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Macrofungi of urban *Tilia* avenues and gardens in Hungary

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ABSTRACT

Macrofungal investigations were performed in gardens and avenues planted with *Tilia* spp. between 2009 and 2020 in Hungary, focusing on the Budapest area. Lime tree (*Tilia*) is recently one of the most favorable commonly used ectomycorrhizal tree in urban landscaping in Budapest, similarly to other European cities. As a result of 71 sampling occasions in total 60 epigeous and hypogeous macrofungal species belonging to 22 families and 33 genera were documented. The nrDNA ITS barcoding region of 56 specimens was sequenced. Fifty-nine species were identified, while one interesting *Inocybe* sp. could not be determined. Phylogenetic analyses of the most frequently collected family, Inocybaceae, including three genera and 17 species were performed. The genera *Russula* and *Tomentella*, two preferred ectomycorrhizal symbionts of *Tilia* in urban environments were also analyzed. *Inocybe alluvionis*, *I. amelandica*, *Mallocybe siciliana* and *Pseudosperma aureocitrinum* were reported for the first time from Hungary. The taxonomic status of other species is also discussed.

1. Introduction

The acceleration of urbanization and urban land use is already well known nowadays (Grimm et al., 2008; Seto et al., 2010; Elmqvist et al., 2013). Recently, urbanization assumed to be the most dangerous and wide-ranging anthropogenic activity to wildlife (Elmqvist et al., 2008). Global annual urban expansion is around 5%, much higher than growth of urban world population rates (Güneralp et al., 2020). Increasing tendency of urbanization is going on and the global population concentrates mainly in the cities and their environments, the research of the urban habitats has become more relevant for the protection of biodiversity (Angel et al. 2005). From 1970 to 2010 most of the newly evolved urban territories were converted from agricultural land use while around one-third was converted from natural areas (Güneralp et al., 2020). Cities and their vicinities suffered the most significant anthropogenic modifications though at the same time the major cities, like Budapest and other capitals built in typically peculiar areas with distinctive natural ecosystems. As a result of human activities new, special urban habitats emerged, meanwhile new ecological niches opened to the new colonizer species (Pál-Fám and Boros, 2006; Pautasso and Zotti, 2009). An important characteristic of these “unique” and surprisingly diverse habitats (like gardens, parks, cemeteries, allotments, landfills, side of roads and streams or tree avenues) is that the continuous disturbance and that long term ecological balance is hardly ever noticeable (Elmqvist et al., 2013). Because of the anthropogenic circumstances urban habitats are usually harsh environments with extreme conditions. Soils known to be compacted

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Table 1
List of the collected and sequenced macrofungi of urban gardens and avenues planted with *Tilia* spp. from Hungary.

Specim. No.	Collected taxa	Location	Occur.	Date of collection	Host	Eco-type	GenBank accessions (ITS)	Matched accessions / identities (%)
1	*Agaricus bitorquis* (Quél.) Sacc.	Alsórákos, Lágymányos	10	2016, 2017, 2018, 2019	*T. cordata, T. tomentosa*	ts	—	—
M22	*A. bitorquis* (Quél.) Sacc.	Lágymányos	—	9/1/2016	*T. tomentosa*	ts	MW354958	AY484696 99%
2	*A. bresadolanus* Bohus	Lágymányos	1	9/27/2017	*T. tomentosa*	ts	—	—
M91	*A. iodosmus* Heinem.	Lágymányos	1	26/7/2016	*T. cordata*	ts	MW354959	DQ182516 99%
3	*A. bisporus* (J.E. Lange) Imbach	Lágymányos	3	2017, 2018, 2019	*T. tomentosa*	ts	—	—
4	*Agrocybe dura* (Bolton) Singer	Lágymányos	1	15/6/2018	*T. cordata*	ts	—	—
5	*A. vervacti* (Fr.) Singer	Lágymányos	1	12/8/2016	*T. tomentosa*	ts	—	—
M60	*A. vervacti* (Fr.) Singer	Lágymányos	1	26/7/2016	*T. tomentosa*	ts	MW425942	UDB011713 100%
6	*Amanita strobiliformis* (Paulet ex Vittad.) Bertill.	Csalogány str. (Budakalász)	4	2018, 2019, 2020	*T. tomentosa*	ecm	—	—
7	*Auricularia auricula-judae* (Bull.) J.Schröt.	Lágymányos	1	15/8/2020	*T. cordata*	ls	—	—
8	*A. mesenterica* (Dicks.) Pers.	Sas str. (Budakalász)	1	1/7/2018	*T. tomentosa*	ls	—	—
9	*Caloboletus radicans* s. str. (Pers.) Vizzini	Industrial park (Törökbálint)	1	22/9/2018	*Tilia* sp.	ecm	MW493385	MH011875 99%
10	*Clitocybe rivulosa* s. str. (Pers.) P. Kumm.	Csalogány str. (Budakalász)	1	10/6/2019	*T. tomentosa*	ts	—	—
11	*Coltricia cinnamomea* (Jacq.) Murrill	Lágymányos	1	18/6/2020	*T. tomentosa*	ecm	—	—
12	*Coprinellus* cf. *truncorum* (Scop.) Redhead, Vilgalys & Moncalvo	Alsórákos	1	18/9/2018	*T. cordata*	ts	—	—
13	*Cortinarius ammophiloides* Bohus	Lágymányos	5	2017, 2018, 2019, 2020	*T. tomentosa*	ecm	—	—
M6	*C. ammophiloides* Bohus	Lágymányos	—	29/9/2017	*T. tomentosa*	ecm	MW354960	MT934866 99%
M64	*C. ammophiloides* Bohus	Lágymányos	—	22/5/2018	*T. tomentosa*	ecm	MW354961	MT934866 99%
M66	*C. ammophiloides* Bohus	Lágymányos	—	28/12/2019	*T. tomentosa*	ecm	MW354962	MT934866 99%
14	*Cyanoboletus pulverulentus* (Opat.) Gelardi, Vizzini & Simonini	Forest Park (Zalaegerszeg)	1	6/9/2018	*T. cordata*	ecm	—	—
15	*Flammulina velutipes* (Curtis) Singer	Lágymányos	2	2019	*T. cordata*	ls	—	—
M69	*Hebeloma ammophilum* Bohus	Lágymányos	1	4/8/2016	*T. cordata*	ecm	MW354963	JF908027 99%
M88	*H. crustuliniforme* (Bull.) Quél.	Lágymányos	1	4/12/2014	*T. tomentosa*	ecm	MW354964	KF309415 100%
16	*H. dunense* L. Corb. & R. Heim	Lágymányos	9	2017, 2018, 2019	*T. tomentosa, T. cordata*	ecm	—	—
M105	*H. dunense* L. Corb. & R. Heim	Lágymányos	—	28/12/2019	*T. tomentosa*	ecm	MW354965	KX687202 99%
M70	*H. dunense* L. Corb. & R. Heim	Lágymányos	—	6/11/2017	*T. tomentosa*	ecm	MW354966	MK305911 99%
M85	*H. dunense* L. Corb. & R. Heim	Lágymányos	—	16/4/2018	*T. tomentosa*	ecm	MW354967	KX687202 99%
M81	*H. mesophaeum* (Pers.) Quél.	Lágymányos	1	1/12/2017	*T. cordata*	ecm	MW425943	MK305920 99%
M101	*H. mesophaeum* (Pers.) Quél.	Alsórákos	1	25/10/2015	*T. cordata*	ecm	MW354968	MK305908 100%
17	*Helvella latispora* Boud.	Lágymányos	1	29/9/2017	*T. tomentosa*	ecm	—	—
18	*Hortiboletus bubalinus* (Oolbekk. & Duin) L. Albert & Dima	Alsórákos, Lágymányos	12	2014, 2016, 2018	*T. cordata, T. tomentosa*	ecm	—	—
19	*H. engelii* (Hlaváček) Biketova & Wasser	Csalogány str. (Budakalász); Lágymányos (Budapest)	3	2018, 2019, 2020	*T. tomentosa*	ecm	—	—
20	*Hymenogaster citrinus* Vittad.		6		*T. tomentosa*	ecm	—	—

