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Article

Vegetation and biotope dynamics in spruce-bilberry forests *Piceetum myrtillosum*: ten years after clearcutting with retention of European aspen *Populus tremula*

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Abstract. The changes in the biotope and in the spectrum of ecological coenotic groups of herb and dwarf shrub tiers of vegetation have been monitored over ten years following the clearcutting of the *Piceetum myrtillosum* (bilberry-rich spruce forest) considering on-site retention of aspen (*Populus tremula* L.) in the Babaevsky District of Vologda Oblast. During the first years after clearcutting, the vegetation cover is unstable, sparse, is characterized by pronounced species changes. The diverse ecotopes resulting from clearcutting contribute to the rapid emergence of new plants, including meadow and swamp species, in disturbed communities. Subsequently, tree tier with the dominance of small-leaved trees forms gradually at after clearcutting site. Additionally, the abundance of the shade-tolerant species increases, while that of the meadow species decreases.

Keywords: clearcuts, secondary succession, aspen, biological diversity, forest restoration, Ellenberg ecological scales, southern taiga, Vologda Oblast

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Научная статья**Динамика растительности и биотопа ельника черничного: 10 лет после вырубки с сохранением *Populus tremula***Д.С. Трошин^{1*}, Д.М. Мирин²

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Аннотация. Исследование посвящено изменениям в биотопе и спектре эколого-ценотических групп растений травяно-кустарничкового яруса в течение десяти лет после рубок ельника черничного на территории Бабаевского района Вологодской области с учетом сохранения на корню осины (*Populus tremula* L.) Показано, что сплошные рубки приводят к нарушению живого почвенного покрова. В первые годы после рубок состояние растительного покрова оказывается неустойчивым, что проявляется в его разреженности и резкой смене видов. Большое разнообразие экотопов, формирующихся в результате лесозаготовительных мероприятий, способствует быстрому появлению новых растений (луговых, опушечных и болотных видов) в нарушенных сообществах. На следующих этапах развития послерубочных участков происходит постепенное формирование древесного яруса, преимущественно представленного мелколиственными деревьями, при этом увеличивается обилие теневыносливых видов и происходит уменьшение и исчезновение луговых видов.

Ключевые слова: сплошные рубки, вторичная сукцессия, осина, биологическое разнообразие, восстановление леса, шкалы Элленберга, южная тайга, Вологодская область

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Introduction

Preserving biological diversity and maintaining ecosystem functions in forests are key issues for sustainable forest management, both in Russia (Karpachevskii et al., 2014) and globally (Aubry et al., 2004; Gustafsson and Perhans, 2010; Work et al., 2003). The conservation of species diversity and ecological balance on clearcut areas is essential to consider to follow this goal. In modern forestry, a difficult choice arises between clearcutting, when the forest stand is cut totally, and selective cutting, when low-value tree species, such as European aspen (*Populus tremula* L.), are retained.

Currently, the issue of harvesting healthy and diseased aspen trees during timber harvesting in various forest types is discussed widely (Bagaev et al., 2016, 2019; Fedrowitz et al., 2014; Gromtsev et al., 2010; Gustafsson et al., 2010; Rudolphi et al., 2014; Zalesov et al., 2015). The money costs associated with aspen disposal are often deemed unjustified, given that this tree species enriches boreal forest ecosystems with various plant, fungal, and animal species by providing specific substrates or resources (Caudullo and De Rigo, 2016; MacKenzie, 2010). While some clearcutting companies acknowledge the importance of preserving biodiversity, considered in voluntary forest certification, there is a clear lack of actual data on the changes in vegetation and environment at the sites with retained aspen trees.

The study aims to analyze the dynamics of the biotope and of the spectrum of ecological coenotic groups in the herb and dwarf shrub tiers over a decade following the clearcutting of bilberry-rich spruce forests. The focus was made on retaining mature aspen trees on the site located in the Babaevsky District, Vologda Oblast, the North-West of Russia. To achieve this goal, several objectives were outlined:

- to track the changes in the state of the tree canopy during after clearcutting succession, including the preservation of aspen trees left on the cutovers, and to assess the development and abundance of tree saplings and understory;
- to analyze the changes in species composition and in the spectrum of ecological coenotic groups in the herb and dwarf shrub tiers over the 10-year period after clearcutting;
- to apply indicative methods in order to describe the changes in soil conditions for plant existence over the 10-year after clearcutting period.

This study is significant for the further development of effective forest management strategies that consider biological diversity and ecosystem sustainability in logged forest areas. The findings may contribute to recommendations for the optimal use of resources in timber harvesting and for the preservation of rare plant species.

Materials and methods

During the study, forest areas and different sections of dated clearcuts were examined within a single forest type **Piceetum myrtillosum**, characterized as a wet bilberry-rich spruce forest with a green moss ground cover of medium sparseness. In 2021, the vegetation was surveyed during the peak of the growing season, lasting here from mid-June to early July.

The studied clearcuts varied in age: 0 years (fresh clearcuts), 3 years, 5 years, and 10 years. Within each clearcutting area, three sample plots were set, where completely cut-down stands, stands with individually retained aspens, and stands with retained tree clumps (with other tree species such as spruce, pine, or birch) were described. In total, 48 sample plots (480 sub-plots of 1×1 m), including 36 plots at the clear-cuts and 12 plots representing natural adjacent forest (control), were analyzed. Phytocenoses were described using standard geobotanical methods for typical areas of 100 m² (10×10 m). The distance between the typical area and the margin of the adjacent forest or neighboring clearcut did not exceed 30 m.

The geobotanical description included the list of parameters: (1) distance from the forest margin and clearcut; (2) crown canopy sparseness; (3) percentage of the area covered by deadwood; (4) presence of epilithic and epixylic vegetation; and (5) species composition of the tree tier, undergrowth, understory, herb, and dwarf shrub tier, moss and lichen cover (accounting for ground bryophytes and lichens, and separately for epiphytic species).

Several parameters were recorded for each species in each canopy of the tree tier: (1) number of stems per sample plot, (2) average and maximum trunk circumference at a 1.3-m height, (3) average and maximum height of individuals, and (4) average vitality score (Andreeva et al., 2002). Additionally, plant pathologies were also noted.

