (Figure 2).

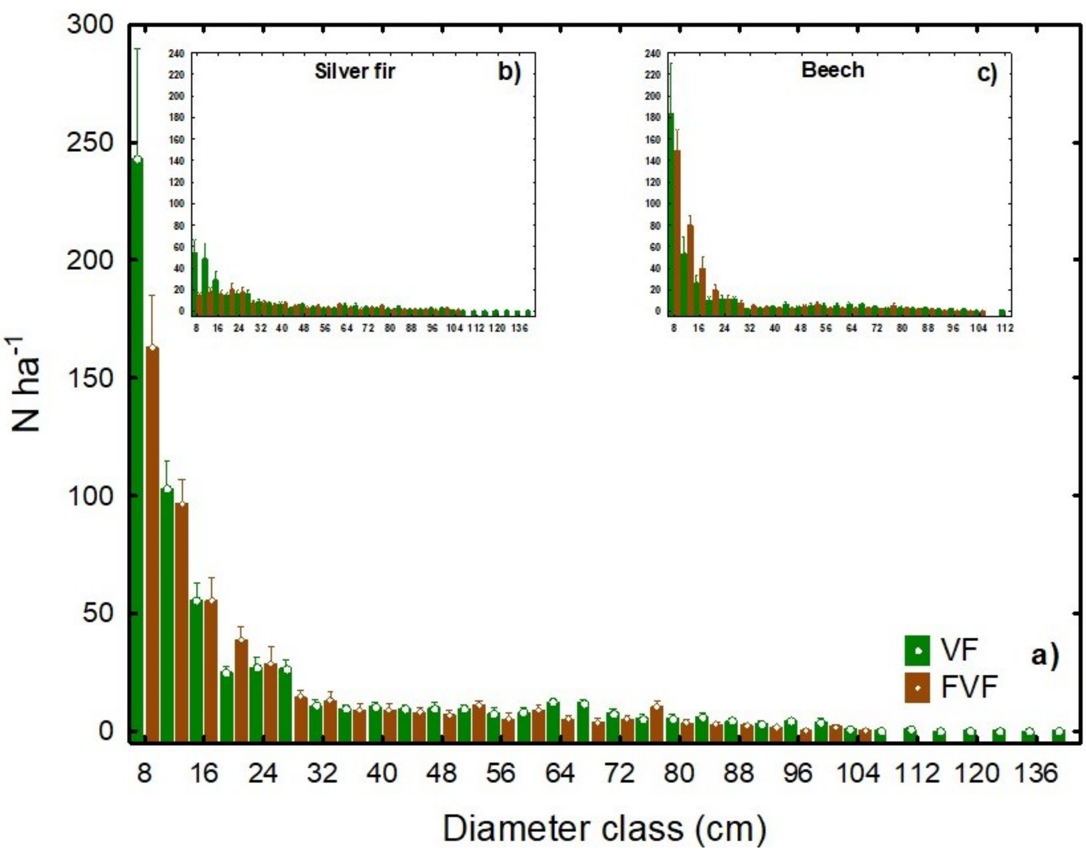

Figure 2. The distribution of the number of trees per diameter class in VF and in FVF (**a**) independent of species and separately for the two main species ((**b**)—Silver fir and (**c**)—Beech).

3.2. Deadwood

The quantity of the total deadwood (DW) in the FVF was approximately half (46%) of that in the VF (112 m^3 ha^{-1} vs. 244 m^3 ha^{-1}, respectively, Table 2). In the former virgin forest, from this total amount, a small proportion (11%) represented DW, resulting from the silvicultural interventions (e.g., woody debris or standing trees left in the forest). The proportion of lying DW was higher (71%) in the VF than in the FVF (60%), while in the FVF, the participation of standing was greater (40%) in comparison with the VF (29%). In both sites, the volume of DW consisted mostly of silver fir, which accounted for 84% of the total DW in the former VF and 63% in the FVF. The average dead-to-live wood ratio was slightly lower in the FVF (18%) than in the VF (21%).

Table 2. Mean, standard error, and range values of deadwood volume (lying and standing deadwood) per species and forest type.

