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REVIEW PAPER

The geographical distribution, trophic modes, and host preferences of *Fomitopsis pinicola* in Central Europe: a comprehensive review

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Abstract

Fomitopsis pinicola [Sw.] P. Karst. is one of the most common wood-decaying macrofungi which is adapted to growth under different environmental conditions, but little is known about its intraspecific variation in spatial distribution, function and substrate specificity in different habitats. To understand how the geographical distribution, trophic mode and host specificity of this fungus vary across different habitat categories, we analysed its habitat and trophic preferences using Slovakia (Central Europe) as an example. For this purpose we studied and compared the archived material (fungarium items and field notes) from 1954 to present, obtained from own collections and external sources. The occurrence of *F. pinicola* in forests and quasi-natural habitats is related to the distribution of Norway spruce. Contrariwise, sites with its presence in public urban spaces are scattered throughout the whole territory of Slovakia. The occurrence of *F. pinicola* as a saprotroph is highest in forests and lowest in public urban spaces, where it accounts for 90.1% and 27.7% of the total number of records, respectively. *F. pinicola* was also shown as an important pathotroph of broadleaves in public urban spaces, where pathotrophy concerns as high as 72.3% of relevant records. *Prunus* species are the most frequently infested woody plants, accounting for 81.3% of these records. *In silico* analysis of available *F. pinicola* ITS sequences indicates its genetic homogeneity in Central Europe and the adjacent regions. Thus, the observed differences in trophic modes and host preferences of *F. pinicola* from different habitats cannot be explained by its intraspecific genetic variability.

Key words: red-banded polypore; trophic adaptation; habitat adaptation; morphospecies

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1. Introduction

In general, *Fomitopsis pinicola* [Sw.] P. Karst. is a common brown-rot fungus found in Central Europe, where it frequently grows on conifers but also occurs on deciduous trees (Niemelä et al. 1995; Zúbrik et al. 2008; Konôpka (ed.) 2010; Černý et al. 2015; Butin 2019). However, it is not clear from the published data, whether it exists primarily as saprotroph for which parasitism is only incidental. On one hand, its role in conifer forests is essential. In fact, it is one of the most important primarily saprotrophic wood-decaying species, which mainly degrades

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**Corresponding author. Branko Slobodník, e-mail: slobodnik@tuzvo.sk* cellulose leaving lignin as structural component intact and thus play important role in the carbon cycle (Penttilä et al. 2004; Bače et al. 2012; Pouška et al. 2013). On the other hand, other authors also draw attention to the parasitic status of this species (Samek et al. 1957; Černý 1976; Soukup & Pešková 2002; Konijnendijk et al. 2005; Mihál & Cicák 2006; Vacek et al. 2007; Zúbrik et al. 2008; Butin 2019).

Many studies suggest that communities of wood-decaying macrofungi vary considerably between different forest stand types, being shaped by specific environmental parameters such as the presence of hosts of the appropriate taxa, substrate succession, humidity and temperature (Heilmann-Clausen 2001; Bače et al. 2012; Pouška et al. 2013; Abrego 2022). The diversity of trophic modes of wood-decaying macrofungi (Agaricomycotina, Basidiomycota) is an important prerequisite for their survival and activity in habitats. Some studies even indicate that some of these fungi "recognize" the habitat naturalness (Antonín & Holec 2015). According to this concept, there exist different possible ecological scenarios, for example: (1) different habitats – different geographical distribution, and (2) different habitats – different trophic modes (phytopathological status, life strategy) and host preferences.

Under the first scenario, the range of hosts that fungal destroyer can infect in geographic areas or habitats is a trait determined by its own evolutionary history and by the evolutionary history of its potential hosts. However, data on host range diversity in urban and other non-forest areas are scarce (Konijnendijk et al. 2005). This study intends to bridge the gap in our understanding of the host range in these areas. Moreover, some fungi, e.g., *Auricularia auricula-judae* [Bull.] Quél., appear to be changing hosts upon climate change (Gange et al. 2011). Under the second scenario, we also assume that some fungi may have different trophic modes in different habitat categories.

In context of these considerations, the goal of this study is to answer the following questions: (1) Can different habitats in the same geographic area affect the host preferences of genetically homogeneous phytopathologically important macrofungi? (2) Can different habitats affect both geographical distribution and trophic mode in these fungi? As a model organism we used the red-banded polypore, *Fomitopsis pinicola*. The main study area was the territory of Slovakia (Central Europe), where we studied the records and specimens, collected since 1954. Previous analyses reveal genetic homogeneity of the European *F. pinicola* specimens collected from coniferous hosts (Högberg et al. 1995, 1999; Haight et al. 2016). To understand whether specimens collected on both coniferous and deciduous woody plants are also genetically homogeneous, we compared patterns of these specimens sourced from various regions of Europe.

