

# *Article* **Changes in the Number of Vascular Plant Species during Reforestation of Clearcut Forests**

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**Abstract:** The article aims to describe the patterns of changes in the number of vascular plant species in communities at different stages of forest regeneration after clearcutting using the space-for-time substitution method. Large-scale logging in boreal forests leads to a simplification of the territory's forest cover (the formation of even-aged stands), which in turn leads to a decrease in the diversity of forest communities and species diversity. These tendencies have been confirmed for many groups of organisms, especially those associated with old trees and dead wood; however, this is not so clear for vascular plants. We investigated plant communities at different stages of regeneration. We used the so-called space-for-time substitution (chronosequence) method of building dynamic series for four forest ecotopes, where industrial clearcuts are most actively carried out. We showed that the fertility of forest ecotopes determines the species pool—the richer the conditions, the more species that can potentially inhabit the community. At the same time, the structure of the tree stand significantly affects the composition and number of species in the community. The lowest species richness was in old-growth forests characterized by the dominance of one species in the tree stand and one or two vascular plant species in the ground cover. With insignificant fluctuations in the average number of species between stages of forest regeneration after logging, some communities at clearcuts in bilberry (*Vaccinium myrtillus* L.) pine (*Pinus sylvestris* L.) and spruce (*Picea abies* (L.) H.Karst.) forests have high species diversity due to the occupation of the site by species of open habitats. These clearcuts are located not far from settlements and close to roads.

**Keywords:** biodiversity; vascular plants; boreal forests; logging; succession; Eastern Fennoscandia

### **1. Introduction**

The conservation of biological diversity is one of the global problems of our time. The world's leading countries agreed to achieve a reduction in the rate of decline of the planet's biodiversity by 2010, but, unfortunately, expectations have not been met [\[1\]](#page-10-0). Land use is one of the main causes of biodiversity decline [\[2\]](#page-10-1). It is generally understood that large-scale logging also leads to the simplification of the forest cover (the formation of even-aged stands) of an area, which in turn should lead to a decrease in forest community diversity and species diversity  $[3,4]$  $[3,4]$ , and a change in forest management is seen as a necessary condition for species conservation [\[1](#page-10-0)[,5,](#page-10-4)[6\]](#page-10-5).

According to data from the space monitoring of the forest zone of the Russian Federation, not only the area covered by forests is decreasing, but also the species composition is changing—the share of deciduous species is increasing [\[7\]](#page-10-6). As a result of large-scale clearcutting that took place in the second half of the 20th century, secondary forests now prevail in the Russian part of Fennoscandia. In Karelia, clearings and young stands currently occupy over 34% of the forested area, middle-aged stands—32%, and mature and overmature communities—approximately 34% (with no more than 5% covered by climax forest) [\[8\]](#page-10-7). First of all, logging affects the species diversity of insects, fungi, and lichens, i.e., those species associated with dead wood and old trees [\[5](#page-10-4)[,9](#page-10-8)[,10\]](#page-10-9). At the same time,



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concerning the species diversity of vascular plants, the impact of logging in the boreal zone is not so obvious [\[11](#page-10-10)[–13\]](#page-10-11) and not as well studied [\[14\]](#page-10-12). Thus, studies in the Komi Republic [\[15\]](#page-10-13) and the Republic of Karelia [\[16\]](#page-11-0) showed that a long period of economic activity did not significantly affect vascular plant species diversity in the area with active forest management, and rare species are successfully preserved in protected areas. In addition, high species diversity is characterized by forests that are of little interest to loggers due to difficult accessibility and low productivity, as well as due to legal restrictions [\[17,](#page-11-1)[18\]](#page-11-2). In general, for a large forest area, species diversity is determined by landscape and habitat diversity and is relatively stable regardless of management activities [\[16](#page-11-0)[,19\]](#page-11-3).

