Natural Regeneration of the Tree Stand in the Bilberry Spruce Forest—Clear-Cutting Ecotone Complex in the First Post-Logging Decade

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Abstract: Bilberry spruce forests are the most widespread forest type in the European boreal zone. Limiting the clear-cuttings size leads to fragmentation of forest cover and the appearance of large areas of ecotone complexes, composed of forest (F), a transition from forest to the cut-over site under tree canopy (FE), a transition from forest to the cut-over site beyond tree canopy (CE), and the actual clear-cut site (C). Natural regeneration of woody species (spruce, birch, rowan) in the bilberry spruce stand—clear-cut ecotone complex was studied during the first decade after logging. The effects produced by the time since cutting, forest edge aspect, and the ground cover on the emergence and growth of trees and shrubs under forest canopy and openly in the clear-cut were investigated. Estimating the amount and size of different species in the regeneration showed FE and CE width to be 8 m—roughly half the height of first-story trees. Typical forest conditions (F) feature a relatively small amount of regenerating spruce and birch. The most favorable conditions for natural regeneration of spruce in the clear-cut—mature bilberry spruce stand ecotone are at the forest edge in areas of transition both towards the forest and towards the clear-cut (FE and CE). Clear-cut areas farther from the forest edge (C) offer an advantage to regenerating birch, which grows densely and actively in this area.

Keywords: boreal forest; reforestation; dynamics; edge effect; spruce; Picea abies; Betula; birch; rowan; prickly rose

1. Introduction

Bilberry spruce stands are the most widespread forest type in the European boreal zone. Spruce timber is widely used in paper-making and construction. A major part of spruce stands has been altered by varying-intensity clear-cutting and selection cutting. Clear-cutting is the main method of timber harvesting in the boreal zone of Russia. This method is the most profitable but causes substantial landscape fragmentation (Figure 1b) and reduction of the natural forest area, thereby jeopardizing the inhabitants of old-growth forest communities [1]. The most critical problems of the consequences of clear-cuttings are reducing the biological diversity of the territory and restoring forests. These problems have been widely discussed in scientific literature since the 1980s. There is now an understanding that vulnerable species can be conserved not only through strict protection of natural forests but also by modifying the logging practices. One of the approaches, termed Variable Retention Forestry (VRF), is to retain trees in cut-over sites, to have a larger cut-over area remaining under the edge of the forest influence, etc. [1–6].
Forests are managed in various ways, one of which is Variable Retention Forestry (VRF). VRF involves retaining trees in cut-over sites, creating a larger cut-over area remaining under the edge of the forest influence, etc. 

![Locations of sampling sites and transect layout.](image)

Alteration of the tree canopy affects the structure of the understory, including the amount and quality of the regeneration. Retention of the regeneration of the main tree species is a way to make VRF more attractive economically, as reforestation costs are reduced. The retained forest elements and the forest edge influence the survival and growth of the existing regeneration and promote the emergence of the next (post-logging) generation of coniferous trees by providing them with a competitive advantage. Still, these relationships are complex and dependent on the stand composition and specific ecological conditions.

Some timber harvesting methods used in Russia meet the principles of VRF. Such systems, first of all, the various selection cutting systems, which both conserve the biodiversity and promote natural regeneration of the tree stand. Improved conditions for spruce growth in shelterwood systems have been highlighted by J. Souček, F.N. Druzhinin, N.N. Terinov, and others. A common practice in clear-cutting in Russia is to leave solo trees or 0.2–0.4 ha forest patches in the cut-over site. Originally, this was done to retain seed sources in the clear-cut, but later on, they were also found to contribute to the conservation of rare species and the forest environment that promotes reforestation. A common perception is that the impact of a tree or forest edge extends to a distance equal to the tree height. The clear-cutting area within the forest impact zone is determined accordingly, and matching regulations and techniques are suggested. Forest impact creates a milder microclimate and the ground cover is affected less severely than in the unsheltered clear-cut. In forestry practice in the taiga zone of Russia, it is accepted that the impact zone of the forest edge is 2/3 of the height of the tree.
studies of post-logging changes in the microclimate and ground cover structure showed the tree stand impact zone to be approximately half the stand height [30,31].

The issue of natural recovery after logging of boreal forests has been studied quite well [32–36] etc. In poor conditions of lichen and cowberry pine forests on sandy soils, cuttings are overgrown with pine [37,38]. In more fertile conditions of pine forests and bilberry spruce forests, the natural restoration of the forest community goes through the stage of the dominance of birch or aspen [36]. Here, for accelerated cultivation of commercial coniferous wood, expensive measures must be carried out [39,40].