(*continued on next page*)

Table 1 (*continued*)

Specim. No.	Collected taxa	Location	Occur.	Date of collection	Host	Eco-type	GenBank accessions (ITS)	Matched accessions / identities (%)
		Lágymányos, Botanical garden		2009, 2014, 2016, 2017				
M110.4	*H. citrinus* Vittad.	Lágymányos	—	2/12/2014	*T. tomentosa*	ecm	MW354969	GU479296 99%
M110.5	*H. citrinus* Vittad.	Lágymányos	—	2/12/2014	*T. tomentosa*	ecm	MW354970	GU479351 99%
M112	*H. citrinus* Vittad.	Lágymányos	—	22/4/2009	*T. tomentosa*	ecm	MW354971	GU479296 99%
21	*Inocybe aeruginascens* Babos.	Alsórákos, Lágymányos	10	2010, 2014, 2016, 2019	*T. cordata, T. tomentosa*	ecm	—	—
M84	*I. aeruginascens* Babos.	Lágymányos	—	26/7/2016	*T. tomentosa*	ecm	MW354972	GU949591 99%
M62	*I. alluvionis* Stangl & J. Veselský	Lágymányos	1	4/8/2016	*T. tomentosa*	ecm	MW354974	MH807260 99%
M31	*I. amelandica* Bandini & B. Oertel	Alsórákos	1	6/6/2018	*T. cordata*	ecm	MW354975	MN512323 99%
M79	*I. decemgibbosa* (Kühner) Vauras	Lágymányos	1	4/8/2016	*T. tomentosa*	ecm	MW354977	KT958905 99%
22	*I. furfurea* Kühner	Alsórákos, Lágymányos (Budapest); Main Park (Üröm)	7	2015, 2016, 2018, 2020	*T. cordata, T. tomentosa*	ecm	—	—
M74	*I. furfurea* Kühner	Alsórákos	—	5/10/2015	*T. tomentosa*	ecm	MW354978	MG012472 100%
M82	*I. furfurea* Kühner	Lágymányos	—	12/8/2016	*T. cordata*	ecm	MW354979	MH366610 100%
M72	*I.* aff. *grammopodia* Malençon	Lágymányos	1	29/9/2017	*T. tomentosa*	ecm	MW354973	MH366591 97%
M77	*I. griseovelata* Kühner	Lágymányos	1	1/12/2017	*T. cordata*	ecm	MW354982	MT006041 99%
M86	*I. griseovelata* Kühner	Lágymányos	1	18/12/2014	*T. tomentosa*	ecm	MW354983	AJ879662 99%
M108	*I. griseovelata* Kühner	Lágymányos	1	29/7/2020	*T. tomentosa*	ecm	MW354980	AJ879662 99%
M109	*I. griseovelata* Kühner	Lágymányos	1	29/7/2020	*T. tomentosa*	ecm	MW354981	FN550931 99%
M16	*I. pruinosa* R. Heim	Lágymányos	1	29/9/2017	*T. tomentosa*	ecm	MW354984	UDB017663 99%
M55	*I. pruinosa* R. Heim	Lágymányos	1	29/9/2017	*T. tomentosa*	ecm	MW354985	UDB017663 99%
23	*I. pusio* P. Karst.	Lágymányos	1	29/7/2020	*T. tomentosa*	ecm	—	—
24	*I. semifulva* Grund & D.E. Stuntz	Lágymányos	3	2017, 2018, 2020	*T. tomentosa*	ecm	—	—
M15	*I. semifulva* Grund & D.E. Stuntz	Lágymányos	—	29/9/2017	T. tomentosa	ecm	MW354986	KX602274 98%
M29	*I. semifulva* Grund & D.E. Stuntz	Lágymányos	—	22/5/2018	T. tomentosa	ecm	MW354987	KX602274 99%
M96	*Inocybe* sp.	Lágymányos	1	22/5/2018	*T. tomentosa*	ecm	MW354988	HQ604215 96%
M68	*I. tabacina* Furrer-Ziogas	Lágymányos	1	26/8/2016	*T. tomentosa*	ecm	MW354989	MK929272 99%
25	*Lepiota lilacea* Bres.	Lágymányos	4	2014, 2016	*T. tomentosa, T. cordata, Tilia* sp.	ts	—	—
M94	*L. lilacea* Bres.	Lágymányos	—	25/9/2014	*Tilia* sp.	ts	MW354990	GQ203822 99%
M95	*L. lilacea* Bres.	Lágymányos	—	4/8/2016	*T. tomentosa*	ts	MW354991	GQ203822 99%
M50	*Lepista sordida* (Schumach.) Singer	Lágymányos	1	25/5/2019	*Tilia* sp.	ts	MW354992	FJ770391 99%
26	*Leucoagaricus subvolvatus* (Malençon & Bertault) Bon	Lágymányos	1	25/9/2014	*Tilia* sp.	ts	—	—
M89	*Mallocybe* aff. *agardhii* (N. Lund) Matheny & Esteve-Rav.	Lágymányos	1	26/7/2016	*T. tomentosa*	ecm	MW354994	KP826751 99%
M111	*M.* aff. *agardhii* (N. Lund) Matheny & Esteve-Rav.	Lágymányos	1	4/8/2016	*T. tomentosa*	ecm	MW354993	KP826754 98%
M71		Lágymányos	1	29/9/2017	*T. tomentosa*	ecm	MW429337	

(*continued on next page*)

Table 1 (*continued*)

