



Analysis of the spatial structure of a natural spruce and beech mixed stand (Slatioara Secular Forest)

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Abstract. Forests are one of the most complex and diverse ecosystems. The complexity of the natural forest ecosystems is determined by the large diversity of structure, the multiple biocenosis connections, the variety and length of trophic chains. Forest ecosystems are highly stratified, each layer having distinct functions. The investigation took place in the Secular Forest Slătioara which presents the structure of multi-year and heterogeneous tree populations and the composition of tree species consists of beech (*Fagus sylvatica*), fir (*Abies alba*) and spruce (*Picea abies*). The main objective of this study was to detect spatial patterns between spruce and beech species from different dimensional classes in the Slatioara Secular Forest in order to test the hypotheses related to the mechanisms underlying the autogenous cohabitation of these forest species. In this paper, the spatial distribution of trees and the extent to which they differ significantly was first analyzed, and secondly, the correlation between the average distance from each tree to the nearest three neighbors was tested, and the extent to which the distribution of seedlings is correlated with the distribution of trees was highlighted, by determining the minimum inhibition distance between seedlings of spruce and beech. Following the univariate and bivariate analyzes, it was concluded that the spatial distribution of spruce and beech seedlings depends on the radius, which identifies the closest neighbors for a particular individual, so if the radius is <2.55 m, the distribution is of aggregate type (spruce seedlings are grouped in meshes and beech seedlings under the crowns of trees) and if the radius is >6.50 m the distribution becomes scattered. When we refer to the spatial distribution of spruce trees, we notice that on a small scale the distribution does not differ significantly from the random one, but on a large scale (over 12 m) there is a tendency to transform in a dispersed type, most likely due to intraspecific competition as well as the fact that spruce is a light-tempered species. The results showed that beech, both in the juvenile and tree stage, seem to be the species with the greatest impact in the equalization and stabilization mechanisms necessary for coexistence but also for maintaining the diversity of tree species within these types of forests.

Key Words: seedlings, spatial distribution, types of forest.

Introduction. The interest in pristine forest began to manifest at the end of the last century, when the first large-scale disturbance occurred in central Europe in man-made coniferous forests, outside their natural distribution range. Since Gayer (1878), many specialists have studied the pristine forest, by trying to determine its growth, development, structure, regeneration and resilience mechanisms, and ecosystem functions (Oliver 2015; Gunderson 2000; Mori 2016). From an ecological point of view, the natural forest ecosystems are represented by a strongly vertical stratification, which is a complex and very dynamic biosystem determined by a great diversity of structure, a complex organization and multiple biocenosis connections, with various and long trophic chains. The classification of forests into a reasonable number of types (units), relatively homogeneous in terms of composition and forest site, is crucial for the development of frameworks for inventory, monitoring, restoration, management and conservation of forest ecosystems (Gafta 2020).

The forest understory is a heterogeneous and dynamic habitat and microsite conditions are continuously changing, as are populations of understory species and, because the understory contains the bulk of the species diversity of vascular plants in temperate forests, is very important to ecosystem functioning, and has important influences on the canopy, understanding of understory plants is critical to forest

management (Antos 2011). The relationship between the trees layer and the understory layer in natural forests continues to present controversial concepts among researchers, especially since the results of the studies do not fully agree and seem to indicate a dependence on the eco-cenotic context (Beatty & Scholes 1988; Ewald 2000; Maltez-Mouro et al 2005; Mölder et al 2008; Chavez & MacDonald 2010; Bartels & Chen 2013), but also on the scale of observation (Gilliam & Roberts 2014). In this regard, various studies stated that the specific composition of the grass layer varies, being sensitive to minor changes in environmental conditions (soil factors, water, gas and soil temperature regimes, its chemical composition) or ecological factors (light quantity and quality, temperature which influences most plant processes including photosynthesis, transpiration, respiration, germination, and flowering) (Bee et al 1989; Qian et al 1997; Sagers & Lyon 1997; Härdtle et al 2003; Tobisch & Sandovar 2005).