In the scientific literature, the issue of overgrowth of the open part of deforestation is more often considered, without taking into account the boundaries of the contiguity of the remaining forest, where the restoration process has its own characteristics [41–43]. Thus, the knowledge of the influence of the remaining spruce stand on the regeneration of tree species is of theoretical and practical importance.

We undertook to investigate the natural regeneration of woody species in different parts of the bilberry spruce forest—clear-cut ecotone complex (EC) in a dynamic perspective—in the first decade after logging. Our task was to assess, firstly, how the amount of undergrowth in the EC changes for some time after logging, and, secondly, to compare the amount of undergrowth in different EC zones.

2. Materials and Methods

2.1. Study Area

The studies were carried out in 2014–2015 in Kholmogorsky District, Arkhangelsk Region (64.4° N, 41.8° E) (Figure 1). The area belongs to the boreal biome. According to the geobotanic zonation adopted in Russia [44], the study area belongs to the northern taiga subzone, bordering forest-tundra in the north and middle taiga in the south, from around 62° N. Absolute elevations in the study area vary within 40–80 m a.s.l., mean annual air temperature (over the past ten years) is +2.8 °C, mean annual precipitation is 660 mm. The coldest month is January (−11.7 °C), with the absolute minimum at −40.0 °C (6 January 2018). The warmest month is July (+17.2 °C), with the absolute maximum at +40.1 °C (1 August 2018). The snow-covered period lasts from early November through April. The duration of the growing season is about 150 days—from mid-May through September (Kholmgory weather archives (www.rp5.ru (accessed on 20 September 2021))). The most common type of forest in the study area is bilberry spruce stands (Piceetum myrtillosum). There are also small areas of Sphagnum pine stands and Polytrichum spruce stands. A brief description of the studied spruce forests is given in Table 1. Pristine spruce-dominated coniferous forest used to prevail until the late 20th century. Nowadays, much of the spruce forest has been logged down, and areas of secondary mixed forest dominated by aspen and birch have become widespread.

2.2. Material

The objects were young trees (regeneration) of spruce (Picea abies (L.) H.Karst.) and birch (Betula pubescens Ehrh.). We also studied aspen (Populus tremula L.), prickly rose (Rosa acicularis Lindl.), and rowan (Sorbus aucuparia L.), which are essential as spruce competitors in the early stages of logging overgrowth.

Surveys were done in adjacent areas of a bilberry spruce forest and a hairgrass-dominated clear-cut (2 to 10 years old), which constitute an ecotone complex (EC). Regeneration in plot 1 was measured twice in the same transects in the 2nd and 3rd years after cutting. Characteristics of the surveyed spruce stands and clear-cuts are given in the Table 1.
Table 1. Characteristics of the spruce stands and clear-cuts.

| Site | Transects | Forest Edge Aspect (º) | Age | Dominant Herbaceous Species | Field Layer Cover (%) | Basal Area (m²/ha) | Average Height (m) | Canopy Cover (%) |
|------|------------|-------------------------|-----|-----------------------------|-----------------------|-------------------|-------------------|------------------|
| 1    | 1          | N (0)                   | 2 (3)| Deschampsia flexuosa, Vaccinium vitis-idaea | 15                    | 110               | Spruce 38.8       | Birch 5.6        |
|      | 2          | E (90)                  | 2 (3)| Deschampsia flexuosa, Vaccinium vitis-idaea | 25                    | 160               | Spruce 31.1       | Birch 1.0        |
| 1    | 3          | S (180)                 | 2 (3)| Deschampsia flexuosa, Vaccinium vitis-idaea | 15                    | 150               | Spruce 31.4       | Birch 2.0        |
|      | 4          | W (270)                 | 2 (3)| Deschampsia flexuosa, Vaccinium vitis-idaea | 15                    | 170               | Spruce 10.5       | Birch 1.0        |
| 2    | 1          | SE (135)                | 5   | Vaccinium myrtillus, V. vitis-idaea         | 35                    | 155               | Pine 2.2          | Birch 1.2        |
|      | 3          | W (270)                 | 5   | Deschampsia flexuosa, Epilobium angustifolium | 30                    | 135               | Aspen 0.8         | Birch 1.5        |
|      | 3          | S (210)                 | 5   | Epilobium angustifolium, Vaccinium vitis-idaea | 30                    | 130               | Spruce 10.2       | Birch 1.0        |
|      | 3          | N (0)                   | 5   | Carex globularis, Vaccinium vitis-idaea     | 40                    | 140               | Spruce 7.2        | Birch 1.2        |
|      | 3          | E (90)                  | 5   | Deschampsia flexuosa, Vaccinium vitis-idaea | 35                    | 180               | Spruce 9.2        | Birch 1.3        |
|      | 3          | S (200)                 | 10  | Vaccinium vitis-idaea, Carex globularis     | 30                    | 140               | Spruce 13.7       | Birch 3.1        |
|      | 2          | W (290)                 | 10  | Epilobium angustifolium, Gymnocarpium dryopteris | 60                    | 160               | Spruce 25.4       | Birch 4.9        |
|      | 3          | E (110)                 | 10  | Vaccinium vitis-idaea, Deschampsia flexuosa | 70                    | 175               | Spruce 30.2       | Birch 3.7        |
|      | 3          | N (0)                   | 10  | Vaccinium vitis-idaea, Carex globularis     | 60                    | 180               | Spruce 27.3       | Birch 5.0        |

