

Epiphytic lichens and bryophytes at different ontogenetic stages of *Pinus sylvestris*

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Summary: We studied the species composition and structure of epiphytic communities at different ontogenetic stages of *Pinus sylvestris* L. in the Tver Region (Central Russia). When distinguishing the ontogenetic stages, we used different morphological and biological features. We investigated structural characteristics of the tree, which determine richness, spatial distribution and ecological spectra of lichens, mosses and liverworts. Analysis of structural changes in the ontogeny of a tree allows us to understand the dynamics of the development of epiphytic communities and patterns of spatial distribution of cryptogamic species. Structural differentiation of the tree increases the heterogeneity of microhabitats, and hereby richness and ecological diversity of lichens and bryophytes are increased.

Keywords: lichens, bryophytes, epiphytic cryptogam cover, lichen and bryophyte communities, liverworts, mosses, *Pinus sylvestris*, tree ontogeny, ontogenetic stages

The distribution and functioning patterns of epiphytic and epixylic lichens and bryophytes in different phytocenoses are currently object of active research (OKSANEN 1988; TIBELL 1992; HILMO 1994; HOLIEN 1996; HUMPHREY et al. 2002; SEDIA & EHRENFELD 2003; FRIEDEL et al. 2006; LÖBEL et al. 2006; ELLIS & COPPINS 2007; CLEAVITTA et al. 2009; HILMO et al. 2009; JÜRIADO et al. 2009; CARUSO et al. 2010; ELLIS 2012; ZARTMAN et al. 2012; ÓDOR et al. 2013; MATOS et al. 2015; MOTA DE OLIVEIRA & TER STEEGE 2015; etc.). Associations of bryophytes and lichens have been analyzed (BAISHEVA et al. 1994; BAISHEVA 1995, 2010; VELLAK & PAAL 1999; LEBEDEVA 2004, 2005; etc.). The abundance of their species depends on many factors. The degree of forest continuity is very important (TIBELL 1992; MARMOR et al. 2011; etc.). It can be calculated using the Index of Forest Continuity (ISIFC) (TIBELL 1992).

Many studies emphasize the connection between epiphytic species abundance and tree age (HILMO 1994; HOLIEN 1996; KUUSINEN 1996; KUUSINEN & SIITONEN 1998; ROLSTAD & ROLSTAD 1999; RANIUS et al. 2008; CLEAVITTA et al. 2009; MEŽAKA et al. 2012; SHRIVER et al. 2012; CALVIÑO-CANCELA et al. 2013; etc.). Tree age often becomes the key factor of the distribution of rare and protected species (FRITZ 2009; FRITZ et al. 2009; LIE et al. 2009; MARMOR et al. 2011). The structural differentiation of trunk and crown in tree ontogenesis plays an important role (KUUSINEN 1996; LEBEDEVA 2004; RANIUS et al. 2008; WOODS et al. 2015). The search for approaches allowing an accurate characterization of these processes is of immediate interest.

Absolute age is also identified as an important characteristic in tree ontogenesis (HYVÄRINEN et al. 1992; KUUSINEN & SIITONEN 1998; JOHANSSON et al. 2007; LIE et al. 2009 etc.). The age of tree is often evaluated based on the trunk diameter or height of the tree (HUMPHREY et al. 2002; FRITZ et al. 2009; NASCIMBENE et al. 2009; SHEN et al. 2014; MOTA DE OLIVEIRA & TER STEEGE 2015). Thus, age or size classes are distinguished (FRITZ 2009; NASCIMBENE et al. 2009; WOODS et al. 2015). Diameter at breast height (DBH) is a commonly used parameter

(FRIEDEL et al. 2006; FLORES-PALACIOS & GARCÍA-FRANCO 2006; FRITZ et al. 2009; LIE et al. 2009; KIRÁLY et al. 2013). However, the actual age of a tree usually doesn't allow an accurate characterization of its developmental stage. The fact that ontogenetic age can be different from chronological age in plants has long been recognized (GREENWOOD 1995; POETHIG 2003; CLIMENT et al. 2011; etc.). Biometric characteristics of the tree mostly depend on ecological conditions, development rates, vitality level and other factors (SMIRNOVA et al. 1999; BOYDEN et al. 2009; ZHUKOVA et al. 2013; etc.). Significant differences in morphology and size are clearly seen, for example, in comparisons of same-age pine tree samples from a sphagnum swamp with samples from a pine forest. Biometric parameters of the swamp form of *Pinus sylvestris* are much lower (PANOV 2007). Additionally, it is necessary to use special devices and methods in order to evaluate absolute age. Therefore it is expedient to use a different periodization of phorophyte ontogenesis when studying the formation dynamics of the epiphytic lichen and bryophyte cover. It is based on correctly identifying ontogenetic stages. This approach has been developed in the works of Russian botanists under the name of 'concept of discrete description of ontogeny' (RABOTNOV 1950; URANOV 1975; GATZUK et al. 1980; WHITE 1985; SMIRNOVA et al. 1999; SMIRNOVA & BOBROVSKII 2001; etc.). Ontogenetic stages are characterized by a complex of different morphological and biological features. This approach has been used many times in regard to trees (ZAUGOLNOVA 1968; SMIRNOVA 1989; EVSTIGNEEV & TATARENKOVA 1995; SMIRNOVA et al. 1999; ANTONOVA & TERTERYAN 2000; SMIRNOVA & BOBROVSKII 2001; etc.).

