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Dendrotelmata (water-filled tree holes) as fungal hotspots – a long term study

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Abstract – Water-filled tree holes (dendrotelmata) are mostly ephemeral micro-ecosystems characterized by high level of heterotrophic microbial activity sustained by allochthonous organic matter. In this paper, description of a five-year long observation of fungal consortia in a Norway maple tree-hole is presented. Overall, 139 fungal taxa were detected. Among them, *Excipularia fusispora*, *Ellisembia leptospora*, *Rebentischia unicaudata*, *Tricladium castaneicola*, *Thielavia terricola* and *Alternaria* spp. occurred most frequently. Our observations suggest that even an individual dendrotelma represents an exceptional microhabitat, forming a hot-spot for microfungi due to its role as a natural spore trap and its (temporarily) aquatic environment. Our results show that this aquatic micro-ecosystem supports highly diverse mycobiota with continuous temporal dynamics, with an important fraction of sporadic taxa.

dendrolimnobionts / diversity / fungal spores / mycobiota / temporal variation

INTRODUCTION

A number of terrestrial plants develop morphological structures collecting and retaining water. These bodies of water (phytotelmata) provide habitats for numerous organisms (Fish, 1983). According to their properties, these microhabitats (Decksbach, 1929) are considered as temporary waters which are fascinating objects to study species adapted to living in highly variable environments (Williams, 2005). Tree holes, also called dendrotelmata (Frank & Lounibos, 1983; Maguire, 1971), form naturally, mostly at boughs, and are small discrete ecosystems characterized by heterotrophic microbial activity (Kaufman *et al.* 2002) driven by allochthonous inputs of soluble and particulate organic matter (Pelz-Stelinski *et al.* 2011; Kitching, 2001). Leaves are the typical source of coarse particulate organic matter (Walker &

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Merritt, 1988) but animal-derived detritus, such as invertebrate carcasses and fecal material, are also important energy supplies (Yee & Juliano, 2006; Daugherty *et al.* 2000). In addition, the rainwater runoff from the canopies discharges dissolved organic carbon and nutrients into tree holes either via throughfall or stemflow (Carpenter, 1982; Kaufman *et al.* 2001; Kaufman *et al.* 2008). Microorganisms in the dendrotelmata have specialized for utilization of these nutrients (Karamchand & Sridhar, 2008).

The majority of water-filled tree-hole studies focused on invertebrates with intensive taxonomical (Kitching & Callaghan, 1982), ecological (Fashing, 1998; Paradise, 1999; Walker *et al.* 1997) and experimental investigations (Paradise, 1998; Walker *et al.* 1988, 1991). Study of dendrotelma-inhabiting fungi, however, was initiated by Gönczöl (1976). Since then, only few studies have been carried out (Gönczöl & Révay, 2003; Karamchand & Sridhar, 2008; Kladwang *et al.* 2003), documenting high diversities of microfungi. These studies dealt with a wide spectrum of different tree species, but were based on only one or two samples per tree. However, the fungal species composition over a longer time scale can vary, causing a significant temporal variation. In this study, we hypothesized that fungal consortia in a single tree-hole maintains high species richness but that it is strongly impacted by disturbances and influenced by different dispersal pathways (stemflow, throughfall), hence, these processes should induce high temporal variation in its composition.

Therefore, our aims were to explore the composition of the fungal consortia and its temporal changes over a period of 5 years in a single dendrotelma with special focus even on the sporadically occurring taxa.

MATERIAL AND METHODS

The examined tree-hole was located in a bough-branching of a Norway maple (*Acer platanoides* L.) in a park (47°30’49.5” N, 19°0’43.6” E; 168 m asl.) in Budapest, Hungary (Fig. 1).

Water samples were taken 89 times at irregular intervals with sterile plastic syringes between 2003 and 2008, always when rainwater was present in the tree-hole. The syringed water samples (8 ml) were composed of 3 subsamples taken from different depths (surface – 3 ml, middle – 2 ml, and disturbed bottom layers – 2 ml) of the water column/sediment. In case of frozen stage, the same volume of sample was taken from the liquid phase under the ice-cover. These combined samples were syringed to sterile centrifuge tubes (10 ml) and fixed by adding 2 ml of F.A.A. solution (Ruzin, 1999). To ensure sedimentation, the samples were stored in fixed vertical position for at least ten days. From these samples, 0.17 – 0.17 ± 0.016 ml of the sediment was pipetted out onto a glass slide and stained with cotton-blue in lactophenol to be observed at 400× magnification (Olympus BX-51). The fungal spores were identified morphologically using a light microscope and phase-contrast illumination at 600× magnifications. Identification of fungal spores was carried out by means of scientific literature and monographs (e.g. Ellis and Ellis 1997, Kendrick 1990, Lacey and West 2006, Seifert *et al.*, 2011).

