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Spatial relationships of trees in middle taiga post-pyrogenic pine forest stands in the European North-East of Russia

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Abstract: Information on the structural organization of forest stands obtained on sample plots is the basis for long-term monitoring of post-fire pine forest structure and dynamics in the European North-East. These data can be used as a marker of native pine stands of the European taiga. Here, we studied vertical and horizontal structure in the post-pyrogenic pine forests of *Vacciniosum, Vaccinioso-cladinosum* and *Myrtillosum* site types in the boreal forest of the Komi Republic. The type of horizontal structure of uneven-aged forest stands changed with age from grouped to random one. Large trees were randomly distributed on the plot. We observed the weak aggregation of undergrowth trees (natural tree regeneration) in stands at distances of 2–6 m. Undergrowth individuals were characterized by group distribution at smaller distances than 1–2 m. Spatial relationships between large, small and codominant trees demonstrated random distribution in most cases. Undergrowth individuals did not show any competitive relations. However, we revealed a "taking off" effect between mature trees of pine and pine undergrowth. The direction of the displacement of tree crown centre projections relative to the bases of their trunks was ambiguous. The shift of the crown space towards the maximum solar radiation was detected in a thinned stand with old age and big size of trees. In other site types, no one-sided orientation of the tree crown development emerged.

Keywords: competitive interactions; Scots pine; spatial pattern; tree stand; undergrowth

Pine forests are the dominant formation of coniferous forests in the European North of Russia. Sustainable self-renewing pine ecosystems are formed as a result of forest evolution. In the Komi Republic, pine forests are most common in the middle taiga subzone and cover about 31% of the forest area of the region. The largest pine forest arrays are on the ancient alluvial terraces of large rivers (Pechora and Vychegda) and conical sandy moraines. Large arrays of pine forests of sphagnum type cover waterlogged watersheds. Regular fires mostly result in the death of a part of the stand

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and other components of the communities without large changes in tree species diversity or tree age generations (Furyaev et al. 2009; Ivanova, Ivanov 2015). Pine forests are affected by fires more often in comparison with other boreal stand-forming tree species. Evolution adaptations to fires, such as high fire resistance of adult trees and the ability to successful regeneration on burnt areas, allow Scots pine (*Pinus sylvestris* L.) to maintain and even expand its range (Sannikov, Sannikova 2009; Furyaev et al. 2009).

Frequency and intensity of forest fires determine the structure, functions and dynamics of the forest communities (Bergeron et al. 2004; Ivanova, Ivanov 2015). Recent studies reported a decrease in fire frequency in the boreal zone due to the anthropogenic influence (Drobyshev et al. 2015; Ryzhkova et al. 2020). This, in turn, may lead to a change in the structure of the pine communities. Climate is another factor important for understanding the processes of pine stand formation (Barhoumi et al. 2020). On the one hand, fire partially or completely destroys the plant community. On the other hand, after fire, the forest stand regeneration and renewal occur, and the soil fertility increases, which, in turn, has a beneficial effect on the emergence of new generations of pine. Thus, fires are important for forest development and forest evolution (Melekhov 1948; Kuuluvainen et al. 2002; Wallenius et al. 2002; Hancock et al. 2009; Pimont et al. 2011). According to Engelmark et al. (1998) and Kuuluvainen and Rouvinen (2000), the age structure of natural pine stands depends on the frequency and intensity of forest fires.

The study of spatial structure is important for analysis in forest ecosystems necessary for understanding the relationships between trees in spatial-temporal aspects (Gavrikov, Stoyan 1995; Dieckmann et al. 2000). In terms of practical implications, the spatial pattern of trees is essential, for example, when planning a forest inventory design and in the forest regeneration management (Grabarnik, Särkkä 2009).

The knowledge of the pattern formation of communities is the basis for a better understanding of the development of forest ecosystems. Information about the structure of tree stand is important for studying the historical development of forest communities, forest formation and growth processes, and also contributes to the sustainable forest management (Wallenius et al. 2002; James et al. 2007; Garet et al. 2012; Kuzmichev 2013). This indicator will also help to answer the question about the amount of carbon accumulated in organic matter at a certain stage in the development of forest communities (Kilpeläinen et al. 2017).

The vertical structure of the tree canopy largely depends on its closeness, the complexity of the stand structure and the vegetation condition. Currently, the tree stand vertical structure is important for the remote sensing (Korpela et al. 2007; Danilin, Favorskaya 2013; Vauhkonen, Mehtätalo 2014), and modelling of the dynamics of the structure and function of forest communities (Stinson et al. 2011; Shanin et al. 2014).

Thus, understanding the leading factors in the formation of the structure and functioning of forests under cyclical fire regimes allows us to expand our knowledge of the forests of the North. Based on this knowledge, it is possible to develop regional approaches to increase sustainability, productivity and effective reproduction of forest ecosystems. By the moment, there is a lack of studies on the structural organization of post-fire pine forests in the European northeast of Russia. The aim of this study is to estimate spatial structure in post-pyrogenic Scots pine forests in the North-East of Europe.

MATERIAL AND METHODS

Study area. We studied native pine forests of different site types on automorphous soils in the middle taiga subzone of the Komi Republic (60°44'N to 62°02'N; 50°28'E to 57°06'E). Seven sample plots (SP) were studied within the boundaries of the Pechoro-Ilychsky Biosphere State Reserve and the Chernamsky Reserve (monitoring station) (Figure 1). Pine forests of *Vacciniosum*, *Vaccinioso-cladinosum* and *Myrtillosum* site types are common in the area under study. These stands are mostly monodominant and confined to the terraces and well-drained watershed areas (Kutyavin 2018).