Species	Beech		Silver Fir		Undefined		Total	
Forest Type	Former Virgin	Virgin	Former Virgin	Virgin	Former Virgin	Virgin	Former Virgin	Virgin
Lying deadwood (m^3 ha^{-1})	10 ± 5.9 (0–45.7)	60.2 ± 13.52 (8.6–144.3)	57 ± 28 (0.5–182.5)	114.4 ± 18.1 (12.8–214.9)	0.3 ± 0.1 (0–3.5)	0.6 ± 0.4 (0–3.5)	67.2 ± 33.7 (1–228)	174.2 ± 21.4 (71.8–277.8)
Standing deadwood (m^3 ha^{-1})	5.6 ± 4.1 (0–34.4)	29.44 ± 10.9 (0.7–117.8)	37.8 ± 8.5 (2.7–65.2)	41.8 ± 11.6 (2.9–101.7)	1.5 ± 0.6 (0–4.9)	0.0	45 ± 9.9 (8.5–80.9)	70.3 ± 14.6 (3.6–145.6)
Total deadwood volume (m^3 ha^{-1})	15.6 ± 6.2 (0.3–45.7)	89.6 ± 22.2 (10.9–262.2)	94.8 ± 30.5 (4.6–230)	154.3 ± 24.5 (15.8–248.1)	1.8 ± 0.6 (0–5)	0.6 ± 0.4 (0–3.5)	112.3 ± 34.7 (10.9–276.2)	244.2 ± 31.3 (75.5–400.4)

The deadwood structure on decay class was more or less similar in the two investigated forests, with more than half of the DW amount (70% vs. 60%) recorded in the most advanced decay classes (i.e., moldering—E class and mull wood—D class) (Figure 3). The fresh deadwood percentage was slightly higher in the FVF compared to VF (11% vs. 6%).

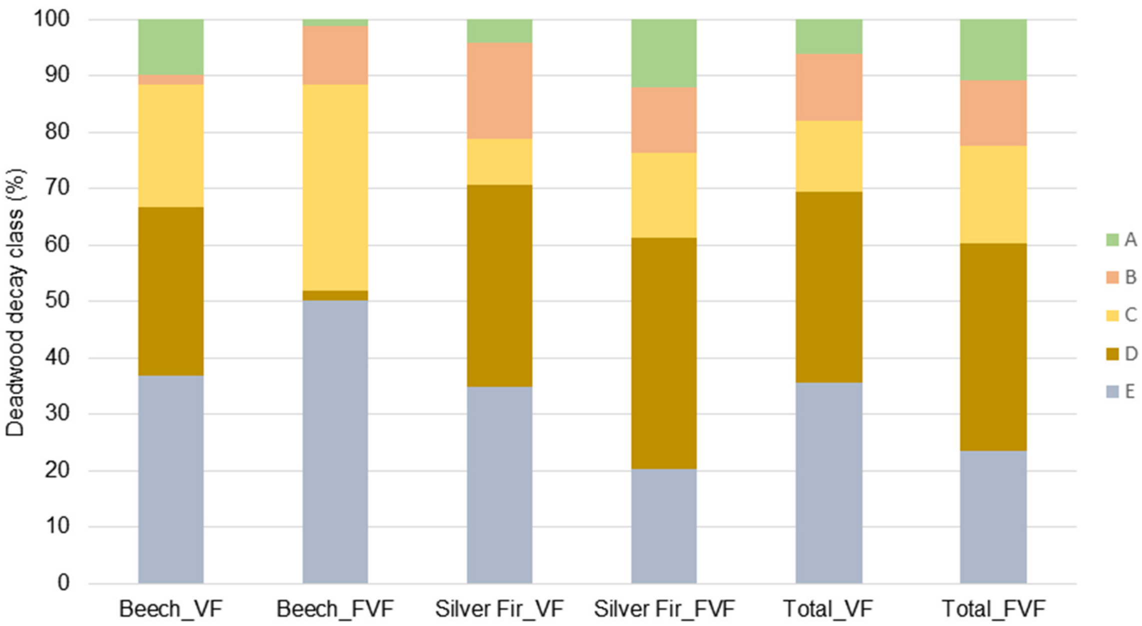

Figure 3. The deadwood structure on decay class (A—fresh, B—hard, C—rotten, D—mouldering, E—mull wood), species, and forest type (VF—virgin, FVF—former virgin forests).