Specim. No.	Collected taxa	Location	Occur.	Date of collection	Host	Eco-type	GenBank accessions (ITS)	Matched accessions / identities (%)
	M. aff. *malenconii* (R. Heim) Matheny & Esteve-Rav.							MN178538 100%
M104	*M.* aff. *malenconii* (R. Heim) Matheny & Esteve-Rav.	Lágymányos	1	18/6/2020	*T. tomentosa*	ecm	MW354995	MH310746 99%
M100	*M. latispora* (Bon) Matheny & Esteve-Rav.	Forest Park (Zalaegerszeg)	1	6/9/2018	*T. platyphyllos*	ecm	MW354996	MN178504 99%
M73	*M. siciliana* (Brugaletta, Consiglio & M. Marchetti) Brugaletta, Consiglio & M. Marchetti	Lágymányos	1	1/8/2017	*T. tomentosa*	ecm	MW354997	NR164583 100%
27	*Paxillus ammoniavirescens* Contu & Dessì	Lágymányos	3	2010, 2016, 2017	*T. tomentosa*	ecm	—	—
M56	*P. ammoniavirescens* Contu & Dessì	Lágymányos	—	29/9/2017	*T. tomentosa*	ecm	MW354998	JN661719 99%
28	*Pleurotus ostreatus* (Jacq.) P. Kumm.	Lágymányos	3	2017, 2019	*T. cordata*	ls	—	—
M99	*Pluteus cinereofuscus* J.E. Lange	Lágymányos	1	26/7/2016	*T. cordata*	ts	MW354999	HM562124 99%
M76	*Pseudosperma aureocitrinum* (Esteve-Rav.) Matheny & Esteve-Rav.	Alsórákos	1	21/5/2018	*T. platyphyllos, T. tomentosa*	ecm	MW355000	MW010047 100%
M61	*P. melliolens* (Kühner) Matheny & Esteve-Rav.	Lágymányos	1	22/5/2018	*T. tomentosa*	ecm	MW355001	FJ904148 99%
M78	*P. obsoletum* (Romagn.) Matheny & Esteve-Rav.	Lágymányos	1	22/5/2018	*T. tomentosa*	ecm	MW355002	MT072905 99%
29	*Russula insignis* Quél.	Alsórákos, Lágymányos (Budapest); Csalogány str. (Budakalász)	4	2016, 2018	*T. tomentosa*	ecm	—	—
M54	*R. insignis* Quél.	Lágymányos	—	1/9/2016	*T. tomentosa*	ecm	MW355003	KJ834553 100%
30	*R. pectinata* Fr.	Alsórákos	3	2018, 2019	*T. platyphyllos, T. tomentosa*	ecm	—	—
M58	*R. pectinata* Fr.	Alsórákos	—	25/5/2018	*T. tomentosa*	ecm	MW355004	UDB031158 99%
M87	*R. pectinata* Fr.	Alsórákos	—	21/5/2018	*T. platyphyllos, T. tomentosa*	ecm	MW355005	UDB031158 99%
31	*Schizophyllum commune* Fr.	Alsórákos, Lágymányos	3	2017, 2019	*T. cordata, T. tomentosa*	ls	—	—
32	*Scleroderma bovista* Fr.	Alsórákos, Lágymányos; Sas str. (Budakalász); Forest park (Zalaegerszeg)	18	2014, 2015, 2016, 2017, 2018, 2019	*T. cordata, T. platyphyllos, T. tomentosa*	ecm	—	—
M97	*S. verrucosum* (Bull.) Pers.	Church Garden (Dunaharaszti)	1	16/7/2018	*Tilia* sp.	ecm	MW355006	UDB027408 100%
M90	*Stropharia coronilla* (Bull.) Fr.	Lágymányos	1	26/7/2016	*T. cordata*	ts	MW355007	MH856747 99%
33	*Suillellus luridus* (Schaeff.) Murrill	Lágymányos (Budapest); Csalogány str. (Budakalász)	7	2010, 2016, 2018, 2019, 2020	*T. tomentosa*	ecm	—	—
34	*Tarzetta cupularis* (L.) Svrček	Margaret Island	1	4/6/2019	*T. tomentosa* (*Pyrus* sp., *Morus* sp.)	ecm	—	—
M63	*Tomentella fuscocinerea* (Pers.) Donk	"Tarzan park"	1	8/9/2018	*T. cordata*	ecm	MW355008	KC966111 99%
35	*Tricholoma argyraceum* (Bull.) Gillet	Alsórákos (Budapest); Csalogány str. (Budakalász)	5	2014, 2015, 2019	*T. cordata, T. tomentosa*	ecm	—	—
M57	*T. argyraceum* (Bull.) Gillet	Csalogány str. (Budakalász)	—	19/11/2019	*T. tomentosa*	ecm	MW355009	GU060277 99%
36	*Tubaria furfuracea* (Pers.) Gillet	Csalogány str. (Budakalász)	1	25/11/2019	*T. tomentosa*	ts	—	—
M80*	*Inocybe amelandica* Bandini & B. Oertel	Alsórákos	1	26/5/2018	*T. cordata, Salix* sp., *Betula pendula*	ecm	MW354976	MN512322 99%
ZB5385*	*Hymenogaster citrinus* Vittad.	Alsórákos	1	16/9/2016	*T. cordata, Salix* sp., *Betula pendula*	ecm	—	—

Registered taxa given with their locations (cities are given in brackets when it is not Budapest), number of all occurrences (from 2009 to 2020) listed with the years or exact date of the collections, the host and eco-type (ls: lignicolous saprotrophs; np: necrotrophic parasites; ts: terricolous saprotrophs; ecm: ectomycorrhizal). Sequenced specimens are labelled with the location and the exact date of collection, GenBank accession, matched accession number based on BLAST and identities (%). Specimens collected associated with different hosts indicated with an asterisk (*) and listed at the end of the table.

with restricted volume, aeration and drainage. Soils may also have significant horizontal and vertical variability (even the absence of structure); modified soil features: higher pH and temperature, decline in organic matters, elevated levels of heavy metal concentrations and negative effects of using de-icing salts (Paul and Meyer 2008; Tume et al., 2008; Lu et al., 2010; Skrbic et al., 2012). On the other hand, some urban habitats could have old history with relatively long ecological continuity like old parks (e.g. Margaret Island in Budapest). Because of the substantial cultural and/or historical background such urban habitats are protected by law and could shelter as old trees as rare species which are sometimes treated in the wild (Nielsen et al., 2014).

Lime trees (*Tilia* spp.) are widely used for urban landscaping in European cities and in human-modified environments as well (Pigott, 1991; Timonen and Kauppinen, 2008; Olchowik et al., 2020). *Tilia* spp. were and continue to be also a very commonly planted trees on the streets and gardens of Budapest and in its vicinities. According to the database of FŐKERT Co. Ltd. (the horticultural company of Budapest) there are more than 14.000 registered lime trees in the city and more than 4.000 new *Tilia* trees were planted in 2018. In addition, according to Rapaics (1934) the first urban walkway (in 1789) were planted with *Tilia* and *Robinia*, furthermore from 1950 to 1960 mentioned as the "epoch of *Tilia tomentosa*" in Budapest when silver lime was the preferred tree with *Sorbus* spp. (Schmidt and Honfi, 2006; Szabó et al., 2014). In Hungary, respectively in Budapest, silver lime (*T. tomentosa*; *T. tomentosa 'Szeleste'*), small-leaved linden (*T. cordata*), large-leaved lime (*T. platyphyllos*) and the hybrid types: crimean lime and "Szent István" lime (*Tilia* × *euchlora* and *Tilia* × *'Szent István'*) are most commonly planted lime trees (according to database of FŐKERT Co. Ltd.). Members of the genus *Tilia* are ectomycorrhiza-forming (ECM) plants and probably the most common ECM trees in the city. Ectomycorrhizal connection between *Tilia* spp. and fungi is a symbiotic/mutualistic relationship, fungi can encourage water and nutrient uptake of the roots and protect from pathogens and soil pollutants (Smith and Read, 1997; Nielsen and Rasmussen, 1999). Proper fungal ECM communities can be important to promote survival of urban trees and develop a strong root system, resulting in healthier trees and thus better environments to the citizens. Garbaye and Churin (1996, 1997) found in autumn better growth and later yellowing leaves of *Tilia* and also *Quercus* spp. in urban conditions after inoculation with ectomycorrhizal fungi. A couple of studies of mycorrhizal status and ECM fungal diversity of *Tilia* spp. is known (Pigott, 1991; Timonen and Kauppinen, 2008; Cui and Mu, 2015; Olchowik et al., 2020) but all of these works focused on examination of soil or mycorrhiza samples, in consequence, none of them described above- and below-ground basidiomata associated with *Tilia* spp. from urban territories. The aim of this study was to investigate macrofungal communities of urban *Tilia* avenues and gardens in Hungary with special regard to Budapest. We also tried to give a taxonomic overview of these communities by phylogenetic analyzes of the typical ectomycorrhiza-forming fungal genera of *Tilia* spp.

