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PLEUROTUS ABIETICOLA (*AGARICALES*, *BASIDIOMYCOTA*) AS A PIONEER XYLOSAPROTROPH ASSOCIATED WITH SPRUCE SITES DIEBACK CAUSED BY *IPS TYPOGRAPHUS*

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The xylosaprotrophic agaricomycete *Pleurotus abieticola*, described in 1997, is still poorly studied in ecological terms. The objective of this paper is to study the ecological characteristics of *P. abieticola* using the material from two large dry spruce sites (causal agent *Ips typographus*) in the Gladyshevsky and Shchuchye Lake protected areas (Saint Petersburg, Russia), where mass fructification of this species was found. The field species identification was confirmed by the results of ITS rDNA sequencing. A detailed study of drying stands revealed new fine features of the ecology and morphology of *P. abieticola*. A saprotrophic pioneer complex which includes *P. abieticola* has been identified (*Fomitopsis pinicola*, *Trichaptum abietinum*, *Gloeophyllum sepiarium*, *Armillaria ostoyae*, *Amaropostia stiptica*, *Exidia nigricans*, *E. saccharina*, *Dacrymyces stillatus*, *Heterobasidion parviporum*, *Phlebiopsis gigantea*, *Stereum sanguinolentum*). The causes of the mass distribution of *Pleurotus abieticola* in spruce stands affected by *Ips typographus* are discussed.

Keywords: dead wood, drying out of spruce forests, Gladyshevsky protected area, oyster mushroom, Shchuchye Lake protected area, xylosaprotrophs

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INTRODUCTION

Pleurotus abieticola was described as an independent species in 1997 (Petersen, Hughes, 1997). Until that, the oyster mushroom specimens associated with conifers, particularly with *Picea abies*, were classified as *Pleurotus ostreatus* (Hilber, 1997). Such substrates as *Abies sibirica*, *Picea obovata* (Petersen, Hughes, 1997; Palamarchuk et al., 2023), *Picea* sp., *Alnus* sp., or *Salix* sp. (Albertó et al., 2002) were indicated for *Pleurotus abieticola*. An analysis of the distribution of this species in Russia showed that *P. abieticola* prefers mountain and foothill forests and is less common on the plain (Palamarchuk et al., 2023). In the Leningrad region (North-West of Russia) only one record is known in the Nizhnesvirsky Nature Reserve (Albertó et al., 2002).

Beginning with 2021, an outbreak of mass reproduction of *Ips typographus* (*Curculionidae*, *Coleoptera*) in the Leningrad region has been observed (Selikhovkin et al., 2022). The centers of drying have approached the protected forests in the Kurortny District of St. Petersburg (Gladyshevsky and Shchuchye Lake protected areas) and it was there, on fresh 2–3-year-old standing deadwood of *Picea abies*, where we discovered mass fruiting of *Pleurotus abieticola*. In some affected sites, the occurrence of this species exceeded that of the basic pioneer of spruce drying, *Fomitopsis pinicola*. Aim of the present report was to develop new data on the ecology and coenology (i.e. identification of the associated complex of fungal saprotrophs on fresh spruce deadwood) of *Pleurotus abieticola* based on the material of two large drying areas in the Gladyshevsky and Shchuchye Lake protected areas (St. Petersburg, Russia).

MATERIALS AND METHODS

The observations were carried out in July – August 2024. The survey covered the areas of drying out of the European spruce (*Picea abies*) in the state nature reserves of Shchuchye Lake and Gladyshevsky in the Kurortny District of St. Petersburg, which were attacked by *Ips typographus* in 2020 and mostly died out by 2021.

Both protected areas are situated on a terraced plain of glacial-lake origin with kame hills and basins, with absolute heights ranging from 25 to 70 m above sea level. Peatlands with a thickness of more than 2 m (Losinovka swamp, etc.) are located in the basin.