Significant structural changes occur in the process of tree ontogenesis (ANTONOVA & TERTERYAN 2000; ZHUKOVA et al. 2013). It is important to identify morphological and anatomical features which determine the distribution of epiphytic cryptogams and their communities (MARMOR et al. 2013; ZHUKOVA et al. 2013). Changes of the pH of the bark are very important environmental factors for lichens and bryophytes (ELLIS & COPPINS 2007; MEŽAKA et al. 2012; SHRIVER et al. 2012; MATOS et al. 2015; etc.).

Pinus sylvestris is a convenient model object for studying developmental patterns of epiphytic lichen and bryophyte cover. The structure of the tree is very labile (STOLL & SCHMID 1998; KULLMAN 2007; MARMOR et al. 2013; ZHUKOVA et al. 2013). Morphology and anatomy of the tree is substantially transformed during the ontogenesis of *P. sylvestris*. Ontogenesis of *P. sylvestris* has been well studied (EVSTIGNEEV & TATARENKOVA 1995; ZHUKOVA et al. 2013).

The general level of diversity of bryophytes and lichens depends on main biogeographical gradients (IGNATOV 2001; WILL-WOLF et al. 2006; NOTOV 2010; MATOS et al. 2015; etc.). Therefore, quantitative characteristics of an epiphytic lichen and bryophyte cover can be different in different regions. This should be considered when selecting a model region.

The aim of the study was to identify the dynamics of the formation of an epiphytic lichen and bryophyte cover at various ontogenetic stages of *P. sylvestris* in Tver Region (Central Russia).

Our studies concerned the following tasks:

- research on *P. sylvestris* ontogenesis,
- identification of morphological and anatomical features of the tree that determine the distribution of lichens and bryophytes
- and exploration of changing patterns in species richness of epiphytes based on the above mentioned features.

Materials and methods

Tver Region (located in Central Russia) has been chosen as a model region. It is part of the territory of the East European plain in the upper reaches of the rivers Volga and Zapadnaya Dvina. The length of the region from West to East encompasses about 450 km (30°50'–38°20'E) and from North to South about 350 km (55°40'–58°50'N) (see NOTOV et al. 2011). The climate is temperate continental. Average annual rainfall is 550–750 mm. The area is generally characterized by flat terrain. Absolute altitudes reach 150–340 m. Most of the territory is located in the southern taiga subzone. Zonal formations are broad-leaved–spruce and spruce forests. The usual components of intrazonal vegetation are different types of pine forests, widespread lowland and highland swamps.

When dividing the ontogenesis of *P. sylvestris* into periods, we identified the following ontogenetic stages: seedlings (p), juvenile trees (j), immature trees (im), virginal trees (v), young generative trees (g₁), mature generative trees, i.e. generative trees of middle age (g₂), old generative trees (g₃), subsenile and senile trees (ss, s). Characteristics of ontogenetic stages of *P. sylvestris* was completed according to Russian studies (SEREBRYAKOV 1962; EVSTIGNEEV & TATARENKOVA 1995; ZABRODIN 2011; etc.). A detailed description of the ontogenetic stages of *P. sylvestris* was has already been published by ZHUKOVA et al. (2013). When analyzing the results we sometimes combined old generative and subsenile trees into one group due to the small size of the sample of subsenile trees.

Data on the occurrence of lichens and bryophytes at different ontogenetic stages of *P. sylvestris* has been gathered by A. Notov during comprehensive floristic studies in 2005–2014 (see NOTOV et al. 2011). All available herbarium materials and observations have been analyzed (ZHUKOVA et al. 2013). We noted for each lichen and bryophyte sample: ontogenetic stage of *P. sylvestris*, altitude levels of the tree (tree base, trunk, branches) and substrates (bark, wood, lichen thallus, the fine-grained deposits, burnt wood). We determined frequency of species on living *P. sylvestris* in the Tver Region using a five-point-scale (Appendix 1).










In the analysis of lichens the authors also noted species of saprobic and lichenicolous fungi that are traditionally studied together with them (SANTESSON et al. 2004). The authors identified associations in the epiphytic lichen and bryophyte cover accordng to BAISHEVA et al. (1994), BAISHEVA (1995, 2010), TARASOVA (2001) and LEBEDEVA (2004, 2005).