In Romania, research has also studied the issue of the competition between trees. Thus, Popa (2004) assessed the spatial variability of competition indices in natural forests and Palaghianu (2009) studied how competition affects the growth of seedlings. Spatial relationships between trees play an important role in the dynamics of forest ecosystems that regulate, together with other factors, the processes of competition, growth, mortality and regeneration of a plant community (Dieckmann & Doebeli 2000). Competition between trees is not symmetrical, usually, a large tree influences the small ones, at least if the dimensions of the trees are very different (Weiner 1990).

The diversity of the tree layer influences the compositional diversity of the lower stratum (subshrub and herbaceous cover) (Augusto et al 2003). The tree layer in natural forests is also characterized by a higher level of compositional diversity compared to similar artificial stands (Duduman et al 2014). The structural diversity of a forest stand indicates the variability of the dimensional characteristics of the constituent trees and is assessed through the distributions of trees in the horizontal and vertical space (Helms 1998). Specific models of spatial trees distribution that depend on the distance between the trees, present the forest as a mosaic dependent on the distance between its parts. Theoretically, the dynamics of each part are described using a model characteristic of an average tree (Bîrsan 2018). The vertical and horizontal structure of trees must be analyzed by models based on the interaction between neighboring trees (Pacala et al 1996) because the development of each tree in a stand is influenced by its neighbors and each tree influences the development neighbors (Hari 1985). Trees can develop to benefit from the existing resources in their growing space, avoiding neighboring trees and managing to reduce the permanent competition within them (Stoll & Schmid 1998; Muth & Bazzaz 2003). However, the interaction between neighboring trees can be not only competitive, but also facilitating, in the sense that, at certain times, one tree can create favorable conditions for the development of another tree in its living space. Over time, this facilitation relationship will turn into a competitive one (Callaway et al 2002).

One of the biggest influences induced by the forest is related to light, changing the quality and quantity of light that pass the forest canopy. In the forest environment, the upper surface of the canopy acts as a reflection screen that interferes with solar radiation. The entire canopy forms a dense and continuous filter that allows light to pass in a smaller amount in comparison to open ground, hence changing the structure and composition of tree populations (Royo & Carso 2006; George & Bazzaz 2014). The light regime inside the forest varies according to the condition, structure, age, composition and season. A dense forest of spruce, beech and fir at the age of their maximum growth, retains up to 98% of full light, preventing the installation of another layer of vegetation inside the forest. Interactions between neighboring trees can lead to positive, negative or zero net effects, depending on the balance between asymmetric competition and facilitation, limitation and diversification of resources (Chi et al 2015; Bulleri et al 2016). Biotic interactions between individuals of tree species occur at different spatial scales, which can range from a few centimeters (in the case of seedlings) to tens of meters (in the case of adult trees) (Gafta 2020). In the same forests, the conditions are different before the canopy closure is being established, as well as after the transition to the mature development stage when the thickness of the forest canopy is smaller and it allows a larger amount of light to enter. Coniferous forests have a constant influence on

light throughout the year, meanwhile deciduous forests are more opaque during the growing season, while in winter, when the trees are leafless, direct sunlight bathes the forest floor. The horizontal distribution of light in the forest environment depends on the horizontal structure of the biocenosis and of course on species composition. In a complex structured biocenosis, for example, an uneven-aged stand, the horizontal variation of light intensity will be higher.

The process of tree species alternation, which consists of the preferential regeneration of one species under the canopy of another one, is largely explained by competition for light but also for water and minerals. As it results from Bândiu's research (1977), in fir-beech stands a cause of alternation is the selective absorption of light by fir and beech. Beech absorbs a greater amount of shortwave radiation (blue) while fir absorbs longwave radiation (red). Even if there is light under the canopy, the beech seedlings have under the fir trees sufficient radiation with the necessary wavelength, just as the fir seedlings find sufficient light conditions under the beech trees. Under the trees of the same species the seedlings do not have the necessary light radiations to survive. This phenomenon of alternation of species is characteristic for beech and fir forests and is also a factor of stability of those forests. The herbal layer cover is influenced by the spatial distribution of the trees. Thus, under spruce trees with a thick crown that causes shading of the ground and soil acidification by the accumulation of litter, the herbal layer cover will be reduced, in many situations completely missing. In the case of the beech trees, at the ground level the herbal cover will be higher, a phenomenon explained by a higher flux of light which reaches the ground level and a reduced litter thickness, respectively (Finzi et al 1998). The herbal layer cover is also influenced by the interspecific competition of herbs for water and minerals. Allelopathic substances inhibit the germination of the seeds of some trees or the growth of plants of their own species through self-inhibition. The role of these allelopathic substances in an ecosystem is to suppress the competition of other species for vital factors (soil nutrients or sunlight), some species managing to occupy exclusively a certain territory in the forest habitat.