The study stands are periodically affected by ground fires. According to the wood samples, we found 2–6 fires in the stands (Table 1). The tree layer of plain pine stands is composed of Scots pine with a mixture of Siberian larch (*Larix sibirica* Ledeb.), Siberian spruce (*Picea obovata* Ledeb.), and birch (*Betula pubescens* Ehrh., *Betula pendula* Roth). About 60% of the undergrowth consists of spruce with a mixture of Siberian pine, birch and aspen (*Populus tremula* L.).

Figure 1. Map of the study area and monitoring study plots

Unlike the plain stands, foothill pine forests of *Vacciniosum* (SP 12) and *Myrtillosum* (SP 1 and SP 10) site types have a slightly greater proportion of codominant tree species (spruce, Siberian pine and birch) in the stand composition. Within these pine forests, both simple single-layer and more complex two-layer stands occur. The undergrowth is dominated by Siberian pine (up to 60%), spruce (up to 50%) and pine (up to 40%). The number of undergrowth individuals varies across the forest types from 1.5 to 7.2 thousand ind·ha^{-1} (Table 1).

Data collection. At the 0.25–0.4 ha plots, we made continuous counts of trees and undergrowth plants taking into account their positions on the area in a rectangular coordinate system (X, Y) using a set of equipment for forest inventory Haglof Postex Laser (Haglof, Sweden). For a more reliable statistical analysis, SP size depended on the number of dominant tree species of at least 150–200 trees on plots. To assess the spatial structure of forest stands and undergrowth with complex structure and mixed composition, they were divided into size categories, tree species and their living state. Undergrowth was assessed at the 0.065 ha plots. The trees with ≥ 6 cm diameter at breast height 1.3 m (*DBH*) were included in the tree layer. Other tree individuals were described as undergrowth. Tree height was measured for all trees.

For each living tree with diameter more than 6 cm, the radii of the crown projection were measured in four directions (north, south, west, and east) as the distance from the centre of the trunk to the crown perimeter using Leica laser rangefinders (Leica, Germany). The height of trees and the length of their crowns were measured with a Haglof laser altimeter (Haglof, Sweden). To date old historical fires in order to clarify the origin of all tree stand generations, we collected samples of dead trunks and woody residues (fallen wood, burned stumps) by sawing (Madany et al. 1982). In order to determine the tree age, we collected at least 100 wood cores using an increment borer on each monitoring

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Table 1. Silvicultural-taxation characteristics of pine forests under study

Site type (SP)	Stand composition* (tree story)	Age (mean age) (years)	Fire years	Tree quantity (n·ha^{-1})	Total basal area (m^2·ha^{-1})	Growing stock (m^3·ha^{-1})
Stands						
Vacciniosum (1)	10PSyl single PO	34–385 (131)	1887, 1805, 1785, 1744, 1727	484	21.3	193.4
Myrtillosum (4)	8PSyl1PO1BP single PS, AS	94–410 (178)	1841, 1769	952	29.7	320.2
Vaccinioso-cladinosum (8)	10 PSyl single B	60–162 (92)	1926, 1935	1 731	27.3	150.3
Myrtillosum (10)	(I) 10 PS	109–211 (114)	1905, 1868, 1842	583	22.7	229.5
	(II) 7PO3B	87–132 (112)				
Vacciniosum (12)	8PSyl1PO1PSib+B	72–173 (113)	2011,1906, 1841, 1772	824	26.0	230.0
Vacciniosum (21)	10PSyl+LS single B	37–425 (5)	2010, 1933, 1885, 1692, 1655, 1653	316	23.0	221.5
Myrtillosum (22)	10PSyl single PO	129–324 (102)	1916	648	32.3	334.5
Undergrowth						
Vacciniosum (1)	9PSyl1PO+PSib single B, PT	–	–	5 696	–	–
Myrtillosum (4)	6PSib2PO1B1PSyl+AS	–	–	2 240	–	–
Vaccinioso-cladinosum (8)	6PO4PSyl+B	–	–	651	–	–
Myrtillosum (10)	5PO4PSib1PSyl singleB	–	–	1 496	–	–
Vacciniosum (12)	4PSib4PSyl2PO single AS, B	–	–	7 240	–	–
Vacciniosum (21)	9PSyl1PT single B	–	–	6 288	–	–
Myrtillosum (22)	6PSyl2PO2PSib single B, PT	–	–	1 312	–	–

*the formula for the composition of the stand and undergrowth consists of the letter name of the tree species (PSyl – *Pinus sylvestris*, PSib - *Pinus sibirica*, PO – *Picea obovata*, LS – *Larix sibirica*, B – *Betula pendula, pubescens*, PT – *Populus tremula*, AS – *Abies sibirica*) and the composition coefficient; the unit of the composition coefficient corresponds to 10% of the stock of a given species in the total wood stock or the amount of a given species in the total amount of undergrowth; + – the proportion of the species 2–5%; single – the proportion of the species < 2%; SP – sample plot

plot. The cores were sampled with increment borer as close to the soil as possible. The age of trees and number fires were determined using a binocular and Lintab 5 instrument (Rinntech, Germany).

Data analysis. Vertical structure of tree canopy was identified by quantifying tree height and crown size. Based on these parameters, we calculated the space filling coefficient for living tree crowns by counting the number of trees with crown-filled space by one-meter height steps, expressed in relative units. The obtained data are presented in graphs [Figure 2, Figure S1, see the Electronic Supplementary Material (ESM)] to compare with different combinations of vertical stand type schemes (Plotnikov 1979).