2. Materials and methods

2.1. Sampling

Mycological observations were performed 71 times by our research group in urban habitats like avenues, gardens and parks planted with *Tilia* spp. (*T. cordata*, *T. tomentosa*, *T. platyphyllos* aggr.) between 2009 and 2020. Epigeous and in some cases hypogeous basidiomata were collected in a few meters range of the lime trees through the years. Sampling dates were randomly selected, not systematical, generally followed the rainy periods of the years. Most of the fungal data were registered in Budapest (capital of Hungary), particularly in Lágymányos and Alsórákos, one of the highest populated quarters of Budapest, according to Central Statistical Office (2018). Some data derived from other Hungarian cities, like agglomeration area of Budapest: Budakalász, Dunaharaszti, Törökbálint, Üröm and a few from a major city in the southwest part of Hungary, Zalaegerszeg. The soil characteristics of the two important locations, Alsórákos and Lágymányos, are really similar, typical pH is between 6.5 and 8.5. Both of the soils have evolved on sandy sediment of the river Danube and are rarely mixed with clay. Lágymányos is located in the southwest part of Budapest, next to the Danube, at an altitude of 100–140 m, planted lime trees are around 10–30 years old. Alsórákos is located in the northeast part of Budapest, at an altitude of 100–130 m, planted lime trees are around 20–45 years old. Between 2009 and 2020 Budapest average mean annual precipitation was about 543 mm/year and the mean annual temperature was 12.9 °C (www.met.hu). All of the surveyed habitats have remarkable anthropogenic influences like neighborhood of roads, continuous reconstruction or landscape-architecture works and other human activities (treading, road salting, use of fertilizers, etc.). During our works we focused on urban habitats planted exclusively with *Tilia* spp., however, some ECM macrofungal data were recorded by chance with other hosts, these mixed records are listed at the end of Table 1 and signed with *. Three soil samples were collected from the surface (layer A) in the closely surroundings of the hypogeous basidiomata and were analyzed the soil properties by the laboratories of University of Debrecen, Faculty of Agricultural and Food Sciences and Environmental Management (2018, standard: MSZ - EU) (see Supplementary Material).

2.2. Morphological and molecular studies

Fresh basidiomata were collected, dehydrated and then placed in the herbarium of the research group at the Department of Plant Physiology and Molecular Plant Biology, Eötvös Loránd University. Hypogeous specimens were deposited in Zoltán Bratek's (ZB) mycotheca (Bratek et al., 2013). Microscopic examination of dried material was achieved by Nikon Optiphot-2 research light microscope in 5% KOH and using a Nikon SMZ-U stereomicroscope. Generally, spores and different cystidia were measured, however, to identify each distinct specimen measurements of other specific microscopic features were needed (e.g. basidia, pileipellis). The length/width ratio (Q value) of the spores and sometimes of the cystidia were also calculated. Aqueous Congo red dye solution was applied in microphotography. Identification to species level in the case of common species was based on macro- and micro-morphological characters. Additionally, we performed molecular phylogenetic analyses when basidiomata could not be identified with certainty by morphological characters. Nomenclature and taxonomy follow Index Fungorum (http://www.indexfungorum.org).

2.2.1. Isolation of DNA, PCR and sequencing

Genomic DNA was isolated primarily from dried or occasionally fresh basidiomata with DNeasy Plant Mini Kit (Qiagen, Courtaboeuf, France) following the manufacturer's instructions with few modifications. Internal transcribed spacer (ITS) region of the fungal nuclear ribosomal DNA locus was amplified. ITS1F/ITS4 primers were used for amplification of the ITS region (White et al., 1990; Vilgalys and Hester, 1990; Gardes and Bruns, 1993). PCR conditions were: initial denaturation 94 °C for 4.5 min, 33 cycles of denaturation 94 °C for 30 s, annealing 51 °C for 30 s, 72 °C elongation for 45 s and after the last cycle the final synthesis 72 °C for 7 min. Gel electrophoresis of amplification products was done on 1% agarose gel. Ethidium-bromide was used for staining. PCR products were purified with the QIAquick® PCR Purification Kit. Sequencing was carried out by BIOMI Ltd. (Gödöllő, Hungary) and BaseClear (Leiden, Netherlands).

2.2.2. Phylogenetic analyses

Phylogenetic analyses were performed in the case of three taxonomically difficult groups that are also mentioned as common ectomycorrhizal partners of *Tilia* spp. FinchTV V. 1.4.0 (Geospiza, Inc., Seattle, WA, USA; http://www.geospiza.com) was used to check the electropherograms. For the phylogenetic analyses, our sequences ("M" specimen no.) of the collected basidiomata (family Inocybaceae, *Russula* spp., *Tomentella* sp.) and reference sequences were analyzed, including sequences of type materials downloaded from GenBank (www.https://www.ncbi.nlm.nih.gov/). For this study, 56 newly generated sequences were submitted to GenBank (Table 1).

In order to find the most similar sequences of the phylogenetically analyzed species a BLAST search was performed in GenBank at NCBI (National Center for Biotechnology Information) (Zhang et al., 2000) and UNITE (Altschul et al., 1997; Nilsson et al., 2018). Alignments of the sequences were carried out with the software MAFFT (Katoh and Toh, 2008) and if necessary were manually corrected with MEGA-X V. 10.0.5 (Kumar et al., 2018). Additionally, other sequences of basidiomata which were not included in the further phylogenetic analyses were identified using the BLAST search tool of GenBank and UNITE public databases. Selection of the matching sequences was based on the current taxonomic results.

Maximum Likelihood (ML) analyses were carried out in RAxML (V. 8.2.12; Stamatakis, 2014) as implemented on CIPRES (Miller et al., 2010). Phylogenetic analyses with the criterion of maximum-likelihood (ML) were controlled with RAxML-HPC2 on XSEDE (8.2.12), using fast bootstrap (1000×) and applying a GTR substitution matrix. Likelihood of final trees was evaluated and optimized under GAMMA model. Phylogenetic trees were visualized by FigTree V. 1.4.4 (Rambaut, 2010). Species of closely related genera were chosen as outgroup in each separate analysis.

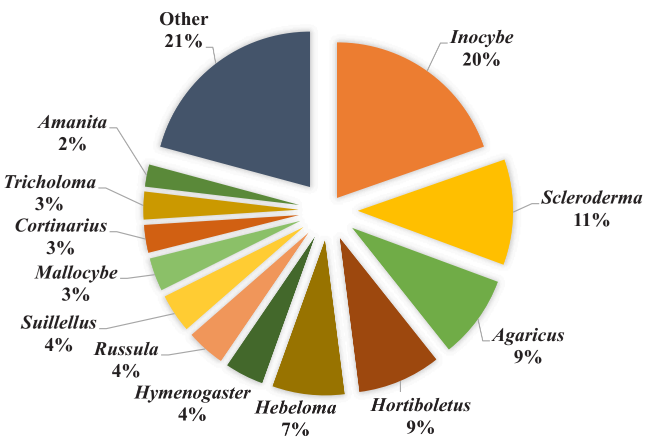

Fig. 1. Proportion of the 12 most frequent genera by occurrence of the collected species.

Fig. 2. ML phylogenetic tree of family Inocybaceae based on nrDNA internal transcribed spacer (ITS) sequences. *Crepidotus applanatus* (KR673659) and *Crepidotus mollis* (JF907959) were chosen as outgroup. Newly generated sequences are in bold. Maximum Likelihood (ML > 70%) bootstrap values are indicated at the branches.