Many authors have developed different competition indices (Becker 1992; Ung et al 1997; Pretzsch et al 2002; Prévosto 2005) that refer to the structural elements of the forest ecosystem, namely tree growth and their position in stands. These indices are classified according to Munro (1974) in: (i) indices according to the distance between the trees; (ii) independent distance indices (based on vertical and horizontal angles). Interpreting such numerous and strongly linked relationships in the network of quasi-virgin uneven-aged ecosystems remain a problem of scientific research in our country. In the recent years, the studies which have been conducted aimed to understand the factors and phenomena that influence the abundance and distribution of cormophytes in natural forest ecosystems. Duduman et al (2014) studied the relationship between the structural diversity of the tree floor and the compositional diversity of the vascular flora from a natural mixture of beech conifers stand in the Slătioara Secular Forest, which confirmed the presence of a high compositional diversity that is directly proportional with the large variability of the dimensions of the component trees (fir, beech and spruce). Another study by Duduman et al (2010) showed that the tree diameter influences the radial growth, especially in the case of shadow intolerant species (Norway spruce); when the preferences for light are decreasing, the correlation level between tree diameter and radial growth is also decreasing (beech, silver fir). In the same study, the influence of competing neighbors on the radial growth was evaluated, through the Hegyi model, and the level of competition exerted by the first ten competing neighbors on reference trees was determined. The result obtained shows that in the natural multi-tree stands, the radial growth is influenced mainly by the competition exerted by the first nine competing neighbors in the case of spruce, by the first two competing neighbors in the case of fir and by the first seven in case of beech. In relation to their orientation, it was observed that the spruce radial growth is mainly influenced by the level of competition exerted by the neighbors in the S and SE and for the fir and the beech the greatest influence on the radial growth is exerted by competing neighbors positioned in the NE and E.

Finally, the impact of biotic interactions on the composition and diversity of species in forest ecosystems can be identified and assessed only by spatial analyzes at

different scales of the relative position of trees in various stages of development. The studies conducted by Dovciak et al (2001), Sterner et al (1986), Moravie & Robert (2003), concluded that primarily there is a positive link between competition and aggregation may arise when competitive thinning of large trees leads to gaps in which clustered off spring regenerate. Spatial heterogeneity induced by edaphic gaps may cause a patchy (clumped) size class distribution, thereby masking the tendency towards regular growth patterns. The aim of the study was to detect spatial patterns between spruce and beech species from different dimensional classes in the Slătioara Secular Forest in order to test the hypotheses related to the mechanisms underlying the autogenous cohabitation of these forest species.

Material and Method. The study was conducted in The Secular Forest Slătioara. Forestry reservation was founded in 1940 and is administrated by the Romanian Academy. The Secular Forest Slătioara is located in the altitudinal belt of: beech, fir mixed beech and fir forests in the Eastern Carpathians, on the southeastern slope of the Rarău Mountains. The study area is located in the southeastern part of the Bîtca cu Plai ridge, in the compartment 36 B of management unit VIII Slătioara. The plot is located at an altitude between 1,150-1,280 m.a.s.l with an area of 6.62 ha. The trees in the study area exceeded 100 cm in diameter and 40 m height. The stand is classified according to the Romanian classification of forest types (Doniță et al 2017), in type 1111 - normal spruce with *Oxalis acetosella* with calcareous rendzina type soil with very good trophicity and moderate active acidity with a slope of the terrain is 30 degrees. The Secular Forest Slătioara is a beech, fir and spruce forest with natural origin, in which the structure of tree populations is uneven-aged and heterogeneous (Cenușă et al 2002). The vertical profile is very varied, multilayered, with a composition and consistency influenced by the process of natural selection of species.