Allocation of trees and undergrowth in a two-dimensional space was considered as a point process, where "points" are the positions of the trunk bases of woody plants relative to the coordinates X and Y (Schabenberger, Gotway 2005). Additional

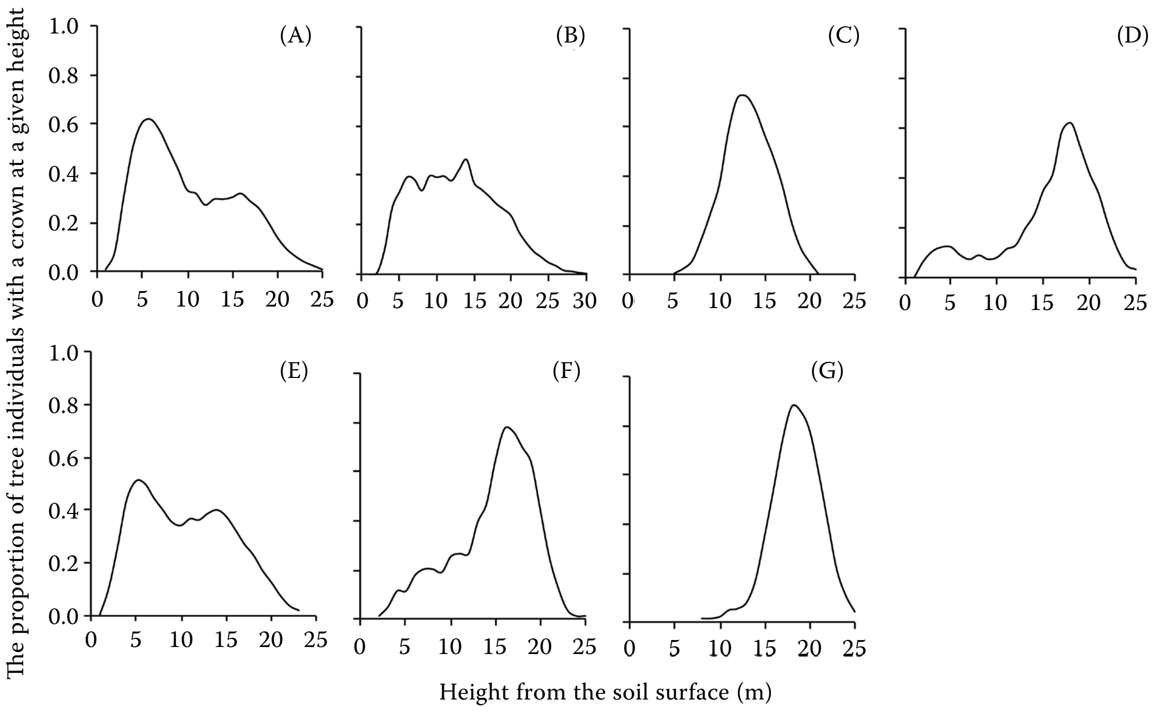

Figure 2. Distribution of space filling coefficients (the proportion of tree individuals with a crown at a given height) with living crowns in pine forests: (A) *Vacciniosum* (SP 1); (B) *Myrtillosum* (SP 4); (C) *Vaccinioso-cladinosum* (SP 8); (D) *Myrtillosum* (SP 10); (E) *Vacciniosum* (SP 12); (F) *Vacciniosum* (SP 21); (G) *Myrtillosum* (SP 22)

information (size, species and other characteristics of plants) is considered as marked point processes. As a statistical tool for assessing spatial interactions in point processes, we used an easy-to-interpret and non-accumulative pair correlation function $g(r)$ (Stoyan, Penttinen 2000). The function $g(r)$ is based on counting pairs of points, the distance (r) between which does not exceed a certain specified value.

The classical analysis of point processes is based on the comparison of the model of observed distribution of trees with the model of complete spatial randomness (CSR), when the "points" are located in a random way. Areas with upper (95%) and lower (5%) confidence intervals for the adoption of the null hypothesis of CSR and the models are calculated based on 999 generations of a homogeneous Poisson process (Wiegand, Moloney 2004). A high number of generations reduces the probability of a type I error (Grabarnik et al. 2011). The hypothesis of the CSR model was tested by the Monte Carlo method, assessing the significance of the deviation of the empirical value of $g(r)$ function from the theoretical one $g(r)$. A point process was defined as aggregated (grouped), random or regular (uniform) if the value $g(r)$ was higher, equal to or lower, respectively, than the confidence intervals.

The spatial relationships between woody plants were studied using the cross-correlation function $g_{ij}(r)$, which, like the pairwise correlation function, depends on the distance (r) between "points". Its values allow us to test the hypothesis of independence or randomness of point marking processes (Stoyan, Penttinen 2000). The methods for estimating the function $g_{ij}(r)$ are similar to $g(r)$.

To study the horizontal structure of forest stands and undergrowth, we analyzed the position of growing trees and living undergrowth on the SP, including conditionally divided trees: large trees ($DBH \geq 20$ cm), small trees (DBH 6–19 cm), pine trees – edificators in the tree layer and other tree species, large undergrowth (height ≥ 0.5 m), small undergrowth (< 0.5 m), pine undergrowth and undergrowth of other tree species. A finer fragmentation of the stand and undergrowth components leads to a small sample of statistical indicators, which leads to a weakening of spatial effects. If there was a small sample size of one of the considered components of the stand and undergrowth, the component was excluded from the analysis.

Statistical processing of spatial data was carried out in the spatstat package (Baddeley, Turner 2005) in the R software environment (Version 3.5.3, 2020).

