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Species richness and substrate specificity of lignicolous fungi in the canopy of a temperate, mixed deciduous forest

Martin UNTERSEHER[1,*], Peter OTTO[1], and Wilfried MORAWETZ[1]

In the more than twenty years in which long-term canopy research has been conducted, mycology has been largely disregarded. Our studies using a construction crane to gain access to the canopy of a forest in Leipzig, Germany are the first long term investigations assessing the diversity and ecology of wood-decaying fungi in a canopy. Thirty-seven individuals of nine different tree species with a large amount of dead wood were selected. Sampling focussed on the four most prominent tree species *Acer pseudoplatanus*, *Fraxinus excelsior*, *Quercus robur* and *Tilia cordata*. In the years 2002 and 2003 dead wood was collected in different canopy strata. Dead branches were removed and stored for two weeks in open boxes with high humidity to allow growth of fructifications in the laboratory. 118 different taxa were identified (108 species, 77 genera). Corticioid fungi (e.g., of Corticiaceae, Stereaceae, Hymenochaetaceae) dominated the fungal composition with 37 species, pyrenomycetes were present with 18 species. Agaric fungi (Agaricales and Cortinariales) were scarce. Species with minute basidiomes dominated the fungal composition of this systematic group. Agarics with larger sporomes were found only once and were restricted to strongly decayed branches in shaded canopy areas. Concerning species richness and fungal composition the four tree species mentioned above differed remarkably. As expected, many fungi that grew on bark or slightly decayed wood showed a distinct host and substratum specifity. It is noteworthy that fungi which are purportedly to be non-specific were found on single tree species only.

Keywords: wood-decaying fungi, canopy research, Leipzig Canopy Crane Project, biodiversity, ecology, indicator species

More than 20 years ago, studies on the diversity of forest canopies revealed a large quantity of organisms dwelling in the tree tops (SUTTON et al. 1983; ERWIN 1982; ERWIN & SCOTT 1980). Many of these organisms are predicted to be canopy specialists (OZANNE et al. 2003). This implies that forest canopies house a large portion of worldwide species diversity (OZANNE et al. 2003; HAWKSWORTH et al. 1995; LOWMAN & MOFFET 1993; ERWIN 1988, 1982). Since the first approaches to study life in tree crowns by rope techniques (PERRY 1978) or fogging (ERWIN 1982; ERWIN & SCOTT 1980), the scientific community has seen a rapid development of different canopy research fields (MITCHELL, SECOY & JACKSON 2002; NADKARNI 2002; MORAWETZ 1998; LOWMAN & MOFFET 1993).

A new era of canopy research was launched in 1990 when the Smithsonian Institute established a construction crane for observation purposes in a Panama forest (WRIGHT 2002). For the first time it was possible to easily gain access to the upper forest regions and to study the canopy of a particular site over many years. In consequence, ten further canopy crane projects have been launched in the last decade. One of them is the Leipzig Canopy Crane Project (LAK) (MORAWETZ & HORCHLER 2004) of which this mycological study is part.

The importance of fungi on forest soils as saprobionts of leaf litter and woody debris and as partners of mycorrhizae is well-known and still a matter of intense research. Studies about diversity and ecological impacts of fungi in forest canopies however are very rare even though intense canopy research has been conducted for more than two decades. Two years ago, mycological research played no significant role in the canopy projects worldwide (MITCHELL, SECOY & JACKSON 2002).

Differences in biotic and abiotic factors like solar radiation (eg. photosynthetic active radiation [PAR]) (HORCHLER 2004; ANHUF & ROLLENBECK 2001), the quantity of available water (BELLOT, ÀVILA & RODRIGO 1999), diurnal and annual gradients in temperature, and the quality and amount of different substrates over time and space, result in distinct mesoclimatic conditions from the forest floor to the canopy. This most probably affects the richness and species composition of lignicolous fungi in the two habitats (e.g., HALLENBERG & PARMASTO 1998; LODGE & CANTRELL 1995).

Dead, hanging branches are naturally occuring, essential parts of nearly every tree crown (e.g., BODDY & RAYNER 1983; BUTIN & KOWALSKI 1983). In the canopy decayed wood desiccates faster than at ground level and may provide niches for xerotolerant and xeroresistant fungi (for definition of xero-

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tolerance and xeroresistance, see BEWLEY 1979). The few studies concerning fungi on dry, weathered wood have concentrated mostly on tropical forests, on the understorey or over short periods of time (e.g., OTTO & GLOWKA 1998; LODGE & CANTRELL 1995; HEDGER, LEWIS & GITAY 1993; NUÑEZ & RYVARDEN 1993; BODDY 1992). Apart from corticioid species of Polyporales, Hymenochaetales and Russulales, pyrenomycete fungi are frequent inhabitants of decayed wood in arid habitats. They are able to continue growth under arid conditions or to survive long periods of drought. (e.g., NUÑEZ 1996; MUNK 1957; INGOLD 1954). Different groups of the Helotiales also tolerate such conditions (BARAL, BARAL & MARSON 2003; SHERWOOD 1981). TEJERA & RODRÍGUEZ-ARMAS (1999) studied the diversity of Aphyllophorales in desert-arid-semiarid areas of the Canary Islands. Their preliminary results showed a comprehensive species richness with 18 new species to the particular islands and four new to the 'Canarian fungal checklist'. In the 1980s a series of studies was published by BODDY and 'co-workers', focussing on the development and ecology of fungal communities on dead attached branches in the understorey. However, many studies were limited to single branches or to early stages of fungal succession (BODDY & RAYNER 1984, 1983, 1982; CHAPELA & BODDY 1988 a, b, c; GRIFFITH & BODDY 1991, 1989, 1988).