The starting point of the present study was the highlighting of two processes that take place in temperate forests that are made up of tree species with shade or semi-shade temperament. Thus, a process refers to direct facilitation, namely the spectral filtration of light at the canopy of trees and this sense we have as an example the easy regeneration of the fir under the crowns of beeches, due to the predominant light transmission from the blue and red spectrum (Bândiu 1977; Dobrowolska 1998). A second process is intraspecific inhibition (auto-allelopathy) and we have as an example the self-inhibition of fir seedlings from pure fir trees (Becker & Drapier 1984, 1985).

In terms of the spatial distribution of trees, the competitive relations for space, light, water, minerals, have a result in dimensional and stage differentiation and natural elimination of less competitive specimens. The regeneration process in the Slătioara Forest has essential ecological peculiarities and it is perfectly integrated in the multisecular and complex circuit of the natural growth and elimination process. Regeneration usually occurs as a result of natural removal, respectively after the fall of some aged trees from the dominant overstory of trees. This creates light meshes in the stand, that represent regeneration points where the seedlings will group together to benefit from the light, heat and nutrients found in these niches. In this sense, we hypothesize that the distribution of seedlings in this forest is not independent of the distribution of trees. So, depending on the temperament of seedlings, spruce trees will group in the meshes created in the canopy and beech seedlings will cluster under the crowns of trees that provide shade.

In this study, (1) the spatial distribution of trees and how it differs significantly from the random spatial distribution was examined; (2) the correlation between the average distance from each tree to the nearest three neighbors and the diameter or the height of the reference tree was tested; (3) the way in which the distribution of seedlings is correlated with the distribution of trees was highlighted, by determining the minimum inhibition distance between spruce and beech seedlings; (4) the scale at which the spatial structures of spruce, beech and seedling are manifested was presented; (5) the correlation between the layer coverage with herbal, mosses, seedlings (spruce and beech) and the spatial distribution of trees was analyzed.

The study of the horizontal structure in forest ecosystems provides a clear highlight of the structural elements and complex connections that characterize the spatio-temporal dynamics of the forest. This represents a fundamental component for ensuring a sustainable forest management (Roibu & Popa 2007). The study area has a rectangular shape (20x50 m) and was delimited with the help of pickets and a ribbon. Taking into account the slope of the terrain, the study area was placed so that the large side of the rectangle was disposed along the contour lines.

The trees, the seedlings, the herbal layer and the bryophytes were inventoried. Seedlings were considered as individuals of tree species, with a diameter smaller than 10 cm. The first step was to determine the coordinates of each tree and seedling, considering the point of origin of the orthogonal axes in one of the corners of the rectangle. The measurement of distances was performed with a 100 m metal roulette. The diameter was measured at the breast height (130 cm), with the forestry caliper. The height was measured using the hypsometer. By means of an imaginary grid, a division of the sample area was made into 250 quadrats with a side of 2 m. In the center of each quadrat, a sub-plot with a side of 0.25 m was delimited, in which the coverage of herbs, mosses, spruce and beech seedlings was evaluated.

Results and Discussion

The distribution of beech, spruce and seedlings (Figure 1) shows that the distribution of beech seedlings on a small scale (up to 5.30 m) is of an aggregate type and beyond this distance it turns into a random type. The aggregation of beech seedlings is probably due to their shade temperament, which groups them under the crowns of large trees.

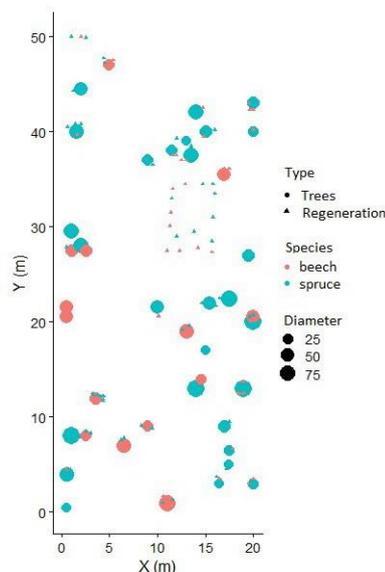


Figure 1. Distribution of beech, spruce and seedlings.