3. Results

3.1. Morphological and molecular phylogenetic analysis

A total of 173 macrofungal records were achieved from different Hungarian urban *Tilia* avenues and gardens between 2009 and 2020 as a result of 71 sampling occasions (Table 1). Two recorded species belong to the phylum Ascomycota and 58 species to the Basidiomycota. Collected basidiomata belong to 22 families and 33 genera, a total of 60 species were detected and 59 of them were assigned to a presumptive species level. We were unable to identify one *Inocybe* specimen (M96) on species level since matching sequences related to this specimen were not found in NCBI and UNITE public databases. 116 specimens belonging to more frequent species were identified based on morphological characteristics and 56 specimens based on molecular phylogenetic analyses. Specimens identified with molecular methods are listed also in Table 1 with the essential identification information. In addition, the specimen vouchers, GenBank accession numbers, the accession numbers with the similarity (%) of the closest matched sequence were indicated. In the case of five specimens (three *Hortiboletus* sp.; two *Hebeloma* sp.) sequencing have failed. This non-success might be due to the older collections or in the case of *Hortiboletus bubalinus* sequencing of nrDNA ITS region is generally difficult (Fig. 1)

3.2. Macrofungal community composition

Total of 41 species are ectomycorrhizal fungi (ECM) while 19 species are altogether saprotrophic (14 terricolous and five lignicolous saprotrophs). The most frequent ECM genera were *Inocybe* with 33 occurrences; *Scleroderma* with 19 occurrences; *Hortiboletus* with 15 occurrences; *Hebeloma* with 13 occurrences and *Suillellus* with seven occurrences. The most common ECM species were *Scleroderma bovista* with 18 occurrence data from four different years, *Hortiboletus bubalinus* with 12 occurrence data from three different years and *Inocybe aeruginascens* with 10 occurrence data from four different years.

Among the saprotrophs, the most frequent genera were *Agaricus* with 15 occurrences and *Lepiota* with four occurrences. The common urban fungus, *Agaricus bitorquis* was registered with 10 occurrences from four different years. We observed also some lignicolous fungi on lime trees, *Pleurotus ostreatus* (three occurrences) and *Schizophyllum commune* (three occurrences) were the most common. One hypogeous species, *Hymenogaster citrinus* was collected six times from four different years under the ground with a specialized truffle searching dog.

3.3. Phylogenetic analyses

The Inocybaceae Jülich (Basidiomycota, Agaricales) were represented in urban *Tilia* habitats as the most diverse group. We documented 12 species of genus *Inocybe* with 33 occurrences, three species of the genus *Pseudosperma* with three occurrences and four species of the genus *Mallocybe* with six occurrences. The ITS region was successfully amplified and sequenced from 27 specimens of Inocybaceae and a phylogenetic tree was generated to investigate phylogenetic relationship in the case of this taxonomically difficult group (Fig. 2).

Four species of Inocybaceae were reported for the first time in Hungary: *Inocybe alluvionis*, *Inocybe amelandica*, *Mallocybe siciliana* and *Pseudosperma aureocitrinum*. Furthermore, *Inocybe decemgibbosa* seems to be a rare or overlooked species in Hungary, with only two other occurrences. Published here in the first time. *Paxillus ammoniavirescens*, a member of the frequent *P. involutus* aggr. was previously found only a few times in Hungary (Seress, 2015).

We found two *Russula* species with seven occurrences from three different years. A phylogenetic tree was generated to discuss the taxonomic position of two *Russula* specimens (Fig. 3). Analysis of the ITS region showed that our specimens belong to two species complexes, namely the European complex clade 6 of *Russula pectinata* and the other is the *Russula insignis* clade, following the taxonomic work of Melera et al. (2016).

Only one basidiome of a *Tomentella* sp. associated with *Tilia* was found. Genetically, our specimen (M64) belongs to the *Tomentella fuscocinerea* group (Fig. 4).

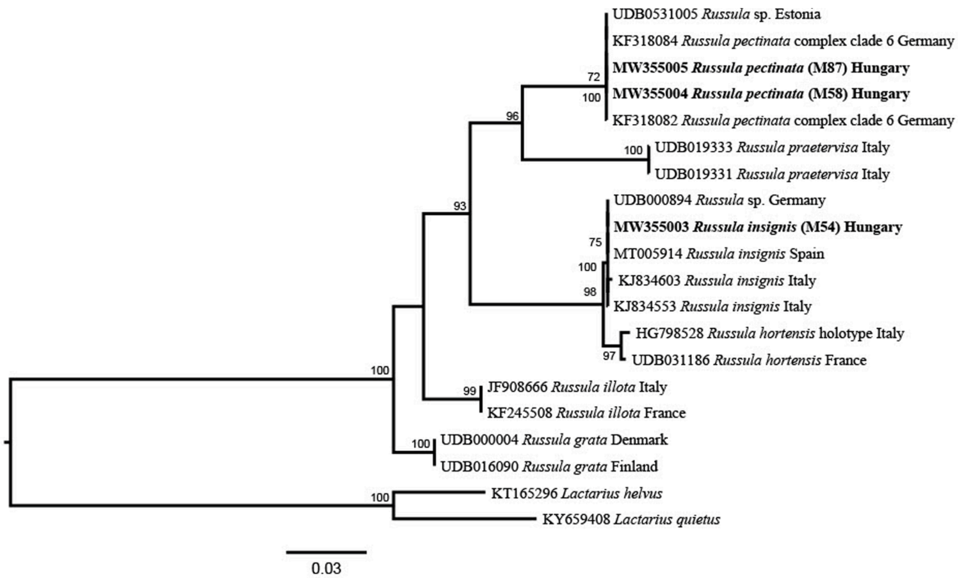

Fig. 3. ML phylogenetic tree of selected *Russula* specimens and their close relatives based on nrDNA internal transcribed spacer (ITS) sequences. *Lactarius helvus* (KT165296) and *Lactarius quietus* (KY659408) were chosen as outgroup. Newly generated sequences are in bold. Maximum Likelihood (ML > 70%) bootstrap values are indicated at the branches.

4. Discussion

4.1. Macrofungal community associated with Tilia

More studies investigated the ECM community of urban *Tilia* habitats (Pigott, 1991; Timonen and Kauppinen, 2008; Cui and Mu, 2015; Olchowik et al., 2020). These works exclusively studied the ectomycorrhizal below-ground root tips of the lime trees and none of them registered any above-ground basidiomata of macrofungi, especially, no notice of saprotrophic fungi was taken. It is known already that results of the below-ground surveys on ECM composition can be different from the results of above-ground basidiomata surveys on ECM composition (Dahlberg et al., 1997; Szabó et al., 2014). ECM communities are often quite diverse and their distribution is patchily below ground similarly to the pattern of the basidiomata above ground. However, remarkable correspondence is hardly ever discoverable between frequent or dominant basidiomata in contrast to the dominant mycorrhizae on root tips (Horton and Bruns, 2001). More studies confirmed that when numerous basidiomata were collected, no related ECM were detectable from the same sampling sites and vice versa (Schmidt and Honfi, 2006; Gebhardt et al., 2007; Smith et al., 2007; Lalli et al., 2015).