Results

Structural features of the ontogenetic stages of *P. sylvestris* are characterized in Table 1. Structural features which are important for the formation of an epiphytic lichen and bryophyte cover are shown in Table 2.

The development of a rhytidome as well as the differentiation between tree trunk and crown are especially important for the formation of connections with bryophytes and lichens. These changes occur at specific stages of *P. sylvestris* ontogenesis. In contrast to a periderm, a rhytidome is characterized by a slow severance rate of elements being shed, a higher capacity for retaining moisture and surface heterogeneity. Niches between rhytidome flakes in the area of the trunk nearest to the roots contribute to its gradual filling with humus and peat substrates. Similar trends for other tree species were described by RANIUS et al. (2008), FRITZ (2009) and FRITZ et al. (2009). Different types of dermal tissues and various conditions of moisture supply guarantee

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CID	no cotyledons (CID)	Skeletal shoots (SSH) of the 2 nd or higher order	
	SSH only of the 1 st order	1) SSH of the 2 nd and 3 rd order 2) no crown 3) no rhytidome 4) no dying branches	1) SSH of 3 rd or higher order 2) crown 3) rhytidome 4) dying branches
		1) no reproductive structures 2) lower branches of the crown are dying off 3) rhytidome is only at the base of the trunk 4) no tree-base elevation	1) reproductive structures or their formation ceases due to organism ageing 2) branches are dying off in various parts of the crown 3) rhytidome covers most of the tree trunk 4) tree-base elevation
		1) tree top is cone-shaped 2) volume of dying canopy is negligible 3) rhytidome is thick and almost smooth 4) tree-base elevation is weakly differentiated	1) tree top has a different shape 2) process of dying in the crown is more pronounced 3) rhytidome is thick with deep cracks 4) tree-base elevation is well differentiated, has deep cracks and protruding root bases
			1) crown top is dome-shaped 2) weak branches are dying off in all parts of the crown
			1) reproductive structures 2) most of the crown is dried out
			1) no reproductive structures 2) crown is deteriorating, the majority of branches is dried out
P	j	im	v
			
			
			

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◀ **Table 1.** Ontogenetic stages of *Pinus sylvestris*: p – seedling, j – juvenile trees, im – immature trees, v – virginal trees, g₁ – young generative trees, g₂ – mature generative trees, g₃ – old generative trees, ss, s – subsenile and senile trees.

level differentiation (Tables 1, 2). The tree base is significantly different in terms of microhabitat formation. In the analysis of epiphytes the tree base and trunk levels are emphasized (LEBEDEVA 2004, 2005).

The elevated tree-base may form some phytocenoses on the tree trunk. In the contact zone the tree base promotes the appearance of components living on the forest floor. Crown differentiation is encouraged by the dying off process of the lower branches. During the course of tree life, dying branches emerge in other parts of the crown as well (Tables 1, 2). The dead rhytidome and dying wood are special microhabitats for lichens and bryophytes. At the last stages of ontogenesis the volume of dying wood increases significantly (Table 1). If the ground tissue integrity is disturbed, parts of dead wood start to show up in the trunk area of the tree as well. Composition and structure of the epiphytic lichen and bryophyte cover depend on dynamics of the tree structure differentiation (Table 2).

Data we obtained in the Tver Region depict the main tendencies in changes to the species richness of lichens, mosses and liverworts in the process of *P. sylvestris* ontogenesis. We identified the general frequency of species occurrence on living samples of pines (Appendix 1).

Only few lichen species have been noted on immature and virginal *P. sylvestris* trees. Among them are typical epiphytic species like *Hypogymnia physodes* and *Pseudevernia furfuracea*. The first one is the most abundant and frequent in the forest area. It is the only species found on dying branches of oppressed, dried out, immature *P. sylvestris* trees. Its abundance on virginal samples increases as their vitality level drops. *Pseudevernia furfuracea* occurs on virginal *P. sylvestris* (v, Table 1) trees only from sphaginous swamps.

Table 2. The dynamics of changes in structural elements of *Pinus sylvestris* during ontogenesis and characteristics of the epiphytic lichen and bryophyte cover.