To reduce the gap of scientific knowledge concerning fungi in tree crowns, our investigations, started in May 2002, have been designed as the first long term investigations to assess the diversity and ecology of wood-decaying fungi in the canopy. The aims of the present study are (i) to create a species list of lignicolous fungi occuring in the canopy, (ii) to analyse beta diversity and (iii) to comment on the influence of ecological factors on species composition in tree crowns.

Material and methods

Canopy access

The interdisciplinary long-term project LAK started in 2001 and is conducted by the University of Leipzig, financed by the UFZ, Centre for Environmental Research Leipzig-Halle and supported by the City of Leipzig. With a construction tower crane (Liebherr 71 EC, height of tower 40 m, jib length 45 m, max. sampling height ca. 33 m), mobile on a 120 twenty metre-long railway track, 1.6 ha of forest can be explored (Fig. 1). Scientists using a remote control to move the crane and standing in a gondola, can raise themselves above the forest then lower the gondola precisely to a location of interest in the canopy. The tips of small distal branches, which were previously inaccessible, are easily reachable (Fig. 2).

Investigation plot

The investigation plot is situated at the margin of a former oak and elm rich floodplain forest [*Querco-Ulmetum minoris* Issler 1924, = *Fraxino-Ulmetum* (R.Tx.1952) Oberd. 1953]. Due to the lack of regular innundations for the last ca. 70 years, succession has tended toward a forest rich in *Acer pseudoplatanus* L. and *Fraxinus excelsior* L. The species *A. pseudoplatanus* and *A. platanoides* L. already are the most dominant tree species in the understorey and sub canopy, indicating the atypical hydrological conditions of this lowland forest. The investigation plot comprises seventeen tree species.

Sampling design

The new challenge to operate in a three dimensional space forced us to apply new methods of collecting fungi. Methods described in previous studies concerning the diversity of lignicolous fungi (e.g., HONG, KLINKA & SONG 1999; LINDBLAD 1997; CHAPELA & BODDY 1988 a; BODDY & RAYNER 1984) could not be used, because sampling was restricted to fallen logs or hanging twigs in the understorey.

Especially because of the limited opportunity to use the crane for mycological studies it was not possible to investigate all tree individuals occuring in the crane site. The following tree species were selected: *Fraxinus excelsior*, *Quercus robur* L., *Tilia cordata* Mill., *Acer pseudoplatanus, Carpinus betulus* L., and *Cerasus avium* (L.) Moench as typical and rather abundant species for floodplain or mixed deciduous forests, additionally *Populus* × *canadensis* Moench, *Quercus rubra* L., and *Robinia pseudacacia* L. as often cultivated species. For selecting individuals of these species the following two criteria were used: (i) tree height at least 25 m and (ii) comparatively large amount of dead wood in different canopy strata. Due to the fact that only few trees of the crane site fulfilled these criteria and further locations in the plot were occupied by other scientists a stochastical choice of individuals was not possible and seemed not to be useful. Either all or many relevant trees of the above mentioned species were sampled to obtain comprehensive data on fungal diversity in the canopy (Fig. 3). Table 1 gives an overview of sampling design.

Sampling took place in the years 2002 and 2003 and was limited mostly to spring (March, April, May) and fall (September, October, November) but also occurred during summer and winter.

Dead twigs were collected at nine or more different locations in each tree crown resulting in a total number of 703 collections. It was intended that the same amount of wood in three different vertical zones (sub canopy [10–17 m], middle canopy [17–24 m], top canopy [24–31 m]) be collected. Often, however, this was not possible because of a generally bad accessibility of the sub canopy (branches blocking the access from above).

Removed twigs, including short bifurcations, were treated only as partial samples because it turned out that this amount of substratum was unsuitable for analyses due to a large amount of variance in twig length. This resulted in selective very low fungal species numbers and therefore unbalanced datasets. Therefore sample size was defined as the amount of

Fig. 1: The construction tower crane of the Leipzig Canopy Project (LAK). The small gondola permits easy access to different levels of the canopy.

twigs collected in an imaginary cube around the gondola with a side length of 3m (Fig. 2). This resulted in a better comparability of total samples. To analyse substrate specificity, a further aggregation of total samples to sample groups was carried out for characterising upper and lower canopy or tree species.

Additional field data included information on stratum (sub, middle, top canopy), height above ground level, tree species and individual number, substratum characters (kind and stage of decay), diameter of branches, coverage with epiphytic algae, lichens and occurrence of old sporomes, location of fructifications on the branch (upper side, lower side) and exposure to sun (estimated as exposed [more than 50 % direct sunlight], semi exposed [10 to 50 %] and shaded [less than 10 % direct sunlight]). Studies on the succession and ecology of 'canopy fungi' based on these data will be treated in a separate publication.