RESULTS

Vertical structure. In the stands of *Vacciniosum* type (SP 1, SP 12), trees vary significantly in height, and the bases of their canopies are approximately at the same distance from the ground level. This type of structure is classified as "ground regular" [Figure 2A, 2E, Figure S1, see the Electronic Supplementary Material (ESM)]. The difference in tree heights is due to the presence of young and old generations of trees. The "regular on top" type of vertical structure emerged in *Myrtillosum* (SP 10) and *Vacciniosum* (SP 21) stands. In this structure type, the tree height is approximately the same, while the canopy length is very different (Figure 2D–F). In the *Vaccinioso-cladinosum* (SP8) and *Myrtillosum* (SP 22) pine stands, trees differed in height and canopy length, but their average part was at the same level. The vertical canopy space of these stands has compact dimensions and may be described as "symmetrical structure" (Figure 2C, 2G). The stand of *Myrtillosum* pine forest (SP 4) demonstrated "diffuse" structure (Figure 2B).

Horizontal structure and space relationships. A slight deviation from the homogeneous Poisson process can be traced in a certain regularity of the old-growth trees distribution in *Myrtillosum* (SP 4, SP 22) forests at distances of up to 1 m (Figure 3I, 3L). Other forest types have a random type of large tree distribution in the area (Figure 3H, 3J, 3K). Distribution of small trees is mostly random at all the study sites (Figure 3N–Q). The presence of many trees of the young second generation in the *Vacciniosum* pine forest (SP 1) is explained by the aggregation of trees at distances up to 8 m (Figure 4M). In the *Myrtillosum* (SP 4) and *Vaccinium* (SP 12) stands, a lot of codominant tree species presented mainly by small individuals of Siberian pine, spruce and birch demonstrates weak aggregation at 2–3 m distance (Figure 3T, 3U). Pine trees are randomly distributed (Figure 3R, 3S).

The amount of undergrowth was different under the stand canopy (Table 1). And the undergrowth distribution in the plot does not obey the CSR hypothesis in any of the studied pine communities. In the *Vacciniosum* (SP 1), *Myrtillosum* (SP 4), *Vaccinioso-cladinosum* (SP 8) and green-moss (SP 22) forests, where large and middle undergrowth prevailed, we found an aggregation of individuals at small distances (less than 1–3 m) (Figure 4A–C, 4G). Tree undergrowth in the *Myrtillosum* (SP 10) and *Vacciniosum* (SP 12, SP 21) sites, where small undergrowth is prevalent, forms large clusters at distances up to 3–6 m (Figure 4D–F). Analyzing the distribution of small and large undergrowth, we found a tendency of large undergrowth to random distribution (Figure 4H–J, 4L). The clustering of large undergrowth is noted under the canopy of the *Myrtillosum* pine forest (SP 10) within a radius of 4 m (Figure 4K). Small undergrowth can aggregate within a radius of 6–8 m (Figure 4M–Q). The degree of undergrowth aggregation decreases with an increase in the undergrowth size, which may be caused by elimination in dense groups of individuals due to competition for soil nutrients. At this stage of the stand development, there is a gradual self-thinning of the group type of distribution of trees in the area, followed by their transition to a random type. Analysis of the spatial distribution of pine and other tree species undergrowth in the *Vaccinioso-cladinosum* stand (SP 8) revealed higher clustering of the codominant tree species at the distance up to 2 m (Figure 4R, 4T). In the green-moss pine forest (SP 22), pine undergrowth tends to be regularly distributed at small distances (up to 2 m), and the codominant tree species are randomly distributed at the site (Figure 4S, 4U).

The tested spatial relationships between large and small trees (Figure 5A–E), and between pine and codominant trees (Figure 5F, 5G) using the cross-correlation function predominantly demonstrate their independent placement. Only the stand of *Vacciniosum* pine forest (SP 1), which has two large generations with a long-term age gap, shows a weak trend for competition for space between large and small trees at a short distance of 2–3 m (Figure 5A). The taking-off is also noted between pine and codominant trees in the *Vacciniosum* stand (SP 12) (Figure 5G). Analysis of the joint placement of trees and undergrowth on an area in some types of forest (SP 1, SP 4, SP 12, SP 21) also reveals a taking-off trend between trees of different stand components (Figure 5H, 5I, 5L, 5M). In undergrowth assemblages, both taking-off and attraction of trees can be observed. For example, in the *Myrtillosum* pine forests (SP 4, SP 10), where the proportion of pine in the undergrowth is lower than 10% (Table 1), small undergrowth individuals are placed among the large ones, forming an aggregated type of spatial distribution (Figure 5P, 5R). On the contrary, stands with a high pine proportion in the under-