Table 1. Basic parameters of tree stands studied in affected sites

Tree stand parameters	Shchuchye Lake protected area	Gladyshevsky protected area
Affected sites coordinates*	60.20890 N, 29.79299 E; 60.20689 N, 29.79715 E; 60.21516 N, 29.79339 E	60.21695 N, 29.56137 E; 60.21778 N, 29.55857 E
Tree species	*Picea abies* (*Pinus sylvestris* sporadic)	*Picea abies* (*Pinus sylvestris* sporadic)
Soil cover dominants	*Vaccinium myrtillus*	*Vaccinium myrtillus*, *Sphagnum* spp.
Number of trees counted	100	100
Mean age	110 years	120 years
Mean diameter**	25 cm	30 cm
Year of dying	2021	2021

Note. *The coordinates of the center of affected sites are indicated. **Visual assessment.

The vegetation of the Shchuchye Lake protected area is represented by green-mosses, fern, sphagnum spruce (*Picea abies*) forests, bilberry-green moss, bilberry, lichen-shrub-green moss spruce-pine (*Pinus sylvestris*) forests, bilberry-green moss, sphagnum, pike birch (*Betula pubescens*) forests, wet-grass birch-black alder (*Alnus glutinosa*) forests, oligotrophic bogs with pine, meso-oligotrophic bogs on the banks of reservoirs and rafts and eutrophic bogs with birch, willow and *Calla palustris*. Some spruce and pine trees reach 100–150 years (Volkova et al., 2017).

The area of the Gladyshevsky Nature Reserve is covered with middle-aged coniferous and deciduous forests considerably disturbed by the Second World War and secondary forest management. The vegetation is also represented by bilberry-green moss or sphagnum pine, spruce, spruce-pine, birch, and aspen (*Populus tremula*) forests. There are gray alder (*Alnus incana*) forests on the steep banks of rivers, and black alder forests grow near the terrace depression of the Gulf of Finland (Khramtsov et al., 2016).

The characteristics of the surveyed tree stands of the Shchuchye Lake and Gladyshevsky protected areas are presented in Table 1.

The observation was carried out along a route without milestones, crossing the center of tree declining focus. Fallen trunks and 100 dead standing trees in each affected site were examined. The presence of fungal fruiting bodies was noted on each tree. As the accounting unit was considered one trunk bearing basidiomata. The percentage of affected trees in a set of 100 examined trunks was taken as the occurrence of the fungal species. Collected specimens were taken for laboratory studies.

The morphological study of collected specimens was carried out using an AxioImager A1 light microscope based in the center for collective use of equipment of the Komarov Botanical Institute of the Russian Academy of Sciences. Micro-preparations were made using a 5% KOH solution and Meltzer's reagent. Microstructure measurements were made in distilled water. The fungi were identified using a number of identification manuals (Ryvarden, Melo, 2017; Jülich, Stalpers, 1980). The material was herbarized at St. Petersburg State Forest Engineering University named after S.M. Kirov (duplicates are stored at the Komarov Botanical Institute of the Russian Academy of Sciences – LE-F). The current species names of the fungi are brought into line with the Index Fungorum database (2024).

Total DNA was isolated from pieces of basidiomata which were freeze-dried at −84°C for 2 days with FreeZone 2.5 Plus (Labconco, USA) freeze dryer. Then in 2-mL tubes together with glass beads the pieces were homogenized for 2 min at 5000 rpm using a Fast prep shaker (Precellys 24, Bertin Technologies, Rockville). Then, 800 μL of CTAB extraction buffer (3% cetyltrimethylammonium bromide, 2 mM EDTA, 150 mM Tris–HCl, 2.6 M NaCl, pH 8) was added to each tube, followed by incubation at 65°C for 1 h. After centrifugation, the supernatant was transferred to new 1.5-mL centrifugation tubes and then mixed with 1 volume of chloroform by gentle vortexing. After centrifugation for 8 min at 14 000 rpm, the supernatant was precipitated with 2 volumes of cold isopropanol, washed with 70% ethanol and dissolved in 50 μL TE buffer.