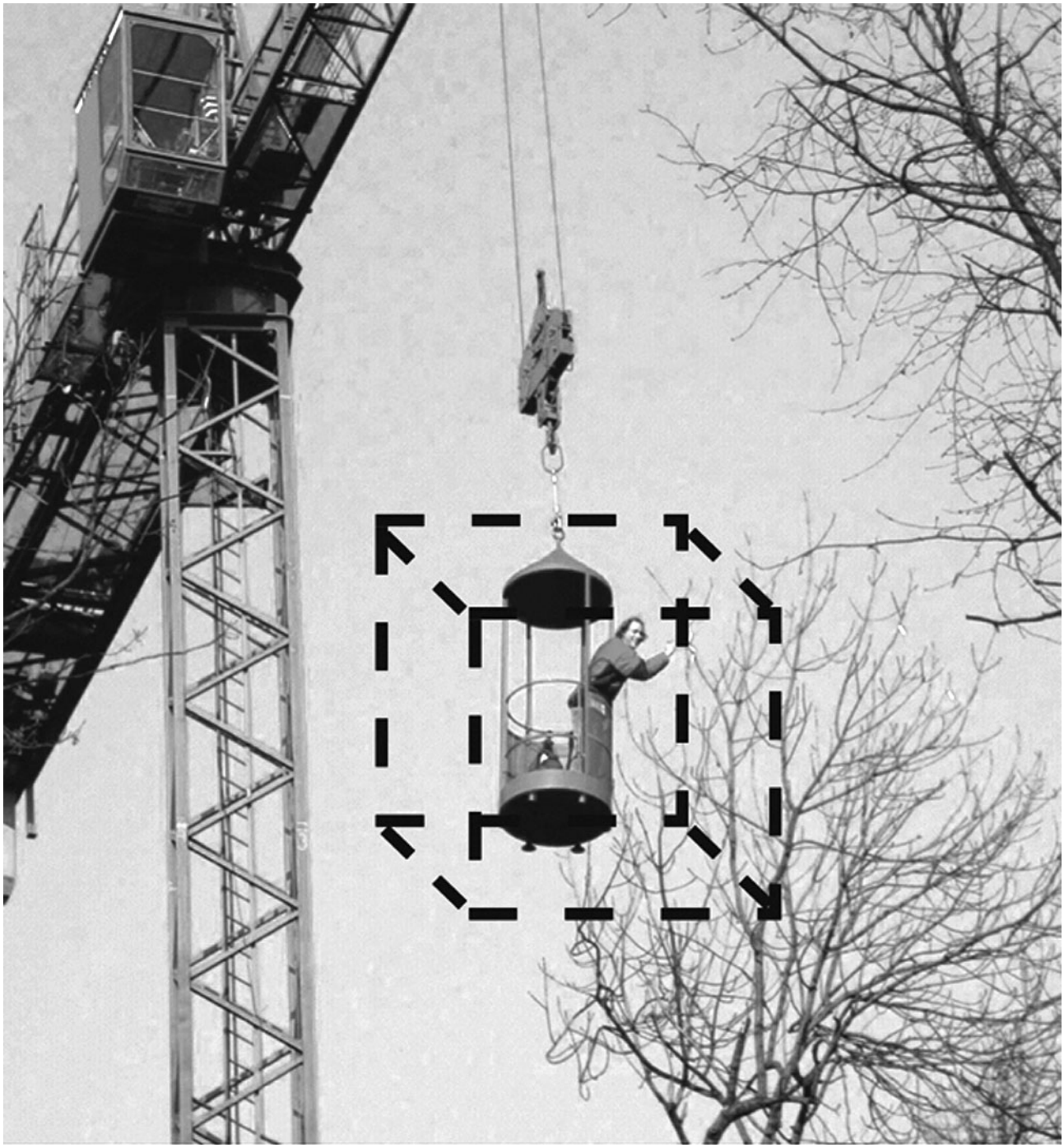

Fig. 2: Definition of an appropriate sample size. A scientist collecting twigs inside an imaginary cube with a side length of about 3 metres.

Several methods for cultivating fungi on natural woody substrates in the laboratory were tested. The following seemed to be suitable to initiate or promote fruitbody development and to simulate conditions in tree crowns during humid weather periods. Samples were put separately in tap water for one day to allow soaking of the wooden tissues. Afterwards they were washed under flowing water, to reduce superficially adhering diaspores. The samples were stored under high humidity in open plastic boxes for two weeks to allow development of sporomes from mycelia previously established in the wood and further growth of fruiting initials. Once a day the samples were sprayed intensively with water to maintain rather high water content of the wood and high air humidity. Using this method the wooden surface could also dry up. The samples were inspected every three to four days for the occurrence of fructifications. All teleomorphic species were recorded, anamorphs were only considered if they grew in deeper layers of bark or wood (Fungi imperfecti with pycnidia ['Sphaeropsi-