Elements and features	Dynamics of changes	Characteristics
Periderm	Increase of surface area and structural changes (increase of phellem, abscission of its outer layers)	Increase of species richness of epiphytic species
Rhytidome	Increase of surface area and structural changes (formation of scale-like elements, emergence and deepening of cracks and cavities)	Increase of species richness of epiphytic species; emergence of epigeic species at tree base
Vertical tree structure	Intensification of branching; formation of the crown, trunk and tree-base elevation; vertical differentiation of each of these elements; increase of the relative amount of old branches	Increase of species richness of epiphytic species; emergence of epigeic species at tree base; increase of their relative role in the ecological spectrum
Dying structural elements of the tree	Intensification of the dying processes; gradual increase of the number of dead branches; emergence of dead wood without ground tissue	Increase of species richness of epiphytic species; emergence of epixylic species at tree base; increase of their relative role in the ecological spectrum
Potential microhabitat	Quantitative and qualitative increase of diversity and heterogeneity	Increase of general species richness; restructuring of the ecological spectrum

All lichen communities typical for coniferous trees are formed on *P. sylvestris* during the generative period. Among them are associations of *Hypocenomycetum scalaris* Hilitzer 1925, *Leprarietum incanae* Hilitzer 1925, *Parmeliopsidetum ambiguae* Hilitzer 1925, *Pseudevernetum furfuraceae* Hilitzer 1925, *Bryorio fuscescenti-Usneetum filipendulae* Hilitzer 1925, *Cladonietum coniocraea* Duvigneaud ex Galinou 1955, *Cladonietum cenoteae* Frey ex Klement 1950, *Chaenothecetum ferrugineae* Barkman 1958 and facies of *Cladonietum cladoniosum digitata* M. Lebedeva ined. (see LEBEDEVA 2005). The first four were noted even on young generative trees of *P. sylvestris*. All others develop on mature generative trees. The mentioned associations form on different altitudinal levels of the tree. Three of them are confined to the tree base area and three to the trunk area. The *Bryorio fuscescenti-Usneetum filipendulae* association forms on dying lower branches of the crown.

The highest species richness of lichens and bryophytes was discovered on old generative and subsenile trees of *P. sylvestris* (Appendix 1). Unique species occurring only on pregenerative or young generative trees were not found. Compared to bryophyte coverage, lichen coverage has a more complex and special structure.

Dynamics of lichen species richness is shown in Fig. 1. The following quantitative indexes are noted: g_1 – 11 species, g_2 – 40 species, g_3 and ss – 67 species. The increase of species number is determined by the differentiation of dermal tissue and the vertical structure of the tree. Emergence of a rhytidome leads to the formation of microhabitats in the tree base area of the trunk. In some phytocenoses on mature generative trees a tree-base elevation occurs. It determines the emergence of some epigeic species that usually grow on the forest floor. The dying process of lower branches of the crown determines the emergence of new substrates. Among them are the dying rhytidome and dead wood. Acidophilic members of *Bryoria*, which are characteristic of coniferous species, live on the rhytidome. Epixylic species colonize dead wood. During the late ontogenetic stages of *P. sylvestris* the volume of dead wood increases significantly, which promotes substantial consolidation of the position of epixylic species. In addition, new epiphytic species emerge (Appendix 1). However, the gradual inclusion of species from other substrate groups leads

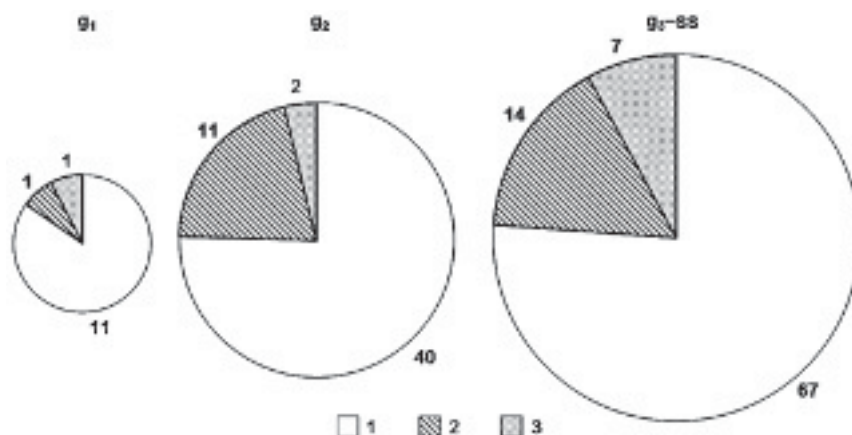


Figure 1. Change in species richness of epiphytic lichen and bryophyte cover during the ontogenesis of *Pinus sylvestris*. Groups: 1 – lichens, 2 – mosses, 3 – liverworts. Ontogenetic stages of *P. sylvestris*: g_1 – young generative trees, g_2 – mature generative trees, g_3 – old generative trees, ss – subsenile trees. Over the sectors indicates the number of species in the group.

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to a decline in the ratio of typical epiphytes (Fig. 2). Following quantitative characteristics were obtained: On g_1 trees – 7 lichen species (63.6%), on g_2 – 19 (47.5%), on g_3 and ss – 25 (37.3%). Lichenicolous fungi may emerge on lichen thalli. For example, *Clypeococcum hypocenomyces* sometimes parasitizes on the thallus of *Hypocenomyce scalaris*.