2. Baseline data, their acquisition and processing

For our studies, we divided the habitats of *F. pinicola* into 3 categories according to the placement and function they have (Jeffrey 2002; Konijnendijk et al. 2005): (a) public urban spaces in cities, towns, and villages, hereafter "public urban spaces" (public parks and similar open spaces, cemeteries, gardens, both paved and non-paved squares, planted streets and pockets of greenery), (b) quasi-natural habitats associated with engineered features, hereafter "quasi-natural habitats" (public recreational areas and sport fields: urban forests, arboretums, spa parks, cottage areas, ski resorts; transport corridor verges: rail sides, roadsides; water margins: riversides, lakesides; public spaces on the urban fringe), and (c) forests.

Concurrently, we considered two types of the trophic modes: wood-decaying saprotrophy and woody plant pathotrophy. *F. pinicola* as the wood-decaying saprotroph derives its nutrition from the dead wood, defined as the wood of stumps and various parts of dead trees, standing or lying. *F. pinicola* as a pathotroph causes a brown rot of living trees.

We identified the woody plant taxa by routine methods and determined them according to standard, widely used keys (Krüssmann 1984; Úradníček et al. 2009). In nomenclature of woody plants, we followed The International Plant Names Index database (IPNI 2024).

The obtained data from Slovak forests are based on the following sources:

a) field notes of J. Gáper, S. Glejdura and K. Bučinová, obtained during their occasional mycological excursions to forest stands since 1982, especially in protected areas. Repeated data, i.e. the same records in several forest stands, mostly in protected areas, were obtained over the past 50 years during excursions, conducted by other field mycologists. These excursions did not provide data other than those reported in our results.
b) museum collections: Herbarium – Slovak National Museum Bratislava, Slovakia (BRA), Herbarium – Charles University, Prague, Czechia (PRC), Herbarium – National Museum, Prague, Czechia (PRM), Herbarium – Moravian Museum, Brno, Czechia (BRNM). A part of the voucher specimens is deposited in the Private fungarium of Stanislav Glejdura, Zvolen, Slovakia (PSG).
c) relevant printed and electronic sources since 1954 (Acta Botanica Universitatis Comenianae; Catathelasma; Časopis Národního Muzea Praha; Česká mykologie – Czech Mycology; Folia Oecologica; Journal of Forest Science; Lesnícky časopis – Forestry Journal – Central European Forestry Journal; Lesnická práce, s. r. o; Mykologické listy; Natura Carpatica; Naturae Tutela; Ochrana prírody; Ochrana

přírody; Proceedings of the Czechoslovak Scientific Society for Mycology; Spravodajca slovenských mykológov; Zborník Oravského múzea; Zborník prác o Tatranskom Národnom Parku; Zprávy lesnického výzkumu; Janitor & Fábry 1981; Kotlaba 1984; Kotlaba & Pouzar 1986; Mihál 1995; Záhorovská 1997; Janitor & Gáper 1998; Škubla 2003; Čadek 2006; Konôpka (ed.) 2010; Baranovič 2024; BioLib 2024; FotoNet 2024; Kunca & Zúbrik 2024).

Most records from both public urban spaces and quasi-natural habitats were obtained by J. Gáper as the result of his systematic field surveys of urban and rural areas of Slovakia in 1982–2024. The collections were conducted mostly in summer and autumn months, but extensive research covered the entire years. We identified the specimens by routine methods and determined them according to standard, widely used keys (Bernicchia 2005; Ryvarden & Melo 2017).

Besides that, a part of records was:

a) excerpted from the polypore card-register of F. Kotlaba (Prague) from January 1953 to February 1989;
b) obtained occasionally in the last 32 years by S. Glejdura, K. Bučinová, S. Gáperová, P. Kollárová and M. Šebesta during their excursions to urban and/or rural areas;
c) excerpted from the relevant printed and electronic sources (Acta Botanica Universitatis Comenianae; Škubla 2003; Kollár 2011; Baranovič 2024; FotoNet 2024);
d) excerpted from the renowned Slovak and Czech herbaria (BRA, PRC, PRM, BRNM).

The nomenclature of fungi follows Index Fungorum database (Cooper & Kirk 2024).

The continuously updated maps with the distribution of *F. pinicola* in Slovakia were generated on the base of all the above-mentioned data sources according to the Tool for searching locations within the squares of vegetation mapping in Slovakia (TOOL) grid square system (Senko et al. 2024). To illustrate changes in the distribution of the species, we presented the records in three above-mentioned habitat categories separately. The points on the maps do not relate to each individual record but show the localities of the fungus in exact TOOL squares. As a result, a single point on the map could include more than one locality.

To evaluate the genetic differences between *F. pinicola* sequences from broadleaved and coniferous hosts, we prepared the custom dataset of *F. pinicola* internal transcribed spacer (ITS) sequences by downloading the GenBank sequences with clearly defined origin (specified host and country). The final dataset consisted of 41 sequences of *F. pinicola* (29 from conifers and 12 from broadleaves) from 12 countries of Central Europe and adjacent regions (Table 1).