3.3. Natural Regeneration and Light Conditions

We found a slightly lower regeneration density (i.e., all saplings with a height > 10 cm and dbh < 6 cm) in the VF site (6015 seedlings per ha) than in the FVF (6744 seedlings per ha), without significant differences. The main difference regarding the regeneration distribution of different height classes (Figure 4) was a higher percentage of taller saplings (h > 130 cm and dbh < 6 cm) in the FVF (32%) than in VF (29%). The species composition of the regeneration was similar between the two forests, with beech being the most common species (94% in virgin and 81% in former virgin forest). The proportion of silver fir was higher in the FVF (16%) than in the VF (5%). The percentage of the other species was slightly higher in the FVF (3% vs. 1%), aside from the spruce, sycamore maple, and pioneer species such as Eurasian aspen found in the FVF (Table S1). The proportion of damaged saplings by browsing of the leading shoot was nearly twofold in the former virgin forest (14%) as opposed to in the virgin forest (7%). The most browsed species was silver fir (double the amount of beech) in both forests. The light conditions were significantly more improved in the former virgin forest (ISF: 24.4 ± 13.2% and DSF: 26.4 ± 11.7%) than in the virgin forest (ISF: 7.2 ± 0.9% and DSF: 6.7 ± 0.8%).

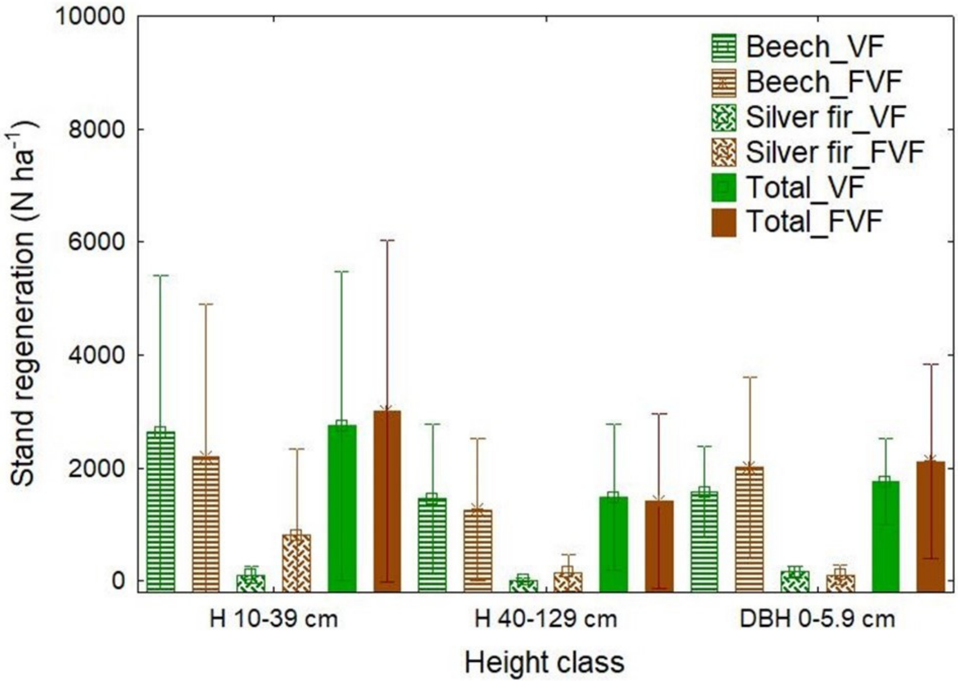

Figure 4. Density of saplings per forest type, species, and regeneration circle (RC1—5 m^2 for seedlings with height of 10–39.9 cm; RC2—10 m^2 for saplings 40–129.9 cm in height; RC3—20 m^2 for saplings with height >130 cm and dbh <6 cm). Error bars represent a 95% confidence interval. According to ANOVA–Tukey's testing, there were no significant differences found ($p > 0.05$) between the sampling category and forest type.

3.4. Soil Microclimate and Soil Respiration

Generally, the soil microclimate and soil respiration showed a seasonal pattern, especially for temperature and respiration (Figure 5). Thus, the soil temperature for all measurement periods (spring, summer, and fall, Figure 5A) was significantly higher ($p < 0.05$) in the FVF than in VF, with the largest difference in summer (5 °C) and the smallest in spring (1.7 °C). The difference between the two forests in terms of soil moisture did not show a clear pattern, being significant only for the spring measurements, with a higher average value in the virgin forest. The differences between the two forests diminished in summer, while in the fall, the soil moisture was slightly higher in the former virgin forest (Figure 5B). The soil respiration followed the seasonal pattern of the soil temperature, with the highest mean value reached in the summer and lowest in fall (Figure 5C). Significantly higher differences between the two forests were found only for summer (the largest one:

5.4 in FVF vs. 3.6 µmol CO_2 m^{-2} s^{-1} in VF) and for fall (2.82 vs. 1.99 µmol CO_2 m^{-2} s^{-1}). Generally, the soil CO_2 emissions were higher in the former virgin forest (Figure 5C).