Spruce seedlings are distributed in groups on a small scale (<5 m) and on a larger scale the distribution becomes random. This is determined by the light temperament of spruce that causes the seedlings to group in the meshes of light created in the canopy. This dispersed distribution can also be explained by the fact that these meshes are dispersed, due to the mortality among the old trees, caused by ecological processes that act on a large scale (wind blows, insect attacks, etc.)

The graphical representations of the univariate analysis of the spatial distribution of trees (Figure 2) and seedlings (Figure 3), and the cumulative analysis of beech, spruce and seedlings (Figure 4) were done using the L function, derived from Ripley's K function (when the number of individuals exceeded 100) or based on the average distance to the nearest k neighbors (if the number of individuals was below 100).

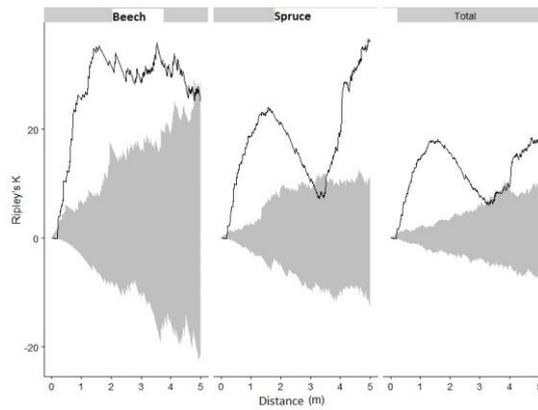


Figure 2. Univariate analysis of the distribution spatial characteristics of spruce and beech trees.

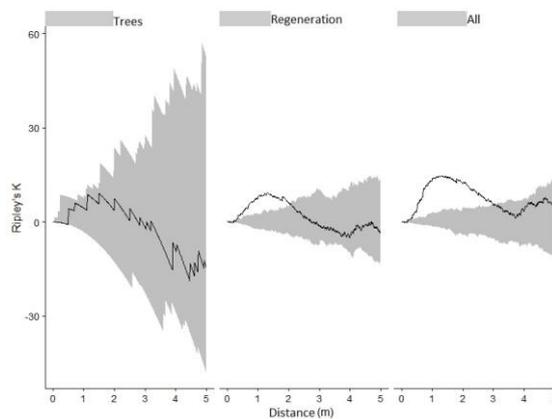


Figure 3. Univariate analysis of the spatial distribution of spruce and beech seedlings (regeneration).

Thus, it is concluded that the spatial distribution of spruce and beech seedlings depends on the radius on which the closest neighbors are identified for a given individual. If the radius is less than 2.55 m (Figure 4), the distribution is of an aggregate type (spruce seedlings are grouped in meshes and the beech seedlings under the crowns of the mature trees). If the radius is greater than 6.50 m the distribution becomes dispersed. Regarding the spatial distribution of spruce trees, it can be noticed that on a small scale the distribution does not differ significantly from the random one, but on a large scale (over 12 m) there is a tendency to transform it into a dispersed type, most likely due to intraspecific competition as well as the fact that spruce has a heliophilic temperament.

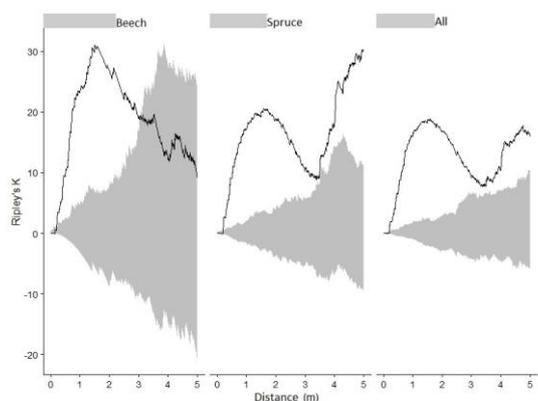


Figure 4. Univariate analysis of spatial distribution of spruce and beech trees and seedlings.

By analyzing the spatial distribution of beech and spruce trees, it can be observed that the distribution is random on a small scale and that on a larger scale (over 9.50 m) it becomes of a dispersed type (Figure 5). The current configuration of trees is similar to the moment they were small, the seedlings settling whenever they find a gap in the canopy, which is a real niche of regeneration (spruce seedlings are predominant). Thus, the competition between trees cannot be considered as a determining factor of this dispersed distribution.