Polymerase chain reaction (PCR) was performed on 15 μl of a mixture containing 3 μl of Screen Mix (Eurogen, Russia), 0.2 μl of each primer (10 μM), 10.5 μl of ddH_2O and 1 μl of DNA template (100 ng). The ITS region of nDNA was amplified using primers ITS1-F and ITS4 (White et al., 1990; Gardes, Bruns, 1993). Amplification of the ITS fragments included preliminary denaturation for 5 min at 95°C and then 33 cycles including: denaturation for 30 s at 95°C, primer annealing for 30 s at 56°C and elongation for 30 s at 72°C, with a final elongation for 5 min at 72°C. The amplification reaction products were visualised by electrophoresis in 1.0%

agarose gel in 1× TAE (tris acetate) buffer solution with ethidium bromide, using a ChemiDoc MP transilluminator (BioRad, USA). The concentration of DNA and PCR products was measured with a SpectroStar Nano (BMG Labtech, Germany) spectrometer. Sequencing was carried out at the Synthol company (Russia).

The obtained sequences were compared with the reference ones using the BLASTn algorithm.

RESULTS

Tree stand declining pattern

Ips typographus attack on the tree stands in the surveyed areas occurred in 2020–2021, and their complete dying off occurred over the course of two growing seasons. In the third to fourth year after the attack, the trees have completely lost their needles and the process of bark shedding began (Fig. 1).

The majority of dead trees retained their bark at the time of the survey, but some of them had completely lost their bark. Bark loss began unevenly in different zones of the trunk, most often above the butt zone. *Ips typographus*, together with the associated cambivorous complex of microfungi, completely destroyed the cambium, and decay products rich in lignocellulose composites were formed under the bark. These composites were quickly colonized by a number of pioneer saprotrophic species of basidiomycetes, among which we were surprised to find a mass development of oyster mushroom species identified in the field as *Pleurotus abieticola* (Fig. 2, a).

To confirm the species identity of this taxon, which had not previously been reported as a mass developing pioneer saprotroph, molecular and morphological studies of the collected samples were carried out.

Fig. 1. The drying European spruce site as a result of the impact of *Ips typographus* (Shchuchye Lake protected area).