In the understory, projective cover and height (both predominant and maximum) were documented. The total projective cover, species composition and relative projective cover (RPC, %) of each plant species were estimated in the herb-dwarf shrub tier and moss layer. The commonly accepted method of plant counts at 1×1 m plots was applied to determine absolute and relative projective cover (Andreeva et al., 2002; Karpachevskii et al., 1980).

The biotopic parameters of the soil were assessed using ecological scale proposed by H. Ellenberg (Bulokhov, 2004; Ellenberg, 1974). The environmental conditions for each sample plot were evaluated using a mean weighted score, considering the projective covers of all herb-dwarf shrub tier species (Oreshkin et al., 2004).

Each species was assigned to a certain aggregated ecological coenotic group regarding the categories indicated in the “Flora of Vascular Plants of Central Russia” database¹ (Zaugol'nova and Khanina, 1996). The vascular plants in the list are given in accordance to S.K. Cherepanov (1995), mosses and liverworts, to Ignatov et al. (Ignatov, 2003; Ignatov and Ignatova, 2003).

For the analysis of the obtained data, such statistical methods were used as pairwise comparison of samples by mean values, Kruskal–Wallis rank test, and multiple comparisons test based on the Fisher's criterion. The statistical analysis was performed using the STATISTICA 10 software package.

Results and discussion

State of the tree stand in clearcuts

The tree vitality was evaluated at all plots studied. A total of 113 individuals were identified in clearcuts of various ages, contrasting with 122 individuals in the adjacent spruce forests bordering each clearcut. The average tree vitality has been assessed by a scale ranging from 0 to 5, where 0 denotes healthy tree, 5 – old deadwood (Fig. 1). All registered tree species (silver birch *Betula pendula* Roth., Norway spruce *Picea abies* ((L.) H. Karst.), Scots pine *Pinus sylvestris* L., and European aspen) were analyzed. Special attention was paid to vitality of European aspen and Norway spruce in order to identify their roles in the forest environment and restoration processes in after clearcutting areas.

Healthy trees predominated at the plots bordering adjacent forests. In recently logged areas, almost all Norway spruce trees were removed. However, during the first year after the clearcut, the vitality of remaining trees was comparable of those in the natural forest. The pattern changed in 3- and 5-year-old clearcuts, where Norway spruce trees, left for seed reproduction, experienced adverse environmental influences. The needles of these individuals faded under direct sunlight, so their vital state has decreased (Martynov, 2008). In 10-year-old clearcuts, fresh deadwood prevailed; moreover, all remaining Norway spruce were assigned as old deadwood. Windthrow and/or deadfall were also observed at the clearcuts.

Consequently, the trees left on the clearcuts had initially the vitality state similar to those in adjacent forests on freshly logged sites, but over the time, their condition deteriorated. The Norway spruce, which was also retained at the clearcuts, exhibited a significant decline in vitality state in 3 years after clearcutting, and all trees became deadwood in ten years after. For aspen, vitality started to decline in 5 years after clearcutting; by the 10th year, the number of living trees significantly decreased, resulting in a deadwood ratio increase.

The effect of clearcutting on sapling pool

The sapling abundance of silver birch, Norway spruce, Scots pine, European aspen, and gray alder *Alnus incana* (L.) Moench differed at the sites with different age of clearcutting, varying from 0 to 6000 ind./ha (Fig. 2). In adjacent forests, the total abundance of saplings amounted to 3350 ind./ha. Spruce saplings comprised 95% of the total sapling pool (3183 ind./ha), the remaining 5% were formed altogether by Scots pine, European aspen, and silver birch.

Healthy saplings predominated across the clearcut plots of different ages. On fresh clearcuts, aspen formed 60% of sapling pool, spruce, approximately 38%. The structure of sapling pool altered at 3-year-old clearcuts, where the absolute number of Norway spruce saplings declined sharply, representing only 12% of the total pool. This decrease resulted from the adverse effects of solar radiation, which was unfavourable for spruce saplings.

¹ Flora of Vascular Plants of Central Russia, 1998–2023. Web page. URL: <https://www.impb.ru/eco/index.php> (accessed: 01.03.2023).

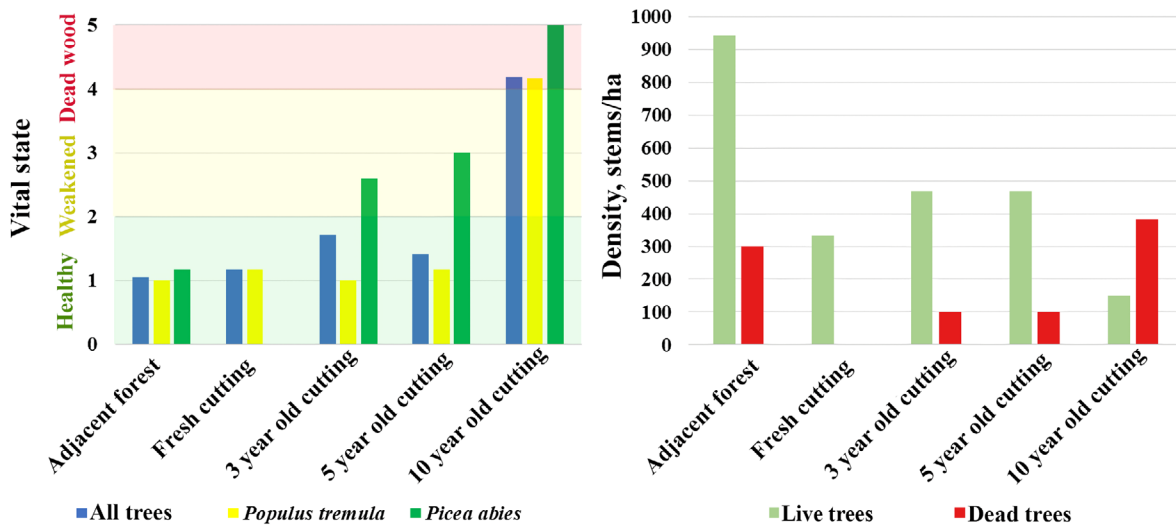


Fig. 1. Vitality state and density of stand components at the clearcuts of different ages and in adjacent forests.