2.3. Methods

Regeneration and understory were surveyed in 100 m long, and 2 m wide transects running from the forest to the clear-cut (Figure 1c). The transects were split lengthwise into adjacent sampling subplots (1 × 2 m). The transect center was at the contact of the forest and the clear-cut so that 50 subplots were situated inside the forest and 50 in the clear-cut. In each surveyed ecotone complex, 2–3 transects were made in the four directions (north, east, south, west). We estimated the regeneration of the woody species most common in the study area: spruce, birch, aspen, rowan, and prickly rose. The analysis of the spatial distribution of regeneration among zones excluded the subplots with soil cover damage (ruts from logging machines) and 100% littering with logging residues, where woody plants were either all gone or heavily damaged. The height of the regeneration was measured. All regenerating woody plants in the subplots were grouped into three categories: small (up to 0.5 m high), medium (up to 1.5 m), and large (taller than 1.5 m) regeneration [29]. The percentage covers of all vascular plant and moss species were determined for each subplot.

All data were divided into 3 groups according to the time since cutting: 3, 5, and 10 year. In the 2-year-old clear-cut, only spruce and birch regeneration was estimated, while prickly rose and rowan were ignored. The position of the transect with respect to the forest edge aspect was taken into account by distinguishing 4 variants: 1—northern, 2—eastern, 3—southern, 4—western aspects. The aspect influences illumination at different times of day and, hence, soil warming and moisture.

Moss species are indicators of the moisture conditions in the site. We estimated the cover of 6 moss species divided into three groups according to their moisture requirements: Sphagnum capillifolium, Sph. centrale, Sph. girgensohnii (these 3 species are hereafter collectively termed Sphagnum spp.)—indicating stagnant conditions, Polytrichum commune—moist sites, Pleurozium schreberi, and Hylocomium splendens—forest mosses growing in well-drained sites without excessive moisture. The percentage cover of each moss species was determined for all subplots, after which the contribution of each of the above species groups to the total percentage cover of mosses was indicated, stating one of the four categories: 1—dominant, 2—subdominant, 3—present (the species’ share is much lower than
that of other species), 4—absent. The interplay between field-layer dominants and woody regeneration was analyzed using 4 classes of abundance: 1—the species’ percentage cover (PC) above 50%; 2—PC of 25 to 50%; 3—PC of 0.5% to 25%, and 4—the species is absent from the subplot.

The analysis of variance (Kruskal-Wallis ANOVA) was applied to determine how the amount of regeneration and understory was related to the forest edge aspect and the abundance of the dominant ground cover species (mosses: *Sphagnum* spp., *Polytrichum commune* Hedw., *Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) Bruch et al.; dwarf shrubs: *Vaccinium myrtillus* L., *V. vitis-idaea* L.; *Deschampsia flexuosa* (L.) Trin., *Epilobium angustifolium* L.) under the forest cover and in the clear-cut.

The relationship between spruce and birch plants was assessed by χ² test—co-occurrence of their small regeneration (up to 0.5 m high) and regenerating plants taller than 0.5 m in the sampling subplots was analyzed.

We applied Kruskal-Wallis ANOVA for comparisons between the data split into four groups based on the EC zone they belonged to: 1—forest (F), 2—forest edge towards the forest (FE), 3—clear-cut along forest edge (CE), 4—clear-cut (C) (Figure 2).