The sequences were aligned using ClustalW algorithm and diversity between sequences (the number of substitutions per nucleotide) was calculated using Kimura 2-parameter model. To visualize differences among sequences, the phylogenetic trees were constructed using Neighbor-Joining, Maximum Parsimony and Minimum Likelihood algorithms implemented in MEGA software version 11 (Tamura et al. 2021). Bayesian inference tree of ITS data was constructed with MrBayes version 3.2 (Ronquist et al. 2012), available at www.phylogeny.fr.

3. Geographical distribution of red-banded polypore in Slovakia

For our study, we analysed data for the past ca 70 years. According to our opinion, the habitat categories have changed considerably in Slovakia during this period. Therefore, the older material would give incorrect information in the present situation.

Table 1. List of *Fomitopsis pinicola* ITS sequences used in this study.

Strain / Voucher	Country of origin	Host	ITS GenBank accession number
RAMG_13114	Austria	*Picea* sp.	KU171413
P3_4908	Austria	*Picea abies* [L.] H. Karst.	KM396268
IB20130042	Austria	*Picea abies* [L.] H. Karst.	KM360140
IB20130040	Austria	*Picea abies* [L.] H. Karst.	KM360139
IB20130024	Austria	*Picea abies* [L.] H. Karst.	KM360135
IB20130030	Austria	*Larix decidua* Mill.	KM360137
IB20130021	Austria	*Picea abies* [L.] H. Karst.	KM360134
IB20130015	Austria	*Picea abies* [L.] H. Karst.	KM360132
IB20130018	Austria	*Picea abies* [L.] H. Karst.	KM360133
IB20130013	Austria	*Picea abies* [L.] H. Karst.	KM360131
IB20130010	Austria	*Picea abies* [L.] H. Karst.	KM360130
Vlasak 1905/1	Czech Republic	*Picea abies* [L.] H. Karst.	ON994728
ZK35/08	Czech Republic	*Picea abies* [L.] H. Karst.	FR717226
CFMR:LT-319	Estonia	*Picea* sp.	KF169652
CFMR:LT-323	Estonia	*Picea* sp.	KF169651
F29	Finland	*Picea abies* [L.] H. Karst.	GU067743
MOGU 117-19	Italy	*Picea abies* [L.] H. Karst.	OM422745
IB20130034	Italy	*Picea abies* [L.] H. Karst.	KM360138
O20.2.1	Latvia	*Picea abies* [L.] H. Karst.	MK911616
P52	Latvia	*Pinus sylvestris* L.	MK801342
B48	Latvia	*Picea abies* [L.] H. Karst.	FJ903310
VL291A	Lithuania	*Pinus mugo* Turra	JF440570
NIBIO 2016-1000/1	Norway	*Picea abies* [L.] H. Karst.	MF511079
TS-Fp-24	Russia	*Picea* sp.	KF169656
O2	Sweden	*Picea abies*[L.] H. Karst.	JQ765681
F11_900	Switzerland	*Picea abies* [L.] H. Karst.	KT943920
D09_821	Switzerland	*Picea abies* [L.] H. Karst.	KT943919
A08_998	Switzerland	*Picea abies* (L.) H. Karst.	KT943917
C08_941	Switzerland	*Picea abies* [L.] H. Karst.	KT943918
IB20130026	Austria	*Alnus incana* [L.] Moench	KM360136
DR_EST_021	Estonia	*Alnus* sp.	KU171403
12391 H	Finland	*Alnus incana* [L.] Moench	JQ700273
NW-FVA7048	Germany	*Fraxinus excelsior* L.	OP023253
NW-FVA5278	Germany	*Fagus sylvatica* L.	MT561407
7	Germany	*Acer platanoides* L.	FR686554
agrAR043	Germany	*Viscum album* L.	FN435658
I220	Latvia	*Alnus incana* [L.] Moench	GU062263
M97	Latvia	*Alnus glutinosa* [L.] Gaertn.	JF340282
olrim956	Lithuania	*Fraxinus excelsior* L.	AY787671
LE-BIN: 3969	Russia	*Populus tremula* L.	OQ053214
LE-BIN: 4361	Russia	*Malus domestica* Borkh.	OM033739

We collected a total number of 508 *Fomitopsis pinicola* records, representing three habitat categories in Slovak territory since 1954. Over half of them (334 records, i.e. 65%) belong to the category forests. 78 records represent the category quasi-natural habitats. In the category public urban spaces, 96 records were detected. Of the 96 records from the latter category and 78 records from quasi-natural habitats, 62 and 90, respectively, are original. The category forests includes 128 original records and 206 records from external sources. However, some of them (more precisely 50 records from this category) could not be used for the synthesis of the geographical distribution data due to the absence of detailed location (missing coordinates or square location). To summarise the distribution of *F. pinicola* in Slovakia, 458 records were therefore used in total (284 from forests, 78 from quasi-natural habitats, and 96 from public urban spaces).