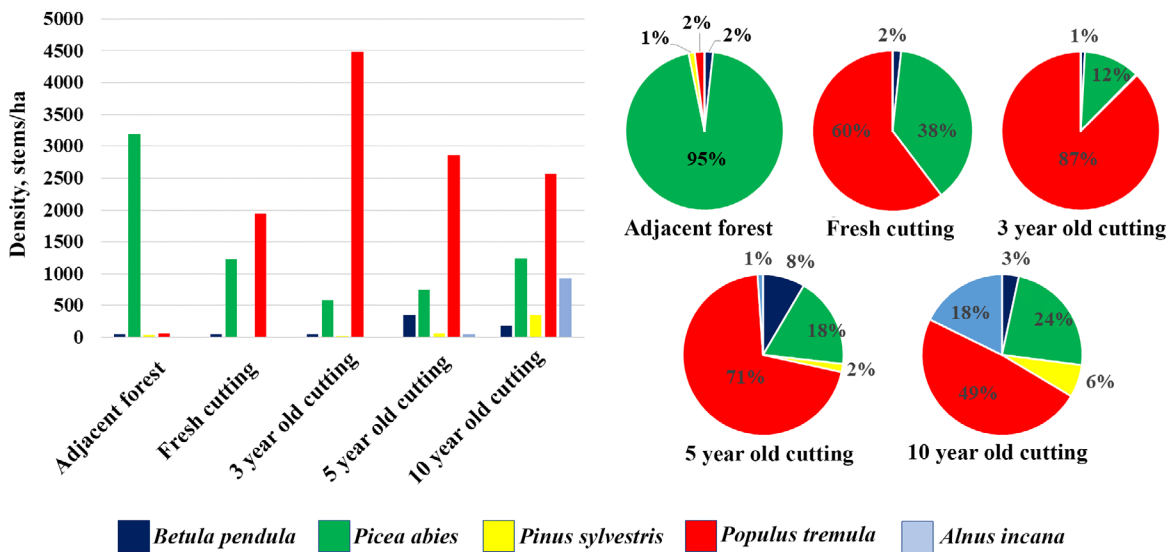


Fig. 2. Population density of forest undergrowth and ratio of tree species at the studied clearcuts and in adjacent forests.

favorable for young undergrowth after clearcutting. Additionally, factors such as frost, strong winter winds, excessive evaporation by plant, and intense resource competition exerted negative impacts (Martynov, 2008; Melekhov, 2003). Over time, some saplings have adapted to the altered environmental conditions. Five years after clearcutting, as the share of European aspen decreased, that of Norway spruce increased. Regard must be paid to gray alder *Alnus incana*, which emerged at 5- and 10-year-old clearcuts, accounting for 1% and 18% of the total sapling pool, respectively. Likely, this was a consequence of waterlogging in these areas.

The effect of clearcutting on the understory

Understory, which performs microclimate mediation and soil protection functions, exerts a positive influence on the reforestation of woody plants both beneath the forest canopy and at clearcuts (Melekhov,

2003). The list of the species of the understory registered during our study is presented in Table 1. All plants were in good vital condition, showing absence of noticeable damage or phytopathologies.

The average sparseness of understory was 17% in the adjacent bilberry-rich spruce forests (control). The highest abundance and frequency of occurrence in these forests were observed for common juniper *Juniperus communis* L., although this species was totally absent at the clearcuts. At fresh clearcuts, the understory consisted of only two species, red raspberry *Rubus idaeus* L. and rowan *Sorbus aucuparia* L. As the clearcuts aged, reaching three years and older, the species composition of the understory became more diverse. Willows *Salix* spp. (particularly, goat willow *S. caprea* L. and cinnamon rose *Rosa majalis* Herrm. joined the understory at this stage. At the 5- and 10-year-old clearcuts, bird cherry *Padus avium* Mill. was also present. However, the abundance of these species was low, and their frequency of occurrence did not exceed 22%. Red raspberry and rowan typically grew in clumps. At the 5-year-old clearcuts, the species composition was further supplemented by downy currant *Ribes spicatum* E. Robson, bay willow *S. pentandra* L., and almond willow *S. triandra* L.

Table 1. Характеристика подлеска на вырубках различной давности.

Years after cutting	Species	Predominant height of specimen, m	Average projective cover, %	Frequency of occurrence, %
Adjacent forest (control site)	<i>Lonicera xylosteum</i>	1.5	1.1	17
	<i>Juniperus communis</i>	0.8	11.1	83
	<i>Sorbus aucuparia</i>	1.4	3.7	50
	<i>Padus avium</i>	2	1.1	8
	<i>Salix caprea</i>	0.5	0.1	8
Fresh clearcut (0)	<i>Rubus idaeus</i>	0.3	1.4	56
	<i>Sorbus aucuparia</i>	0.3	4.4	100
3	<i>Rubus idaeus</i>	0.7	4.7	78
	<i>Sorbus aucuparia</i>	0.6	13.1	89
	<i>Rosa majalis</i>	0.4	1.3	33
	<i>Salix caprea</i>	0.6	2.4	44
5	<i>Ribes spicatum</i>	0.3	0.1	11
	<i>Rubus idaeus</i>	0.7	2.3	56
	<i>Sorbus aucuparia</i>	1.1	10.8	78
	<i>Padus avium</i>	1.9	0.9	22
	<i>Rosa majalis</i>	0.6	1.4	33
	<i>Salix caprea</i>	1.4	1.9	22
	<i>Salix pentandra</i>	1.1	0.7	33
10	<i>Salix triandra</i>	0.5	0.6	11
	<i>Rubus idaeus</i>	0.8	0.4	22
	<i>Sorbus aucuparia</i>	1.6	9.4	89
	<i>Padus avium</i>	3	0.6	11
	<i>Rosa majalis</i>	1	0.3	11
	<i>Salix caprea</i>	1.5	0.3	11

Changes in biotope characteristics during plant community succession after clearcutting

Recently, analysis and consideration of various factors in the natural environment is a key issue of phytocoenology. Plants may serve as indicators of habitat conditions, making possible to determine some environmental parameters without the need for applying specialized measuring instruments. In this study, we have assessed the studied biotopes using G. Ellenberg's optimal ecological scales for light, moisture, acidity, and soil nitrogen availability (Fig. 3).