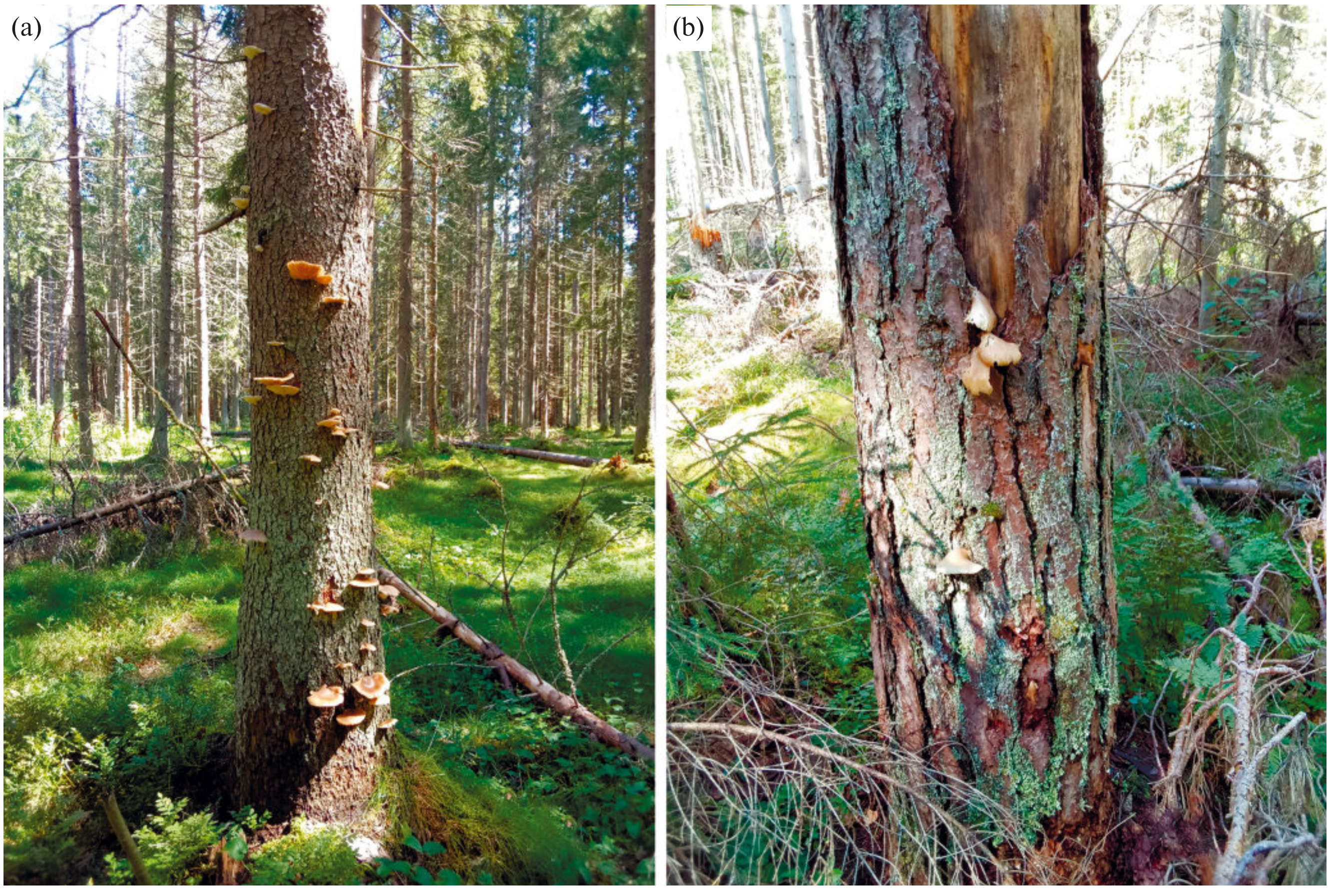

Fig. 2. *Pleurotus abieticola* basidiomata: a – on a dead trunk of *Picea abies* in stand attacked by *Ips typographus* (Shchuchye Lake protected area); b – on a dead trunk of *Pinus sylvestris* affected by *Tomicus piniperda* (Gladyshevsky protected area).

Molecular evidence

For the five studied specimens, sequences containing 580, 637, 621, 552 and 634 nucleotide pairs were obtained and submitted to GenBank (http://www.ncbi.nlm.nih.gov/genbank/). The sequences were provided with GenBank accession numbers PQ273839, PQ273840 PQ273841, PQ273842, PQ273843, respectively (Table 2). All these specimens showed 100% identity to reference sequences of *P. abieticola* from GenBank database.

Thus, we confirmed the species identification of the taxon we have identified. Interestingly, one of the samples was associated with dead wood of *Pinus sylvestris* (Fig. 2, b). This substrate is indicated for *Pleurotus abieticola* for the first time.

Table 2. Results of comparison of the obtained ITS sequences of *Pleurotus abieticola* samples with the most similar sequences deposited in the GenBank database

GenBank Sample, accession number	Region of origin (reference)	Coverage/Identity, %				
		PQ273839 580 bp	PQ273840 637 bp	PQ273841 621 bp	PQ273842 552 bp	PQ273843 634 bp
P. abieticola, OP821377.1	Russia, Republic of Komi (Palamarchuk et al., 2023)	100/100	100/100	100/100	100/100	100/100
P. abieticola, OP821378.1	Russia, Republic of Komi (Palamarchuk et al., 2023)	100/100	99/100	100/100	100/100	100/100
P. abieticola, AY450348.1	Russia, Primorsky Territory (Petersen, Hughes, 1997)	100/100	97/100	100/100	100/100	100/100
P. abieticola, KX836361.1	China (Li et al., 2017)	100/100	96/100	98/100	100/100	96/100

Morphological description

Pleurotus abieticola R.H. Petersen et K.W. Hughes, Mycologia 89 (1): 175, 1997 (Fig. 3).