A completely different situation is seen if considering separate forest patches, i.e., forest areas similar in species composition, age, completeness, and ground cover. Under conditions of low soil fertility, changes in the species diversity of vascular plants may not be observed after clearcutting. For example, in cowberry or lichen pine forests remote from settlements, it is not the number of species that changes but the ratio of their abundance. In richer conditions after logging, a sharp increase in diversity may be observed at the expense of open-habitat species [\[20\]](#page-11-4), especially in plots located near settlements or agricultural fields [\[13](#page-10-11)[,21\]](#page-11-5). If only forest species are considered, some data suggest that diversity can be expected to increase with community age [\[22\]](#page-11-6). It should be noted that there are not many continuous observations on permanent sample plots established after logging and they are limited, as a rule, to a few years or at best a couple of decades [\[13,](#page-10-11)[23\]](#page-11-7). At the same time, it is also possible to use another approach—a large number of descriptions of communities at different stages of recovery after logging—the so-called space-for-time substitution (chronosequence) method, for which, however, there are questions [\[24\]](#page-11-8). The main problem here is that the studied communities may not always line up in a time series due to habitat conditions and disturbance history differences. Therefore, when considering the diversity of forest communities united not by territorial principles but by the similarity of ecotope (forest conditions), it is very important to clearly define the similarity (identity) of forest conditions and the history of their development. The main habitat property (determining biodiversity in the taiga zone) is moisture conditions [\[25](#page-11-9)[,26\]](#page-11-10), which are determined by topography and groundwater depth.

A discussion of the possibility of preserving forest ecosystem functions in commercial logging areas [\[27](#page-11-11)[,28\]](#page-11-12) has continued over the last decade with a focus on biodiversity conservation [\[14\]](#page-10-12). One possible way to solve this problem is to simulate natural disturbances [\[29\]](#page-11-13). Experience has shown, however, that it is impossible to accurately simulate natural forest disturbances, and the question of whether we should try to simulate natural situations as closely as possible is still open [\[30](#page-11-14)[,31\]](#page-11-15). To answer this question, we must first understand how natural disturbances are similar to clearcuts. Natural disturbances differ not only in the type of impact but also in scale (area) [\[32\]](#page-11-16) and, consequently, differ in the rate and characteristics of regeneration. Similar criteria can be applied to clearcuts, which, in Russia, differ in both area and the proportion of wood removed [\[18\]](#page-11-2). In our study, we limited ourselves to clearcuts; the analog among natural disturbances in the study region is windthrow. How are these fundamentally different and can they be compared in terms of regeneration and biodiversity dynamics? For example, 20-year monitoring of middle taiga spruce forests in areas of clearcut windthrow [\[33\]](#page-11-17) showed that regeneration of the indigenous community can occur without the stage of hardwood dominance, which, in clearcuts under similar conditions, is possible only with active human activity [\[34,](#page-11-18)[35\]](#page-11-19). The main difference between natural disturbances and commercial clearcutting is that in the latter case, the main part of tree biomass is removed, while for natural disturbances it all remains on the site. Therefore, the processes in the upper soil layers [\[36\]](#page-11-20) and the species composition of fungi [\[37\]](#page-11-21), insects [\[38\]](#page-11-22), and other groups of organisms [\[39,](#page-11-23)[40\]](#page-11-24) are also different. The number of vascular plant species can increase after windthrow, but not as dramatically as in clearcuts [\[12,](#page-10-14)[41\]](#page-12-0), although changes in the abundance of some herbaceous species can be significant [\[12,](#page-10-14)[42\]](#page-12-1).

We aimed to investigate changes in vascular plant species diversity with forest community restoration after logging. munity restoration after logging.

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# **2. Materials and Methods** *2.1. Data Collection*

# *2.1. Data Collection*

This study was conducted in Eastern Fennoscandia within the middle and northern taiga (according to the geobotanical zoning of Russia [\[43\]](#page-12-2)) or the middle boreal and southern taiga (according to the geobotanical zoning of Russia [43]) or the middle boreal and south-habitative contains to the good chanceled zones (Figure [1\)](#page-2-0) according to Ahti et al. [\[44\]](#page-12-3). In habitats with automorphic soils (deep groundwater) mostly occupied by exploitation forests, descriptions of the tree layer, (deep groundwater) mostly occupied by exploitation forests, descriptions of the tree layer, ground cover, and soil have been made, as presented in published databases [45,46]. ground cover, and soil have been made, as presented in published [dat](#page-12-4)[aba](#page-12-5)ses [45,46].  $T$  is studied in Eastern Fennoscandia with the middle and northern Fennoscandia with the middle and northern Fenn

<span id="page-2-0"></span>

**Figure 1.** Biogeographic zoning of Northern Europe (according to Ahti et al. 1968 [44]). The study **Figure 1.** Biogeographic zoning of Northern Europe (according to Ahti et al. 1968 [\[44\]](#page-12-3)). The study area is marked with a blue-shaded area. area is marked with a blue-shaded area.