In the adjacent bilberry-rich spruce forests, shade-tolerant plants were predominantly represented by common species, such as wood sorrel *Oxalis acetosella* L., lady fern *Athyrium filix-femina* (L.) Roth, liverwort *Hepatica nobilis* Schreb., etc. At fresh clearcuts, the species composition of the ground cover was similar to that of the background spruce forest. However, there was a decrease in species abundance because of the negative impact of heavy timber equipment. At the 3–10-year-old clearcuts, light-loving species dominated, including fireweed *Chamaenerion angustifolium* (L.) Scop., common heather *Calluna vulgaris* (L.) Hull, wild strawberry *Fragaria vesca* L., meadow buttercup *Ranunculus acris* L., meadowsweet *Filipendula ulmaria* ((L.) Maxim., etc. When the age of clearcut reached five years, their share decreased gradually due to the increasing light intensity here compared to the natural spruce forests. The light intensity at clearcuts tended to decrease only five years after clearcutting (Fig. 3A).

The average soil moisture gradually increased as five years have passed after clearcutting. In the adjacent (natural) forest, as well as at the sites with fresh and 3-year-old clearcuts, the moisture level was around average values, so mesophytic plant species predominated: European blueberry *Vaccinium myrtillus* L., lingonberry *V. vitis-idaea* L., lily of the valley *Convallaria majalis* L., etc. At the 5-year-old clearcuts, some hygromesophytic and hygrophytic species appeared, while at the 10-year-old clearcuts, moisture-loving species settled actively, increasing their abundance. Dominant species here were represented by meadowsweet *Filipendula ulmaria*, elongated sedge *Carex elongata* L., true fox sedge *C. vulpina* L., and wild angelica *Angelica sylvestris* L. The waterlogging process becomes prominently evident only by the 10th year after clearcutting (Fig. 3B).

The soil nitrogen richness exhibit a pronounced wave-shape dynamics (Fig. 3C). In the spruce-bilberry forests, species characteristic of nitrogen-poor soils dominated, such as European blueberry, lingonberry, club moss *Lycopodium clavatum* L., etc. After clearcutting, there was a significant increase in nitrogen content. At the 3-year-old clearcuts, the nitrophilous species have appeared, including fireweed, common nettle *Urtica dioica* L., wood cranesbill *Geranium sylvaticum* L., etc. In 5–10 years after clearcutting, the abundance of nitrophilous species decreased slightly and then stabilized. Likely, such dynamics was related to the biological nutrient cycling rate, which was influenced by certain factors. The latter might include constant production rate of tree biomass and low decomposition rate of litter due to climatic zone (low-temperature conditions) and conifer needle thus which both acting as inhibitors. However, after clearcutting, the soil surface generally warmed up, accelerating litter decomposition and nutrient cycling, and so resulting in better nitrogen nutrition for plants (Bobkova and Likhanova, 2019).

In the adjacent forests, a low pH level was observed, reflected by the presence of typical acidophilic plants here: European blueberry, lingonberry, common cow-wheat *Melampyrum pratense* L., etc. At fresh clearcuts, species characteristic of both moderately acidic and slightly acidic conditions appeared, including fireweed, ground elder *Aegopodium podagraria* L., and common nettle. In ten years after clearcutting, soil acidity did not change significantly (Fig. 3D), indicating the stability of this parameter during the first decade of restorative succession.

Dynamics of ecological coenotic groups in the herb and dwarf shrub tiers during overgrowth of clearcuts

The number of plant species, indicating the emergence of new ecological coenotic groups at the clearcuts of various ages, increased during the community succession after clearcutting. Presumably, the influence of heavy timber equipment on skid roads promoted development of dense and altered soils, fostering the emergence of ruderal-meadow species. Colonizing of such areas by meadow species was facilitated by shading cessation from the tree stand, while various pits, depressions, and furrows contributed to the settlement of wetland plants. The most substantial increase in species occurred where the soil became looser after clearcutting and interfaced with non-forest areas.