Following distribution according to the altitude levels on the tree was noted at the last stages of the formation of lichen coverage on *P. sylvestris* trees: In total, 19 species of lichens were found on the tree base, 50 on the trunk and 29 on the branches of trees. The number and ratio of sector-specific lichen species (which were found only within one altitude level) are as follows: In the tree base 8 sector-specific species were found (42.1% of all species registered within this altitude level), 19 on the trunk (38%), 6 on the branches (20.7%). The majority of species confined to the tree base (7 species) are primarily epigeic lichens. More than half of the species confined to the trunk and branches are typical epiphytes. Their altitude level differentiation is rather clear-cut. *Alectoria sarmentosa*, *Bryoria capillaris*, *Usnea dasypoga* are confined to drying branches. Epixylic species are less specialized with regard to altitude levels.

In some cases a slight modification of the special distribution of lichens and bryophytes is possible. For example, in pine forests located at the edges of black alder swamps, a 'rising' of tree base synusia to the trunk area can be observed. In certain cases species that are rare and atypical for *P. sylvestris* occur. For example, *Hypocenomyce anthrocophila* and *Mycoblastus sanguinarius* are often met on charred wood of trunks that are partially damaged by fire. *Psilolechia lucida* and *Chaenotheca furfuracea* were observed by the authors on peaty substrate between roots and on the roots of fallen live pines. Typical epigeic bryophytes sometimes occur on roots and between roots of pines with a partially exposed root system.

Bryophyte species richness is considerably lower than that of lichens (Fig. 1). In total, 14 species of mosses and 7 species of liverworts were identified. There were no species observed exclusively on *P. sylvestris*. Almost all mosses (13 out of 14) and all liverworts are confined to the tree

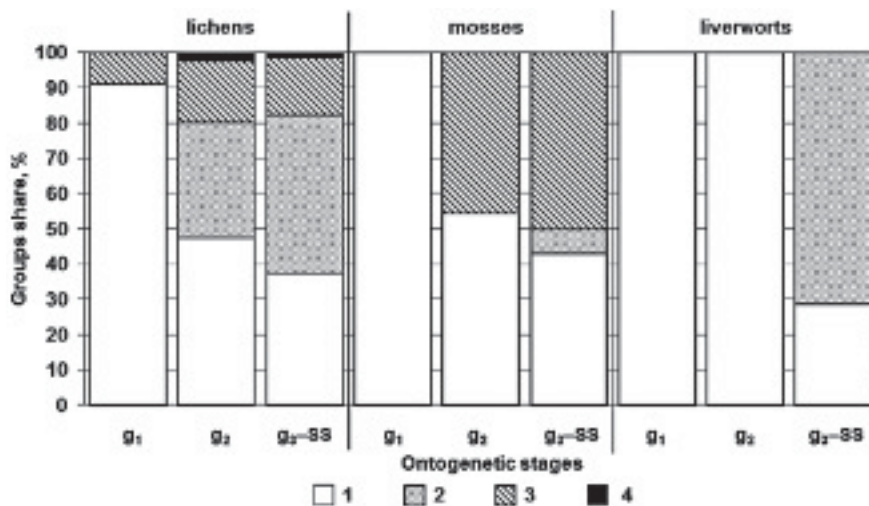


Figure 2. Changes in the role of substrate groups in ecological spectra of lichens, bryophytes and liverworts during the ontogenesis of *Pinus sylvestris*: substrate groups: 1 – epiphytes; 2 – epixylic; 3 – epigeic; 4 – lichenicolous fungi; ontogenetic stages of *P. sylvestris*: g_1 – young generative trees; g_2 – mature generative trees; g_3 – old generative trees; ss – sub-senile trees.

base. *Dicranum montanum* develops somewhat regularly on the trunks. Other species are rare (Appendix 1). Substrate spectra are different for mosses and liverworts (Fig. 2). Typical epigeic species (7 out of 14) and species observed on the tree bark and soil (2) are dominant in mosses. All identified liverworts can be noticed with varying frequency on decomposing dead wood. 4 out of 7 species are typical epixylics.

Mosses and liverworts appear only on trees in the generative stage. Their development is connected with the differentiation of the tree base. On the young generative tree of *P. sylvestris* two species of mosses (*Dicranum montanum*, *Plagiothecium laetum*) and two species of liverworts (*Chiloscyphus profundus*, *Ptilidium pulcherrimum*) were found. They appear only in high moisture conditions. Mature generative trees are usually covered with the majority of moss species (11 of 14 species) (Appendix 1). In the mature generative stage typical associations of mosses like *Orthodicrano montanii-Plagiothecietum laeti* (BAISHEVA et al. 1994) are more or less consistently formed (see BAISHEVA et al. 1994; BAISHEVA 1995, 2010). However, they are not growing exclusively on *P. sylvestris*. The only association with a diagnostic species of liverworts (*Ptilidio pulcherrimi-Hypnetum pallescentis* Barkman ex Wilmanns 1962) forms very rarely on *P. sylvestris*. This association is more typical of other tree species. More than half of the liverwort species abundance appears only on old generative *P. sylvestris* trees.