Basidiomata annual, of pleurotoid morphotype, gymnocarpic, with a well-developed or reduced eccentric stipe, growing solitary or in small clusters. Pileus semicircular, kidney-shaped or ear-shaped, 4–17 × 3–8 cm, often lobed, initially convex with an inrolling margin, then plane, usually concave at the attachment point. The upperside is ingrown fibrous, smooth or felted at the base, hygrophanous, sometimes slightly radially striped along the edge, gray, bluish-gray, grayish-brown, when dry – dirty beige (sometimes with an olive or cherry tint), matt. The context is fleshy-elastic, flexible, initially hygrophanous, then dry and easily crumbling, whitish. Hymenophore gilled or on the descending part of the stem with a favoloid pattern due to strongly developed anastomoses, gills descending onto the stipe, of three levels, white. Stipe eccentric or lateral, short, sometimes almost reduced, 0.7–1 cm long, 0.5–1 cm thick, ribbed white to grey-brown, usually finely tomentose. Spore print white.

Hyphal system monomitic. Generative hyphae 3.5–12 µm in diam., with clamp connections, thin-walled in the gill trama and rather thick-walled in the context. Trama irregular. Pileipellis a cutis. Pleurocystidia not differentiated. Cheilocystidia fusiform, clavate, cylindrical, often septate, (15)20–60(70) × 4.5–15 µm. Basidia narrowly clavate, 25–35 × 5.0–7.5 µm, 4-spored. Basidiospores 7.0–12.5 × 3.5–5.5 µm.

Material examined: Russia, St. Petersburg, Kurortny District, Shchuchye Lake protected area, 60.215788 N, 29.793347 E, on bark penetration of dry standing *Picea abies*, leg. D.A. Shabunin, 13.07.2024 (LE 287757, PQ273839). – *ibid*., 60.210145 N, 29.795031 E, on bark penetration of dry standing *P. abies*, leg. D.A. Shabunin, 13.07.2024 (LE 287758, PQ273840). – *ibid*., 60.210112 N, 29.795002 E, on bark penetration of dry standing *P. abies*, leg. D.A. Shabunin, 13.07.2024 (LE 287759, PQ273841).

New data on ecology

In the observed sites, *P. abieticola* demonstrated an unusually high occurrence (Table 3), reaching the parameters of occurrence up to 53.0% in the Shchuchye Lake protected area. Fruiting bodies usually appear on bark-covered areas. Fruiting bodies have not been observed on decorticated areas of the trunk. The first basidiomata were registered on 12.06.2024 and sporulation continued until the end of August 2024. During this time, several generations of basidiomata appeared, and the June basidiomata did not collapse, but monotonously increased in size and underwent age-related changes (hardening of the context, disappearance of hygrophanity and fading of the cap surface). The oyster mushroom *P. abieticola* was recorded only on dead standing trunks; fruiting bodies were usually noted from the base of the trunk to a height of 3 m.

In addition, fruiting of *P. abieticola* was recorded on a dead trunk of Scots pine, dried out as a result of an attack by *Tomicus piniperda* in the center of died spruce tree stand in the Gladyshevsky protected area.

Together with *Pleurotus abieticola*, the following pioneer xylosaprotrophs were noted in the sites affected by *Ips typographus*: *Fomitopsis pinicola*, *Trichaptum abietinum* (two dominants of the pioneer saprotrophic

Table 3. Occurrence of pioneer saprotrophic fungi developing in observed *Picea abies* affected sites

Fungal species	Tree state	Species occurrence in different affected sites in different protected area, %				
		Shchuchye Lake			Gladyshevsky	
		1	2	3	4	5
Amaropostia stiptica (Pers.) B.K. Cui, L.L. Shen et Y.C. Dai	standing	–	–	2.0	1.0	–
****Armillaria ostoyae* (Romagn.) Herink	fallen*	5.3	–	–	1.0	1.0
****Botryobasidium laeve* (J. Erikss.) Parmasto	fallen	5.3	–	–	–	–
****Dacrymyces stillatus* Nees	standing	–	–	–	1.0	–
Exidia nigricans (With.) P. Roberts	fallen	1.0	–	–	1.0	1.0
« «	fallen	–	6.7	–	3.8	6.7
E. saccharina Fr.	standing	–	–	–	–	1.0
***Fomitopsis pinicola* (Sw.) P. Karst.	standing	30.0	18.0	7.0	53.0	62.0
« «	fallen	21.0	20.0	41.2	50.1	26.7
Gloeophyllum sepiarium (Wulfen) P. Karst.	fallen	–	–	5.9	–	–
Heterobasidion parviporum Niemelä et Korhonen	fallen	–	–		3.8	–
Phlebiopsis gigantea (Fr.) Jülich	fallen	–	–	5.9		–
****Pleurotus abieticola* R.H. Petersen et K.W. Hughes	standing	7.0	25.0	53.0	30.0	21.0
Stereum sanguinolentum (Alb. et Schwein.) Fr.	fallen	–	–	–	–	6.7
Trichaptum abietinum (Pers. ex G.F. Gmelin) Ryvarden	standing	3.0	5.0	2.0	1.0	–
« «	fallen	57.9	60.0	29.4	11.5	6.7