![Figure 2. Ecotone complex arrangement and zone notations. See text for explanations.](image)

Having pooled together the data on the total amount of regeneration in the ecotone from spruce forest to clear-cuts of different ages, we applied the analysis of variance for different sizes of the forest edge and clear-cut edge zones (3 to 12 m). Based on the amount of regeneration, we determined the distance covered by the edge effect, i.e., the width of EC zones in which distinctions between the four zones were significant (Figure 2). Taking into account the changes in air temperature, illumination, and ground cover structure revealed in our previous studies, the width of the forest-to-clear-cut transitional zone was identified as approximately half the height of first-story trees, i.e., 8 m in each direction from the forest edge [31]. Thus we hypothesized the average distance of the edge effect on regeneration as 8 m. Having found the said width for the zones FE and CE, we performed a statistical analysis of the temporal and spatial variation of the amount of spruce and birch regeneration in the EC taking the size categories into account.

3. Results

3.1. Significant Factors for the Distribution of Regeneration in the Forest and the Clear-Cut

We studied the key factors that can influence the total amount of woody regeneration and understory: forest edge aspect and the most abundant moss and vascular plant species (Table 2) under the forest canopy (F and FE) and in the clear-cut (CE and C).
Table 2. ANOVA results for the distribution of young birch, spruce, rowan, and prickly rose plants in the ecotone complex in connection with microhabitat ecological and coenotic characteristics.

| Main Effects          | Birch | Spruce | Rowan | Prickly Rose |
|-----------------------|-------|--------|-------|--------------|
|                       | Forest| Clear-Cut| Forest| Clear-Cut| Forest| Clear-Cut| Forest| Clear-Cut |
| **Aspect**            |       |        |       |              |       |        |       |          |
| H-value               | 13.12 | 20.41  | 23.82 | 15.81        | 30.71 | 27.67  | 60.65 | 34.01     |
| p-value               | 0.49  | <0.001 | 0.0025 | 0.008         | <0.001 | <0.001 | <0.001 | <0.001     |
| df/n                  | 3/650 | 2/527  | 3/650 | 2/527        | 3/650 | 2/527  | 3/650 | 2/527     |
| **Sphagnum spp. abundance** |       |        |       |              |       |        |       |          |
| H-value               | 26.27 | 100.92 | 15.28 | 22.20        | 6.09  | 7.06   | 3.11  | 5.84      |
| p-value               | <0.001 | <0.001 | 0.0016 | <0.001        | 0.10  | 0.070  | 0.37  | 0.12      |
| df/n                  | 3/325 | 3/325  | 3/325 | 3/325        | 3/325 | 3/325  | 3/325 | 3/325     |
| **Polytrichum commune abundance** |       |        |       |              |       |        |       |          |
| H-value               | 5.63  | 44.62  | 6.11  | 26.89        | 2.58  | 1.73   | 0.67  | 3.31      |
| p-value               | 0.13  | <0.001 | 0.10  | <0.001        | 0.46  | 0.63   | 0.87  | 0.34      |
| df/n                  | 3/325 | 3/325  | 3/325 | 3/325        | 3/325 | 3/325  | 3/325 | 3/325     |
| **Pleurozium schreberi abundance** |       |        |       |              |       |        |       |          |
| H-value               | 6.03  | 14.95  | 8.83  | 15.32        | 4.21  | 4.87   | 2.49  | 4.87      |
| p-value               | 0.11  | 0.0018 | 0.032 | 0.0015        | 0.24  | 0.18   | 0.47  | 0.18      |
| df/n                  | 3/325 | 3/325  | 3/325 | 3/325        | 3/325 | 3/325  | 3/325 | 3/325     |
| **Hylocomium splendens abundance** |       |        |       |              |       |        |       |          |
| H-value               | 15.68 | 56.41  | 13.46 | 7.97         | 3.12  | 8.32   | 2.40  | 2.93      |
| p-value               | 0.0013 | <0.001 | 0.0037 | 0.046        | 0.37  | 0.039  | 0.49  | 0.40      |
| df/n                  | 3/325 | 3/325  | 3/325 | 3/325        | 3/325 | 3/325  | 3/325 | 3/325     |
| **Vaccinium myrtillus abundance** |       |        |       |              |       |        |       |          |
| H-value               | 0.83  | 4.09   | 6.17  | 7.20         | 0.94  | 4.16   | 3.49  | 2.60      |
| p-value               | 0.84  | 0.25   | 0.10  | 0.065        | 0.82  | 0.24   | 0.32  | 0.45      |
| df/n                  | 3/325 | 3/325  | 3/325 | 3/325        | 3/325 | 3/325  | 3/325 | 3/325     |
| **Vaccinium vitis-idaea abundance** |       |        |       |              |       |        |       |          |
| H-value               | 0.35  | 4.50   | 0.84  | 6.79         | 4.29  | 1.85   | 4.29  | 4.15      |
| p-value               | 0.84  | 0.21   | 0.65  | 0.078        | 0.12  | 0.60   | 0.12  | 0.24      |
| df/n                  | 2/325 | 2/325  | 2/325 | 2/325        | 2/325 | 2/325  | 2/325 | 2/325     |
| **Deschampsia flexuosa abundance** |       |        |       |              |       |        |       |          |
| H-value               | 1.67  | 4.37   | 0.005 | 0.14         | 19.98 | 5.08   | 3.67  | 1.65      |
| p-value               | 0.19  | 0.22   | 0.94  | 0.98         | <0.001 | 0.16  | 0.055 | 0.64      |
| df/n                  | 1/325 | 1/325  | 1/325 | 1/325        | 1/325 | 1/325  | 1/325 | 1/325     |
| **Epilobium angustifolium abundance** |       |        |       |              |       |        |       |          |
| H-value               | 0.18  | 2.56   | 5.80  | 9.13         | 0.94  | 10.07  | 0.17  | 8.75      |
| p-value               | 0.67  | 0.46   | 0.012 | 0.027        | 0.33  | 0.018  | 0.68  | 0.032     |
| df/n                  | 1/325 | 1/325  | 1/325 | 1/325        | 1/325 | 1/325  | 1/325 | 1/325     |