The data (presence-absence of species) were compiled into a data matrix using MS Excel 2003 (Microsoft, Redmondton, USA). The Hellinger transformed dissimilarity matrix was then calculated using binary Bray-Curtis (Sørensen-)

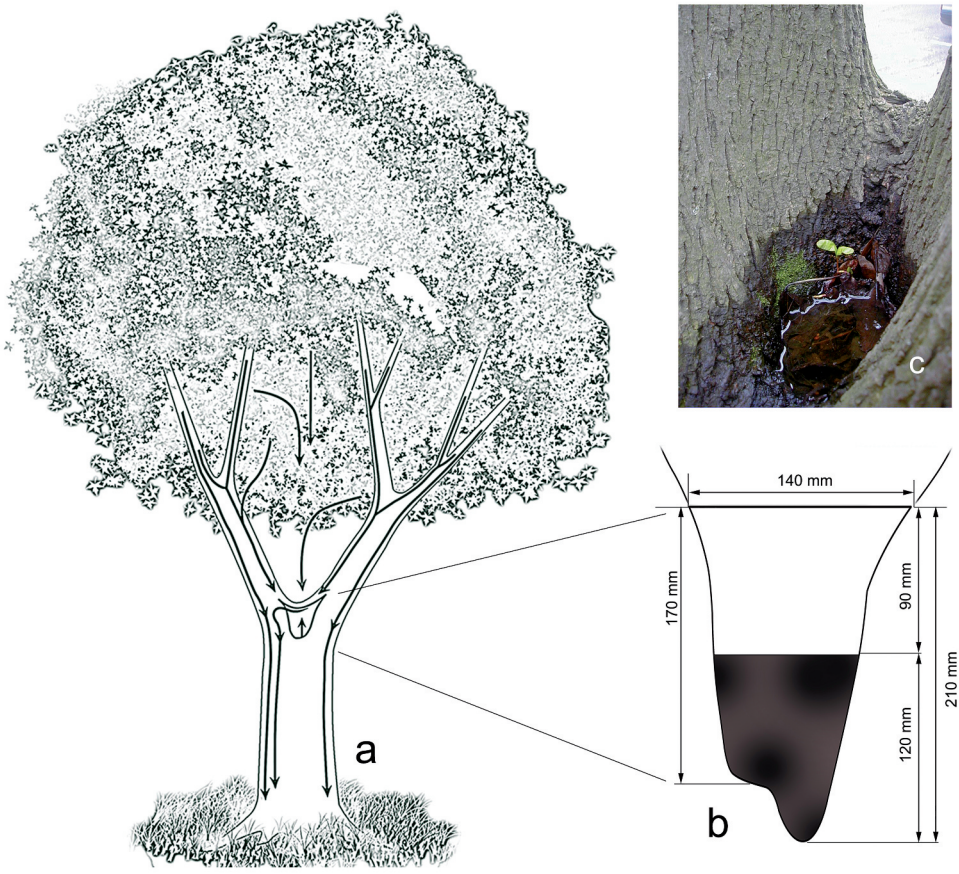


Fig 1. The examined tree-hole in a Norway maple tree. **a.** the host tree. Arrows show the observed movements of rainwater (stemflow, splash and throughfall). **b.** the side view of the three-hole. **c.** the water-filled three hole.

distance using "vegan" package (Oksanen *et al.*, 2013). The non-metric multidimensional scaling (NMDS) plot was generated to assess the differences among fungal consortia. After this, permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) was applied to compare compositions of samples grouped by year with 999 permutations. An important assumption for PERMANOVA consisted in implying a similar multivariate spread among groups (in this case, among years), hence multivariate homogeneity of groups (years) dispersions (variances) was also tested (*betadisper* in "vegan" package (Oksanen *et al.*, 2013) and verified by ANOVA before applying PERMANOVA.