was carried out within its boundaries; in the case of a relatively large homogeneous site, the most characteristic part of the site was determined and, depending on the age, completeness, and composition of the stand, an area sufficient to reflect the stand structure and ground cover (at least 400 square meters) was described. The composition, age, height, diameter, fullness, composition, and abundance of the undergrowth and woody understory were<br>taken into account when describing the two standard and international advertising of the ground cover was performed at each site. Species composition was studied in the whole plot. At each plot, we determined its "history"—anthropogenic and natural disturbances and a description of the ground cover was performed at each site. Species composition of the ground compositio In the case of a small-sized forest site, the geobotanical description of the community taken into account when describing the tree stand. A soil pit was dug and a description of

(scale and timing)—using a set of characteristics (the soil profile; presence and condition of stumps; composition and structure of the tree stand; presence and nature of tree damage; and composition and structure of the ground cover). We considered it important to include in the analysis only those sample plots that could be confidently attributed to the type of forest conditions and did not raise questions about the history of natural disturbances and anthropogenic activities.

All descriptions were grouped according to the type of forest conditions and stand age class. The allocation of forest condition types was preceded by the development of habitat classifications, which began with the work under the CORINE-biotopes program [\[47\]](#page-12-6) and the subsequent adaptation of the results to create a model of forest coenotic diversity [\[48\]](#page-12-7). For East Fennoscandia, we have distinguished three types of habitats (ecotopes) on automorphic sandy soils with the following corresponding forest types: lichen (*Cladonia* P.Browne spp.) pine (*Pinus sylvestris* L.) forest (Pinetum cladinosum, Pinus sylvestris- [Cladonia]—P.s-Cl.), cowberry (*Vaccinium vitis-idaea* L.) pine forest (Pinetum vacciniosum, Pinus sylvestris-Vaccinium vitis-idaea—P.s.-V.v.-i.) and bilberry (*Vaccinium myrtillus* L.) pine forest (Pinetum myrtillosum, Pinus sylvestris-Vaccinium myrtillus—P.s.-V.m.) [\[48\]](#page-12-7). In addition, two types of ecotopes on sandy loam soils were also identified in automorphic conditions: bilberry spruce (*Picea abies* (L.) H.Karst.) forest (Piceetum myrtillosum, Picea abies—Vaccinium myrtillus—P.a.-V.m.) and sorrel (*Oxalis acetosella* L.) spruce (Piceetum oxalidosum, Picea abies—Oxalis acetosella—P.a.-O.a.). The latter type of forest conditions is characterized by relatively rich soils and, understandably, these habitats were first of all used for agriculture. Currently, there are practically no old-growth forests of this type and all age stages are poorly represented, so descriptions of the P.a.-O.a. conditions were not included in our study. Brief characteristics of the climax communities of the other conditions are presented in Table [1.](#page-3-0)

<span id="page-3-0"></span>**Table 1.** Specific features of old-growth communities in the studied ecotopes.



Note. The studied ecotopes included P.s.-Cl. (Pinus sylvestris–Cladonia type), P.s.-V.v.-i. (Pinus sylvestris– Vaccinium vitis-idaea type), P.s.-V.m. (Pinus sylvestris–Vaccinium myrtillus type), and P.a.-V.m. (Picea abies– Vaccinium myrtillus type).

Relying on the results from years of route surveys and research into the structure of forest communities in permanent sample plots, we have built regeneration series for the forest habitat types (Figure [2\)](#page-4-0) [\[49\]](#page-12-8). For all the series, we have identified the stages of <span id="page-4-0"></span>forest development objectively distinguished in nature by the tree stand and ground-cover development objectively distinguished in nature by the tree stand and ground-cover structure: clearcuts–young stands–middle-aged stands–mature communities–subclimax– structure: clearcuts–young stands–middle-aged stands–mature communities–subclimax– climax (we joined the last three stages together in this study because of the stable species climax (we joined the last three stages together in this study because of the stable species composition, and we refer to them in this paper as old-growth forests). composition, and we refer to them in this paper as old-growth forests).