Note: p-values below 0.05 are in bold type.

3.2. Forest Edge Aspects

The CE zone at the north-facing forest edge contained a reliably greater amount of birch and spruce regeneration than in all other variants (Figure 3). Understory species (rowan and prickly rose) respond to the forest edge aspect differently, and they were significantly more abundant at the west-facing forest edge.

3.3. Mosses as Indicators for Moisture and Trophic Conditions

*Sphagnum* species tend to occupy microdepressions and other stagnant sites. It is likely that soil moisture, of which *Sphagnum* mosses are an indicator, was the determinant for the distribution of woody seedlings and then the regeneration. Regenerating birch was found to be significantly more abundant in *Sphagnum*-dominated and *Sphagnum*-subdominated sites in the clear-cut and in *Sphagnum*-dominated sites under the forest canopy (Figure 4).
3.2. Forest Edge Aspects

The CE zone at the north-facing forest edge contained a reliably greater amount of regeneration than at forest edges facing other cardinal directions: northern, eastern, southern, and western. Letters indicate differences between means (based on the analysis of variance).

![Figure 3](image-url) Amount of woody regeneration and understory in the clear-cut adjoining the forest edge in different cardinal directions: ■ northern, ■ eastern, ■ southern, ■ western. Letters indicate differences between means (based on the analysis of variance).

![Figure 4](image-url) The amount of woody regeneration in the forest and the clear-cut depending on the share of Sphagnum mosses in the percentage cover: ■ dominant, ■ subdominant, ■ present, ■ absent. Letters indicate differences between the means for the forest and the clear-cut (based on the analysis of variance).

The effect of Sphagnum spp. presence and abundance on the distribution of spruce regeneration were much lower. Regenerating spruce was reliably more abundant only in Sphagnum-dominated sites.

Similar to Sphagnum spp., Polytrichum commune indicates high soil moisture in the subplot. In contrast to Sphagnum, Polytrichum commune tolerates tree stand removal and increased insolation quite well, so its percentage cover does not decrease in clear-cuts compared to the original forest community. Clear-cut subplots lacking Polytrichum commune had significantly fewer regenerating birch trees than the subplots with a relatively high abundance of the moss. Spruce regeneration in the clear-cut was also significantly more abundant in sites containing this moss species. For sites under the forest canopy, no correlation was revealed between spruce and birch regeneration amounts and the percentage cover of Polytrichum commune (Table 2).

The distribution of rowan and prickly rose plants did not correlate with the abundance of Sphagnum and Polytrichum (Table 2).

True mosses (Pleurozium schreberi and Hylocomium splendens) are typical boreal species forming a moss cover under a forest canopy. They respond negatively to stand removal, and their high abundance in the clear-cut suggests that the moisture conditions have remained similar to what used to be under the cut-over forest canopy. Subplots lacking
true mosses had a significantly higher amount of spruce regeneration under the forest canopy, and their C zone also contained more regeneration of birch.

3.4. Vascular Plants

Forest grasses (*Deschampsia flexuosa* and *Calamagrostis phragmitoides*) are expectedly more abundant in gaps and dominate in clear-cuts. A positive correlation for hairgrass abundance was found only with the amount of rowan regeneration in the forest (Table 2)—both species occurred in the subplots situated in canopy gaps.