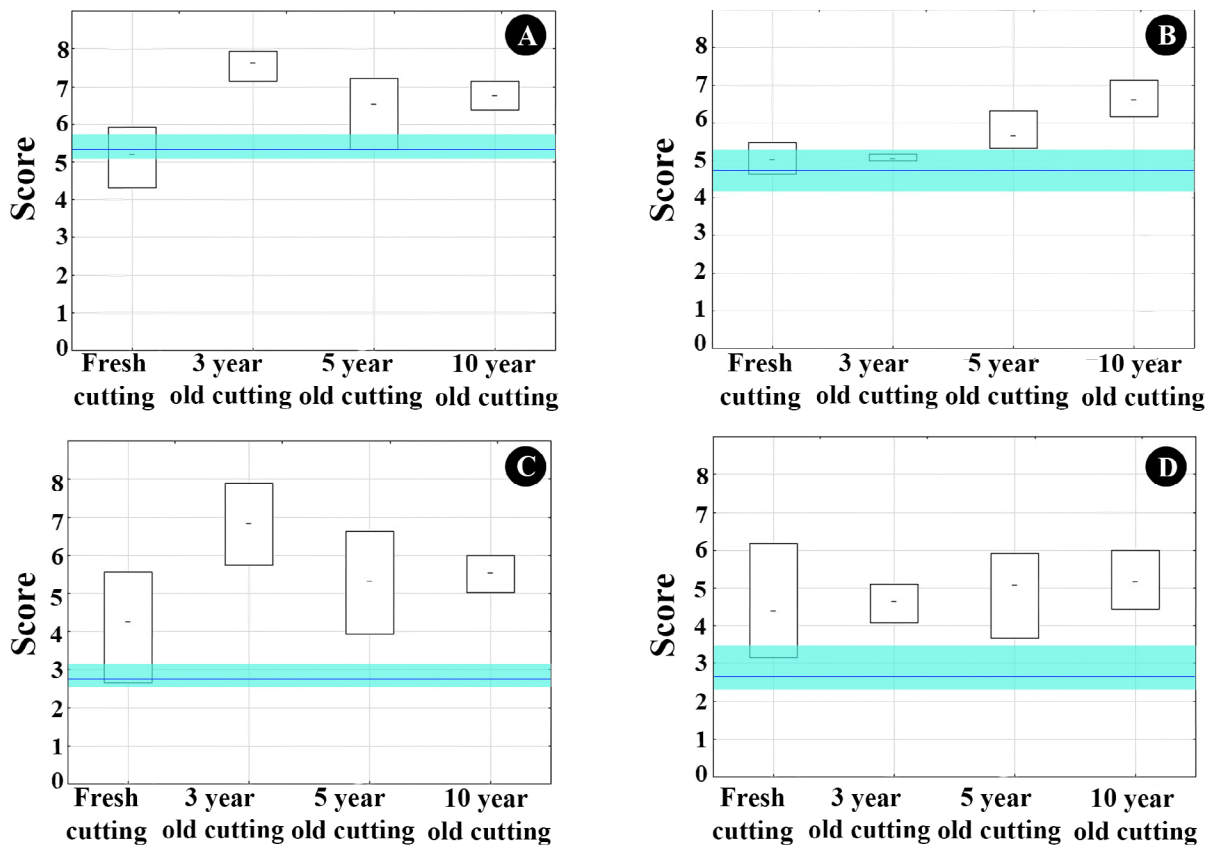


Fig. 3. Relation to illumination (A), moisture (B), nitrogen richness of soil (C) and acidity (D) in the areas of different clearcutting age according to Ellenberg scale. Dash line indicates the mean value; “boxes”, limits of variation; the horizontal line in the blue insert is the mean value and limits of variation in the forests adjacent to the clearcuts.

The taiga species hold a dominant position, constituting 47% of the total species number, when referring to the distribution of ecological coenotic groups based on the number of species and projective cover in the structure of the herb and dwarf shrub tiers of phytocenoses in adjacent forests (Fig. 4). Subdominant groups included nemoral and nemoral-boreal species, jointly representing 94% of the projective cover. Despite this dominance, meadow species (constituting 3% of the total number of species) were also present in the forest areas, although their RPC was less than 1%.

At fresh clearcuts, meadow species prevailed (29%), represented by common species large-leaved lupine *Lupinus polyphyllus* Lindl., dandelion *Taraxacum officinale* F.H. Wigg., bush vetch *Vicia sepium* L., creeping thistle *Cirsium arvense* (L.) Scop., and others. This species composition was due to disappearance of most tree shading after clearcutting. However, changes in plant composition were not immediate and apparent, as it took some time for the community to respond to this anthropogenic impact.

Even at the 3-year-old clearcuts, meadow species dominated significantly in the herb and dwarf shrub tiers. Most frequently, common starwort *Stellaria graminea* L., lady's mantle *Alchemilla* spp., mugwort *Artemisia vulgaris* L., and couch grass *Elytrigia repens* ((L.) Nevski were registered. However, marginal species with a wide ecological optimum, such as fireweed, had maximum abundance. In five years after clearcutting, wetland species became part of the community; such meadow species as field horsetail *Equisetum arvense* L., large-leaved lupine, and meadow crane's-bill *Geranium pratense* L. being dominants. In ten years after clearcutting, the composition of ecological coenotic groups in the herb and dwarf shrub tiers remained relatively stable, but wetland species (meadowsweet, true fox sedge, elongated sedge, etc.) began to predominate, while meadow species sharply reduced their projective cover (Fig. 4).

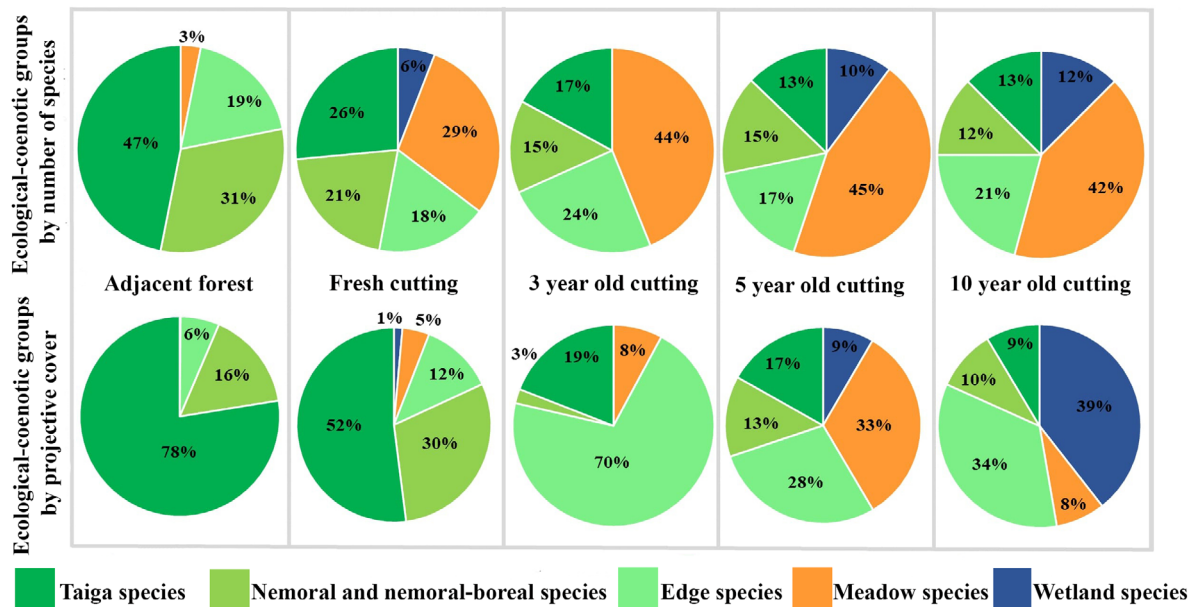


Fig. 4. Ratio of ecological coenotic groups by the species number and projective cover in the herb and dwarf shrub tiers at the sites with different clearcutting age and in the adjacent forests.

When analyzing the dynamics of the total number of species and the abundance of each ecological-coenotic group separately (Fig. 5), the number of taiga species was generally low. It has noticeably decreased immediately after clearcutting and remained approximately the same over the next ten years. The total projective cover of taiga species has noticeably decreased in the first year after clearcutting, followed by a monotonous but insignificant decrease. Nemoral and nemoral-boreal species were poorly represented in the studied communities, with no trends in species diversity and total projective cover.

Meadow species were absent in the adjacent forests. After clearcutting, there was a sharp increase in their number and abundance, reaching a maximum at the 5-year-old clearcuts. However, by the 10-year period, both the number of species and projective cover of this group have decreased.

Wetland species were absent in the adjacent forests and at the 3-year-old clearcuts. Both the number of species and their abundance increased significantly at the 5–10-year-old clearcuts, indicating waterlogging of these areas.