**Figure 2.** Restoration series of climax forest communities in different types of ecotopes (shown in **Figure 2.** Restoration series of climax forest communities in different types of ecotopes (shown in the title of each diagram). Names of plant associations are given in the blocks; association names are composed of characteristic species and/or dominant trees (if any) and herbaceous–shrub and mossare composed of characteristic species and for dominant trees (if any) and netbaccous shade and moss–lichen layers. The arrows show the directions of the succession. The large shaded arrow shows<br>. the dynamic series under unchanged post-cutting moisture conditions.

The stages of forest regeneration after logging can be characterized as follows: The stages of forest regeneration after logging can be characterized as follows:

Clearcut is the period from the year of felling to the tree layer forming. Clearcut is the period from the year of felling to the tree layer forming.

Young stand is the period from the forming of the tree layer to 40–60 years (the end Young stand is the period from the forming of the tree layer to 40–60 years (the end of of the natural thinning of a dense stand). the natural thinning of a dense stand).

Middle-aged stand is the period until the beginning of the processes of the second Middle-aged stand is the period until the beginning of the processes of the second natural thinning or natural dying of deciduous trees (birch or aspen) (100–120 years). natural thinning or natural dying of deciduous trees (birch or aspen) (100–120 years).

Old-growth forest in this study is the stage of mature stands (with an average age of Old-growth forest in this study is the stage of mature stands (with an average age of pine or spruce in the tree layer of more than 100–120 years). pine or spruce in the tree layer of more than 100–120 years).

We analyzed 418 geobotanical descriptions collected in 2001–2022 throughout the ritory of the Republic of Karelia and its neighboring territories (Figure 1): P.s.-Cl.—29, territory of the Republic of Karelia and its neighboring territories (Figure [1\)](#page-2-0): P.s.-Cl.—29, P.s.–V.v.-i.—99, P.s.-V.m.—95, and P.a.-V.m.—195; Clearcuts—94, Young forests—117, P.s.-V.v.-i.—99, P.s.-V.m.—95, and P.a.-V.m.—195; Clearcuts—94, Young forests—117, Middleaged—99, and Old-growth—108. The sample ratios reflect the actual distribution of forest types on the one hand and their age structure on the other.

When defining the species composition of a community, we place special emphasis When defining the species composition of a community, we place special emphasis on considering the natural boundaries of the plot under study. It should be taken into on considering the natural boundaries of the plot under study. It should be taken into account that clearcutting allotment was carried out within the natural forest patches. For account that clearcutting allotment was carried out within the natural forest patches. For this research, we chose relatively homogeneous forest plots away from roads and other this research, we chose relatively homogeneous forest plots away from roads and other

anthropogenically disturbed habitats, like farm fields, settlements, and power lines. This is particularly important when studying natural processes of community formation.

#### *2.2. Data Analysis*

Simpson's diversity index was calculated using the formula: D (Simpson's diversity index) =  $\sum (n/N)^2$ , where n is the percentage cover of a particular species, and N is the total percentage cover of all species [\[50\]](#page-12-9).

Differences in the number of plant species between communities at different age stages were identified using the non-parametric Kruskal–Wallis test. The Kruskal–Wallis test was followed by Dunn's multiple comparison tests to identify which groups are different. To determine the factors of community formation under the different types of forest conditions and for the different age stages, geobotanical descriptions of plant communities were ordinated based on nonmetric multidimensional scaling (NMS) using the PC-ORD program (version 6.0, MjM Software Design [\[51\]](#page-12-10)). The coverings of moss– lichen and grass–shrub species were taken into account in the analysis. Axis loads were calculated using the Sörensen coefficient.

#### **3. Results**

The total number of species in different types of forest ecotopes is determined by habitat fertility. Thus, in P.s.-Cl., the total number of species at all stages of forest development was 22, and in P.s.-V.v.-i.—50, P.s.-V.m.—91, and P.a.-V.m.—240 (Figure [3\)](#page-5-0). At the same time, in each type of forest ecotope, there are different patterns of phytocenosis composition formation at various stages of succession. In the poor, dry conditions of P.s.-Cl. and P.s.- V.v.-i., the number of species changed insignificantly. In general (Figure [3\)](#page-5-0) and on average for communities (Figure [4\)](#page-6-0), under the poorest conditions, the highest species diversity of vascular plants was observed at the clearcutting stage. Species diversity changed differently under the P.s.-V.m. conditions. Here, the restoration of the climax community usually went through a change in the dominant tree species (Figure [2\)](#page-4-0). The maximum species diversity of vascular plants both in general for all studied sites (Figure [3\)](#page-5-0) and on average (Figure [4\)](#page-6-0) was observed at the middle-aged stage, characterized by relatively sparse and usually mixed coniferous–deciduous tree stands.