3.5. Competition between Spruce and Birch Regeneration

Studying the relationship of spruce and birch regeneration of different height categories in the surveyed clear-cuts, we analyzed the occurrence of small regeneration plants (up to 0.5 m high) and those taller than 0.5 m in the sampling subplots. We found that small spruce regeneration was significantly more abundant in the subplots lacking medium-size and large birch (*p*-value = 0.029). Similarly, small birch was significantly less abundant in sites with medium-size and large spruce (*p*-value < 0.001).

Analyzing the occurrence of small and >0.5 m spruce regeneration, we found that small regeneration was significantly more abundant in the subplots simultaneously containing regeneration plants taller than 0.5 m (*p*-value < 0.001). Birch regeneration also exhibited a pronounced positive association between small and large plants (*p*-value < 0.001). This pattern speaking of spruce, may suggest that larger regeneration plants create a favorable environment for seed sprouting as they suppress ground-cover plants.

3.6. Transitional Zone Width

Comparison of the combined amounts of birch and spruce regeneration across EC zones shows the effect of the forest on the clear-cut extends to a distance of up to 8 m. This is the distance (in the CE zone) at which the amount of regenerating birch is transitional from low values in the adjacent forest to high values in the clear-cut. The total amount of spruce in this zone is significantly higher than in the forest and the clear-cut (Figure 5). Thus, CE width for regeneration is 8 m. Although there was no significant difference between the F and FE zones in the amount of regeneration (Figure 5), we assume, proceeding from our previous studies [30], that FE width is also equal to CE width—8 m.

Regeneration of birch in the forest was represented by solo plants in some sampling subplots (density varying from 200 to 1800 plants/ha, i.e., not more than 1 plant per 3 subplots). Its density in the FE zone increased in some transects to 3000 plant/ha, but the difference with subplots in the F zone was generally insignificant. Starting from the forest edge towards the clear-cut, the amount of birch regeneration multiplied: to 5000–8000 plants/ha in the CE zone, and to 8000–10,000 plants/ha in the C zone (Figure 5).

Spruce regeneration density grew from inside the forest (4100 plants/ha on average) towards its edge, reaching a maximum in the CE zone (5400 plants/ha). Regenerating spruce density was the lowest in the C zone—1800–2500 plants/ha, twice lower than in the F zone (Figure 5).

The density of rowan regeneration in open spaces (in C and CE zones) was about 1.5 times higher than under the forest canopy (F and FE zones) (Figure 5).

The amount of prickly rose regeneration was significantly higher in the clear-cut (C zone) than in other EC zones (Figure 5).

Aspen regeneration in most transects occurred as solo plants, and only one subplot contained the species in an amount sufficient for the analysis of spatial distribution. The density of aspen regeneration under the forest canopy (F and FE zones) was an order of magnitude lower than in the clear-cut (C zone) (100, 200, and 2000 plants/ha, respectively).
3.2. Forest Edge Aspects

The CE zone at the north-facing forest edge showed the highest density of naturally regenerating birch in regenerating birch species.

Amount of woody regeneration and understory in the clear-cut adjoining the forest edge in different cardinal directions.

**Figure 6.** Variation of birch regeneration amounts in the EC by size categories: small (up to 0.5 m high), medium (up to 1.5 m high), and large (higher than 1.5 m). Means values and standard errors are shown.

3.7. Temporal and Spatial Variation of the Amount of Regeneration concerning Size Categories

The distribution of birch regeneration over the bilberry spruce forest—clear-cut EC showed its amount to be significantly lower under the spruce canopy (F zone) than in the adjacent clear-cut (C zone) irrespective of the time since cutting (Figure 6). Only the FE zone in the 10-year-old clear-cut has an increased amount of regenerating birch up to 0.5 m high. The amount of naturally regenerating birch in the CE and C zones increased with time since cutting.
The 2-year-old clear-cut contained very little birch regeneration, its amount being 260 plants/ha on average. The amount of birch regeneration grew abruptly in the 3-year-old clear-cut due to mass germination. Besides, small regeneration was twice more abundant in the open clear-cut (C zone) compared to the CE zone. Five-year-old clear-cuts also contained more small-size regeneration in zone C than in zone CE. By the age of ten, the birch canopy has closed in zone C, and this community could be classified as a young stand. The newly formed canopy notably reduces the possibility of further seedling emergence. By the tenth year, small- and medium-size regenerating birch in the transitional zone (CE) was no longer fewer than in the clear-cut, but large regeneration was much less abundant, and the birch stand canopy had not reached closure.

The total amount of spruce regeneration in the forest was 4000 plants/ha on average in all the surveyed subplots. Two years after cutting, the amount of regenerating spruce in zone F differed little from other zones (Figure 7). Another year later, in the 3rd year after cutting, the number of spruce seedlings increased several times both in the CE zone and in the open clear-cut (C zone).