The distribution of *F. pinicola* in forests (Fig. 1) and quasi-natural habitats (Fig. 2) is similar and overlaps with the distribution of the Norway spruce (*Picea abies* [L.] H. Karst.). This means that the occurrence of *F. pinicola* from these two habitat categories is linked mostly to the mountainous regions. Its distribution in the public urban spaces has a larger range and represents the scattered occurrence on the whole territory of Slovakia (Fig. 3).

At the turn of the 1930s/1940s, the first list of *F. pinicola* records in Slovakia was published by Pilát (1936–42). All the records available up to the beginning of the 1980s,

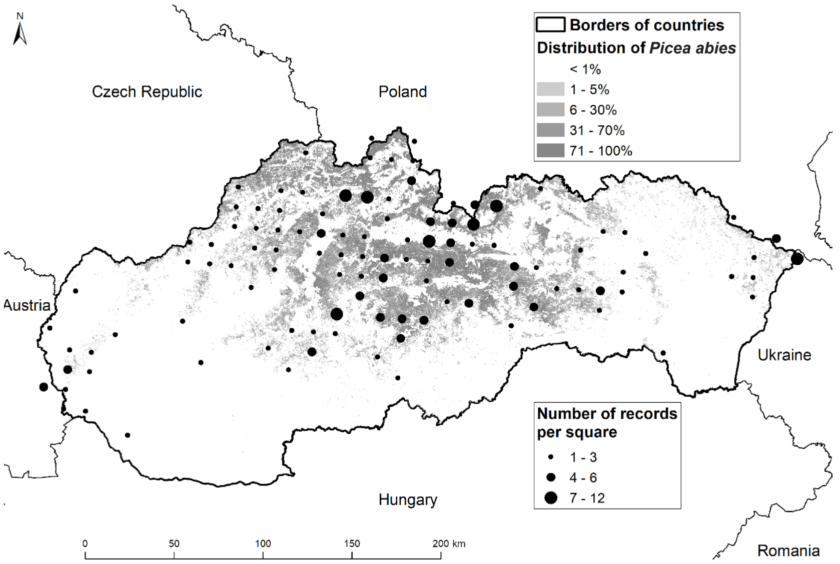

Fig. 1. Distribution map of *Fomitopsis pinicola* records in Slovak forests within the quadrants of the square system of the vegetation mapping in Slovakia TOOL (Senko et al. 2024). The distribution of Norway spruce is coloured in grey.

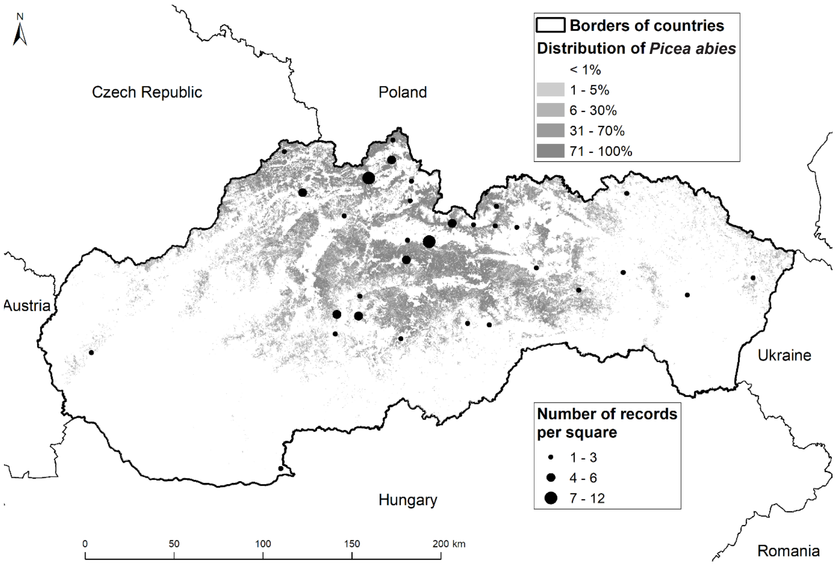

Fig. 2. Distribution map of *Fomitopsis pinicola* records in Slovak quasi-natural habitats within the quadrants of the square system of the vegetation mapping in Slovakia TOOL (Senko et al. 2024). The distribution of Norway spruce is coloured in grey.

including those of Pilát mentioned here, were processed by Kotlaba (1984). Based on this knowledge of geographical distribution, he wrote that *F. pinicola* preferably grows in Northern and Central Slovakia. Our findings show that these Slovak regions are certainly the best ones for this fungus in both forests and quasi-natural habitats (Figs. 1, 2). However, 96 records from the category public urban spaces published here are not from these typical Slovak regions but from the entire territory of Slovakia (Fig. 3).