Besides the ordination method, the analysis of alpha-diversity (α-diversity) and temporal beta-diversity (β-Sørensen) was also applied. The former tests differences in fungal richness among years using one-way ANOVA model followed by a Tukey's post-hoc test (multiple comparisons of means at significance level 0.05). Eventually, due to the potentially high portion of sporadically occurring taxa (SOT), we analyzed the contribution of SOT to temporal shift (temporal beta-

diversity) in community structure among mycobiota, following the method of Ashley *et al.* (2014) with a minor modification (using different distance method, namely Sørensen-distance). To identify the SOT, we set a maximum frequency of occurrence (FOC% = number of samplings in which a taxon was recorded/total samplings × 100) threshold of < 10%. Thus, fungal taxa with less than 10% of FOC% were considered to constitute the SOT subset of the whole fungal consortia.

RESULTS

The maximum water capacity of the tree-hole was 300 ml, its maximum depth was 210 mm. The ratio of the free water column and the sediment in the tree-hole, checked by a simple metal stick, was about 4:3.

By microscopical examination, a total of 139 different types of fungal spores were detected (Table 1) in the following proportions: hyphomycetes 67%, Ascomycota 14%, Basidiomycota 6%, coelomycetes 5%, unknown 7%. The predominant majority of detected fungi were saprotrophic. At genus and species level 45 and 50 taxa were identified, respectively. The number of fungal taxa per sample varied between 4 and 55 during the five-year period of observation. Fifty five % of the fungal taxa (77) occurred sporadically (i.e. their frequency of occurrence was less than 10%; Table 1). None of the taxa was present in all samples, and only 15 taxa were detected in more than half of the samples (occurrence FOC% = > 50%; Table 1), hence, these taxa represented more or less the constant mycobiota consortium during periods that the tree holes were filled with water.

The structure of the community composition of the studied dendrotelma varied between years (2003-2008; Fig. 2). There is already a distinct evolution in the mycobiota from 2003 to 2005, but the biggest changes occurred between 2005 and 2006, while in the subsequent years (2007-2008) the temporal variation in the structure of mycobiota hardly changed. Due to the non-significant (F = 1.749, P = 0.133) difference in the multivariate homogeneity of groups (years) dispersions, the PERMANOVA test was possible to apply. The result of PERMANOVA test showed that there is a significant (F = 4.662, R^2 = 0.219, P = 0.001) clustering by years.

Besides, there was a significant overall interannual difference (ANOVA: F = 6.258, P = < 0.001) also manifested in total fungal richness (α-diversity) between years (Fig. 3). More specifically, this significant difference originated from the following pairs of years (the results of the Tukey's test): 2004-2006 (P = 0.0215), 2004-2007 (P = 0.0022), 2005-2006 (P = 0.0305), 2005-2007 (P = 0.0067).

The fact that there are numerous fungi (in total 77 of 139 taxa) with sporadic occurrence (SOT) has prompted us to analyze the contribution of SOT (the fraction of Sørensen dissimilarity attributable to SOT) to the temporal dynamics of the community (temporal β-diversity). This analysis showed that the SOT had an important role in β-diversity. Specifically, the temporal variation (β-diversity) was 0.58 (Fig. 4), meaning that there was a 58% "pure" species temporal variation during the five-year study period (total community dissimilarity between all possible sampling points). Within this variation (58%), the contribution of SOT to this temporal dynamic ranged from 0.0 to 48.8% (Fig. 4). In average, 18% of the temporal dynamic of mycobiota was the result of SOT.

Table 1. List of fungal taxa present as spores or conidia in the water-filled tree-hole and their values of frequency of occurrence (FOC%) between 2003-2008