Figure 7. Variation of spruce regeneration amounts in the EC by size categories: small (up to 0.5 m high), medium (up to 1.5 m high), and large (higher than 1.5 m). Means values and standard errors are shown.

Five and ten years after cutting, the conditions for the emergence and survival of regenerating spruce remained favorable only in the FE and CE zones. In 10-year-old clear-cuts (C zone) with the regeneration made up of birch, the total amount of regenerating spruce was lower than in the adjacent bilberry spruce forest (F zone).

4. Discussion
4.1. Environment Characteristics in the Forest, Transitional Zone, and the Clear-Cut

The study of the regeneration distribution over the EC and its determinant factors confirmed our previous findings [31] of the four distinct zones: forest, a transition from forest to clear-cut under forest canopy, a transition from forest to clear-cut beyond forest
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canopy, and the clear-cut per se. Each one has its specific microclimate and coenotic features, as well as the amount and quality of regeneration.

This study corroborated the previously determined 8 m width of the transitional zones FE and CE, which is roughly half the average tree stand height in the surveyed north-taiga bilberry spruce forests. Microclimate parameters (illumination, surface air temperature) in the bilberry spruce forest and the clear-cut change at 8–10 m distance into the forest [31]. The width of transitional zones in other regions and for other woody species varies from a half to the whole tree height, sometimes more. According to a study of microclimate parameters in a 50–60 m high *Pseudotsuga menziesii* stand [20], the impact zone of the adjacent clear-cut reached 30–60 m into the forest community for parameters such as shortwave solar radiation and soil temperature, and up to 240 m inwards for air temperature and humidity, and wind speed. Where the stand of *Abies lasiocarpa* and *Picea engelmannii* was 21 m high, the transitional zone, in which temperature and soil moisture parameters changed, was estimated to be 7–18 m in both directions from the forest edge [25].

Differences between zones were also seen in the ground cover structure. The main ground cover dominants in zones F and FE were true mosses (*Hylocomium splendens* and *Pleurozium schreberi*) and forest dwarf shrubs (*Vaccinium myrtillus* and *V. vitis-idaea*). The field layer in CE was generally similar to that in the forest—the contribution of grasses was minor. At the same time, mosses associated with moist habitats (*Sphagnum* spp. and *Polytrichum commune*) were more abundant than in the F zone. The average abundance of mosses in zone C was lower than in other zones of the EC. The most conspicuous distinctive feature of zone C was the dominance of grasses (*Deschampsia flexuosa*, *Calamagrostis phragmitoides*), which accounted for 20% of the percentage cover on average. Microelevations and areas around stumps had a higher percentage cover of *V. vitis-idaea* [45,46].

Regeneration under the canopy (F zone) was predominantly represented by spruce, while birch were scarce, although they were present in the original canopy. The fact that the light-loving birch and pine cannot grow under a spruce canopy and, hence, that these species are little involved in the natural regeneration has been highlighted by several authors [47,48]. The understory species rowan and prickly rose occurred throughout in minor amounts.

The structure of regeneration in FE in the first years after cutting was the same as inside the forest community, but ten years later, there was significantly more small-size regenerating spruce and birch in this zone.

CE featured the greatest amount of regenerating spruce compared to all other zones. Other studies have also demonstrated that this zone contained the greatest amount of small-size coniferous regeneration [49,50], and this pattern persisted 20 years after stand removal [51] and 30–35 years later [30,52]. The environment in the CE zone was the most favorable for the emergence and growth of the young spruce generation—temperature, light, and moisture conditions, no competition from herbaceous and woody vegetation [25,27]. Furthermore, regenerating birch was significantly less abundant here than in the clear-cut, permitting spruce to populate this zone and form the tree stand actively. Thus, both our studies and data from the literature show that a peculiar environment favoring the regeneration of spruce is formed at the forest edge.

In the center of the hairgrass-dominated clear-cut (C zone), on the contrary, birch regeneration predominated. Birch being a light-demanding pioneer species with high growth energy, rapidly occupies the cut-over space and competes both with spruce seedlings and with previous-generation spruce (retained after stand removal), outgrowing and suppressing them [33,53,54]. The analysis of competition between spruce and birch occurrence evidences a clearly negative association of spruce and birch regeneration. This zone is likely to develop a birch-dominated community with spruce in the second story. Also, clear-cuts more often than the adjacent forest contain rowan—a frequent shade-tolerant understory species in European Russia [55]. Under the canopy of actively regenerating birch in clear-cuts, rowan numbers grow insignificantly. Although aspen was rare and
scant in the surveyed stands, it does populate clear-cuts very actively, propagating by root sprouts and seeds [56]. Prickly rose, like rowan, is a widespread understory species but is more light-demanding [57] and forms single-species stands in open sites.