4. Trophic modes and woody plants as hosts

After the exclusion of the records with the missing information about the trophic mode, a dataset of 363 records of *F. pinicola* (202 from the category forests, 67 from quasi-natural habitats and 94 from public urban spaces) was used to compare and quantify its main trophic modes. As Fig. 4 shows, saprotrophy is the dominant trophic mode of *F. pinicola* in forests, where it accounts for 90.1% of the total number of records for which we indicated the trophic mode. In contrast, *F. pinicola* is important as a pathotroph of woody plants in the public urban spaces, where the pathotrophy is related to 72.3% of the total number of considered records.

To analyse the taxonomic spectra of the hosts for *F. pinicola*, we used the dataset representing 384 records in total, from which 235 belong to the category forests, 61 to quasi-natural habitats, and 88 to the category public urban spaces. The rest of 508 records did not contain the information about host.

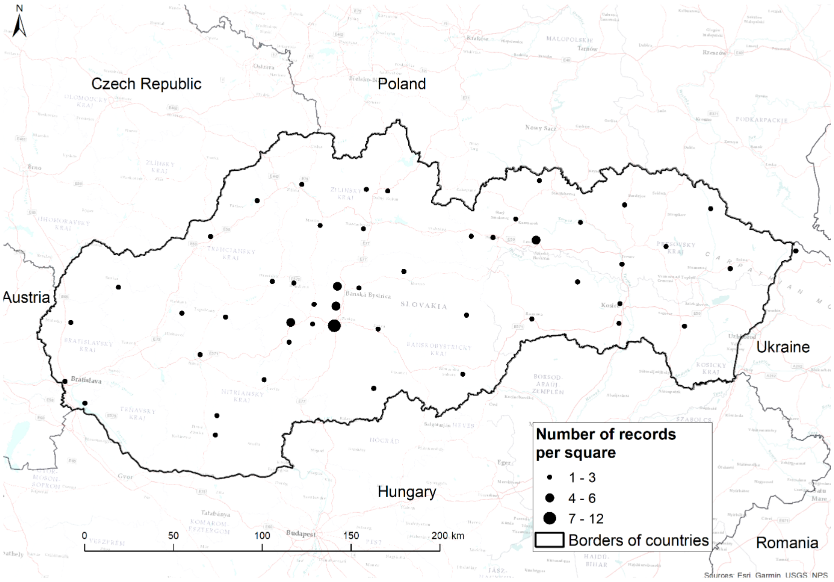

Fig. 3. Distribution map of *Fomitopsis pinicola* records in Slovak public urban spaces within the quadrants of the square system of the vegetation mapping in Slovakia TOOL (Senko et al. 2024).

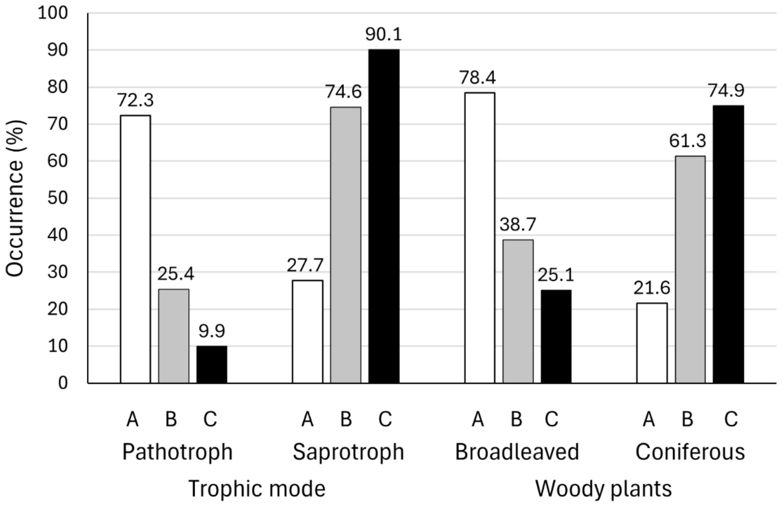

Fig. 4. The occurrence of *Fomitopsis pinicola* in Slovakia over the past ca 70 years, according to the trophic mode and the woody plants within three habitat categories. (A: public urban spaces; B: quasi natural habitats; C: forests).

Conifers are the main hosts of *F. pinicola* in forests and quasi-natural habitats, where they represent 74.9% and 61.3% of the total number of analysed records, respectively. However, this number is only 21.6% in public urban spaces (Fig. 4). From among coniferous trees, the dominant host of *F. pinicola* is the Norway spruce. Contrariwise, broadleaved woody plants are the dominant hosts of *F. pinicola* in the public urban spaces, accounting for 78.4% of the total number of records for which we indicated the host, followed by the quasi-natural habitats (38.7%) and the forests (25.1%), respectively (Fig. 4). From among the broadleaves from public urban spaces, the predominant hosts of *F. pinicola* are the species of *Prunus* (81.3% of 69 reliable records), followed by only a few records on seven another woody plants (Table 2, Fig. 5).