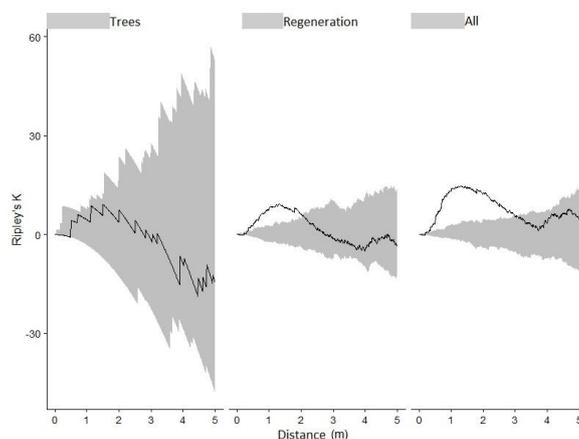


Figure 5. Bivariate analysis of the spatial distribution of spruce, beech and seedlings.

From the interpretation of the random spatial models it cannot be necessarily inferred that there are no interactions at all or that the processes governing the tree distribution are purely random. But we can say that beech is the supporting species cohabitation of forest species in the studied grove, while the spruce that has a scattered or grouped distribution in the canals created in the canopy, it generates a lower local forest diversity. The high value of the Spearman correlation coefficient indicates a good correlation between the soil coverage with grasses and the distance to the nearest spruce tree (Table 1). A fairly high value of the correlation coefficient is also characteristic for the correlation curve between the herbal coverage and the distance to the nearest beech tree.

Table 1
Spearman correlation coefficients and their associated probability

<i>Covering (%)</i>	<i>Dist_Fa_1</i>	<i>Prob(>r)</i>	<i>Dist_Mo_1</i>	<i>Prob(>r)</i>
Herbs	0.40	<0.0001	0.47	<0.0001
Moss	-0.07	0.27	-0.15	0.01
Seedling beech	0.02	0.68	0.06	0.33
Seedling spruce	0.10	0.09	0.08	0.19

The regression curve between the herbal coverage and the distance to the nearest spruce is a parabola (Figure 6). The herbal coverage does not increase monotonically with the distance to the nearest spruce because for a distance of more than 5.5 m it starts to decrease. This is probably due to the fact that, starting from this distance, the herbal layer is negatively influenced by beech trees. Light is the main factor influencing the herbal coverage: the bigger the distance between the trees (the crowns do not touch), the higher the growth rate of grass, which is facilitated by the penetrating light. The litter, by the acidification level, influences the growth and development of herbs.

The different chemical composition of the litter between beech and spruce could influence the phytomas of the grasses; this is due to the fact that spruce leaves cause a high acidification by decomposition, which inhibits the growth and development of grasses.

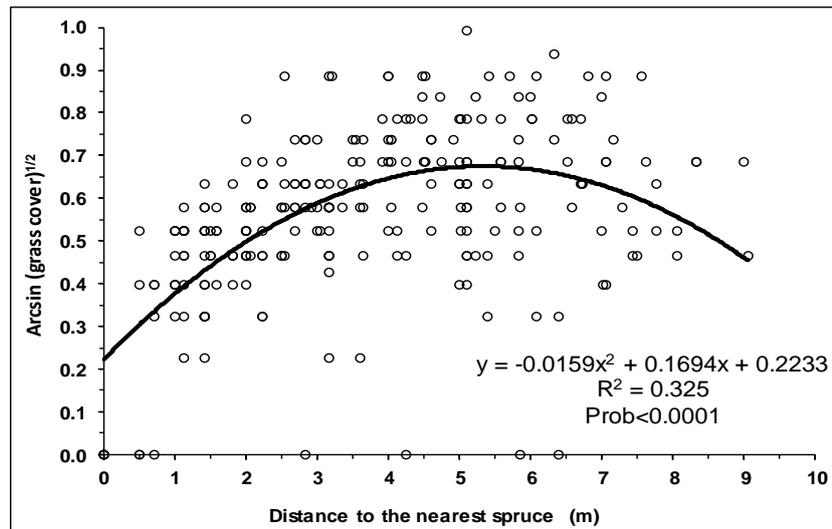


Figure 6. The regression model between herbal coverage and distance to nearest spruce.