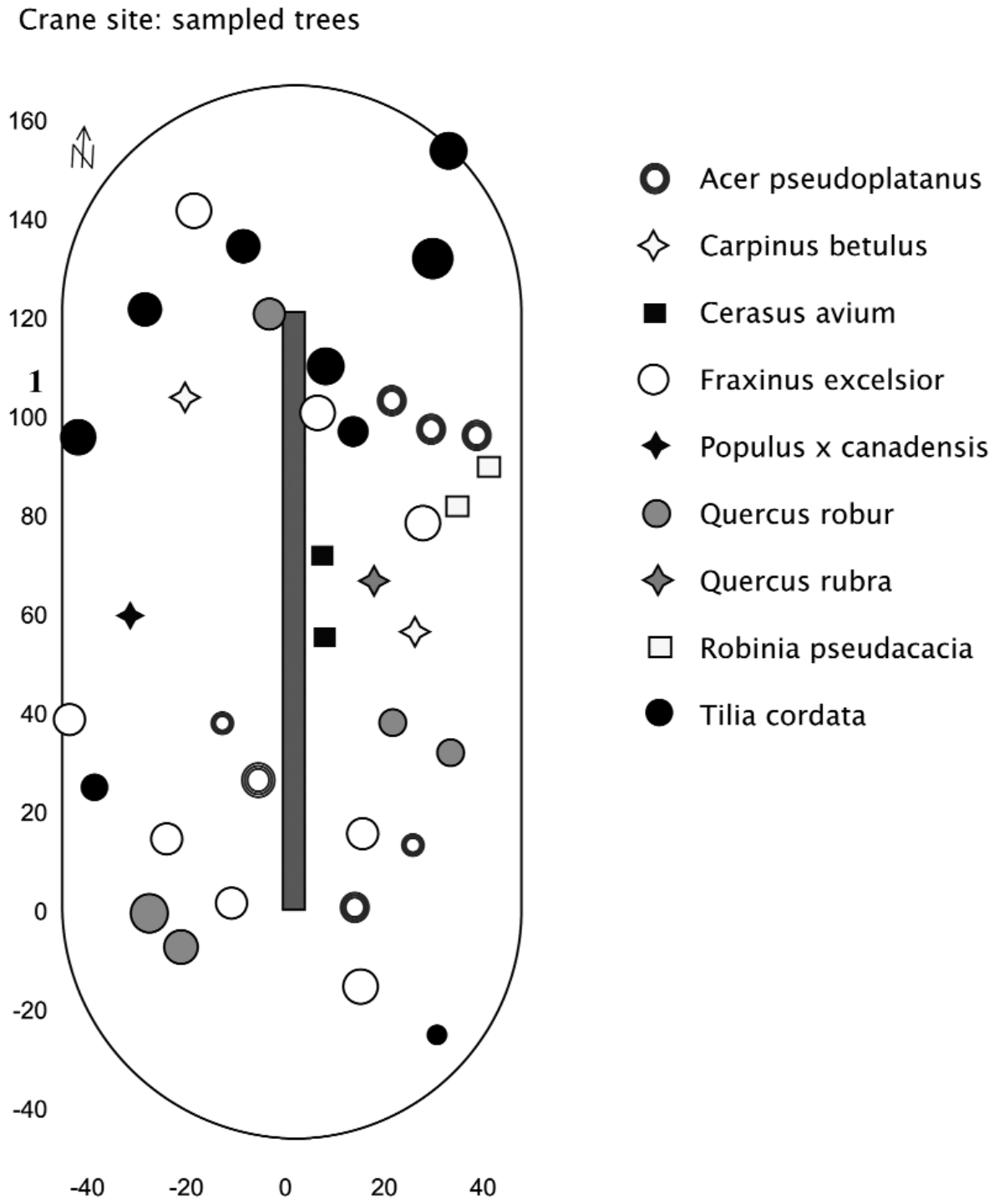

Fig. 3: Distribution of sampled trees at the canopy crane site. The long grey bar marks the 120 metres long railway track on which the tower crane can be moved. The black line encircles the area reachable by crane.

dales'], acervuli ['Melanconiales'] or immersed sporodochia [Moniliales pp.]). Imperfect fungi with rapidly developing, mostly superficial mycelia were deliberately excluded because they could have occurred as secondary colonisers and probably do not belong to typical wood inhabiting species of the canopy. The collected fungi are stored in the Herbarium LZ, University of Leipzig.

Stages of wood decay

Previous studies were used as a guideline to define states of wood-decay (Lumley, Gignac & Currah 2001; Winterhoff 2001; Lindblad 1997): State 0: living but obviously weak, bark intact without fissures, wood unchanged. State 1: dead, bark cracked, slightly decayed, wood mostly unchanged.

Tab. 1: Overview of sampling design and amount of sampled wood.

Tree species	No. of sampled trees	No. of total samples			Total length of sampled twigs (m)
		subcanopy	middle canopy	top canopy	
Acer pseudoplatanus L.	7	6	6	8	45
Carpinus betulus L.	2	3	4	4	20
Cerasus avium (L.) Moench	2	2	1	1	ND
Fraxinus excelsior L.	8	4	9	12	28
Populus x canadensis Moench	1	1	2	1	ND
Quercus robur L.	5	6	6	9	23
Quercus rubra L.	1	2	1	1	ND
Robinia pseudacacia L.	2	2	2	3	ND
Tilia cordata Mill.	9	11	10	7	26
total	**37**	**37**	**41**	**39**	**more than 150**

State 2: bark clearly to heavily decayed, often covered with algae, often present as small patches, wood superficially decayed, heartwood mostly unchanged. State 3: decay of sapwood advanced to about half of the branch's diameter, wooden structure mostly destroyed, easily removable with a knife. State 4: branches mostly decorticated, wooden tissue spongy, heartwood often clearly decayed, resulting in conspicious reduction of weight. Following this classification, the state of decay directly near the sporomes was noted as proposed by HØILAND & BENDIKSEN (1996).