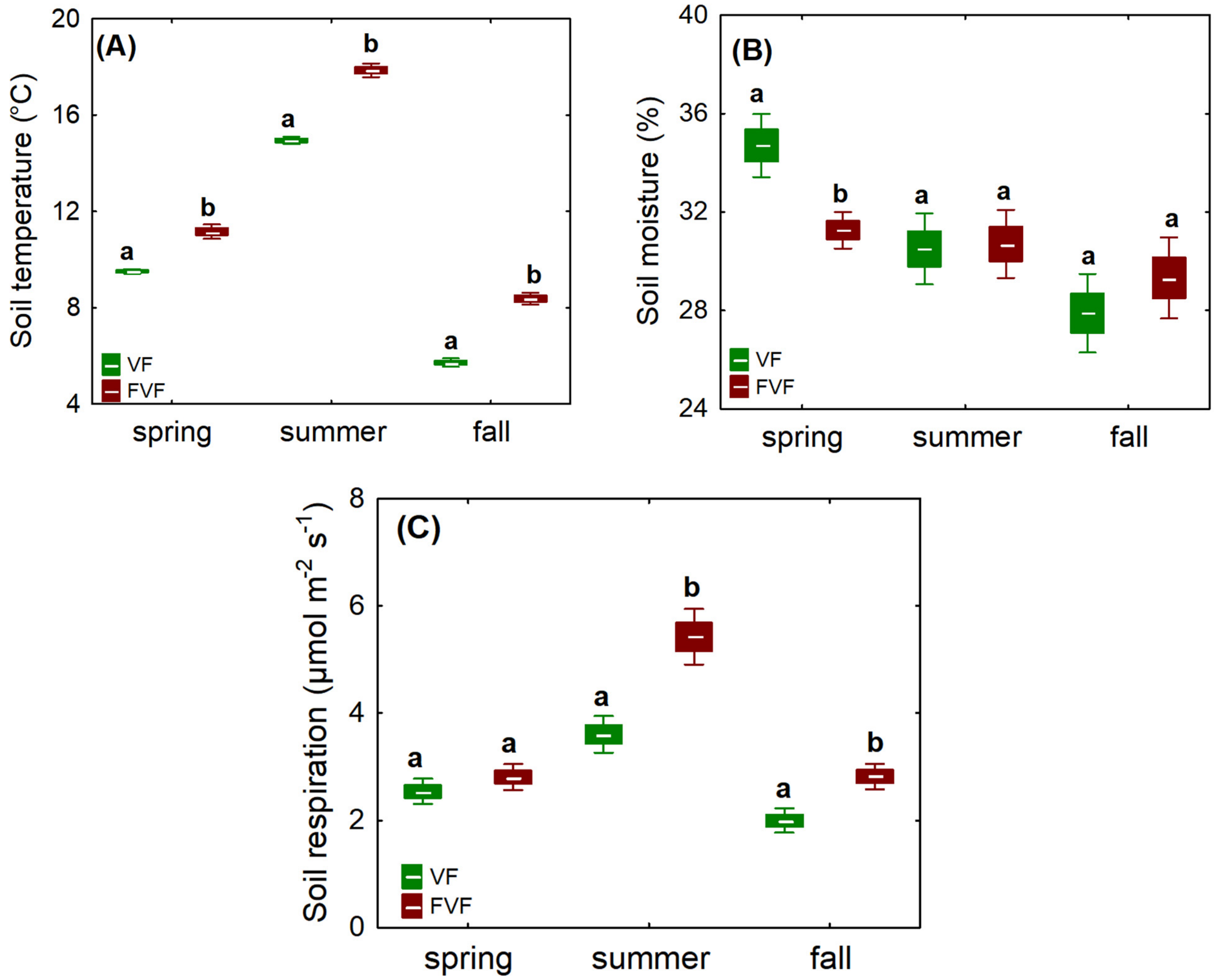

Figure 5. Boxplots of (**A**) soil temperature, (**B**) soil moisture, (**C**) and soil respiration along seasons per forest type (i.e., VF and FVF). Different letters (i.e., (**a**) and (**b**)) mean significant differences between the VF and FVF within each season. Boxes bound the standard errors of the mean. Whiskers represent the 95% confidence intervals and horizontal lines within boxes represent the mean values.