4.2. Characteristics of ectomycorrhizal macrofungal communities

In the present work we found basidiomata of 41 different ECM species and the most frequent genera were *Inocybe* (Inocybaceae, Agaricales), *Scleroderma* (Sclerodermataceae, Boletales), *Hortiboletus* (Boletaceae, Boletales), *Hebeloma* (Hymenogastraceae, Agaricales) and *Suillellus* (Boletaceae, Boletales). In other European studies on urban *Tilia* ECM communities, the most frequent ECM taxa were: in Finland *Boletus* (Boletaceae, Boletales), *Cenococcum* (Gloniaceae, Mytilinidiales), *Inocybe*, *Russula* (Russualceae, Russulales) and *Tuber* (Tuberaceae, Pezizales) (Timonen and Kauppinen, 2008); while in Poland, according to Olchowik et al. (2020): *Inocybe*, *Tylospora* (Atheliaceae, Atheliales), *Tuber* (Tuberaceae, Pezizales) and *Cenococcum* were found. Van Geel et al. (2018) investigated the ECM communities of urban *Tilia tomentosa* habitats in three major European cities, Leuven (Belgium), Strasbourg (France) and Porto (Portugal), on different soil types. *Inocybe*, *Tomentella* (Thelephoraceae, Thelephorales), *Tuber* and *Russula* were common genera in all of the three cities. Interestingly ECM of *Scleroderma* was found frequently in neither case, however, in our present work *Scleroderma bovista* gives the impression of being a very frequent ectomycorrhizal colonizer of *Tilia* and usually we found a lot of basidiomata near the lime trees (even in drought periods). Members of *Scleroderma* (together with *Paxillus* and *Pisolithus*) are frequently mentioned as primary colonizers, often fruiting in freshly cleared habitats (e.g. coal spoil) (Newton, 1992; Jeffries, 1999) and *S. bovista* referred as fungi of disturbed habitats, mostly growing on sandy, clayey soils. Members of the genus *Russula* proved to be frequent genus near the urban lime trees according to Timonen and Kauppinen (2008) and also Van Geel et al. (2018). We reported only two species with seven occurrences altogether. One possible explanation of this result is that *Russula* spp. usually prefer acidic soils and are often considered to be late-stage fungi (Visser, 1995; Twieg et al., 2007). We could not detect any sclerotia of *Cenococcum* (*Cenococcum* is not producing conspicuous reproductive structures) which is considered the most abundant anamorphic ECM fungus and associates with a variety of host plants like *Tilia* also in urban environments (Nielsen and Rasmussen, 1999; Obase et al., 2017).

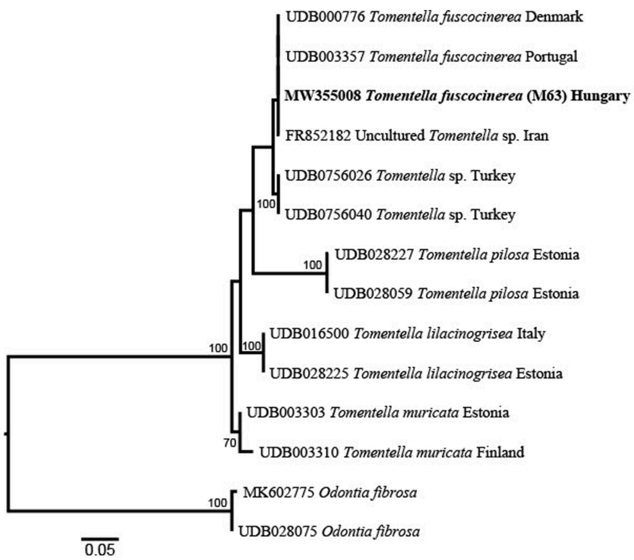

Fig. 4. ML phylogenetic tree of *Tomentella fuscocinerea* group and their close relatives based on nrDNA internal transcribed spacer (ITS) sequences. *Odontia fibrosa* (MK602775 and UDB028075) were chosen as outgroup. Newly generated sequences are in bold. Maximum Likelihood (ML > 70%) bootstrap values are indicated at the branches.

4.3. Familiy Inocybaceae, the richest ectomycorrhizal group

Inocybe (Inocybaceae) proved to be the most common group in our present work (Fig. 2) and were also really frequent in all of the above mentioned studies. Inocybaceae is one of the most taxonomically diverse families of Agaricales, now considered as an independent family based on recent molecular phylogenetic works (Matheny, 2005; Ryberg et al., 2010). Seven major clades of family Inocybaceae have been adopted already on genus level: *Inocybe* sensu stricto, *Nothocybe*, *Pseudosperma*, *Mallocybe*, *Inosperma*, *Auritella* and *Tubariomyces* and were elevated to generic rank (Matheny et al., 2019). Members of the family are usually considered as early colonizers and able to grow with younger trees and also seedlings (Visser, 1995; Twieg et al., 2007) that may resulting successful colonization in urban *Tilia* habitats. According to the present work *Inocybe aeruginascens* (10 occurrences, four different years) and *I. furfurea* (seven occurrences, four different years) proved to be the most frequent *Inocybe* species. *Inocybe aeruginascens* and *I. furfurea* were also reported as fungi of dry, sandy soils, routinely fruiting in urban environments with diverse broad-leaved trees (Nagy and Nagy, 2011; Bandini et al., 2018). *Inocybe griseovelata* and *I. semifulva* which have quite similar morphological characters, seem to be more common in *Tilia* planted gardens and avenues primarily on sandy soils. We observed them from three different years with several occurrences.

Among the first reported inocyboid species in Hungary, *Mallocybe siciliana* (syn. *I. siciliana*) and *Pseudosperma aureocitrinum* (syn. *I. aureocitrina*) were described from the Mediterranean region. Holotype of *M. siciliana* was found near to *Salix* spp. from a river valley on sandy alluvial soil while *P. aureocitrinum* was described from a humid and warm evergreen *Quercus ilex* forest on calcareous soil (Brugaletta et al., 2017; Esteve-Raventós, 2014). The holotype of *Inocybe amelandica* was described from Netherlands and usually fruiting on white sand dunes near to *Salix* sp. (www.inocybe.org). *Inocybe alluvionis* was reported from alluvial–riverine, sandy soils and mostly grows in moist habitats or shaded places for example near to *Alnus* sp. (Bandini et al., 2019).

There is a considerable incoherence in the case of the specimens M71 and M104, both of them tentatively named as *Mallocybe* aff. *malenconii* based on the labelling of highly similar sequences in public databases (UNITE, NCBI). However, our phylogenetic tree shows that both sequences belong to two different species level clades (Fig. 3). Specimen M96, an unknown *Inocybe* sp. seems to be a really peculiar *Inocybe* sample, the closest hits in the public databases (maximum similarity 96%) are from Canada and USA. Here further taxonomic investigations are necessary to unveil whether M96 belongs to an undescribed species or this is an already described species not yet sequenced and present in the available databases.

5. Conclusions

The current study confirms that urban landscapes can serve as proper habitats for macrofungi and are able to tolerate the anthropogenic influences. Taxonomic diversity of the ectomycorrhizal family Inocybaceae and relevant occurrences of other genera (e.g. *Scleroderma*, *Agaricus*) in urban *Tilia* planted gardens and avenues points to that these habitats can be excellent for certain fungi. Further studies on urban macrofungi, included phylogenetic and ecological analyses, can encourage the knowledge of fungal diversity which is also part of the global diversity, moreover, in regard to urgent urban expansion.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01672.