Statistical analysis

To analyse species diversity and tree specifity, presence-absence data were used. Analysis of tree specificity was done using the four most abundant canopy tree species in the plot, *A. pseudoplatanus*, *F. excelsior*, *Q. robur* and *T. cordata* and the most abundant fungi with three or more counts per tree. The species composition was analysed by two common ordination methods, Correspondence Analysis (CA) (GAUCH 1982), and Nonmetrical Multidimensional Scaling (NMS) using a Sørensen similarity matrix (MC CUNE & GRACE 2002). The CA was performed using the software 'Canoco 4.5 for Windows' (TER BRAAK & SMILLAUER 1998), the NMS using 'PC-ORD' (MC CUNE & MEFFORD 1999). Substrate specificity could be assessed by the results of the CA. Additionally we analysed specificity by calculating indicator values using the free software 'IndVal 2.0' (DUFRÊNE & LEGENDRE 1997). Significance levels of the indicator values were calculated applying a Monte-Carlo permutation procedure. Estimations of species richness were performed using the free software 'EstimateS 6 beta' (COLWELL 2000). Selected software options of all methods are given in the captions of figures and tables.

Nomenclature and systematical arrangement

The Index Fungorum (www.indexfungorum.org) , that is consistent with the 'Dictionary of the Fungi', 9th edition (KIRK, CANNON, DAVID & STALPERS 2001) was used as a guideline to species and authorities names.

Results

Species richness

118 different taxa were determined at species or generic level (Tab. 2). With a total sample number of 128 imaginary cubes (see Fig. 2), 50 species were singletons, another 22 were doubletons. Approximately 10 % of all samples could not be identified or were placed in larger groups or orders. They are not included in the species list. Members of the corticioid Russulales were present with 37 species (29,7 % of the total observed species richness), 18 pyrenomycete species were recorded. They belong to the orders Diaporthales, Xylariales, Dothideales, Pyrenulales and Sordariales. 16 mitosporic species (incl. Coelomycetes) were identified. Agaric fungi were scarce. Except *Gymnopilus penetrans* (Fr..) Murrill, *Pluteus cervinus* P. Kumm and *Mycena galericulata* (Scop.) Gray, which were found once, only species with minute basidiomes were present: *Pleurotellus chioneus* (Pers.) Kühner, *Resupinatus applicatus* (Batsch) Gray, *R. trichotis* (Pers.) Singer, *Episphaeria fraxinicola* (Berk. & Broome) Donk, *Cyphellopsis anomala* (Pers.) Donk, *Crepidotus subtilis* P.D. Orton and *Lachnella spp*.

The host trees are also listed in table 2. The highest species richness was observed on lime trees (*T. cordata*) with 47 different species. Sycamore (*A. pseudoplatanus*) was colonised by 23 fungal species, ash (*F. excelsior*) by 19 and oak (*Q. robur*) by 34. Considering the different amounts of sampled wood, sycamore was least populated with a mean of about 0.5 species per metre or one species every 2.2 metres. The mean density of occurrence of teleomorphs on ash was one species every 1.4 metres or about 0.7 species per metre. The mean density on lime and oak trees was similar with about two species per metre. Figure 4 shows original species accumulations (line with grey coloured circles) and species accumulations curves (line with black squares) for the four tree species (a-d) and for all existing data (e). After 100 samples each, the species number calculated by rarefaction was 23 on *A. pseudoplatanus*, 16 on *F. excelsior*, 25 on *Q. robur* and 40 on *T. cordata*.

Tab. 2: All fungi identified to species or generic level are listed. Their host trees (*), the number of counts (**) and abbreviations of species (***) that are presented in the CA-diagrams (Figs. 5, 6) are also shown. *: Ap = *Acer pseudoplatanus*, Cb = *Carpinus betulus*, Ca = *Cerasus avium*, Fe = *Fraxinus excelsior*, Pc = *Populus* × *canadensis*, Qr = *Quercus robur*, Qru = *Quercus rubra*, Rp = *Robinia pseudacacia*, Tc = *Tilia cordata*. **: Number of counts based on 128 samples (sample size was imaginary cube).

Fungal Species	Tree Species *	Counts **	Abbr***
Ascomycetes			
Diaporthales			
Diaporthe oncostoma (Duby) Fuckel	Rp	3	ND
Melanconium atrum Link	Cb	2	ND
Valsa ambiens (Pers.) Fr.	Pc	2	ND
Dothideales			
Karschia lignyota (Fr.) Sacc.	Qr	1	ND
Teichospora obducens (Schumach.) Fuckel	Fe	1	ND
Helotiales			
Ascocoryne cylichnium (Tul.) Korf	Tc	2	ND
Hyalinia rosella (Quél.) Boud.	Qr	1	ND
Hyalorbilia inflatula (P. Karst.) Baral & G. Marson	Qr	1	ND
Mollisia cinerea (Batsch) P. Karst.	Ca	2	ND
Mollisia melaleuca (Fr.) Sacc	Cb	1	ND
Mollisia sp.	Ca	1	ND
Orbilia cf. coccinella (Sommerf.) P. Karst.	Cb, Qr, Tc	7	orbicocc
Orbilia crystallina (Quél.) Baral	Tc	1	ND
Orbilia euonymi Velen.	Qr	1	ND
Orbilia sarraziniana Boud.	Cb	1	ND
Hypocreales			
Hypocrea rufa (Pers.) Fr.	Ap, Fe, Qr, Tc	9	hyporufa
Hypocrea sp.	Tc	1	ND
Nectria cinnabarina (Tode) Fr.	Qr	1	ND
Patellariales			
Patellaria atrata Cooke	Tc	5	pateatra
Pleosporales			
Fenestella vestita (Fr.) Sacc.	Ap	1	ND
Melanomma pulvis-pyrius (Pers.) Fuckel	Pc	1	ND
Pleomassaria carpini (Fuckel) Sacc.	Cb	2	ND
Pyrenulales			
Massaria anomia (Schwein.) Petr.	Rp	4	ND
Massaria pupula (Fr.) Tul. & C. Tul.	Ap	4	ND
Rhytismatales			
Colpoma quercinum(Pers.) Wallr.	Qr	3	ND
Sordariales			
Coniochaeta pulveracea (Ehrh.) Munk	Tc	3	ND
Coniochaeta sp.	Tc	1	ND
Coronophora gregaria (Lib.) Fuckel	Ca	1	ND
Lasiosphaeria ovina (Pers.) Pat.	Tc	2	ND
Lasiosphaeria sp.	Cb, Qr	1	ND
Nitschkia cupularis (Pers.) P. Karst.	Fe	17	nitscupu
Nitschkia sp.	Ap	1	ND
Xylariales			
Cryptosphaeria eunomia (Fr.) Fuckel	Fe	22	crypeuno
Diatrypella quercina (Pers.) Cooke	Qr, Qru	13	diatquer
Eutypa maura (Fr.) Sacc.	Ap	16	eutymaur
Eutypa sp.	Rp	1	ND
Basidiomycetes			
Agaricales			
Crepidotus sp.	Fe	1	ND
Crepidotus subtilis P.D. Orton	Fe	1	ND
Cyphellopsis anomala (Pers.) Donk	Ap, Pc, Tc	4	cyphanom
Episphaeria fraxinicola (Berk. & Broome) Donk	Fe	12	episfrax