Note. *Only fallen logs resulting from windfall of trees killed by *Ips typographus* are considered. **The species was noted on a trunk affected by *Pleurotus abieticola*. ***Species first noted for the Shchuchye Lake and Gladyshevsky protected areas.

Fig. 3. Basidiomata of *Pleurotus abieticola* (LE 287757, LE 287758) appeared on dead wood of *Picea abies* (Gladyshevsky protected area): a – upperside of young fruiting bodies; b – upperside of mature fruiting bodies; c – young fruiting bodies from the front; d – hymenophore of mature fruiting bodies (the favoloid pattern is visible on the part of descending onto the stipe). Scale bar – 5 cm.

complex), *Gloeophyllum sepiarium*, *Armillaria ostoyae*, *Amaropostia stiptica*, *Exidia nigricans* (an ecotype previously considered as *E. pithya*), *E. saccharina*, *Dacrymyces stillatus*, *Heterobasidion parviporum*, *Phlebiopsis gigantea*, *Stereum sanguinolentum* (Table 3). *Fomitopsis pinicola* was most frequently encountered in the surveyed foci of spruce drying out earlier. Its fruiting was recorded on dead trunks at a height from the base to 2–3 m, as well as on stumps and windfallen trunks. It is interesting to note that the honey fungus (*Armillaria ostoyae*) was either not found in the dried-up plantations, or its prevalence did not exceed 1%.

Within aforementioned species, only one fungus developed in a strong association with *Pleurotus abieticola* on one trunk, *Fomitopsis pinicola*.

Fig. 4. Basidiomata of *Pleurotus abieticola* grown on a necrotic area of a living *Picea abies* tree (Leningrad Region, Vaskelovo settlement, 12.09.2014, leg. I.V. Zmitrovich).

DISCUSSION

It is known that *Ips typographus* is a carrier of a pool of cambivorous fungal species (Linnakoski et al., 2012). Therefore, the attack of this insect on tree stands leads to detrimental consequences for trees in the shortest possible time, i.e. the transition of the entire stand to a state of dead wood, which begins to be colonized by fungal xylosapotrophs.

The species composition of wood-destroying fungi in the first stages after the drying of spruce stands as a result of the impact of *Ips typographus* is still poor. Probably, this should be explained by the rapidity of the drying process. The most fungal species that infests the wood of the trunks of the European spruce in the affected sites after the impact of the bark-beetle is *Fomitopsis pinicola*. The development of this fungus leads to the break of dead trunks and their transition to the category of fallen trees.

An unexpected fact is the occurence of the fungus *Pleurotus abieticola*, previously not noted in either St. Petersburg or the Leningrad Region. This is a saprotrophic species causing white rot. There is a finding on living *Picea abies* (Fig. 4), but the fruiting bodies developed at the site of necrosis that occurred as a result of pruning, so the saprotrophic status of the species is not disputed in this case either. This species was considered rare (Palamarchuk, 2023), but our studies revealed an outbreak of its mass development, exceeding that of *Fomitopsis pinicola* in one of the affected sites. Probably, outside the development of forest epiphytoties, this species has a competitive limitation, since its niche is occupied by its ecological analogue, the white rot fungus *Trichaptum abietinum*.