F. pinicola colonizes, especially in mountain and foothill forests, primarily the wood of dead or dying, standing or lying trunks and stumps of conifers, mostly *Picea abies*, *Abies alba*, *Pinus sylvestris*, and *Larix decidua*. However, it may also grow as a pathotroph on older, overmature living trees (Samek et al. 1957; Mihál & Cicák 2006) or the trees in poor health damaged by animals (Příhoda 1964), diseases (Černý et al. 2015), mechanical wounds from forest machines or logs, or wind stress and other abiotic stressors (Příhoda 1964; Černý 1976; Soukup & Pešková 2002; Vacek et al. 2007; Zúbrik et al. 2008; Konôpka (ed.) 2010). In connection with its action as a pathotroph, it is necessary to note that *F. pinicola* has been reported as a heart rot pathogen and subsequently as a mortality agent of old-growth spruces in pristine northern forests of Europe, China, and Alaska. These data were summarized by Vasaitis (2013). In addition, it was observed that the spreading of this fungus is facilitated by bark beetles (Coleoptera: Curculionidae, Scolytinae) and can reach high densities after their outbreaks. Living basidiomata on dead wood appear even after 1 year after bark beetle outbreak but are lacking on living trees (Příhoda 1964; Pouška et al. 2013; Vasaitis 2013; Vogel et al. 2017). According to Zúbrik et al. (2008), *F. pinicola* also serves as the major decomposer of deciduous trees.

Fig. 5. Basidioma of *F. pinicola* as a pathotroph on the *Prunus serrulata* branching point in Zvolen town, Slovakia (photo: Svetlana Gáperová).

Our results from Slovak forests correspond to the available literature data from the coniferous forests of Central Europe. However, as shown in Table 3, its pathological impact on broadleaved trees in Central European

Table 2. Occurrence (% of all broadleaved/coniferous host individuals) of *Fomitopsis pinicola* in Slovakia over the past 70 years, according to the host tree species within three habitat categories (A: public urban spaces; B: quasi-natural habitats; C: forests).

Tree species	Occurrence (% of host individuals)		
	A	B	C
Broadleaved			
Alnus incana [L.] Moench	0.0	14.3	1.8
Alnus glutinosa [L.] Gaertn.	0.0	0.0	3.6
Alnus sp.	0.0	4.8	9.0
Betula pendula Roth	0.0	23.8	3.6
Betula pubescens Ehrh.	0.0	0.0	1.8
Betula sp.	0.0	4.8	12.5
Cerasus avium [L.] Moench	2.9	0.0	0.0
Corylus avellana L.	0.0	4.8	1.8
Fagus sylvatica L.	2.9	9.5	32.1
Frangula alnus Mill.	0.0	0.0	1.8
Fraxinus sp.	0.0	0.0	1.8
Malus domestica Borkh.	7.2	0.0	0.0
Paulownia tomentosa Steud.	1.5	0.0	0.0
Populus alba L.	0.0	0.0	3.6
Populus tremula L.	0.0	9.5	3.6
Populus sp.	0.0	0.0	1.8
Prunus armeniaca L.	1.5	0.0	0.0
Prunus avium [L.] L.	18.8	4.8	1.8
Prunus cerasifera Ehrh.	10.1	0.0	0.0
Prunus cerasus L.	1.5	0.0	0.0
Prunus domestica L.	11.6	0.0	0.0
Prunus serrulata Lindl.	34.8	0.0	0.0
Prunus subhirtella Miq.	1.5	0.0	0.0
Prunus sp.	1.5	0.0	0.0
Quercus robur L.	0.0	4.8	0.0
Quercus sp.	0.0	4.8	1.8
Salix alba L.	0.0	4.8	7.1
Salix silesiaca Willd.	0.0	0.0	1.8
Salix sp.	0.0	0.0	5.4
Sorbus aucuparia L.	1.5	0.0	0.0
Tilia cordata Mill.	1.5	4.8	0.0
Tilia platyphyllos Scop.	1.5	4.8	0.0
Tilia sp.	0.0	0.0	1.8
Ulmus sp.	0.0	0.0	1.8
Coniferous			
Abies alba Mill.	5.6	5.6	13.6
Larix decidua Mill.	0.0	0.0	1.1
Picea abies [L.] H. Karst.	55.6	88.9	77.3
Picea pungens Engelm.	5.6	0.0	0.0
Picea sp.	16.7	0.0	0.0
Pinus nigra J. F. Arnold	0.0	0.0	1.1
Pinus /sylvestris L.	5.6	0.0	3.4
Pinus sp.	0.0	5.6	3.4
Pseudotsuga menziesii [Mirb.] Franco	11.1	0.0	0.0

Table 3. List of *Fomitopsis pinicola* trophic modes in Central European forests (S – wood-decaying saprotroph, P – pathotroph, * – overmatured trees, ** – weakened and/or stressed trees).