Taxon name	*FOC%*	*Taxon name*	*FOC%*
Acrogenospora sphaerocephala (Berk. & Broome) M.B. Ellis	22	*Excipularia fusispora* (Berk. & Broome) Sacc.	95
Agaricomycetes	31	*Exserohilum* sp.	5
Aglaospora profusa (Fr.) De Not.	1	*Fusarium* spp.	59
Alternaria spp.	79	*Fusicladium* sp.	1
Anguillospora sp.	15	*Ganoderma* sp.	7
Anthostomella/*Herpotrichella* sp.	3	*Helicodendron triglitziense* (Jaap) Linder	24
Arborispora paupera Marvanová & Bärl.	5	*Helicomyces* anamorph of *Tubeufia palmarum*(Torrend) Samuels, Rossman & E. Müll.	5
Arthrinium sp.	6	*Hyalodidimae* spp.	19
Asterosporium asterospermum (Pers.) S. Hughes	1	*Isthmolongispora ampulliformis* (Tubaki) de Hoog & Hennebert	8
Bipolaris sp.	6	*Isthmolongispora minima* Matsush.	15
Camarosporium sp.	8	*Leptosphaeria* spp.	30
Camposporium ontariense Matsush.	41	*Leptosphaeria thurgoviensis* E. Müll.	1
Cephaliophora muscicola G.L. Barron, C. Morik. & Saikawa	22	*Lylea tetracoila* (Corda) Hol.-Jech.	10
Cephaliophora sp.	4	*Macrodiplodiopsis desmazieri* (Mont.) Petr.	1
Ceratosporium fuscescens Schweinitz	1	*Massaria inquinans* (Tode) De Not.	1
Chaetomium sp.	55	*Melanospora* sp.	1
Chaetosphaerella sp.	3	Myxomycetes	11
Cladosporium spp.	56	*Neohendersonia kickxii* (Westend.) B. Sutton & Pollack	7
Clypeosphaeria sp.	<1	*Nigrospora* sp.	3
Cornutispora sp.	1	*Oidium* spp.	1
Corynespora proliferata Loer.	10	*Oncopodiella hungarica* Révay	1
Coryneum sp. 1	3	*Oncopodiella trigonella* (Sacc.) Rifai	66
Coryneum sp. 2	1	*Oncopodium elaeagni* D. Magyar	1
Cruciger lignatilis R. Kirschner & Oberw.	12	*Ovulariopsis*-like	1
Curvularia spp.	2	*Periconia* sp.	4
Cymadothea trifolii (Pers.) F.A. Wolf	1	*Phaeodidymae* spp.	64
Dictyosporium toruloides (Corda) Guég.	7	*Phomopsis/Polystigmina* sp.	18
Diplocladiella scalaroides G. Arnaud ex M.B. Ellis	1	*Phyllactinia fraxini* (DC.) Fuss	18
Diplodia spp.	33	*Pithomyces chartarum* (Berk. & M.A. Curtis) M.B. Ellis	14
Discosia sp.	1	*Pleospora* spp.	13
Discostroma corticola--like (Fuckel) Brockmann	2	*Polylobatispora deltoidea* Matsush.	2
Drechslera/*Helminthosporium* sp.	14	Pucciniales	34
Dwayaangam sp.	<1	*Pyrigemmula aurantiaca* D. Magyar & Shoemaker	43
Dyatripaceae	7	*Rebentischia unicaudata* (Berk. & Broome) Sacc.	80
Ellisembia leptospora (Sacc. & Roum.) W.P. Wu	90	*Repetofragma inflatum* (Berk. & Ravenel) W.P. Wu	1
Epicoccum nigrum Link	60	*Retiarius bovicornutus* D. L. Olivier	1

Table 1. List of fungal taxa present as spores or conidia in the water-filled tree-hole and their values of frequency of occurrence (FOC%) between 2003-2008 *(continued)*