In the adjacent forest areas and at fresh clearcuts, marginal species were initially present in small diversity and abundance. Nevertheless, after just three years, their projective cover has increased significantly. Despite a subsequent decrease in projective cover, the number of marginal species remained substantial.

Our results demonstrate that the increase in the number of the meadow, marginal, and wetland plants contributes to higher species richness in the first years after clearcutting. We suggest that as a canopy formed by trees and shrubs develops, the species spectrum of ecological-coenotic groups in the herb and dwarf shrub tiers will gradually align with that of the natural adjacent forest.

In addition, our findings indicate that formation of shrub canopy and tree undergrowth over 10 years in the western part of Vologda Oblast exhibits a lower rate for meadow and wetland species, on one hand, and nemoral, nemoral-boreal, and taiga species, on the other hand, compared to that described for Estonia (Zobel et al., 1993).

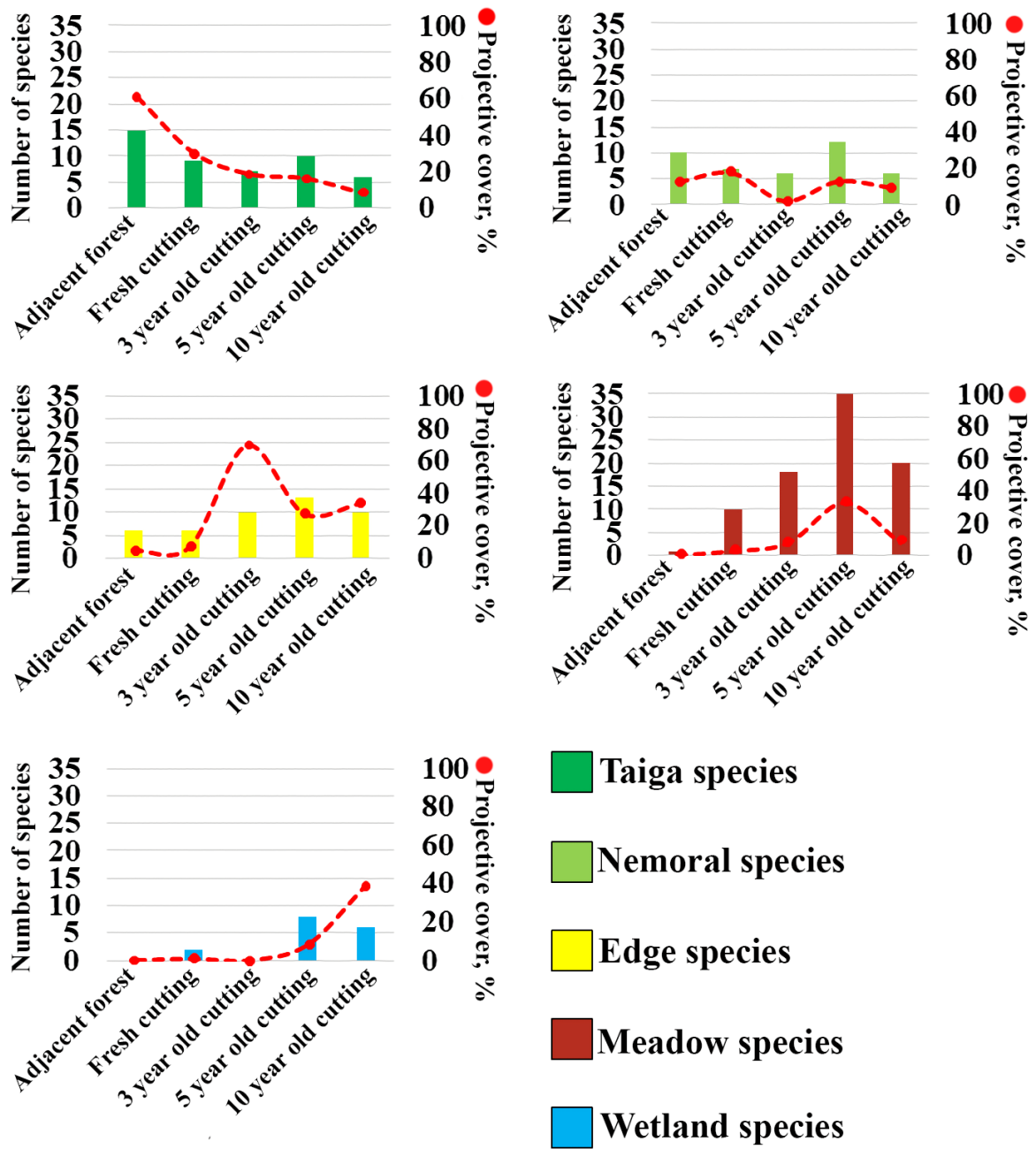


Fig. 5. Dynamics of the total species number (columns) and of the projective cover (dotted line) in different ecological-coenotic plant groups in the herb and dwarf shrub tiers after clearcutting of spruce-bilberry forests.

Changes in moss cover during community succession after clearcutting

The moss cover at clearcuts had a population density loss of about 50% after clearcutting when comparing to that in the adjacent forests. In these areas, the primary dominant species at almost all sites was glittering woodmoss *Hylocomium splendens* (Hedw.) Bruch et al., co-dominated often by red-stemmed feathermoss *Pleurozium schreberi* (Willd. ex Brid.) Mitt., and accompanied occasionally by knights plume moss *Ptilium crista-castrensis* (Hedw.) De Not. At both fresh and the 3-year-old clearcuts, moss cover did not exceed 5%, and no dominant species were registered. Moss projective cover at the 5- and 10-year-old clearcuts reached about 10% and less, with big shaggy-moss *Rhytidiadelphus triquetrus* (Hedw.) Warnst. being the most abundant, especially at the 10-year-old clearcuts. Further studies are required for comprehensive analysis of changes in moss cover.