Author(s)	Trophic mode	Geographical origin	Host(s)
Orłoś (1955)	S, P**	Central European forests	Conifers and broadleaves
Samek et al. (1957)	S, P	Slovakia (High Tatra Mts.)	*Picea abies*
Příhoda (1964)	S, P**	Slovakia (High Tatra Mts.)	*Picea abies*
Černý (1976)	S, P**	Czech and Slovak forests	Conifers
Kotlaba (1984)	S, P	Czech and Slovak forests	Conifers and broadleaves
Kuthan (ed.) (1989)	S	Slovakia (High Tatra Mts.)	*Picea abies*
Jankovský et al. (2002)	S	Czechia (Krkonoše Mts.)	*Picea abies*
Soukup & Pešková (2002)	P**	Czech forests	Conifers
Penttilä et al. (2004)	S	Central European forests	*Picea abies*
Mihál & Cicák (2006)	S, P*	Slovakia (Slovenské rudohorie Mts.)	*Picea abies*
Vacek et al. (2007)	S, P**	Czechia (Krkonoše Mts.)	*Picea abies*
Zúbrik et al. (2008)	S, P**	Slovak forests	Conifers and broadleaves
Vogel et al. (2017)	S	Germany (Bavarian Forest NP)	*Picea abies*
Butin (2019)	S, P	Central European forests	Conifers
Scholler et al. (2021)	S	Germany (Black Forest NP)	*Picea abies*

forests is little studied and appreciated (Orłoś 1955; Kotlaba 1984; Zúbrik et al. 2008). Therefore, the question arises about its pathogenic role and incidence on these trees in forests ecosystems. Data scarcity is still a common barrier to adequately understanding trophic modes of wood-decaying fungi in Central European urban and other non-forest areas. As a results, we believe that our study has at least started to fill the gap in our understanding of the trophic strategies in these areas.

Survey data, including those from the forests of Slovakia and Central Europe found, that in both forests and quasi-natural habitats, where *F. pinicola* is widespread and abundant, it associates predominantly with conifers. The host survey data demonstrate that it is an important saprotroph, especially of species in the Pinaceae. Contrariwise, in the urban settings, where *F. pinicola* is restricted in its distribution, it associates especially with broadleaved trees, which are its rarer hosts in both forests and quasi-natural habitats. A survey of 88 records from the Slovak public urban spaces indicates that *F. pinicola* is an important pathogen in urban trees, especially *Prunus* spp. (Rosaceae).

These differences among habitat categories primarily arise from the different composition of the woody plant species spectrum present and the fungus adaptation in the landscape.

Although some data suggest a role of *F. pinicola* in urban tree pathogenesis, the available information is scarce. Our results correspond to these previously published data (Konijnendijk et al. 2005; Butin 2019).

Between 1999 and 2001 a pilot study was conducted on the main pests and diseases in urban forests and trees in 18 European countries. From four of them including Slovakia *F. pinicola* was reported to be a fungus causing decay rated as important (Konijnendijk et al. 2005). Similarly, Butin (2019) wrote that it is may also attack living trees in parks. Similar conclusions were also reached by the Lederer (2007), who confirmed that *F. pinicola* colonizes living tree trunks of *Prunus* spp. in the Czech Republic's urban areas.

5. *In silico* analysis of genetic diversity within *F. pinicola*

To evaluate genetic differences within *F. pinicola* in Central Europe and adjacent territories, ITS sequences phylogenetic analysis was performed. The set of ITS sequences from broadleaved hosts, despite lower numbers of sequences, exhibits 3-times higher variability than the set from conifers (0.0034 versus 0.0011 base substitutions per nucleotide). The observed within-groups divergences are low and the diversity between broadleaved and coniferous host groups was even lower than the diversity within coniferous group (0.0021 base substitutions per nucleotide). It indicates that the variability of ITS sequences cannot discriminate between *F. pinicola* ITS sequences from broadleaved and coniferous hosts.

Careful examination of phylogenetic trees constructed by Neighbor-Joining, Maximum Parsimony, Minimum Likelihood or Bayesian inference did not lead to the identification of any pattern based on either the host or the geographical origin of the strains/vouchers (data for Maximum Parsimony and Neighbor-Joining trees are shown in Fig. 6). We can therefore conclude that there are no genetic bases for the observed differences between *F. pinicola* isolates infecting deciduous and coniferous hosts.