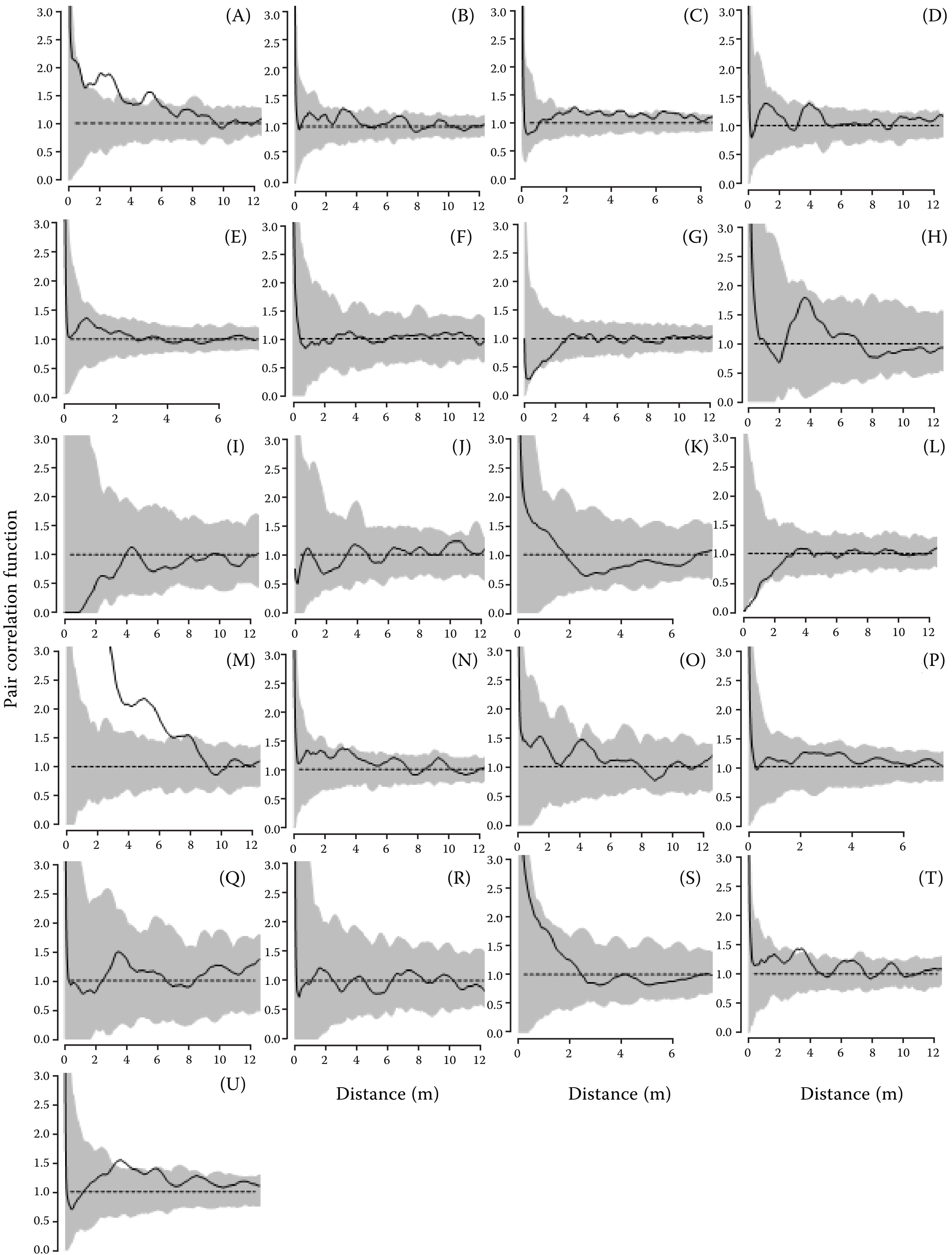

Figure 3. Assessment of empirical pair correlation of function ĝ(r) (solid line) and the area of acceptance of the null hypothesis about the randomness of a point process (grey area) for: (A–G) trees at SP 1, SP 4, SP 8, SP 10, SP 12, SP 21, SP 22; (H–L) large trees at SP 1, SP 4, SP 10, SP 12, SP 22; (M–Q) undergrowth at SP 1, SP 4, SP 10, SP 12, SP 22; (R–S) pine trees (SP 4, SP 12); (T–Y) trees of co-dominant species (SP 4, SP 12)

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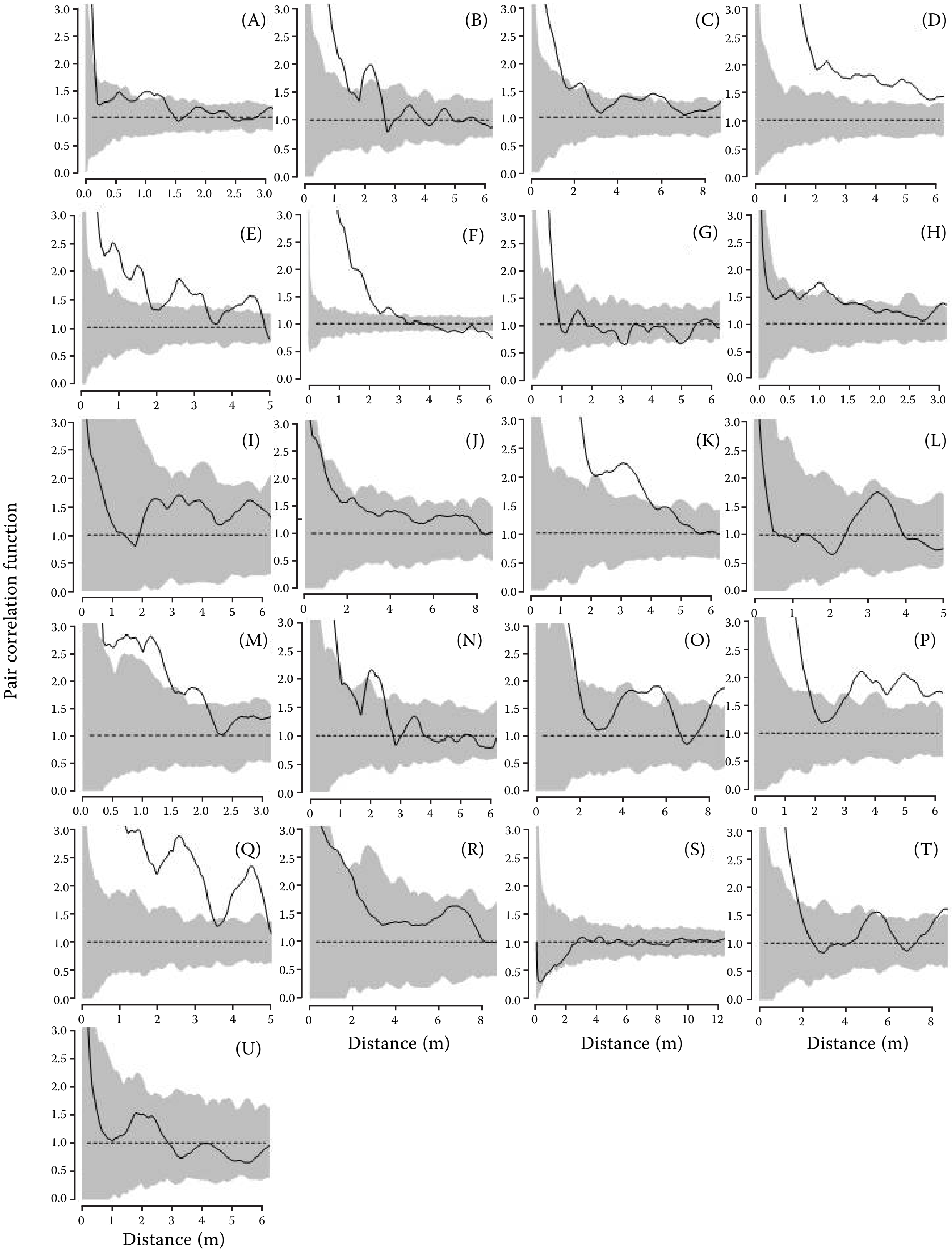