Peculiarities of the species composition at different stages of succession after clearcutting

A total of 137 plant species were documented at the clearcuts of various ages and in the adjacent forests. Analysis of species distribution, considering their abundance, allowed us defining several plant groups:

(1) "Cross-cutting species". Species found both in the forests and at all clearcuts regardless of the age. This group includes common cow-wheat, European blueberry, May lily *Maianthemum bifolium* (L.) F.W. Schmidt, rowan, lady fern, lingonberry, big shaggy-moss, red-stemmed feathermoss, common haircup *Polytrichum commune* Hedw., glittering woodmoss, broom forkmoss *Dicranum scoparium* Hedw., woody thyme-moss *Plagiomnium cuspidatum* (Hedw.) T.J. Kop., and juniper haircap *Polytrichum juniperinum* Hedw. The group is subdivided into two sub-groups: (1) the frequency of occurrence of certain species increases along the clearcut age (big shaggy-moss, red-stemmed feathermoss, common haircup, and juniper haircap), (2) this parameter decreases (common cow-wheat, European blueberry, and arctic starflower *Trientalis europaea* L.;

(2) Growing only at the clearcuts. This group comprises red clover *Trifolium pratense* L., meadow buttercup, field horsetail, wild strawberry, red raspberry, large-leaved lupine, and fireweed;

(3) Noted both in forests and at the 5-year-old and elder clearcuts: stone bramble *Rubus saxatilis* L., bird cherry, hypnum moss *Hypnum cupressiforme* Hedw., and herb Paris *Paris quadrifolia* L.;

(4) Growing at the 2- to 10-year-old clearcuts: common nettle, germander speedwell *Veronica chamaedrys* L., cinnamon rose, smooth brome *Bromopsis inermis* (Leyss.) Holub, brown knapweed *Centaurea jacea* L., mugwort, and meadow horsetail *Equisetum pratense* Ehrh.;

(5) Found at the 5- to 10-year-old clearcuts: wood clubrush *Scirpus sylvaticus* L., wild angelica, Kentucky bluegrass *Poa pratensis* L., St John's wort *Hypericum perforatum* L., meadow crane's-bill, true fox sedge, and water avens *Geum rivale* L.;

(6) Noted only in the forests: common juniper, stiff clubmoss *Lycopodium annotinum* L., flat pea *Lathyrus sylvestris* L., fly honeysuckle *Lonicera xylosteum* L., groundcedar *Diphasiastrum complanatum* (L.) Holub, sickle moss *Sanionia uncinata* (Hedw.) Loeske, lesser butterfly-orchid *Platanthera bifolia* (L.) Rich., and knights plume moss.

At a fresh clearcut, the most abundant species were common cow-wheat, *Hepatica nobilis*, European blueberry, and May lily; their projective cover ranged from 6.0 to 11.8%. The number of species at this stage was 47. At the 3-year-old clearcuts, phytocoenotic and ecotopic selection was manifested in the herbaceous-undershrub community; at this stage, the species clearly divided into dominant and subordinate. Pioneer plant species became dominant, seeking to colonize new areas. In three years after clearcutting, fireweed, rowan, and May lily dominated (RPC = 7.8–62.5%), with fireweed as absolute dominant. At this stage, 55 species were noted, indicating an increase in biodiversity in the first years after disturbance.

The dominant species remained the same five years after clearcutting. There was a slight decrease in the projective cover of fireweed, likely due to the settlement of the new species on the clearcuts, predominantly of meadow and ruderal flora, which led to competition for resources. The number of species at this succession stage reached 102, which was maximum within the considered 10-year period.

Ten years after clearcutting, the dominant species was meadowsweet, followed by fireweed and rowan (RPC = 9.4–32.1%). Meadowsweet dominance was linked to the waterlogging of the area. A total of 71 plant species were registered at the 10-year-old clearcuts. This stage was characterized by

a pivotal shift in species composition, as the undergrowth of small-leaved tree species actively formed a dense and light-preventing tier, leading to a change in dominant species and disappearance of a meadow vegetation.

In the natural forests adjacent to the clearcuts, the most abundant species were European blueberry (absolute dominant in the herb and dwarf shrub tiers), along with glittering woodmoss and red-stemmed feathermoss in the moss cover. The total number of species was 57 in the forest areas, constituting approximately 40% of the overall plant diversity. The results of the statistical analysis of the obtained data are shown in Table 2.

According to the tests performed, the species have been divided into five main groups depending on the age of the clearcut (Fig. 6). The “control” group (natural forest) included 11 species, represented by six moss species and five herb and dwarf shrub species.

Four species (ground elder, liverwort, common cow-wheat, and arctic starflower) were found exclusively at fresh clearcuts. These were forest species; therefore, their abundance decreased as the environmental conditions were changing. By the third year of succession, lily of the valley, mugwort, smooth brome, brown knapweed, and May lily reached maximum abundance. Similar to fresh clearcuts, forest species were present in these communities, but they were partly displaced by meadow species. At the 5-year-old clearcuts, a number of meadow species became notably abundant.

The group of species found predominantly at the 10-year-old clearcuts included lady fern, true fox sedge, field horsetail, herb Paris, and common nettle. In addition, “local” species were noted, whose abundance was notable at the clearcuts for two or more observation periods. Goat willow was an example of such species, which abundance was notably high throughout the entire 10-year survey. The species response to clearcutting observed in our study fits well to the data obtained for the mid-taiga subzone of Karelia, Russia (Kryshen', 2006), although with some peculiarities. According to our data, May lily increased its abundance at early stages of after-clearcutting succession, goat willow did not exhibit significant trend in abundance dynamics, and the share of cereals was extremely insignificant in the clearcut community. Similar pattern was reported for the mid-taiga subzone of the Komi Republic, Russia (Il'chukov, 2003).

Table 2. Analysis of differences (Kruskal–Wallis test) in species abundance in forests and clearcuts of different ages. Significance level (p-value): * – 10%; ** – 5%; *** – 1%. “+” – species has a confinement to a certain category; blank cell – no significant confinement is observed; *H* – Kruskal–Wallis test value.