Taxon name	*FOC%*	*Taxon name*	*FOC%*
Splanchnonema quercicola M.E. Barr	2	hyalophragmosporae sp. 5	1
Sporidesmium sp.	13	hyalophragmosporae sp. 6	1
Stegonsporium sp.	3	hyalophragmosporae sp. 7	1
Stemphylium vesicarium (Wallr.) E.G. Simmons	13	phaeoamerosporae sp. 1	37
Stigmina negundinis (Berk. & M.A. Curtis) M.B. Ellis	2	phaeoamerosporae sp. 2	23
Taeniolella spp.	60	phaeoamerosporae sp. 3 (*Humicola*-like)	5
Tetracladium sp. 1	1	phaeoamerosporae sp. 4	39
Tetracladium sp. 2	1	phaeodidymosporae sp.	64
Tetraploa sp.	1	phaeodictyosporae sp.	2
Thelephoraceae	1	phaeohelicosporae sp.	2
Thielavia sp. (possibly *T. terricola* (J.C. Gilman & E.V. Abbott) (C.W. Emmons)	53	phaeophragmosporae sp. 1	1
Titaea complexa K. Matsush. & Matsush.	10	phaeophragmosporae sp. 2	3
Torula sp.	10	phaeophragmosporae sp. 3	2
Tranzschelia spp.	12	phaeophragmosporae sp. 4	3
Trematosphaeria pertusa Fuckel	72	scolecosporae spp.	33
Triadelphia heterospora Shearer & J.L. Crane	1	scolecosporae sp. 1	1
Triadelphia uniseptata (Berk. & Broome) P.M. Kirk	41	scolecosporae sp. 2 (*Mycocentrodochium curvisporum*-like)	12
Trichothecium roseum (Pers.) Link	1	scolecosporae sp. 3	3
Tricladium castaneicola B. Sutton	62	scolecosporae sp. 4	1
Trifurcospora irregularis (Matsush.) K. Ando & Tubaki	16	scolecosporae sp. 5	45
Trimmatostroma salicis Corda	6	scolecosporae sp. 6	7
Trinacrium gracile Matsush.	2	scolecosporae sp. 7	2
Trinacrium incurvum Matsush.	12	scolecosporae sp. 8	7
Trinacrium parvisporum Matsush.	3	scolecosporae sp. 9	22
Trinacrium robustum Tzean & J.L. Chen	10	scolecosporae sp. 10	16
Trinacrium sp. 1	19	scolecosporae sp. 11	8
Trinacrium sp. 2	10	scolecosporae sp. 12	2
Trinacrium tothii D. Magyar	30	scolecosporae sp. 13	46
Tripospermum sp.	18	scolecosporae sp. 14	9
Urocystis sp.	2	scolecosporae sp. 15	19
Ustilaginales	10	staurosporae spp.	7
Ustilago reticulata Liro	9	staurosporae sp. 1	6
Xylariaceae	16	staurosporae sp. 2	13
Zopfiella-like	3	staurosporae sp. 3	2
hyalodidymosporae sp.	39	staurosporae sp. 4	10
hyalophragmosporae sp. 1	15	staurosporae sp. 5	1
hyalophragmosporae sp. 2	22	staurosporae sp. 6	16
hyalophragmosporae sp. 3	9	staurosporae sp. 7	3
hyalophragmosporae sp. 4	3		

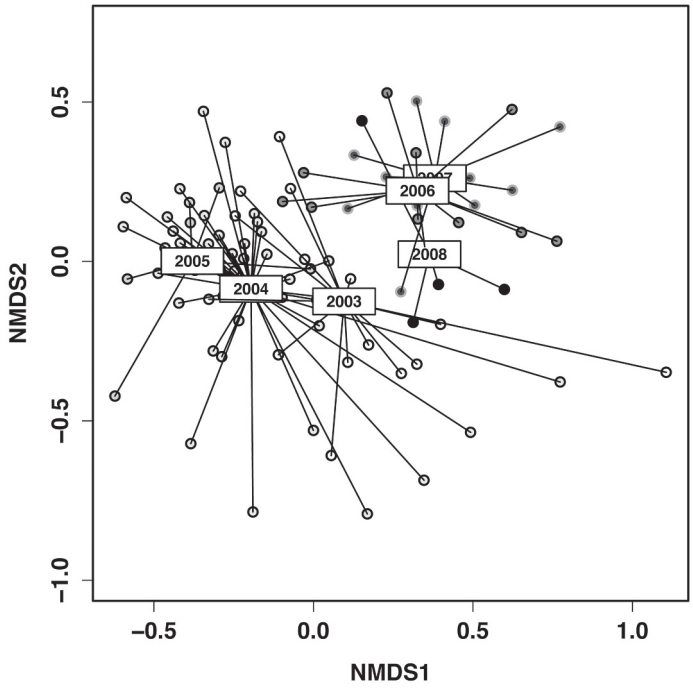


Fig. 2. The interannual changes (2003-2008) in community structure of mycobiota. Non-metric multidimensional scaling (run: 20, stress: 0.25) based on the binary Bray-Curtis distance of community matrices for fungal taxa of the tree-hole.