Tab. 2: Continued

Fungal Species	Tree Species *	Counts **	Abbr***
Gymnopilus penetrans (Fr.) Murrill	Tc	2	ND
Lachnella filicina (P. Karst.) W.B. Cooke	Ap, Pc, Tc	4	lachfili
Lachnella sp.	Ap, Fe, Tc	4	lach_sp
Lachnella villosa (Pers.) Gillet	Fe	2	ND
Mycena galericulata (Scop.) Gray	Qr	1	ND
Pleurotellus chioneus (Pers.) Kühner	Ca, Tc	4	ND
Pleurotus cornucopiae (Paulet) Rolland	Fe	1	ND
Pluteus cervinus P. Kumm.	Tc	1	ND
Resupinatus applicatus (Batsch) Gray	Cb, Tc	2	ND
Resupinatus trichotis (Pers.) Singer	Cb, Qr	2	ND
Unguicularia cf. millepunctata (Lib.) Dennis	Qr, Tc	4	ungumill
Auriculariales / Tremellales			
Auricularia auricula-judae (Fr.) J. Schröt.	Ap, Pc, Rp, Tc	5	auriauri
Basidiodendron eyrei (Wakef.) Luck-Allen	Tc	1	ND
Exidia cartilaginea S. Lundell & Neuhoff	Tc	3	ND
Exidia glandulosa (Bull.) Fr.	Ap, Qr, Qru, Tc	4	ND
Exidia thuretiana (Lév.) Fr.	Tc	7	exithur
Exidia villosa Neuhoff	Tc	1	ND
Sebacina calcea (Pers.) Bres.	Qru	1	ND
Dacrymycetales			
Dacrymyces cf. lacrymalis (Pers.) Sommerf.	Fe	1	ND
Dacrymyces stillatus Nees	Ca, Fe, Qr, Rp, Tc	9	dacrstil
Hymenochaetales			
Hyphodontia microspora J. Erikss. & Hjortstam	Tc	2	ND
Hyphodontia nespori (Bres.) J. Erikss. & Hjortstam	Qr	2	ND
Hyphodontia sambuci (Pers.) J. Erikss.	Ap, Fe	3	ND
Phellinus contiguus (Pers.) Pat.	Qr	5	phelcont
Phellinus sp.	Ca, Qr, Rp, Tc	8	phell_sp
Schizopora radula (Pers.) Hallenb.	Cb, Qr, Qru, Tc	13	schiradu
Polyporales			
Brevicellicium sp.	Cb	1	ND
Byssomerulius corium (Pers.) Parmasto	Tc	2	ND
Cerrena unicolor (Bull.) Murrill	Ap	2	ND
cf. Lopharia spadicea (Pers.) Boidin	Tc	1	ND
Coriolopsis gallica (Fr.) Ryvarden	Ap	1	ND
Cylindrobasidium laeve (Pers.) Chamuris	Cb	1	ND
Daedaleopsis confragosa (Bolton) J. Schröt.	Ca	2	ND
Galzinia incrustans (Höhn. & Litsch.) Parmasto	Cb	1	ND
Hapalopilus rutilans (Pers.) P. Karst.	Qru, Tc	2	ND
Hyphoderma medioburiense (Burt) Donk	Tc	1	ND
Hyphoderma mutatum (Peck) Donk	Tc	1	ND
Hyphoderma praetermissum (P. Karst.) J. Erikss. & Å. Strid	Qr, Rp	1	ND
Hyphoderma radula (Fr.) Donk	Cb, Ca, Qru Tc	4	ND
Hyphoderma setigerum (Fr.) Donk	Ca, Tc	3	hyphseti
Hypochnicium eichleri (Bres.) J. Erikss. & Ryvarden	Qr	1	ND
Hypochnicium polonensis(Bres.) Å. Strid	Tc	1	ND
Hypochnicium vellereum (Ellis & Cragin) Parmasto	Cb	1	ND
Laetiporus sulphureus (Bull.) Murrill	Qr	1	ND
Merulius tremellosus Schrad.	Tc	1	ND
Oligoporus subcaesius (A. David) Ryvarden & Gilb.	Fe	2	ND
Phlebia cf. centrifuga P. Karst.	Tc	1	ND
Phlebia radiata Fr.	Qr	1	ND
Polyporus ciliatus (P. Karst.) Sacc.	Qr, Tc	2	ND
Radulomyces confluens (Fr.) M.P. Christ.	Cb, Fe, Pc, Rp, Tc	8	raduconf
Radulomyces cf. hiemalis (Laurila) Parmasto	Tc	1	ND
Radulomyces molaris (Chaillet) M.P. Christ.	Cb, Ca, Qr, Qru	9	ND
Trametes versicolor (L.) Lloyd	Qr	1	ND
Vuilleminia comedens (Nees) Maire	Qr	14	vuilcome
Russulales			
Peniophora cinerea (Pers.) Cooke	Ap, Ca, Fe, Qr, Qru, Tc	18	penicine