Species	<i>H</i>	<i>p</i> -value	Species confinement				
			Adjacent forest	Fresh clearcut	3-year-old cutting	5-year-old cutting	10-year-old cutting
<i>Aegopodium podagraria</i>	31.328	0.000***		+			
<i>Angelica sylvestris</i>	7.109	0.130					
<i>Artemisia vulgaris</i>	10.906	0.028**			+		
<i>Athyrium filix-femina</i>	11.568	0.021**					+
<i>Bromopsis inermis</i>	13.686	0.008***			+		
<i>Calluna vulgaris</i>	18.936	0.001***	+				
<i>Carex vulpina</i>	22.841	0.000***					+
<i>Centaurea jacea</i>	9.717	0.046**			+		
<i>Chamaenerion angustifolium</i>	41.641	0.000***		+	+	+	
<i>Convallaria majalis</i>	14.347	0.006***		+			

Species	<i>H</i>	<i>p</i> -value	Adjacent forest	Species confinement			
				Fresh clearcut	3-year-old cutting	5-year-old cutting	10-year-old cutting
<i>Dicranum scoparium</i>	28.846	0.000***	+				
<i>Equisetum arvense</i>	10.149	0.038**					+
<i>Filipendula ulmaria</i>	40.694	0.000***				+	+
<i>Fragaria vesca</i>	23.357	0.000***		+	+	+	
<i>Geranium sylvaticum</i>	16.219	0.003***			+	+	
<i>Hepatica nobilis</i>	26.970	0.000***		+			
<i>Hylocomium splendens</i>	28.462	0.000***	+				
<i>Hypericum perforatum</i>	15.525	0.004***				+	
<i>Hypnum cupressiforme</i>	26.813	0.000***	+				
<i>Lathyrus vernus</i>	25.270	0.000***	+			+	
<i>Lupinus polyphyllus</i>	32.070	0.000***				+	
<i>Lycopodium clavatum</i>	30.350	0.000***	+				
<i>Maianthemum bifolium</i>	13.140	0.011**			+		
<i>Melampyrum pratense</i>	19.461	0.001***		+			
<i>Oxalis acetosella</i>	18.402	0.001***	+	+			
<i>Padus avium</i>	3.696	0.449					
<i>Paris quadrifolia</i>	17.060	0.002***					+
<i>Plagiomnium cuspidatum</i>	30.710	0.000***	+				
<i>Pleurozium schreberi</i>	30.774	0.000***	+				
<i>Polytrichum commune</i>	24.662	0.000***	+				
<i>Polytrichum juniperinum</i>	17.966	0.001***	+			+	+
<i>Pteridium aquilinum</i>	9.912	0.419					
<i>Ranunculus acris</i>	30.920	0.000***				+	
<i>Rhytidiadelphus triquetrus</i>	22.642	0.000***	+				+
<i>Rosa majalis</i>	8.738	0.068*			+	+	
<i>Rubus idaeus</i>	19.757	0.001***			+	+	
<i>Rubus saxatilis</i>	24.067	0.000***	+				
<i>Salix caprea</i>	8.218	0.084*	+	+	+	+	+
<i>Sorbus aucuparia</i>	16.010	0.003***			+	+	
<i>Trientalis europaea</i>	15.435	0.004***		+			
<i>Urtica dioica</i>	15.631	0.004***					+
<i>Vaccinium myrtillus</i>	30.947	0.000***	+				
<i>Vaccinium vitis-idaea</i>	26.560	0.000***	+				
<i>Veronica chamaedrys</i>	28.622	0.000***			+	+	

Adjacent forest	Age of cutting			
	Fresh cutting	3 year old cutting	5 year old cutting	10 year old cutting
<i>Calluna vulgaris</i>				
<i>Dicranum scoparium</i>				
<i>Hylocomium splendens</i>				
<i>Hypnum cupressiforme</i>				
<i>Lycopodium clavatum</i>				
<i>Plagiomnium cuspidatum</i>				
<i>Pleurozium schreberi</i>				
<i>Polytrichum commune</i>				
<i>Rubus saxatilis</i>				
<i>Vaccinium myrtillus</i>				
<i>Vaccinium vitis-idaea</i>				
<i>Oxalis acetosella</i>				
<i>Aegopodium podagraria</i>				
<i>Hepatica nobilis</i>				
<i>Melampyrum pratense</i>				
<i>Trientalis europaea</i>				
		<i>Chamaenerion angustifolium</i>		
		<i>Fragaria vesca</i>		
		<i>Convallaria majalis</i>		
		<i>Artemisia vulgaris</i>		
		<i>Bromopsis inermis</i>		
		<i>Centaurea jacea</i>		
		<i>Maianthemum bifolium</i>		
		<i>Geranium sylvaticum</i>		
		<i>Rosa majalis</i>		
		<i>Rubus idaeus</i>		
		<i>Sorbus aucuparia</i>		
		<i>Veronica chamaedrys</i>		
		<i>Hypericum perforatum</i>		
		<i>Lupinus polyphyllus</i>		
		<i>Ranunculus acris</i>		
<i>Polytrichum juniperinum</i>			<i>Polytrichum juniperinum</i>	
<i>Lathyrus vernus</i>			<i>Lathyrus vernus</i>	
			<i>Filipendula ulmaria</i>	
			<i>Athyrium filix-femina</i>	
			<i>Carex vulpina</i>	
			<i>Equisetum arvense</i>	
			<i>Paris quadrifolia</i>	
			<i>Urtica dioica</i>	
<i>Rhytidadelphus triquetrus</i>			<i>Rhytidadelphus triquetrus</i>	
		<i>Salix caprea</i>		

Fig. 6. Grouping of plant species by abundance depending on the age of clearcuts.

Therefore, significant changes occurred both in the species composition of plants and in their abundance at the clearcuts of the spruce-bilberry forests. A total of 27 species were notably associated with the communities of different clearcutting age (up to 10 years).

Conclusion

1) The vitality of retained spruce trees at the clearcuts declines noticeably within two years after clearcutting, while such decline for aspen is evident by the 10th year. A significant reduction in the number of survived (living) trees at the clearcuts is particularly notable five and ten years after clearcutting.

2) In the first years after clearcutting, aspen plays a main role in reforestation, but the population density of undergrowth of other species, including spruce, increases only by the 10th year. Understory expands and species diversity increases between the 3rd and the 5th year after clearcutting.

3) Soil nitrogen richness and alkalinity is higher at the 3–10-year-old clearcuts compared to that in the natural forest, due to accelerated biological cycling in these disturbed areas. Moreover, the pH level shifts from acidic to slightly acidic. Soil moisture starts increasing after five years, and waterlogging processes become evident at the 10-year-old clearcuts. Changes in the spectrum of ecological coenotic

groups in the herb and dwarf shrub tiers reflect biotope alterations. The diversity of the meadow species surges at the fresh clearcuts, their abundance reaches maximum by the 5th year. Wetland species emerge at the 5-year-old clearcuts and become prevalent at the 10-year-old ones. Nemoral-boreal herbs settle predominantly in the first year after clearcutting. Forest species are better conserved at the clearcut sites where stand elements are retained.

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