The effect of the litter varies considerably depending on its quantity and type and can influence the vegetation having influence both physically and chemically but also by its decomposition rate which is as follows: herbaceous plants with flowers > deciduous tree leaves > herbs > softwood tree leaves. Litter thickness is another parameter that negatively influences the diversity and density of plant species through the large amount of litter, especially in the advanced stages of spruce colonization because when, in addition to spruce needles, the formation of litter substantially contributes to its branches, cones and bark. At the same time, the evergreen spruce that shades the soil and during the winter, thus keeping the snow for a longer time under the massif, makes the vegetation period of the grasses start later. This can be explained by the fact that needles (softwood leaves) have a higher resistance over time which amplifies the physical effect on plants in the herbaceous layer of coniferous forests while perennial herbaceous species that appear in autumn or deciduous shrub species exercise only competitive effects during the growing season and this time gap can provide enough photosynthetic and growth opportunities to allow trees to survive and grow through the litter layer.

Conclusions. The results showed that in the studied natural perennial shrubs, beech, both in the juvenile and tree stage, seems to be the species with the greatest impact in the equalization and stabilization mechanisms necessary for coexistence, but also for maintaining the diversity of tree species within these types of forests. In contrast, spruce spatial dissociation in the stands induces a much lower local forest diversity. In the case of the quasi-virgin forest from the study area, it was pointed out that, it offers a distribution to the beech seedlings grouped under the canopy of the tree that filters the light entering the forest, thus protecting the seedlings from drought and heat. Besides this, the light that penetrates through the crowns of spruce trees has a short wavelength (towards blue) that satisfies the radiation needs of the beech seedlings.

According to the results, the spruce seedlings also have a grouped distribution but, unlike the beech seedlings, they are grouped in the meshes of light that are created in the canopy of large trees. The gaps that were formed by the fall of dry old trees, but also by breaking other categories of trees, are real niches of regeneration in which pre-existing seedlings or later installed seedlings develop and in which and in which the phenomenon of competition it manifests itself at first with the existing tree on the edges of the hollow, and then, as the seedling rises, to develop intraspecific competition of seedlings. The dispersed distribution of the spruce trees is determined by the relationships between them, in particular by the competition for space, light, water and minerals, resulting in a differentiation of ecological niches or in the natural elimination of spruce trees. Because spruce and beech have complementary temperaments, being mutually tolerant, it is observed that mixed forests with these species are stable, with a

higher trophicity and a lower inter-species competition. As the trees increase in size, their space demand increases (in special on a foraging purpose), at the expense of the neighboring trees, whose growth might be inhibited or which can even dry up and die, leaving the space to the remaining ones, that are better adapted to the ecological factors. As for the degree of grass cover of the soil, it is influenced by the light that penetrates inside the forest, which is facilitated by a larger distance between the trees (so the crowns do not touch each other), favoring the light penetration and consequently the herbs development. As for the degree of grass cover of the soil, it is influenced by the light that enters the inside the forest. Thus, the greater the distance between the trees (so the crowns do not touch), the more it penetrates a greater amount of light that favors the development of grasses. The higher the correlation between the degree of grass cover and the distance to the nearest spruce can be due to: spruce litter which is acidic and influences the growth and development of herbs as well as the thickness of which prevents growth the evergreen spruce that shades the soil and in winter so the snow is maintained for a while longer under the massif which makes the vegetation period of the grasses start later. Knowing the fact that grasses start this period earlier than trees and seedlings this will make you a competition disloyalty that will result in the removal of weeds. Another important factor in removing weeds is rooting the spruce which is truncated occupying a large area around the tree.

The present results are limited by the study area of 0.10 ha, which did not allow the detection of spatial patterns to be highlighted on a larger scale. At the same time, the ecological response of the forest species evaluated in this study is also limited only to the lower submountain-mountain floor (800-1,300 m), where the climatic conditions are optimal for beech and spruce. Taking into account all this, the results obtained in this study require validation by identical observations made in equivalent stands from the point of view of ecological conditions. The distribution of spruce and beech seedlings in space is closely correlated with the limits of tolerance they have towards light as well as with their level of competition for light.

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Conflict of interest. The author declares no conflict of interest.

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