The constant discarding of dead wood that is characteristic of *P. sylvestris* promotes the formation of epixylic synusia of lichens and liverworts in the forest phytocenoses. Many types of these synusia do not appear on living trees. Among the epiphytic species, early and late epixylics and later on ground flora species occur (SÖDERSTRÖM 1988).

Discussion

Our materials relate to an important topic of ecology: studies on the determinants of diversity and structure of plant communities. It was in the Journal of Ecology where discussions about the relationship between photophytes and epiphytes broke out (LÖBEL et al. 2006; ZARTMAN et al. 2012; MATOS et al. 2015; MOTA DE OLIVEIRA & TER STEEGE 2015; WOODS et al. 2015; etc.). The authors consider the tree as a determinant of epiphytic communities.

We obtained preliminary data on epiphytic lichens and bryophytes at different ontogenetic stages of *P. sylvestris*. We plan further studies of different types of pine forests. However, the used approach has helped to identify the importance of age-related changes of tree structure of *P. sylvestris* regarding the spatial distribution of cryptogamic epiphytes. A rather complete and correct identification of ontogenetic stages takes into account the dynamics of the main morphological, anatomical and biological features of the tree. It also takes into account the stages of differentiation of trunk, crown and tree base, the dynamics of changes of the dermal secondary tissues and the rate of decay of different structures. All these features of the ontogenetic stages are associated with the dynamics of increasing heterogeneity of microhabitats. Therefore, the structural characteristics of ontogenetic stages correlate well with the dynamics of the formation of epiphytic cryptogam cover.

Anatomical and morphological changes occurring in the ontogenesis of *P. sylvestris* strengthen above all the differentiation of the vertical structure of the tree. The trunk, crown and tree base are differentiated, the secondary dermal tissue changes and different structures gradually die. Morphological and anatomical differentiations hit the peak on old generative and subsenile trees.

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These differentiations increase the diversity of microhabitats which are populated by various species of bryophytes and lichens in accordance with their biological and ecological features. The intensity of interaction between each *P. sylvestris* tree with lichens and bryophytes gradually increases. A tree-base elevation ensures a closer connection with ground coverage.

Lichens, mosses and liverworts are characterized by different dynamics of species richness and ecological spectra of substrate groups. The formation of epiphytic lichen and bryophyte cover begins on immature or virginal trees of *P. sylvestris*. Bryophytes appear for the first time only on young generative trees. Species richness of all cryptogamic groups culminates on old generative and subsenile trees. In different groups it varies considerably: lichens – 67 species, mosses – 14 species, liverworts – 7 species (Fig. 1). All typical associations of lichen and bryophyte communities are also formed on generative trees.

The increase of the volume of dead wood causes the occurrence of epixylic species. Old generative and subsenile trees provide substrate for epixylic lichens, mosses and liverworts. Some of these lichens already appear on young generative trees. Lichens and liverworts have more epixylic species than mosses (Fig. 1). Epigeic species only inhabit the elevated tree base of old generative and subsenile trees. Among them are some lichens. Single moss species only grow on the border of tree base and trunk. Marked differences are determined by the features of ecological-phytocenotic characteristics of forest lichens, mosses and liverworts in Central Russia.

Our proposed approach can be useful for the analysis of the diversity and ecology of epiphytes on other tree species, too. Such studies may help to reveal specific features in the dynamics of changes in the epiphytic lichen and bryophyte cover on trees with different crowns and rhytidome structures as well as various pH factors of the bark. They will allow a deeper understanding of the patterns of organization of plant communities and the mechanisms of maintaining their stability. However, further studies using ontogenetic approaches are not only of academic interest. They are necessary for the an effective solution to problems of protection and sustainable use of forest resources. Only old generative and subsenile trees are characterized by a maximum species richness and the occurrence of rare and protected cryptogamic species. Their preservation in the forest will ensure the conservation of biodiversity of bryophytes and lichens.

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Appendix 1. List of lichens and bryophytes found at different ontogenetic stages of *Pinus sylvestris*. Ontogenetic stages of *P. sylvestris*: im – immature trees, v – virginal trees, g₁ – young generative trees, g₂ – mature generative trees, g₃ – old generative trees, ss – subsenile trees. Altitude levels of the tree: Tr – trunk, TB – tree base, Br – branches. Substrates: Ba – bark, W – wood, Oth – others: lt – lichen thallus, du – decomposing underlay, silt substrate, bw – burnt wood. F – frequency of occurrence of species on living *P. sylvestris* trees in the Tver Region: 0 – single finding, 1 – very rarely (not more than three findings), 2 – rare (4–10 findings), 3 – sporadic (11–25 findings), 4 – frequent (26–50 findings), 5 – very frequent (more than 50 findings). Names of diagnostic species of associations of epiphytic lichen and bryophyte communities are in bold font.