3.5. Ground Vegetation Diversity

Within each forest type, the diversity profiles of the plot curves were, in general, similar for low alpha values and diverged with an increase in the alpha up to alpha = 3, and for high alpha values (around a value of 4), they tended to converge again (Figure 6). Although as an average pattern, the decrease in lines was more abrupt for the former virgin forest (alpha varying from 0 to 2), there were also two plots among virgin plots where this decrease was pronounced.

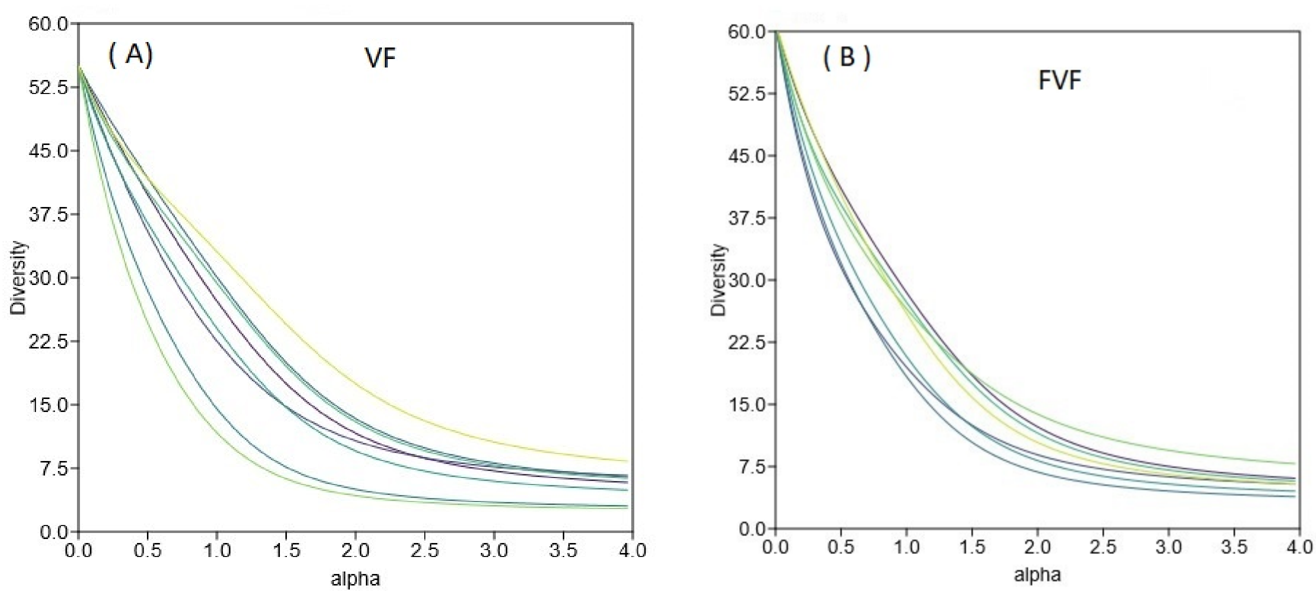

Figure 6. Diversity profiles of both forest types using the exponential of the Renyi diversity index. ((**A**)—virgin forest (VF), (**B**)—former virgin forest (FVF)). The scale alpha values: alpha = 0—provides the total number of species, alpha = 1—gives a measure directly proportional to the Shannon index, alpha = 2—similar to Simpson's index, high alpha value estimate the Berger–Parker index. Different color of lines represents the sampled plots within each forest type.

The assessment of the ground vegetation diversity in the two forests using different diversity indices showed different patterns of higher values (Margalef, Menhinick, evenness, equitability, Simpson), lower values (dominance, Brillouin, Fisher's alpha), or similar values (Shannon, Berger–Parker) in the virgin forest compared to the former virgin forest (Figure 7). Nevertheless, all tests failed to show significant diversity differences between both forest types (VF vs. FVF).