Tab. 2: Continued

Fungal Species	Tree Species *	Counts **	Abbr***
Peniophora incarnata (Pers.) P. Karst.	Cb	1	ND
Peniophora laeta (Fr.) Donk	Cb, Pc	7	ND
Peniophora lycii (Pers.) Höhn. & Litsch.	Ap, Fe	5	penilyci
Peniophora quercina (Fr.) Cooke	Qr	5	peniquer
Peniophora rufomarginata (Pers.) Bourdot & Galzin	Tc	19	penirufo
Peniophora violaceolivida (Sommerf.) Massee	Pc	2	ND
Stereum hirsutum (Willd.) Gray	Qr	2	ND
Stereum ochraceo-flavum (Schwein.) Fr.	Cb, Qr	2	ND
Stereum rameale (Schwein.) Burt	Cb, Qr	7	sterrame
Schizophyllales			
Schizophyllum commune Fr.	Ap, Qr, Tc	6	schicomm
Fungi imperfecti			
Camarosporium sp.	Rp	1	ND
Corniculariella spina (Berk. & Ravenel) DiCosmo	Fe	1	ND
Epicoccum nigrum Link	Ap	1	ND
Exosporium tiliae Link	Tc	5	exostili
cf. Flagellospora curvula Ingold	Qru	1	ND
Micropera sp.	Cb	1	ND
Phoma epicoccina Punith., M.C. Tulloch & C.M. Leach	Ap	1	ND
Phoma sp.	Ap	1	ND
Trichoderma sp.	Ap, Cb, Fe, Qr, Tc	5	ND
Tubercularia vulgaris Tode	Ap, Tc	6	tubevulg
Rabenhorstia tiliae (Fr.) Fr.	Tc	4	rabetili
Stegonsporium acerinum Corda	Ap	7	stegacer
Stegonsporium pyriforme (Hoffm.) Corda	Ap	8	stegpyri

Beta diversity

Regarding the fungal composition, the four tree species differ considerably (Figs. 5 and 6, Tab. 3). The ordination biplot diagrams (Figs. 5 and 6) display similarities and dissimilarities between fungi and tree species. The further two fungal species are apart, the less similar they are concerning their occurrence on different trees. The more distant two tree species are, the less similar they are concerning the composition of their mycota. Distinct groupings of samples and fungal species are apparent. In Fig. 5, axis 2 is plotted against axis 1. *Eutypa maura* (Fr.) Sacc., *Tubercularia vulgaris* Tode, *Stegonsporium acerinum* Corda and *Stegonsporium pyriforme* (Hoffm.) Corda are located clearly in the centroid of the examined individuals of sycamore (upper part of diagram). Individuals of oak group around *Peniophora quercina* (Pers.) Cooke, *Diatrypella quercina* (Pers.) Cooke, *Radulomyces molaris* (Chaillet) M. P. Christ, *Phellinus contiguus* (Pers.) Pat., *Stereum rameale* (Schwein.) Burt and *Vuilleminia comedens* (Nees) Maire respectively (lower left of diagram). In order to obtain a better resolution for fungal species clustering with *T. cordata*, axis 3 was plotted against axis 2 in figure 6. In addition to the above mentioned groupings, it is apparent that *Patellaria atrata* Fr., *Exosporium tiliae* Link, *Exidia cartilaginea* S. Lundell & Neuhoff, *Peniophora rufomarginata* (Pers.) Bourdot & Galzin, *Pleurotellus chioneus* and *Hypho-derma setigerum* (Fr.) Donk also exhibit strong association to their hosts. In contrast to this, other fungi lie between tree species like *Peniophora lycii* (Pers.) Höhn. & Litsch., *Peniophora cinerea* (Pers.) Cooke, *Lachnella filicina* (P. Karst.) W. B. Cooke, *Dacrymyces stillatus* Nees or *Radulomyces confluens* (Fr.) M. P. Christ. These fungi were found on different tree species and showed no substrate specificity. The arch effect, which occurrs often when using CA, was not obvious (for computation of CA by reciprocal averaging see GAUCH [1982] or TER BRAAK & SMILLAUER [1998]). Analyses using NMS with 'PC-ORD' (MC CUNE & MEFFORD 1999) resulted in similar diagrams (not shown). Additionally table 3 displays values and significances to define fungal species assemblages on each tree species. In consequence, indicator species can be named but is not done here.