Species	im	v	g ₁	g ₂	g ₃ , ss	Tr	TB	Br	Ba	W	Oth	F
LICHENS												
<i>Absconditella celata</i> Döbblers & Poelt					+	+				+		0
<i>Absconditella lignicola</i> Vězda & Pišut					+	+				+		0
<i>Alectoria sarmentosa</i> (Ach.) Ach.					+			+	+			0
<i>Bryoria capillaris</i> (Ach.) Brodo & D. Hawksw.			+	+	+			+	+			2
<i>Bryoria furcellata</i> (Fr.) Brodo & D. Hawksw.				+	+	+		+	+			2
<i>Bryoria fuscescens</i> (Gyeln.) Brodo & D. Hawksw.				+	+	+		+	+			3
<i>Buellia schaeferi</i> De Not.				+	+	+			+	+		1
<i>Calicium denigratum</i> (Vain.) Tibell					+	+				+		0
<i>Calicium glaucellum</i> Ach.					+	+				+		0
<i>Calicium trabinellum</i> (Ach.) Ach.					+	+				+		2
<i>Calicium viride</i> Pers.					+	+			+			0
<i>Chaenotheca chrysocephala</i> (Turner ex Ach.) Th. Fr.				+	+	+			+			3
<i>Chaenotheca ferruginea</i> (Turner ex Sm.) Mig.				+	+	+		+	+	+		4–5
<i>Chaenotheca furfuracea</i> (L.) Tibell					+		+				du	0
<i>Chaenotheca trichialis</i> (Ach.) Th. Fr.					+	+			+	+		1
<i>Chaenothecopsis pusilla</i> (Ach.) Alb. Schmidt					+	+				+		1
<i>Chaenothecopsis pusiola</i> (Ach.) Vain.					+	+				+		0
<i>Chaenothecopsis savonica</i> (Räsänen) Tibell					+	+				+		0
<i>Cladonia arbuscula</i> (Wallr.) Flot. s.lat.					+		+		+			2
<i>Cladonia botrytes</i> (K.G. Hagen) Willd.					+		+		+	+		2
<i>Cladonia cenotea</i> (Ach.) Schaer.				+	+		+		+		du	3
<i>Cladonia chlorophaea</i> (Flörke ex Sommerf.) Spreng.				+	+	+	+		+	+		3
<i>Cladonia coniocraea</i> (Flörke) Spreng.				+	+	+	+	+	+	+		3
<i>Cladonia cornuta</i> (L.) Hoffm.				+	+		+		+			2
<i>Cladonia digitata</i> (L.) Hoffm.			+	+	+		+		+			5
<i>Cladonia fimbriata</i> (L.) Fr.			+	+	+	+	+		+	+		3
<i>Cladonia furcata</i> (Huds.) Schrad.					+		+		+			1
<i>Cladonia macilenta</i> Hoffm.				+	+		+		+	+		2
<i>Cladonia rangiferina</i> (L.) F.H. Wigg					+		+		+			2
<i>Clypeococcum hypocenomyces</i> D. Hawksw.				+	+	+	+				lt	2
<i>Elixia flexella</i> (Ach.) Lumbsch					+	+				+		0
<i>Evernia prunastri</i> (L.) Ach.				+	+	+			+			3
<i>Evernia mesomorpha</i> Nyl.			+	+	+	+		+	+	+		4–5
<i>Hypocenomyce anthracophila</i> (Nyl.) P. James & Gotth. Schneid.				+	+	+				+	bw	0