Figure 4. Assessment of empirical pair correlation of function $\hat{g}(r)$ (solid line) and the area of acceptance of the null hypothesis about the randomness of a point process (grey area) for: (A–G) undergrowth SP 1, SP 4, SP 8, SP 10, SP 12, SP 21, SP 22; (H–L) large undergrowth SP 1, SP 4, SP 8, SP 10, SP 12; (M–Q) small undergrowth SP 1, SP 4, SP 8, SP 10, SP 12; (R–S) pine undergrowth (SP 8, SP 22); (T–Y) undergrowth of co-dominant tree species (SP 8, SP 22)

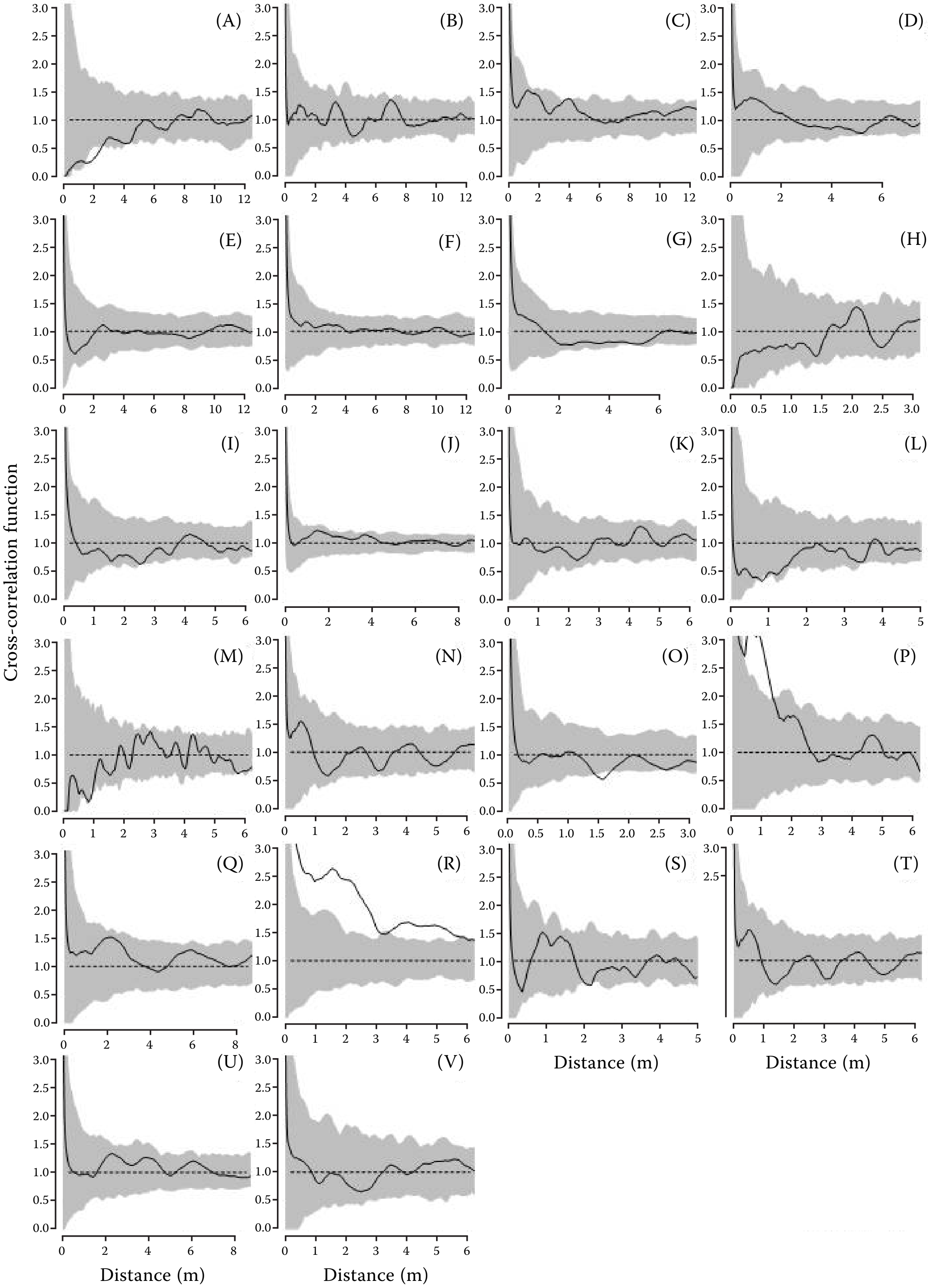

Figure 5. Assessment of empirical cross-correlation function $\hat{g}_{ij}(r)$ and the area of acceptance of the null hypothesis about the randomness of a point process for each pair of categories of tree species: (A–E) large trees/small trees; (F–G) pine trees/co-dominant trees; (H–N) trees/undergrowth; (O–T) large undergrowth/small undergrowth; (Y–V) pine undergrowth/co-dominant undergrowth

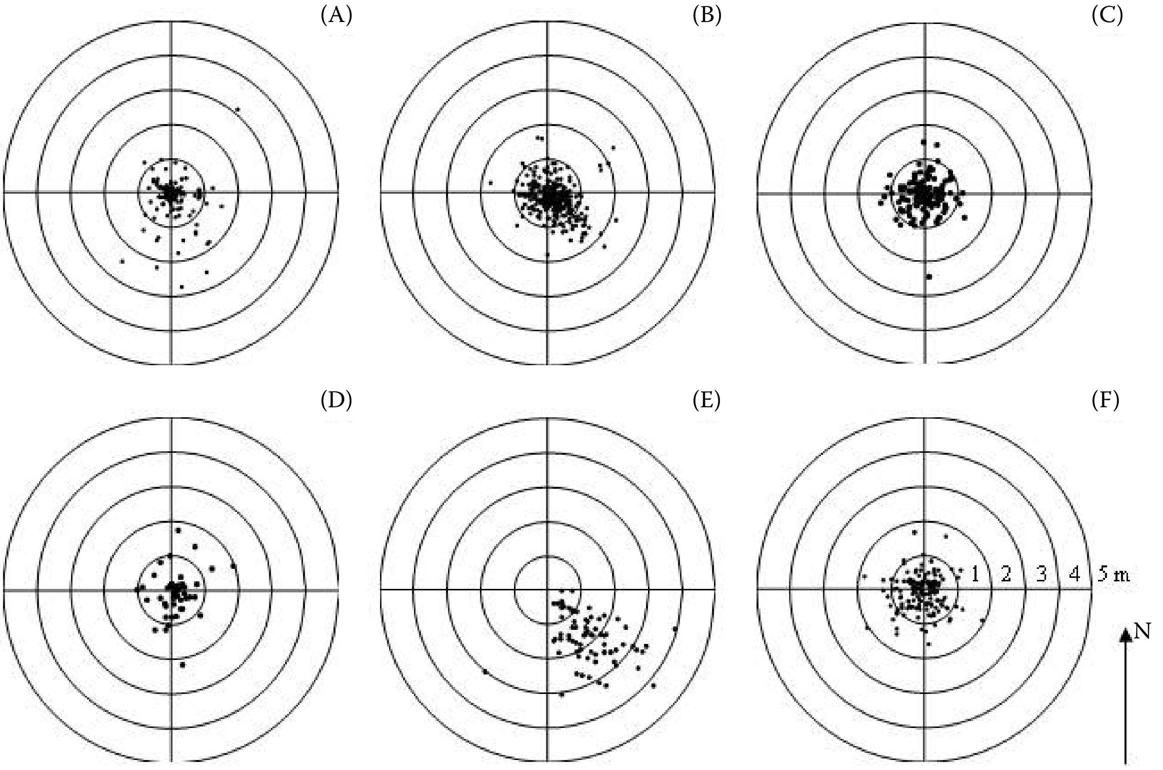

Figure 6. The direction of development of tree crowns in pine forests: (A) *Vacciniosum* (SP 1); (B) *Vaccinioso-cladinosum* (SP 8); (C) *Myrtillosum* (SP 10); (D) *Vacciniosum* (SP 12); (E) *Vacciniosum* (SP 21); (F) *Myrtillosum* (SP 22)

Dots – the centers of tree crowns relative to their trunks; the arrow – direction north

growth (SP 1 and SP 12) demonstrate a competition between large and small undergrowth individuals (Figure 5O, 5S). In another site type, the distribution of large and small undergrowth is random. Joint placement of pine undergrowth with undergrowth of codominant trees is random in the *Vaccinioso-cladinosum* (SP 8) and green-moss (SP 22) pine forests (Figure 5U, 5V).

The stands under study have an asymmetrical canopy development (Figure 6). The displacement of tree crown projection centres relative to the base of their trunks is highly variable. The trees in the *Vacciniosum* pine forest (SP 21) forming a sparse stand with a predominant generation of large old-growth individuals with a wide crown have a greater displacement of the centres of crown projections. In this type of community, phototropism is manifested very clearly. Under the influence of uneven solar radiation in the tree canopy, mature trees stretch their branches towards the light, which leads to the formation of an eccentric crown shape with a shift in the centres of the crown projection in the southeast direction (Figure 6E). The phototropism is not clear in other denser stands under study, where the crown development is randomly directed (Figure 6A–D, 6F).