GenBank search of available *F. pinicola* sequences allowed us to generate the custom database of ITS sequences of European origin from multiple coniferous or broadleaved hosts. Unfortunately, limited number of sequences of other molecular markers used in the molecular taxonomy of fungi, e.g., partial translation elongation factor 1-α (tef1-α), large subunit ribosomal ribonucleic acid (LSU rRNA), or RNA polymerase II gene (Rpb2) were available in GenBank database. The final dataset included the sequences from 12 countries and was dominated by sequences from *Picea abies* as a host. The observed between-group and within-group variability was at least 10-times lower than commonly used cutoff divergence (0.03) for sequences belonging to

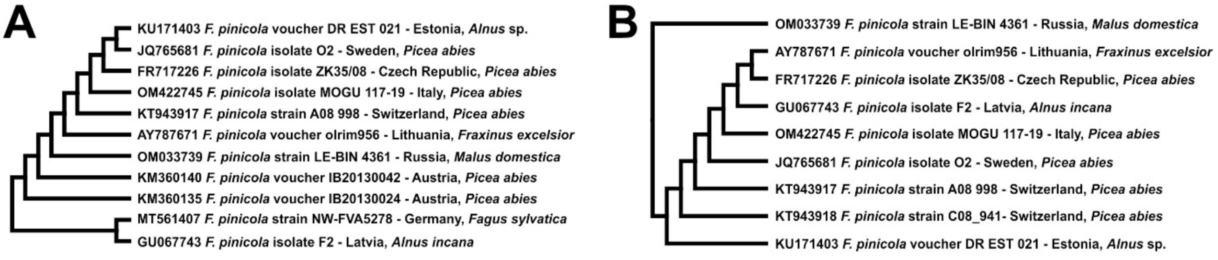

Fig. 6. Selected parts of unrooted phylogenetic trees showing relatedness among *F. pinicola* ITS sequences obtained by Neighbor-Joining (part A) and Maximum Parsimony algoritms (part B). GenBank accession numbers, country of origin, and host are shown.

the different operational taxonomic unit – species (Wu et al. 2019) and observed divergences within groups were 3-times lower than intraspecies ITS variability in members of *Ganoderma* genus (Pristaš et al. 2023). By comparison of *F. pinicola* sequences from a wide range of coniferous or broadleaved hosts and from all over Europe we reveal genetic homogeneity among European populations of *F. pinicola* and confirm that host jumps and preference has not been a major driver of speciation in this species (Haight et al. 2016).

Theoretically, considerable genetic variation within fungal morphospecies could be due to different host spectrum over their geographic ranges, though this variation may not always be evident when analysing the phenotypes (Haight et al. 2016; Pristaš et al. 2023). *F. pinicola* is the first polypore that was studied from the viewpoint of genetic diversity (Högberg et al. 1995, 1999). In these studies, genetic differentiation among populations in Swedish, Finnish, Russian and Lithuanian coniferous forests (often with the dominance of Norway spruce) was found to be very low. No population differentiation was detected over large geographic distances among the populations studied and so, they were found to be members of one intersterility group. These findings were also confirmed by more recent researchers.

Using sequence data of the ITS regions of the rDNA, Dresch et al. (2015) found only very little sequence divergence between 14 Austrian and Italian strains. Besides that, no grouping of 8 *F. pinicola* ITS sequences from *Picea abies* host from Austria was observed, and the sequence of *F. pinicola* strain 7 from broadleaves *Acer platanoides* from Germany showed the highest similarity to *F. pinicola* sequence of strain VL291A from Lithuania and coniferous *Pinus mugo* host. Only sequences from USA or Asia showed a stronger sequence divergence.

Similarly, the analysis of three molecular markers (ITS, tef1-α, and Rpb2) found very little sequence divergence among the six European strains isolated from basidiomata collected on coniferous hosts in Estonia, Sweden, and Russia (Haight et al. 2016). In addition, the data of the last cited authors suggest that the European clade, which has a geographic range confined to Eurasia, is *Fomitopsis pinicola* sensu stricto (s. str.), while other three North American clades represent separate species in the *F. pinicola* complex. Using the same three molecular markers, the above-mentioned assumption was confirmed by Liu et al. (2021).

6. Conclusion

Until the late 1980s, the species of wood-decaying fungi were described mostly on the basis of their macro- and micromorphological characteristics. However, subsequent studies have repeatedly shown that even the traditional morphospecies, such as *Fomes fomentarius* sensu lato (s. l.) or *Heterobasidion annosum* s. l., often shelter extensive cryptic diversity. According to recent studies, cryptic species are a common phenomenon throughout the fungal taxa and are usually to have different host associations from one another in different habitats.

Although genetically homogeneous populations are generally rare in the wild, *Fomitopsis pinicola* is a widespread genetically homogeneous species in Central Europe. Despite this, it has different both geographical distribution and host associations in different habitats. The occurrence of this fungus in both forests and quasinatural habitats associated with engineered features is related to the distribution of Norway spruce (*Picea abies*). The occurrence of *F. pinicola* in the public urban spaces in cities, towns and villages is scattered, but covers practically all the regions of Slovakia. *F. pinicola* appears to be primarily a wood-decaying saprotroph in Central European coniferous forests (especially Norway spruce forests) while in the public urban spaces in cities, towns and villages it is important as a pathotroph of broadleaved trees. The species of *Prunus* are very susceptible to the fungus within this habitat category. Our results show that local adaptation of *F. pinicola* to different habitat conditions, expressed by intraspecific variation in geographic distribution, function, and host specificity, occurred without processes of cryptic speciation during the long-term occurrence of *F. pinicola* in Central Europe.

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