References

Altschul, S.F., Madden, T.L., Schaffer, A.A., Zhang, J., Zhang, Z., Miller, W., Lipman, D.J., 1997. Gapped BLAST and PSI-BLAST: a new generation of protein database search programs. Nucleic Acids Res 25, 3389–3402. https://doi.org/10.1093/nar/25.17.3389.

Angel, S., Sheppard, S.C., Civco, D.L., 2005. The Dynamics of Global Urban Expansion. Transport and Urban Development Department, World Bank, Washington, DC.

Bandini, D., Oertel, B., Ploch, S., Ali, T., Vauras, J., Schneider, A., Scholler, M., Eberhardt, U., Thines, M., 2018. Revision of some central European species of *Inocybe* (Fr.: Fr.) Fr. subgenus *Inocybe*, with the description of five new species. Mycol. Prog. 18, 247–294. https://doi.org/10.1007/s11557-018-1439-9.

Bandini, D., Oertel, B., Ploch, S., Thines, M., 2019. *Inocybe heidelbergensis*, eine neue Risspilz-Art der Untergattung *Inocybe*. Z. Mykol. 85 (2), 195–213.

Bratek, Z., Merényi, Zs, Varga, T., 2013. Changes of hypogeous funga in the Carpathian-Pannonian region in the past centuries. Acta Mycol. 48, 33–39. https://doi.org/10.5586/am.2013.005.

Brugaletta, E., Consiglio, G., Marchetti, M., 2017. *Inocybe siciliana*, una nuova specie del Sottogenere *Mallocybe*. Riv. Micol. 60 (3), 195–209.

Central Statistical Office, 2018. In: Vukovich, G. (Ed.), Gazdaság és Társadalom. Xerox, Hungary, p. 3.

Cui, L., Mu, L.Q., 2015. Ectomycorrhizal communities associated with *Tilia amurensis* trees in natural versus urban forests of Heilongjiang in northeast China. J. For. Res. 27, 1–6. https://doi.org/10.1007/s11676-015-0158-1.

Dahlberg, A., Jonsson, L., Nylund, J.E., 1997. Species diversity and distribution of biomass above and below ground among ectomycorrhizal fungi in an old-growth Norway spruce forest in south Sweden. Can. J. Bot. 75, 1323–1335. https://doi.org/10.1007/3-540-27043-4_15.

Elmqvist, T., Alfsen, C., Colding, J., 2008. Urban systems. In: Jørgensen, S.E., Fath, B.D. (Eds.), Encyclopedia of Ecology, 1st ed. Academic Press, Oxford, pp. 3665–3672.

Elmqvist, T., Fragkias, M., Goodness, J., Güneralp, B., Marcotullio, P.J., McDonald, R.I., Parnell, S., Schewenius, M., Sendstad, M., Seto, K.C., et al., 2013. Urbanization, biodiversity and ecosystem services: challenges and opportunities. In: Fragkias, M., Goodness, J., Marcotullio, P.J., McDonald, R.I., Parnell, S. (Eds.), Global Assessment. Springer, Dordrecht, pp. 13–30.

Esteve-Raventós, F., 2014. *Inocybe aureocitrina* (Inocybaceae), a new species of section Rimosae from Mediterranean evergreen oak forests. Plant Biosyst. 148 (2), 377–383. https://doi.org/10.1080/11263504.2013.877532.

Garbaye, J., Churin, J.L., 1996. Effect of ectomycorrhizal inoculation at planting on growth and foliage quality of *Tilia tomentosa*. Arboric. J. 22, 29–34.

Garbaye, J., Churin, J.L., 1997. Growth stimulation of young oak plantations inoculated with the ectomycorrhizal fungus *Paxillus involutus* with special reference to summer drought. For. Ecol. Manag. 98, 221–228. https://doi.org/10.1016/S0378-1127(97)00105-9.

Gardes, M., Bruns, T.D., 1993. ITS primers with enhanced specificity for basidiomycetes application to the identification of mycorrhizae and rusts. Mol. Ecol. 2, 113–118. https://doi.org/10.1111/j.1365-294x.1993.tb00005.x.

Gebhardt, S., Neubert, K., Wöllecke, J., Münzenberger, B., Hüttl, R.F., 2007. Ectomycorrhiza communities of red oak (*Quercus rubra* L.) of different age in the Lusatian lignite mining district, East Germany. Mycorrhiza 17 (4), 279–290. https://doi.org/10.1007/s00572-006-0103-4.

Van Geel, M., Yu, K., Ceulemans, T., Peeters, G., van Acker, K., Geerts, W., Ramos, M.A., Serafim, C., Kastendeuch, P., Najjar, G., Ameglio, T., Ngao, J., Saudreau, M., Waud, M., Lievens, B., Castro, P.M., Somers, B., Honnay, O., 2018. Variation in ectomycorrhizal fungal communities associated with Silver linden (*Tilia tomentosa*) within and across urban areas. FEMS Microbiol. Ecol. 94 (12) https://doi.org/10.1093/femsec/fiy207ff.ffhal-01904404.

Grimm, N., Faeth, S., Golubiewski, N., Redman, C., Wu, J., Bai, X., Briggs, J., 2008. Global change and the ecology of cities. Science 319, 756–760. https://doi.org/10.1126/science.1150195.

Güneralp, B., Reba, M., Hales, B., Wentz, E., Seto, K., 2020. Trends in urban land expansion, density, and land transitions from 1970 to 2010: a global synthesis. Environ. Res. Lett. 15 (4), 044015 https://doi.org/10.1088/1748-9326/ab6669.

Horton, T.R., Bruns, T.D., 2001. The molecular revolution in ectomycorrhizal ecology: peeking into the black-box. Mol. Ecol. 10, 1855–1871. https://doi.org/10.1046/j.0962-1083.2001.01333.x.

Jeffries, P., 1999. Scleroderma. In: Cairney, J.W.G., Chambers, S.M. (Eds.), Ectomycorrhizal Fungi Key Genera in Profile. Springer-Verlag, Berlin, pp. 187–200.

Katoh, K., Toh, H., 2008. Recent developments in the MAFFT multiple sequence alignment program. Brief. Bioinform. 9, 286–298. https://doi.org/10.1093/bib/bbn013.

Kumar, S., Stecher, G., Li, M., Knyaz, C., Tamura, K., 2018. MEGA X: molecular evolutionary genetics analysis across computing platforms. Mol. Biol. Evol. 35 (6), 1547–1549. https://doi.org/10.1093/molbev/msy096.

Lalli, G., Leonardi, M., Oddis, M., Pacioni, G., Salerni, E., Iotti, M., Zambonelli, A., 2015. Expanding the understanding of a forest ectomycorrhizal community by combining root tips and fruiting bodies: a case study of *Tuber magnatum* stands. Turk. J. Bot. 39 (3), 527–534. https://doi.org/10.3906/bot-1406-50.

Lu, X., Wang, L., Li, L., Lei, Y.K., Huang, L., Kang, D., 2010. Multivariate statistical analysis of heavy metals in street dust of Baoji, NW China. J. Hazard. Mater. 173, 744–749. https://doi.org/10.1016/j.jhazmat.2009.09.001.

Matheny, P.B., 2005. Improving phylogenetic inference of mushrooms using RPB1 and RPB2 sequences (*Inocybe*; Agaricales). Mol. Phylogenet. Evol. 35, 1–20. https://doi.org/10.1016/j.ympev.2004.11.014.

Matheny, P.B., Hobbs, A., Esteve-Raventós, F., 2019. Genera of Inocybaceae: new skin for the old ceremony. Mycologia 112, 1–38. https://doi.org/10.1080/00275514.2019.1668906.