The reason for such a wide local spread of *P. abieticola* may be the appearance of numerous dead spruce tree trunks in the declining forests after the development of *Ips typographus*. However, the lack of records of this species from well-studied surrounding forests raises the question of the propagule fund sufficient to affect the sharply declining forest stand. In this sense, the hypothesis that the carriers of the propagules of this fungus are outbreaks forming bark-beetles is also of interest. In the future, this hypothesis will be of interest for testing.

CONCLUSION

Pleurotus abieticola is a recently described and, therefore, still poorly studied species, which is revealing new facets of its ecology. In 2014, we discovered it on the Karelian Isthmus on a living *Picea abies* on a dead shoot, and in 2024, in another place on the Karelian Isthmus, as a pioneer saprotroph that widely colonized dead spruce stands.

A detailed study of these stands allowed us to identify new subtle features of the ecology and morphology of this species. In particular, eutrophic basidiomata of this species with large caps up to 17 cm wide were identified, which allowed us to expand the morphological diagnosis of this species. The phenological features of this species were also clarified, and it was shown that fruiting bodies that appeared in June can exist until the end of summer, slowly increasing in size and bearing spores. During the observations in the surveyed areas, a new substrate of *P. abieticola* was also identified, namely *Pinus sylvestris*, affected by *Tomicus piniperda*.

A saprotrophic pioneer complex was identified, where the *Pleurotus abieticola* has entered, including such species as *Fomitopsis pinicola*, *Trichaptum abietinum* (two dominants of the pioneer xylosaprotrophic complex), *Gloeophyllum sepiarium*, *Armillaria ostoyae*, *Amaropostia* *stiptica*, *Exidia nigricans*, *E. saccharina*, *Dacrymyces stillatus*, *Heterobasidion parviporum*, *Phlebiopsis gigantea*, *Stereum sanguinolentum*. Such species as *Armillaria ostoyae*, *Botryobasidium laeve, Pleurotus abieticola* were first noted in the Shchuchye Lake and Gladyshevsky protected areas, although all species, except the latter, are quite common in the coniferous forests of the region.

The discovery of a free niche in the form of sharply dead *Picea abies* stands seems to be a significant but insufficient explanation for the sharp increase in the number of *Pleurotus abieticola* in the surveyed area, since the fund of propagules of this rare species in these areas is by definition poorer than that of the dominant pioneers *Fomitopsis pinicola* and *Trichaptum abietinum*. In this regard, it is of interest to test the hypothesis about the transfer of *Pleurotus abieticola* propagules by bark-beetles forming outbreaks.

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Pleurotus abieticola (*Agaricales*, *Basidiomycota*) как пионерный ксилосапротроф, ассоциированный с очагами усыхания ельников, вызванного короедом-типографом

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Ксилосапротрофный агарикомицет *Pleurotus abieticola*, описанный в 1997 г., еще плохо изучен в экологическом отношении. Цель данного сообщения – изучение экологических особенностей *P. abieticola* на материале двух обширных очагов усыхания ели в заказниках “Гладышевский” и “Озеро Щучье” (Санкт-Петербург, Россия), в которых обнаружили массовое плодоношение этого вида. Идентификация этого вида в полевых условиях была подтверждена результатами секвенирования участка ITS рДНК. Подробное исследование древостоев позволило выявить новые тонкие особенности экологии и морфологии этого вида. Выявлен сапротрофный пионерный комплекс, в состав которого внедрился *P. abieticola* (*Fomitopsis pinicola*, *Trichaptum abietinum*, *Gloeophyllum sepiarium*, *Armillaria ostoyae*, *Amaropostia stiptica*, *Exidia nigricans*, *E. saccharina*, *Dacrymyces stillatus*, *Heterobasidion parviporum*, *Phlebiopsis gigantea*, *Stereum sanguinolentum*). Обсуждаются причины массового развития *Pleurotus abieticola* в еловых древостоях, пораженных короедом-типографом.

Ключевые слова: вешенка, заказник “Гладышевский”, заказник “Озеро Щучье”, короеды, ксилосапротрофы, лубоеды, ООПТ, сухостой, усыхание ельников