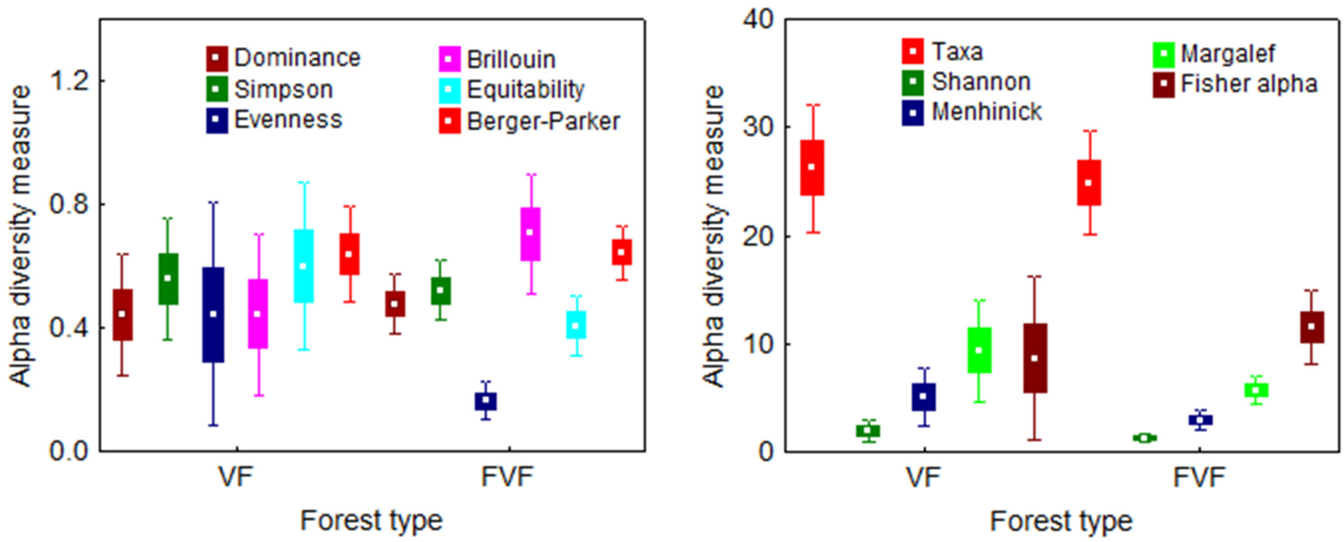

Figure 7. Ground vegetation diversity comparison between a virgin forest (VF) and former virgin forest (FVF). Alpha diversity measures: dominance, Simpson, evenness, Brillouin, equitability, Berger–Parker, taxa (richness), Shannon, Menhinick, Margalef and Fisher's alpha index. Boxes: means ± standard errors of the mean, whiskers: 95% confidence intervals.

4. Discussion

Our study found that the first silvicultural intervention in a former beech–silver fir mixed virgin forest did not significantly change the distribution of trees on diameter classes, still following an inverted J-shaped form (Figure 1) for both the silver fir and European beech species (Figure 2b,c). The inverted J shape is the typical diameter distribution for natural forests with shade-tolerant silver fir and beech species [3,12,21], suggesting a general structural stability and resilience [42,53] but also susceptibility to disturbance events of low-to-moderate severity [33,54]. This suggests that a single harvest did not change the characteristic shape of the tree distribution in our former virgin forests, as was the case in forests with long-term historical management, which showed a more bell-shaped distribution, clearly different from those of virgin forests [11]. Furthermore, the former virgin forest showed a similarly high vertical diversity. However, although the tree density was not significantly reduced in the former virgin forest, the number of trees with a dbh greater than 80 cm became significantly lower (Table 1), which is in agreement with the general removal of large-diameter trees in managed forests [35]. In the same way, some Bosnian, Croatian, and Slovenian virgin forests were transformed into managed forests approximately 120 years ago. The cutting intensity there was also around 40% for the first time, and later, it was up to 20% by applying a single-tree selection system or an uneven aged silvicultural system [21,35,55,56]. We supposed a similar evolution for our former virgin forest, which became a buffer zone for the virgin forest, after its inclusion as part of a UNESCO World Heritage Site in 2017. Related to the management goal for the forests in the buffer zone, according to the proposed (but not yet approved) guidelines (about what should be done in the buffer zones of UNESCO areas), forest managers should apply only selection systems (single-tree selection or a group selection system) nearby UNESCO reserves, which will maintain the uneven-aged structure into the future. Other structural forest characteristics such as the basal area, volume, Hdom, and Ddom were significantly reduced in the former virgin forest in comparison with the virgin forest, shown by the main differences between the virgin and managed forests [11,22]. The species composition in both forests was dominated by beech. This finding is in line with data presented in the work of Vandekerkhove et al. [57] for beech-dominated old-growth forest where silver fir and spruce were in small proportions. Previous studies [21,42,58] have reported a decline in silver fir in several old-growth forests in Central and Southeastern Europe. In contrast to these researchers, Keren et al. [59] observed, in the Dinaric Mountains of Bosnia, that fir and spruce dominated in the upper layer of the stand compared to beech. Moreover, during the last 50 years, European Beech has become the most competitive and vital tree forest species from sub-mountain to mountain regions, especially in the Central European mountains [60].