4.2. Time since Cutting

Birch regeneration in clear-cut sites gained in numbers as time passes since cutting. Birch is known for frequent and abundant seed-bearing and intensive growth [58,59]. It can, therefore, rapidly capture the released spaces, occupying the dominant position [56]. Another factor is its capacity for vegetative propagation—after a stand comprising birch is logged down, birch begins to regenerate rapidly and grow actively [60].

Spruce amounts, on the contrary, were the highest in the early stages of post-logging regeneration due to the ample presence of the previous spruce generation retained from the cut-over forest. As time passed since cutting, the amount of spruce regeneration declined confidently. There are several possible reasons for that. Firstly, in 2–3 years, the open cut-over space gets overgrown with sod-forming grasses, which prevent the germination of spruce seeds [61] and cause the death of small regeneration plants [62]. Secondly, since the fifth year after cutting, the main competitors for spruce regeneration are birch plants derived both from seeds and through sprouting [63]. Although spruce can for a long time survive under tree canopy, it cannot stand competition from birch regeneration.

4.3. Forest Edge Aspect

The greatest amount of spruce and birch regeneration in the clear-cut was found at the north-facing forest edge. This is likely because such sites remain in the shade during the daytime, preventing desiccation of the plants [41,64,65].

Prickly rose and rowan plants, on the contrary, develop more intensively in clear-cuts near the west-facing forest edge, i.e., in the most thoroughly warmed sites.

4.4. Mosses Associated with Moist Habitats (Sphagnum spp. and Polytrichum commune) and Mosses Associated with Well-Drained Habitats (Hylocomium splendens and Pleurozium schreberi)

A positive correlation was found between Sphagnum spp. and Polytrichum commune abundance and regeneration of birch and spruce, which was the most explicit in the clear-cut. Conversely, the number of birch and spruce regeneration is significantly higher at sites with the absence or small presence of Hylocomium splendens and Pleurozium schreberi. The positive correlation between birch and spruce regeneration and the moss cover structure can be explained by a set of factors. The thick cover of true mosses physically hinders the rooting of woody seedlings [66]. The cover of Polytrichum and Sphagnum mosses, on the other hand, has a different structure and indicates excessive moisture conditions, where seed germination is not hindered, and constantly high moisture is guaranteed.

The importance of high moisture is also evidenced by the fact that birch seedlings are abundant in the microdepressions created by the uprooting of large trees and in the tracks of logging machines, where the soil cover was damaged. Birch is an intensively transpiring species [67], which is the reason for its positive correlation with moisture.

5. Conclusions

When bilberry-type spruce stands are clear-cut and part of the forest is left intact, there forms the following ecotone complex: the forest site (F), the transition from forest to the cut-over site under tree canopy (FE), the transition from forest to the cut-over site beyond tree canopy (CE), and the actual clear-cut site (C). All four zones are clearly distinguished through a set of traits. Judging by the amounts and sizes of regeneration of different species, the width of zones FE and CE is 8 m each—roughly half the height of first-story trees.

The effect of the mother stand canopy is vividly illustrated by changes in the structure of regeneration in zones of the ecotone complex. Typical forest conditions (F) are noted for relatively low amounts of regeneration of spruce, birch, rowan, and prickly rose. The FE and CE zones contain a significantly higher amount of regenerating spruce, mainly recently germinated seedlings and small regeneration, while CE also features a sharp rise
in the amount of small and medium-size birch regeneration. In the C, the total amount of birch regeneration 5–10 years after cutting is approximately the same as in CE, but large regeneration plants are significantly more abundant. These patterns evidence quite convincingly that the sparse spruce stand offers optimal conditions for regeneration of spruce, while for a pioneer species such as birch, optimal conditions are found in an open clear-cut, where birch was regenerating actively through both root sprouts and seeds, and growing at a high rate throughout the period of observations. By the 10th year after cutting, one can speak of an established (closed) tree canopy—the average number of birch taller than 1.5 m in the clear-cuts was 4000–6000 plants/ha.

In addition, the transitional zones formed after clear-cutting differ depending on the forest edge aspect. Surveys show that north-facing sites contain greater amounts of spruce and birch regeneration due to the microclimate and less variable temperature and moisture conditions.

Overall, the most favorable conditions for natural regeneration of the spruce forest in the clear-cut—bilberry spruce stand ecotone complex are found in the transitional zones near the forest edge, both towards the forest and towards the open clear-cut.

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