<span id="page-5-0"></span>

Figure 3. Total species diversity of vascular plants of communities at different stages of forest generation after clearcutting in the studied ecotopes. The y-axis shows the number of species. regeneration after clearcutting in the studied ecotopes. The y-axis shows the number of species.

As noted earlier, the conditions of P.a.-V.m. are fundamentally different from the others in terms of soils, the dominant species in the climax state, and the dynamics of regeneration after harvesting—without human influence always through hardwood (*Betula* L. spp. or *Populus tremula* L.) dominance stages. There were also peculiarities in the change of species diversity of vascular plants during the recovery of the climax community after logging. In general, the cutting stage was characterized by high diversity, but mainly due to sites in agriculturally developed areas (Figure [3\)](#page-5-0). On average, the diversity in individual descriptions was practically the same at all stages of restoration (Figure [4\)](#page-6-0).

<span id="page-6-0"></span>

**Figure 4.** Variation in the mean number of vascular plant species (herbaceous–shrub layer species **Figure 4.** Variation in the mean number of vascular plant species (herbaceous–shrub layer species only) in the plant communities grouped by forest types and age stages (1—clearcuts, 2—young stands, stands, 3—middle-aged stands, and 4—old-growth forests). Different letters at the top of the figure 3—middle-aged stands, and 4—old-growth forests). Different letters at the top of the figure indicate significant differences between age stages within one type of forest condition (Kruskal-Wallis test). Wallis test).

as the evenness of species distributions in terms of abundance (Figure [5\)](#page-6-1)—the higher the value, the more the dominance of one or several species. In pine forests, the minimum values of the dominance index were found in clearcut communities, indicating the presence of several dominants. It is remarkable that the value of the index for the communities of young forests (P.s.-Cl.) is sharply out of the general trend as well as the logically high  $\alpha$  young for old growth forests under the conditions of the  $\beta_S$ .  $V_m$  and  $\beta_S$ ,  $V_m$  explores values for old-growth forests under the conditions of the P.s.-V.m. and P.a.-V.m ecotopes. We calculated the Simpson diversity index, which shows not so much the abundance

<span id="page-6-1"></span>

**Figure 5.** Variation in Simpson index values calculated for plant communities (based on herbaceous– **Figure 5.** Variation in Simpson index values calculated for plant communities (based on herbaceous– subshrub species abundance data) grouped by ecotope types and age stages (1—clearcuts, 2—young subshrub species abundance data) grouped by ecotope types and age stages (1—clearcuts, 2—young stands, 3—middle-aged stands, and 4—old-growth forests). stands, 3—middle-aged stands, and 4—old-growth forests).

# **4. Discussion**

In all the studied ecotope types, one pattern was observed both for the composition of vascular plants for the successional stage as a whole and on average for the site; the number of species was higher in clearcuts than in an old-growth forest. Similar patterns have been described for Canadian boreal forests [\[52\]](#page-12-11). We discussed these issues in detail in a long-term study of post-cutting communities [\[13\]](#page-10-11). Two main points should be emphasized here that provide an increase in diversity after felling. First, the removal of the "pressure" of the tree stand allows species of neighboring communities to inhabit the clearcut site [\[20](#page-11-4)[,21\]](#page-11-5). To illustrate the unpredictability of species composition of annual clearcuts, we can cite examples that contain weeds brought in with planting material from forest nurseries or agricultural fields if the clearcut is directly adjacent to a road of regular use [\[13](#page-10-11)[,21\]](#page-11-5). Their presence is very short-term (1–2 years) and does not have a significant impact on the subsequent formation of community structure, but should be taken into account in the study of species diversity. The second point is that no matter how destructive the impact of machines on the ground and soil cover may be, most of the boreal forest species find refuge near stumps, coarse woody debris, undercuts, and forest edges. Moreover, most forest species can regenerate via vegetative reproduction or seed reserves in the soil [\[53\]](#page-12-12). Only a few species can be considered extremely vulnerable, which not only reduce in abundance but, as a rule, "leave" the clearcutting area. The orchid *Goodyera repens* (L.) R.Br. and the fern *Athyrium filix-femina* (L.) Roth ex Mert [\[16\]](#page-11-0) are examples of such species among those widespread in the study area. The list could be extended to species of wet habitats, but we limited ourselves in this study to automorphic soils. Quite strict requirements on loggers for biodiversity conservation remove the richest streamside habitats from logging plans, and poor bog habitats are not cut for economic reasons. At the same time, not only wetland species but also aquatic plants are on the general list of clearcutting species. The point here is that the destruction of the tree layer in the lower parts and at the bases of slopes leads to the formation of overwatered areas and even persistently wet, non-drying puddles [\[13\]](#page-10-11). In other words, the tree layer smooths and equalizes the variations in forestpatch conditions within a forest type, and its destruction leads to an increase in habitat diversity and, consequently, species diversity (Figure [3\)](#page-5-0) [\[54\]](#page-12-13). At the same time, when considering species diversity within one patch, the differences in the number of species are not so great (Figure [4\)](#page-6-0).