DISCUSSION

Vertical structure of the tree canopy largely depends on its closeness, the complexity of the stand structure and the vegetation condition (Shanin et al. 2016). Our studies have shown different types of structures that fill the space of the tree crown in primary pine forests. On SP 1 and SP 12 with "ground regular" vertical structure, a difference in tree heights is due to the presence of two generations. The same height of canopy bases is possibly associated with the competition for light between young individuals when growing in groups. This competition causes the active growth of the second generation trees, which may result in the raise of the canopy base of these trees to the height of adult plants (Figure 2A, 2E). The structure on SP 10 and SP 21 is composed of the abundant old trees of maximal height (Figure 2D, 2F). The stands SP 8 and SP 22 have relatively high density and short age series, which had probably led to the compact canopy dimensions due to interspecies competition for light in the dense stands (Figure 2C, 2G). Stand SP 4 shows "diffuse" structure, when the trees are different in height, but they are similar in the relative length of the canopies. As a result the living canopy is stretched in the vertical direction (Figure 2B). Accordingly, this method of displaying information on the vertical vegetation structure allows to combine the stands with similar structure of the recorded plant height vertical framework, crown size and horizon of the maximum concentration of photosynthetic biomass (Plotnikov 1979).

Many authors (Plotnikov 1979; Storozhenko 2007; Kuzmichev 2013) noted a grouped pattern of trees in the natural stands at the stage of forestation. This pattern becomes more random with age. According to Storozhenko (2007), the regeneration and decaying processes are constant during the whole life-time of stable native forest and result in the formation of a complex spatial stand structure. This result is confirmed by the patterns of horizontal structure of post-pyrogenic pine forests on automorphic soils. Statistical analysis of spatial point process models revealed the diversity in the horizontal structure of stands and undergrowth in the pine forests under study. Several deviations from the CSR hypothesis were found in the tree distribution in the *Vacciniosum* (SP 1) and *Vaccinioso-cladinosum* (SP 8) stands. Also, this result might be explained by the fact that large pine trees form a "plate" root system on the automorphous soils, intercepting elements of mineral nutrition from the upper horizons of the soil, and causing a competitive relationship between individuals of different size categories. At these plots, we found the weak aggregation of trees at a distance of 2–6 m (Figure 3A, 3E), caused by the presence of the second generations of relatively young trees, affected by the tree elimination processes due to high stand density and increased competition for space and soil nutrients. There are no spatial dependences in tree distribution in the stands of *Myrtillosum* (SP 4, SP 10), *Vacciniosum* (SP 12, SP 21) and *Myrtillosum* (SP 22) site type (Figure 3B, 3D, 3E, 3F). These stands are mainly composed of old trees. The self-regulation processes are weakened, and there is practically no replenishment of stands by the young tree generation.

The resistance of Scots pine to the pyrogenic impact is a part of the species adaptive response to stress developed in the course of evolution and proceeding under the climatic background of the local region (Furyaev et al. 2009). These processes are an endogenous mechanism of the forest community dynamics, allowing it to withstand an adverse environment. A few studies (e.g. Getzin, Wiegand 2007; Shanin et al. 2016) revealed that the regular pattern of tree crown centres is typical of the random type of tree distribution on the plot due to the use of the inter-crown space. Our research in pine forests indicated that the structure of distribution of tree crown centre projections repeats the type of distribution of trunk bases on the plot. The independent placement of large and small trees is predetermined by the distance between them, at which the strength of competition between trees of different size for elements of mineral nutrition and living space directly depends on the degree of aggregation of individuals (Ipatov, Tarkhova 1975).

Studies of Siberian pine stands (Gavrikov, Stoyan 1995) showed the changes in the crown distribution with age from group to regular pattern. Old light-demanding tree species may demonstrate a tendency to the regular pattern. High thermal stability of the bark of the lower part of the pine trunk and after-fire regeneration peaks of the pine are evolutionary adaptations allowing pine to grow in conditions of cyclic ground fires (Sannikov, Sannikova 2009). These adaptive features are an endogenous mechanism of the forest community dynamics, which allows to maintain the balance of matter and energy and to withstand adverse environment (Storozhenko 2007). Our results are in line with the theory of structural organization of pine forest ecosystems and confirm that fires are one of the main factors affecting the structure of boreal forests (Bowman et al. 2013; Shanin et al. 2016). The considered pine forests formed a complex structure of woody plant populations due to different fire dynamics that led to changing the type of horizontal structure from group to random one. Thus, pine forests have an optimal structure of forest stands which has allowed for hundreds of years in most cases to prevent the transition of ground fire to crown fire which could lead to their complete destruction.

CONCLUSION

The studied pine communities with different pyrogenic patterns formed a complex structure of tree populations. These stands are in the regime of natural dynamics. In pine forests, tree stands have a complex spatial structure. The spatial distribution of trees on the plots changes with age and mainly has an aggregated type at the stage of post-pyrogenic regeneration. Due to the competition for mineral elements, dense groups of undergrowth are gradually dissociated with the formation of random distribution type. Undergrowth demonstrates weak grouping in the stand. Large trees are randomly distributed on the plots. All the pine stands have an asymmetric development of tree crowns. In the open stands, we found an eccentricity of the crown shape in the direction of maximum sunlight. Thus, the pine forests form an optimal stand structure, allowing for hundreds of years, in most cases, to prevent the transition of ground fire to crown fire, which could lead to their complete destruction. The data on the structural organization of forest stands collected from the test plots can be used as a basis for long-term monitoring of the post-fire pine forest structure and dynamics in the European North-East, and may be a marker of native pine stands of the European taiga when comparing them with bordering areas.

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