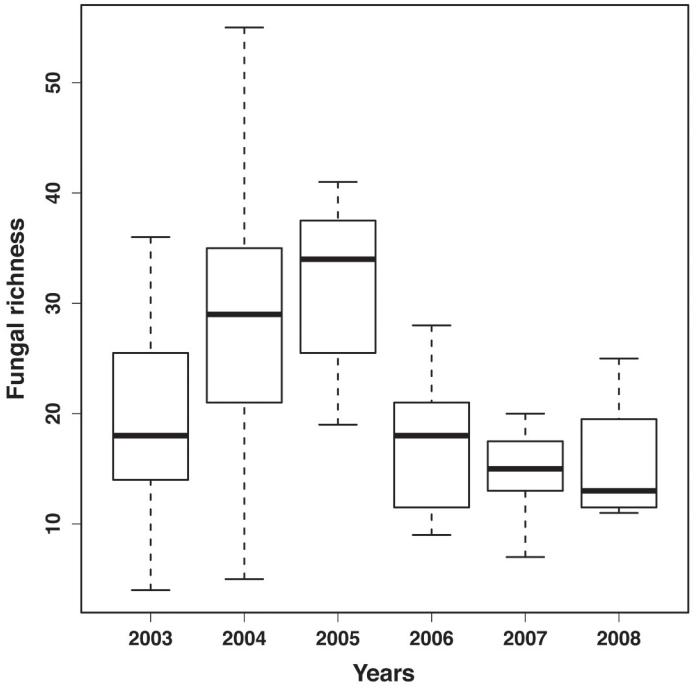


Fig. 3. Variation of fungal richness (α-diversity) among years (2003-2008).

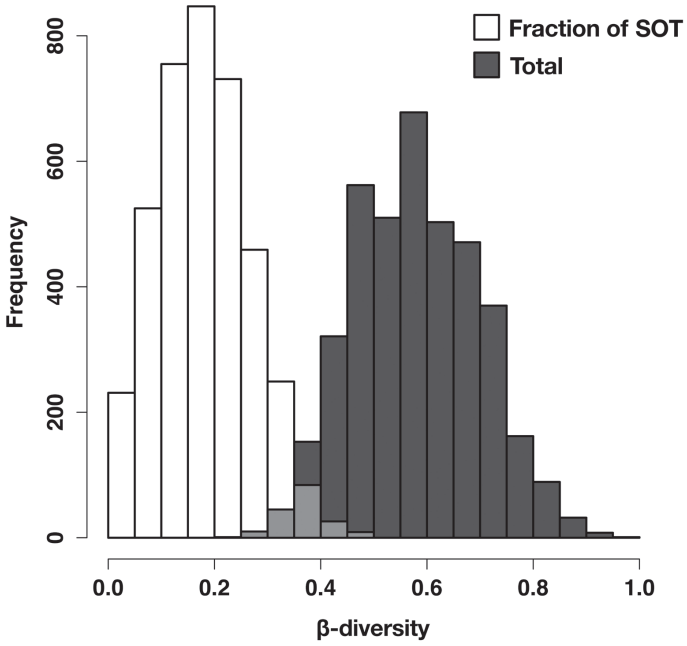
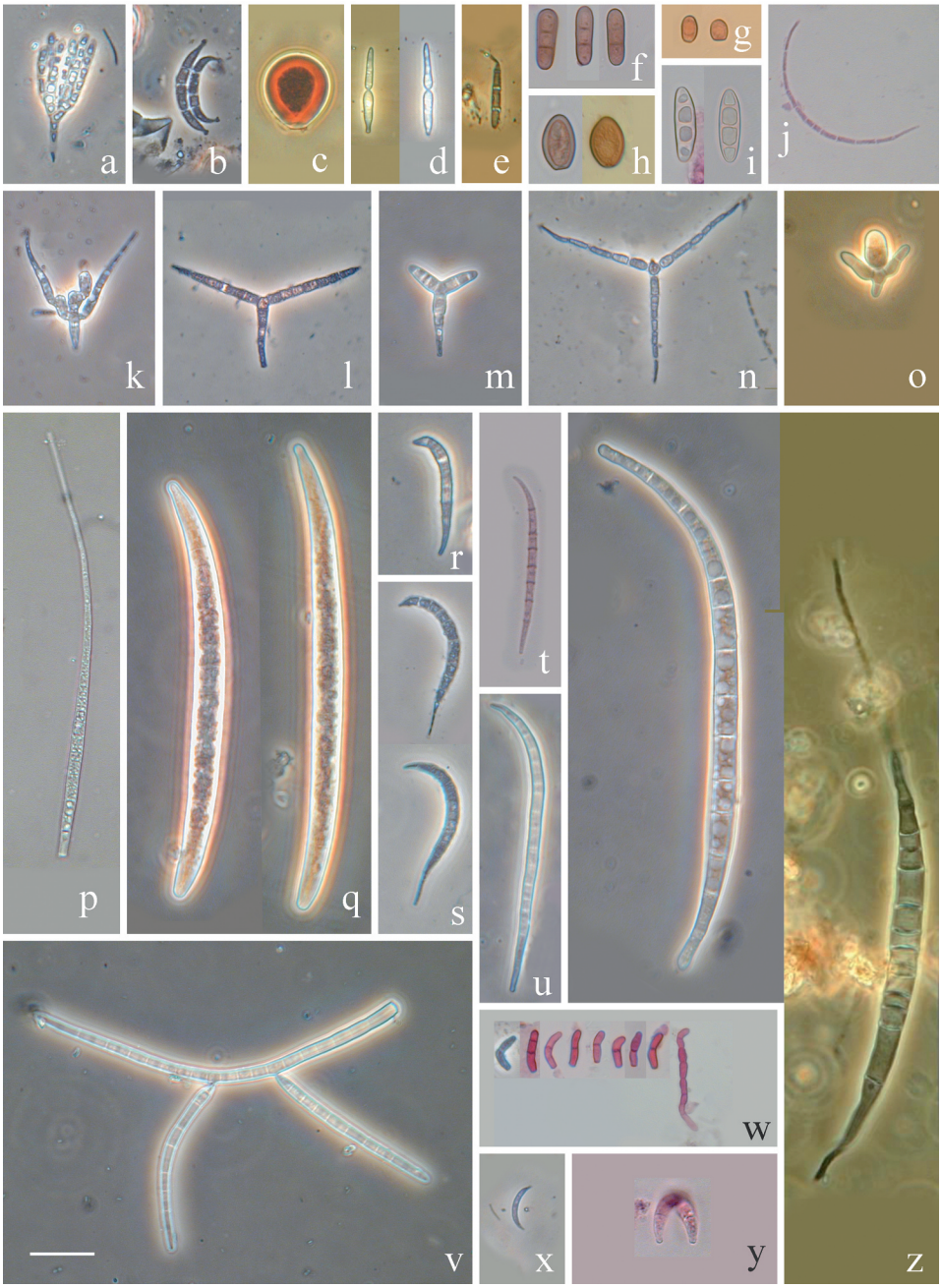