The amount of deadwood was arguably clearly different between the managed and unmanaged forests [11,61], with a significantly lower quantity in the managed forests, especially because in the past, the retention of deadwood in forests was not desired or allowed. Deadwood has been seen as a risk for the propagation of diseases and as a potential trigger of disturbance events [62], but since its crucial role in the preservation of forest biodiversity and ecosystem functioning has been scientifically proven [63], the retention of a certain amount of deadwood in managed forests from biodiversity goals has become an important task as part of numerous integrative forest management approaches [64]. The amount of deadwood in our former virgin forest reached only half of the amount in the virgin forest, but its amount (112 m^3 ha^{-1}) was still superior to that found in the managed forests. An amount of about 60–70 m^3 ha^{-1} of deadwood was found in the silver fir mixed managed forests of the Dinaric Mountains, three to five times lower than in virgin forests [11,65]. Moreover, Glatthorn et al. [15] found a much lower biomass stocked in the deadwood in managed forests in comparison with virgin Slovakian beech forests. However, the amount of deadwood in our former virgin forest was much greater than those found in the nemoral beech–oak forests of Western Romania (35–57 m^3 ha^{-1}) [63] or than the average volume in European forests (20 m^3 ha^{-1}, Forest Europe, 2020) and exceeded the quantity (30–40 m^3 ha^{-1}) proposed as the threshold for mixed montane European forests [66]. According to our study, where the proportion of DW in each forest was highest for silver fir compared with European beech (i.e., 84% of the total DW in FVF and 63% in VF, Table 2), our results confirmed that silver fir is in decline in both forests, which is consistent with numerous studies across Europe that have made observations over several decades [21,67].