Melera, S., Ostellari, C., Roemer, N., Avis, P., Tonolla, M., Barja, F., Narduzzi-Wicht, B., 2016. Analysis of morphological, ecological and molecular characters of *Russula pectinatoides* Peck and *Russula praetervisa* Sarnari, with a description of the new taxon *Russula recondita* Melera & Ostellari. Mycol. Prog. 16, 117–134. https://doi.org/10.1007/s11557-016-1256-y.

Miller, M.A., Pfeiffer, W., Schwartz, T., 2010. Creating the CIPRES science gateway for inference of large phylogenetic trees, Proceedings of the Gateway computing environments workshop (GCE), New Orleans, Louisiana. ⟨10.1109/GCE.2010.5676129⟩.

Nagy, I., Nagy, G.L., 2011. *Inocybe aeruginascens* and *Inocybe javorkae* (Agaricales, Basidiomycota), two species described from Hungary. Clusiana 50 (1), 23–35.

Newton, A.C., 1992. Towards a functional classification of ectomycorrhizal fungi. Mycorrhiza 2, 75–79. https://doi.org/10.1007/BF00203253.

Nielsen, J., Rasmussen, H., 1999. Mycorrhizal status and morphotype diversity in *Tilia cordata* - a pilot study of nurseries and urban habitats. Acta Hortic. 496, 451–459. https://doi.org/10.17660/ActaHortic.1999.496.56.

Nielsen, A.B., van den Bosch, M., Maruthaveeran, S., van den Bosch, C.K., 2014. Species richness in urban parks and its drivers: a review of empirical evidence. Urban Ecosyst. 17, 305–327. https://doi.org/10.1007/s11252-013-0316-1.

Nilsson, R.H., Larsson, K.-H., Taylor, A.F.S., Bengtsson-Palme, J., Jeppesen, T.S., Schigel, D., Kennedy, P., Picard, K., Glöckner, F.O, Tedersoo, L., Saar, I., Kõljalg, U., Abarenkov, K., 2018. The UNITE database for molecular identification of fungi: handling dark taxa and parallel taxonomic classifications. ⟨10.1093/nar/gky1022⟩.

Obase, K., Douhan, G.W., Matsuda, Y., Smith, M.E., 2017. Progress and challenges in understanding the biology, diversity, and biogeography of *Cenococcum geophilum*. In: Tedersoo, L. (Ed.), Biogeography of Mycorrhizal Symbiosis. Springer International, Switzerland, pp. 299–317. https://doi.org/10.1007/978-3-319-56363-3.

Olchowik, J., Suchocka, M., Jankowski, P., Malewski, T., Hilszczanska, D., 2020. The ectomycorrhizal community of urban linden trees in Gdańsk, Poland. 10.1101/2020.07.30.228668.

Pál-Fám, F., Boros, V., 2006. Macrofungi examination in Kaposvár city, Somogyi Múzeumi Közlemények 17(B): 7–16. (article in Hungarian with an abstract in English).

Paul, M., Meyer, J., 2008. Streams in the Urban Landscape. Annu. Rev. Ecol. Syst. 32 (1), 207–231. https://doi.org/10.1146/annurev.ecolsys.32.081501.114040.

Pautasso, M., Zotti, M., 2009. Macrofungal taxa and human population in Italy's regions. Biodivers. Conserv. 18, 473–485. https://doi.org/10.1007/s10531-008-9511-4.

Pigott, C.D., 1991. *Tilia cordata* Miller. J. Ecol. 79, 1147–1207.

Rambaut, A., 2010. FigTree v1.3.1. Institute of Evolutionary Biology. University of Edinburgh, Edinburgh.

Rapaics, R., 1934. Magyar Kertek, A Kertművészet Magyarországon, Magyar Könyvbarátok. A Királyi Egyetemi Nyomda, Hungary, Budapest.

Ryberg, M., Larsson, E., Jacobsson, S., 2010. An evolutionary perspective on morphological and ecological characters in the mushroom family Inocybaceae (Agaricomycotina, Fungi). Mol. Phylogenet. Evol. 55, 431–442. https://doi.org/10.1016/j.ympev.2010.02.011.

Schmidt, G., Honfi, P., 2006. Budapesti fák élete és halála. Budapest 29 (7), 2–6.

Seress, D., 2015. Diversity and Morphology of Ectomycorrhizas (Ph.D.). Eötvös Loránd University, Budapest, Hungary.

Seto, K.C., Sanchez-Rodriguez, R., Fragkias, M., 2010. The new geography of contemporary urbanization and the environment. Annu. Rev. Environ. Resour. 35, 167–194. https://doi.org/10.1146/annurev-environ-100809-125336.

Skrbic, B., Milovac, S., Matavuly, M., 2012. Multielement profiles of soil, road dust, tree bark and wood-rotten fungi collected at various distances from high-frequency road in urban area. Ecol. Indic. 13 (1), 168–177. https://doi.org/10.1016/j.ecolind.2011.05.023.

Smith, M.E., Douhan, G.W., Rizzo, D.M., 2007. Ectomycorrhizal community structure in a xeric *Quercus* woodland based on rDNA sequence analysis of sporocarps and pooled roots. New Phytol. 174 (4), 847–863. https://doi.org/10.1111/j.1469-8137.2007.02040.x.

Smith, S.E., Read, D.J., 1997. Mycorrhizal Symbiosis, 2nd ed. Academic Press, Cambridge.

Stamatakis, A., 2014. RAxML version 8. A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30, 1312–1313. https://doi.org/10.1093/bioinformatics/btu033.

Szabó, K., Boll, S., Erős-Honti, Zs, 2014. Applying artificial mycorrhizae in planting urban trees. Appl. Ecol. Environ. Res. 12, 835–853. https://doi.org/10.15666/aeer/1204_835853.

Timonen, S., Kauppinen, P., 2008. Mycorrhizal colonisation patterns of *Tilia* trees in street, nursery and forest habitats in southern Finland. Urban For. Urban Green. 7, 265–276. https://doi.org/10.1016/j.ufug.2008.08.001.

Tume, P., Bech, J., Sepulveda, B., Tume, L., Bech, J., 2008. Concentrations of heavy metals in urban soils of Talcahuano (Chile): a preliminary study. Environ. Monit. Assess. 140, 91–98. https://doi.org/10.1007/s10661-007-9850-8.

Twieg, B.D., Durall, D.M., Simard, S.W., 2007. Ectomycorrhizal fungal succession in mixed temperate forests. New Phytol. 176, 437–447. https://doi.org/10.1111/j.1469-8137.2007.02173.x.

Vilgalys, R., Hester, M., 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. J. Bacteriol. 172, 4238–4246. https://doi.org/10.1128/jb.172.8.4238-4246.1990.

Visser, S., 1995. Ectomycorrhizal fungal succession in jack pine stands following wildfire. New Phytol. 129, 389–401. https://doi.org/10.1111/j.1469-8137.1995.tb04309.x.

White, T.J., Bruns, T., Lee, S., Taylor, J.W., 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis, M.A., Gelfand, D.H., Sninsky, J.J., White, T.J. (Eds.), PCR Protocols: A Guide to Methods and Applications. Academic, New York, pp. 315–322. https://doi.org/10.1016/b978-0-12-372180-8.50042-1.

Zhang, Z., Schwartz, S., Wagner, L., Miller, W., 2000. A greedy algorithm for aligning DNA sequences. J. Comput. Biol. 7 (1–2), 203–214. https://doi.org/10.1089/10665270050081478.