The species diversity of intermediate stages (young and middle-aged stands), compared to the diversity of clearcuts and old-growth forests, are not so evident and differ depending on the type of forest conditions.

The two-factor ANOVA showed the dependence of the number of species mainly on the type of ecotope and confirmed our methodological assumptions about the need to strictly associate communities with the type of ecotope. Next, we review changes in the number of species by stages of vegetation recovery for each ecotope type separately. For P.s.-Cl., the clearcutting stage (until the formation of a closed tree stand) sometimes lasts for 15–20 years. Under these conditions, the restoration of the pine canopy and its density depend on silvicultural activities: whether seed trees were left, how close the forest edge is, and whether planting or support of natural regeneration was carried out. In most cases, forest regeneration is successful. The tree canopy intercepts light and water and can be said to "squeeze out" alien grasses and forbs from the community [\[22\]](#page-11-6). This is favored by the dominance of *Calluna vulgaris* L., which significantly increases its abundance in clearcuts as well as after fires. In contrast to richer conditions, where fluctuations in species abundance are quite sharp, here, the increase in the cover of heather and its following decrease during the formation of the tree layer is prolonged over the years. Therefore, a relatively high Simpson's index value is observed in young stands of lichen pine forests (Figure [5\)](#page-6-1). In middle-aged communities, the projected cover of *Calluna vulgaris* decreases and is leveled by the cover of other shrubs (*Empetrum nigrum* L., *Vaccinium vitis-idaea* L., and *V. myrtillus* L.).

P.s.-V.v.-i. plant communities are much more widespread in Karelia than the P.s.-Cl type. The growing conditions here are characterized by higher moisture content, lichens are replaced by green mosses in the ground cover, and boreal grasses and sedges appear at all stages of community development after logging. Species diversity at the first three stages changes insignificantly, decreasing in general only at the final stage—in old-growth communities. Old-growth P.s.-V.v.-i. forests are characterized by monodominant stands and sparse undergrowth, which explains the "compact" ecological range of old-growth P.s.-V.v.-i. forests (Figure [6\)](#page-8-0). The diversity of microhabitats is, thus, provided by canopy structures and woody debris. These factors do not increase the species diversity of vascular<br>*Pacifical pacifical* plants [\[10\]](#page-10-9) but drive only a change of dominants, usually *Vaccinium vitis-idaea*, *V. myrtillus*, and, in the north, also *Empetrum nigrum*.

<span id="page-8-0"></span>

**Figure 6.** Ordination diagram of plant community distributions in the factor space (NMS ordination **Figure 6.** Ordination diagram of plant community distributions in the factor space (NMS ordination based on cover data for grass–shrub and moss–lichen species). Designations: different icons indicate based on cover data for grass–shrub and moss–lichen species). Designations: different icons indicate different types of forest ecotopes, and different colors indicate age stages (1—clearcuts, 2—young different types of forest ecotopes, and different colors indicate age stages (1—clearcuts, 2—young stands, 3—middle-aged stands, and 4—old-growth forests). stands, 3—middle-aged stands, and 4—old-growth forests).