Fig. 4. Histogram showing the range of total β-diversity (black bars) and its fraction (white bars) attributable to sporadically detected taxa (SOT).

Dendrotelma-inhabiting fungi – Some microfungi might be characterized as specific dendrotelma-inhabiting fungi or dendrolimnobionts, although some of these fungi are known from various freshwater habitats (streams, lakes and ponds) and from litter: *Acrogenospora sphaerocephala*, *Anguillospora* sp., *Cephaliophora muscicola*, *Fusarium* spp., *Helicodendron triglitziense*, *Helicomyces* anamorph of *Tubeufia palmarum*, *Isthmolongispora ampulliformis*, *Isthmolongispora minima*, *Thielavia terricola*, *Tricladium castaneicola* and scolecosporae sp. 14.

Besides these fungi, some apparently undescribed species (Fig. 5b,p) and other rarely reported species were also found (Fig. 5).

Fig. 5. Potential dendrotelma-inhabiting (dendrolimnobionts) fungi and other observed taxa in the water-filled tree-hole during the five-year period of observation (2003-2008); **a.** staurosporae sp. 6., **b.** staurosporae sp. 1, **c.** *Acrogenospora sphaerocephala*, **d.** *Isthmolongispora minima*, **e.** *Isthmolongispora ampulliformis*, **f.** phaeophragmosporae sp. 1, **g.** phaeoamerosporae sp. 1, **h.** phaeoamerosporae sp. 3, **i.** hyalophragmosporae sp. 1, **j.** scolecosporae sp. 2, **k.** *Tetracladium* sp. 1, **l.** *Trinacrium* sp. 1, **m.** *Trinacrium tothii*, **n.** *Trifurcospora irregularis*, **o.** *Tetracladium* sp. 2, **p.** scolecosporae sp. 14, **q.** *Cephaliophora muscicola*, **r.** scolecosporae sp. 6, **s.** scolecosporae sp. 10, **t.** scolecosporae sp. 16, **u.** scolecosporae sp. 7, **v.** *Tricladium castaneicola*, **w.** hyalodidymospore sp. 1, **x.** scolecosporae sp. 3, **y.** scolecosporae sp. 8, **z.** *Anguillospora* sp.; scale bar = 20 µm. ▶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DISCUSSION