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Species	im	v	g ₁	g ₂	g ₃ , ss	Tr	TB	Br	Ba	W	Oth	F
<i>Hypocnomyce friesii</i> (Ach.) P.James & Gotth. Schneid.				+	+	+			+	+		1
<i>Hypocnomyce scalaris</i> (Ach.) M. Choisy			+	+	+	+	+		+	+		5
<i>Hypogymnia physodes</i> (L.) Nyl.	+	+	+	+	+	+	+	+	+	+		5
<i>Imshaugia aleurites</i> (Ach.) S.L.F. Mey.				+	+	+			+	+		2
<i>Lecanora albellula</i> (Nyl.) Th. Fr.				+	+	+		+	+	+		2
<i>Lecanora hagenii</i> (Ach.) Ach.				+	+	+		+		+		1
<i>Lecanora pulicaris</i> (Pers.) Ach.				+	+	+		+	+	+		2
<i>Lecanora subintricata</i> (Nyl.) Th. Fr.					+			+	+	+		1
<i>Lecanora symmicta</i> (Ach.) Ach.				+	+	+		+	+	+		4
<i>Lecidea nylanderii</i> (Anzi) Th. Fr.					+	+			+			1
<i>Lepraria incana</i> (L.) Ach.			+	+	+	+	+		+			5
<i>Micarea denigrata</i> (Fr.) Hedl.					+			+		+		1
<i>Micarea melaena</i> (Nyl.) Hedl.					+			+		+		0
<i>Mycoblastus sanguinarius</i> (L.) Norman				+	+	+				+	bw	0
<i>Mycocalicium subtile</i> (Pers.) Szatala				+	+	+		+		+		3
<i>Parmelia sulcata</i> Taylor			+	+	+	+		+	+	+		4–5
<i>Parmeliopsis ambigua</i> (Wulfen) Nyl.			+	+	+	+	+		+	+		5
<i>Parmeliopsis hyperopta</i> (Ach.) Arnold				+	+	+	+		+	+		3
<i>Physcia tribacia</i> (Ach.) Nyl.					+	+			+			1
<i>Placynthiella icmalea</i> (Ach.) Coppins & P.James				+	+	+		+		+		2
<i>Placynthiella uliginosa</i> (Schr.) Coppins & P.James					+			+		+		1
<i>Platismatia glauca</i> (L.) W.L. Culb. & C.F. Culb.				+	+			+	+			2
<i>Pseudevernia furfuracea</i> (L.) Zopf		+	+	+	+	+			+			4–5
<i>Pycnora sorophora</i> (Vain.) Hafellner				+	+	+		+		+		2
<i>Ramalina farinacea</i> (L.) Ach.					+	+			+			1
<i>Scoliciosporum chlorococcum</i> (Graewe ex Stenh.) Vězda					+	+		+		+		2
<i>Scoliciosporum sarothamni</i> (Vain.) Vězda					+			+		+		2
<i>Strangospora moriformis</i> (Ach.) Stein				+	+	+		+	+	+		2
<i>Trapeliopsis flexuosa</i> (Fr.) Coppins & P.James					+			+		+		3
<i>Tuckermannopsis chlorophylla</i> (Willd.) Hale				+	+	+		+	+	+		3
<i>Usnea dasypoga</i> (Ach.) Röhl.				+	+			+	+			2
<i>Usnea hirta</i> (L.) Weber ex F.H. Wigg.				+	+	+		+	+	+		4
<i>Vulpicida pinastri</i> (Scop.) J.-E. Mattsson & M.J. Lai			+	+	+	+	+	+	+	+		4–5
MOSESSES												
<i>Amblystegium serpens</i> (Hedw.) Bruch et al.				+	+		+		+			2
<i>Dicranella heteromalla</i> (Hedw.) Schimp.					+		+				du	1
<i>Brachythecium salebrosum</i> (Web. & Mohr) Bruch et al.				+	+	+	+		+			2
<i>Dicranum flagellare</i> Hedw.				+	+		+		+			2
<i>Dicranum montanum</i> Hedw.			+	+	+	+	+		+			3–4
<i>Dicranum polysetum</i> Sw.				+	+		+				du	
<i>Dicranum scoparium</i> Hedw.				+	+		+				du	
<i>Plagiomnium cuspidatum</i> (Hedw.) T. Kop.				+	+		+		+		du	4

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Species	im	v	g ₁	g ₂	g ₃ , ss	Tr	TB	Br	Ba	W	Oth	F
<i>Plagiothecium laetum</i> Bruch et al.				+	+		+		+			5
<i>Pleurozium schreberi</i> (Brid.) Mitt.					+		+		+		du	3
<i>Pohlia nutans</i> (Hedw.) Lindb.				+	+		+		+		du	3
<i>Sanionia uncinata</i> (Hedw.) Loeske				+	+	+	+		+			3
<i>Stereodon pallescens</i> (Hedw.) Mitt.				+	+	+			+			4
<i>Tetraphis pellucida</i> Hedw.					+		+			+	du	
LIVERWORTS												
<i>Calypogeia integristipula</i> Steph					+		+		+		du	2
<i>Cephalozia bicuspidata</i> (L.) Dumort.					+		+		+		du	1
<i>Chiloscyphus profundus</i> (Nees) Engel & Schust.			+	+	+		+		+			3–4
<i>Lepidozia reptans</i> (L.) Dumort.					+		+		+		du	2
<i>Lophozia longiflora</i> (Nees) Schiffn.					+		+			+		0
<i>Orthocaulis attenuatus</i> (Mart.) A. Evans					+		+		+			0
<i>Ptilidium pulcherrimum</i> (Weber) Vain.			+	+	+	+	+		+			4

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