A single silvicultural intervention did not significantly influence the distribution of deadwood by different decay classes (Figure 3); in both forests, the most decayed deadwood was predominant. The low percentages of "fresh" and "hard" deadwood indicate that intermediate or severe disturbances did not occur in the investigated virgin forest [42], which is in agreement with the findings of Visjnic et al. [11], while in the former virgin forests, part of the deadwood probably perceived as fresh and good was removed. Furthermore, the proportion of deadwood in relation to the total volume of trees was similar between the virgin and former virgin forest (22% vs. 27%, respectively). These small differences in the ratios of deadwood to live tree populations highlight the similar structure of FVF to VF, prior to anthropogenic disturbance. A similar proportion of DW in relation to the total wood mass was found in other virgin forests [11], while in managed forests, this ratio was significantly lower [65]. Moreover, the presence of DW for all decay classes in both sites highlights the highest level of ecosystem stabilization, especially for biodiversity conservation and soil biochemistry [42,68,69]. Despite much better light conditions, the regeneration in the former virgin forest showed only slightly higher density values than in the virgin forest (6744 vs. 6015 seedlings per ha, respectively). This may be a consequence of the short time after intervention (only seven years), but also of the increased competition of the understory vegetation [37]. However, a slightly higher density of seedlings (10–39 cm height) and of the tallest saplings (H > 1.3 m and dbh < 6 cm) in the former virgin forest suggests that the greater light availability created by tree harvesting stimulated the production of new seedlings and accelerated the growth of larger saplings, in accordance with the main objective of the group shelterwood system [40]. The better light conditions in the former virgin forest led to the improvement of regeneration diversity, even though the proportion of other species was insignificant (Acer pseudoplatanus, 0.2%; Picea abies, 0.3%, Populus tremula, 1.0%). In the future, it is expected that the larger gaps, specifically made by silvicultural practices (i.e., group shelter wood system) in FVF, will accelerate the tree recruitment process with consequences for its structure and composition [65]. Beech was the main species of the regeneration layer in both forests, but the proportion of silver fir regeneration in the former virgin forest was three times higher than in the virgin forest (Table S1). This tendency could have been a consequence of both soil microclimate conditions and the spectral composition of the light which can influence seedling emergence. A prior study [70] observed that the natural regeneration of fir trees is hindered by a low proportion of the blue component and a surplus of the green and red components of the light spectrum. Nevertheless, the higher proportion of silver fir seedlings in managed forests is considered as a result of silvicultural interventions [71], which induced more economically valuable conifer species such silver fir compared to beech, as is a common practice in many European beech–conifer mixtures [11,72]. One of the main factors controlling seed germination may be set by the soil microclimate. The dynamics of a soil microclimate along seasonal growth vegetation, and especially the soil temperature, which was significantly higher in the former virgin forest (Figure 5A), can accelerate the dynamics of natural regeneration with consequences in the structure and composition of seedlings or recruits. Forest microclimatic buffering capacity increases in periods with warmer and drier years. For instance, intact forest canopies mitigated increases in vapor pressure deficits and temperature extremes by 20% and 15%, respectively, compared to disturbed forests [3]. Another factor that can influence regeneration is browsing. As in other studies [42,73], we found beech to be less susceptible to browsing by ungulates (i.e., roe deer and red deer) than silver fir. A greater proportion of damaged saplings was found in the FVF (almost two times more) than in VF. Therefore, silver fir seedlings can lose the competitive advantage of early height growth, mainly by beech or pioneer species [74]. In addition, changes in the forest canopy, mainly due to human disturbance (e.g., silvicultural interventions), could greatly affect not only the soil microclimate but also soil respiration [75,76]. Furthermore, silvicultural interventions (e.g., group shelterwood system according to a forest management plan) can lead to soil compaction, which could thus restrict root growth and microbial activities. On the one hand, the significant differences in soil temperature between forest types, especially in summer (Figure 5C), was the main factor contributing to increased soil respiration in the FVF. On the other hand, silvicultural interventions could reduce competition for soil moisture and nutrients, which would help to stimulate the root growth of seedlings and recruits [77]. In addition, wood harvesting and organic matter mixed into the mineral soil would increase substrate availability, which could increase microbial activity and accelerate the decomposition of litter and soil organic matter [78]. Even though harvesting operations started less than ten years ago, it was still observed that adventive geoelements [43] appeared in the FVF, unlike in the VF. The category of adventive geoelements is characteristic of species (e.g., *Festuca drymea*, *Erigeron annuus*, *Erectites hieracifolia*) that are massively dispersed by humans [79]. Therefore, the presence of these geoelements is justified in forests where forest management is practiced, because only within them is the anthropogenic factor present.

5. Conclusions

The effect of the disturbance regime did not considerably change the shape of the distribution of trees per diameter class between each forest type, showing structural similarities between the two forest types before disturbance events. Furthermore, the differences in soil microclimate and the proportion of regenerated species between forests (i.e., VF and FVF) may affect the future of the natural forest type, such as its composition. On the one hand, this temporal fluctuation in natural regeneration will allow foresters to take beneficial and rapid measures to preserve natural species composition over time and space to, for instance, promote more silver fir. On the other hand, turning virgin forests into managed forests is not the right way to go. However, on the basis of the obtained results, the forest management applied here (i.e., group shelterwood system) was not always "bad". It promoted the regeneration and recruitment of silver fir, which according to the latest research, will disappear in many European old-growth forests or its share will fall to a negligible percentage in these forests in the near future. This is what makes sense in terms of our study area for future ecological research in the next 10–20 years, at least regarding silver fir dynamics.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f14040742/s1, Table S1: Natural regeneration per forest type, species, and regeneration circle (RC1—5 m^2 for seedlings with height of 10–39.9 cm; RC2—10 m^2 for saplings 40–129.9 cm in height; RC3—20 m^2 for saplings with height >130 cm and dbh <6 cm) (N ha^{-1} mean $\pm$ standard error). Minimum and maximum values (indicated in brackets) correspond to the average of the four regeneration sub-plots per plot.

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