In previous snapshot works (Gönczöl, 1976; Gönczöl & Révay, 2003; Karamchand & Sridhar, 2008), the precious diversity of dendrotelma-inhabiting fungi was already shown, and it is likely that fungal diversity of tree holes depends on local factors and climate. Gönczöl & Révay (2003) found *Alatospora acuminata* (a fungus common in streams) dominating in tree holes, but in our study this species had not been detected. *Tricladium castaneicola*, which seems to be a typical dendrolimnobiont species, and some undescribed fungi with staurospores matched previous findings from Hungary from dendrotelmata of different tree species. Comparing our results with those obtained in a study conducted in India (Karamchand & Sridhar 2008), it can be stated that except of *Anguillospora* and *Tripospermum* species there were no matches.

Fungal species occurring in dendrotelmata have different origins. Those arriving as airborne spores are known from the literature and surrounding air samplings (Járai-Komlódi, 1991; Járai-Komlódi & Tóth, 1993-94; Magyar, 2008). Phylloplane (phyllosphere) and tree bark inhabiting taxa were inferred from mycological examination on tree canopies (Ellis & Ellis, 1987; Magyar & Tóth, 2003; Magyar, 2006; Sudheep & Sridhar, 2010; Révay & Gönczöl, 2011) and are represented by some of the most dominant fungi (*Excipularia fusispora* (95%), *Phomopsis* sp. (18%) and *Alternaria* spp. (79%)). Several aquatic fungi known from streams (i.e., *Anguillospora* sp., *Tricladium* spp.) were found as well. Gönczöl & Révay (2003) confirmed that tree holes serve as habitats for some water-borne conidial fungi, thus the occurrence of aquatic hyphomycetes is not surprising in such habitats. The majority of the bark-inhabiting species likely originated from the host tree, but, in the tree-hole, plant detritus of other tree species than maple were also found, such as litter and fruits of neighboring *Fraxinus excelsior* trees and explaining the presence of chasmothecia of *Phyllactinia fraxini*. However, clear evidence of distant sources was also found, such as conidia of *Oncopodium elaeagni* deriving from a Russian olive tree, *Elaeagnus angustifolia*, ca. 300 meters away from our maple tree. Some plant-pathogenic taxa were also found in the tree-hole. Among ubiquitous airborne phytopathogens smut and rust spores were best represented.

As our results showed, the fungal consortia represents a dynamic system in which the species turnover (β-diversity) has a significant part shaping the composition of the mycobiota in time scale. Although, the interannual fungal composition variation (during the five years) was not further analyzed in this study, but it might be the result of circumstantial changes as well as random processes, e.g., due to changes in the quantity and quality of the litter-inputs (as the major energy source in such systems) (Sridhar *et al.* 2013), and also the frequency and stochasticity of passive transport pathways (i.e., stemflow and throughfall). The importance of stemflow and throughfall due to rain events represent an important role in passive transport of a broad group of fungi living in tree canopies (Lodge, 1995; Stone *et al.* 1996; Magyar *et al.* 2016). Several studies focusing on stemflow and throughfall show high fungal diversity in such samples (Ando & Tubaki, 1984; Czeczuga & Orłowska, 1998; Gönczöl & Révay, 2004, 2006; Sridhar & Karamchand, 2009; Sudheep & Sridhar, 2010). Our results suggest that a great portion of the transported fungal spores can be sporadic and these rare species likely have a prominent role in forming temporal dynamics of the mycobiota in dendrotelmata. Nevertheless, these transported fungi might have low competitive ability in aquatic habitats or serve as food for smaller animals such as insect larvae or testate amoebae living in dendrotelmata.

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