spruce undergrowth, and in old-growth forests, spruce is often abundant in the main canopy. The total species diversity is much higher here (Figure 3) as the community set is more diverse and the regeneration of bilberry pine forests on clearcuts can naturally proceed through the birch-dominating stage (Figure [2\)](#page-4-0). Why, in contrast to lichen and The transition from P.s.-V.v.-i. to P.s.-V.m. is well marked in nature by relatively dense

lingonberry conditions, is the maximum diversity both as a whole and on average in the community here observed at the middle-aged stage? We explain this by the specific changes in the community that occur by the middle-aged stage. Several tree species still dominate here, but natural (or anthropogenic) thinning of the tree stand has already occurred. The uneven canopy structure increases the set of microhabitats, which ensures the existence of a species in the community. In the early stages (in the absence of thinning), the tree canopy is very dense and prevents the growth of light-loving species, and, at a later stage, there will be a loss of deciduous species that have reached the age limit. These changes in the tree layer will lead to a decrease in the species diversity of the ground cover (Figure [4\)](#page-6-0).

The ecological conditions of old-growth bilberry spruce forests (P.a.-V.m.) are the widest of all the studied ecotope types, and overlap to a large extent with P.s.-V.m. (Figure [6\)](#page-8-0). Since the structure of the tree canopy is one of the determinants of species diversity, and both of these ecotope types have the same set of main tree species, it is not surprising that their ecological ranges, determined by the structure of the ground cover, overlap. It is also not surprising that the highest species diversity is observed in the P.a.-V.m ecotope. The distribution of P.a.-V.m. is confined mainly to southern areas with a large number of settlements and relatively developed agriculture. A large number of species were generally found in clearcuts under these conditions. At the same time, on average, in one description, species richness does not differ from that in young stands and is even slightly lower than in middle-aged stands. The latter is explained by the same reasons as for the P.s.-V.m. ecotope—the diversity of species in the tree stand and the relative sparseness of the stand.

Based on our research, is it necessary to carry out special activities when harvesting stands in order to preserve biodiversity and improve the regeneration of the original community? In this article, we have discussed changes in species assemblage but not in their projected cover. The removal of stands leads to localized outbreaks of some forest species. For instance, under the poor conditions of the northern taiga, *Calluna vulgaris* and *Vaccinium vitis-idaea* tend to grow, while in the richer southern communities, species like *Epilobium angustifolium* L., *Avenella flexuosa* (L.) Drejer, and *Calamagrostis arundinacea* (L.) Roth are found. This list can be continued, but the point is that all these species grow under the canopy of the stand, and the described processes have no effect on the number of species. However, a sharp increase in the cover of these species can be critical for conifer regeneration; therefore, the approach to commercial harvesting called variable retention forestry is certainly worthy of attention and approval. The fact is that the trees left in the clearcuts preserve the forest environment and the dominance of mature forest species, which is useful for the early regeneration of the natural community.

## **5. Conclusions**

In this article, we focused on changes in the number of species but not their composition. Our research has demonstrated the dependence of the species richness of vascular plants on the type of ecotope (the complex fertility of the site) and the influence of the tree layer. The first factor is evident and does not require special explanation—the more fertile the conditions, the greater the set of vascular plant species that can potentially inhabit the territory of one forest site. The second factor, in terms of the degree of influence on diversity, is the tree layer. There are some laws and regulations here as well. First of all, the diversity of the ground layer is determined by the composition of the tree layer. Each tree species creates special conditions, i.e., increases the diversity of microhabitats under the canopy. These factors act in combination, which is visible in Figure 6-the higher the soil fertility, the more complex the tree canopy and the wider the "spread" of canopy cover variations. Correspondingly, the total number of species associated with forest conditions and regeneration stage is also higher. The question remains: why are these potentialities rarely realized in the species diversity of a particular section, with the average numbers of species in the plant communities at different regeneration stages within an ecotope differing little from each other? The point is that most inventories were made under conditions remote from settlements, agricultural areas, and public roads, i.e., open habitats with high

species diversity. In addition, our study is limited to managed forests on automorphic soils, i.e., remote from bogs, rivers, lakes, and streams. Accordingly, the species pool of wetland habitats is not available for most of the studied communities. At the same time, there are exceptions, shown as "outliers" in Figures [4–](#page-6-0)[6.](#page-8-0) These exceptions are forest areas bordering diverse anthropogenic communities, which significantly expand the pool of vascular plant species. In general, the total list of species growing at the initial stages of forest community regeneration in clearcuts is much broader than in old-growth forests, but only because of areas located near settlements, agricultural fields, and public roads, which provide seeds of species that are not native to these forest communities.

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