Many fungal species were found fruiting on and in outer layers of the twig (bark, phloem fibres, sapwood) of one tree species exclusively. *Rabenhorstia tiliae* (Fr.) Fr., *Exosporium tiliae*, and *Peniophora rufomarginata* grew on *T. cordata*, *Cryptosphaeria eunomia* (Fr.) Fuckel, *Nitschkia cupularis* (Pers.) P. Karst. and *Episphaeria fraxinicola* on *F. excelsior*, *Diatrypella quercina*, *Peniophora quercina* and *Vuilleminia comedens* on *Q. robur*, *Peniophora laeta* (Fr.) Donk, *Pleomassaria carpini* (Fuckel) Sacc. on *C. betulus* and *Stegonsporium acerinum*, *S. pyriforme* and *Eutypa maura* occurred on twigs of *A. pseudoplatanus*.

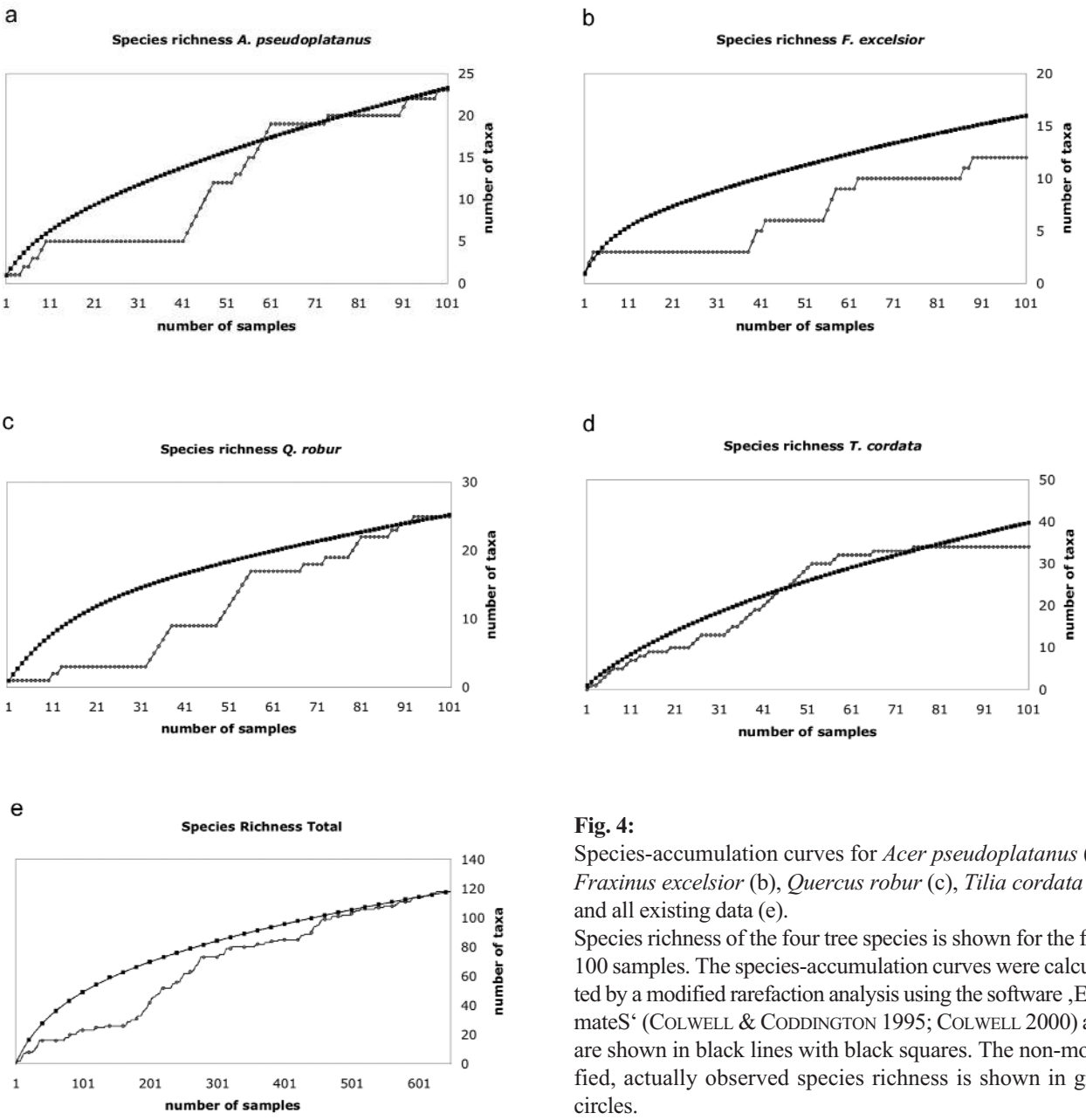

Fig. 4:
Species-accumulation curves for *Acer pseudoplatanus* (a), *Fraxinus excelsior* (b), *Quercus robur* (c), *Tilia cordata* (d) and all existing data (e).
Species richness of the four tree species is shown for the first 100 samples. The species-accumulation curves were calculated by a modified rarefaction analysis using the software ‚EstimateS' (COLWELL & CODDINGTON 1995; COLWELL 2000) and are shown in black lines with black squares. The non-modified, actually observed species richness is shown in grey circles.

Discussion

Sampling and cultivation

As stated previously the number of examined individuals per tree species as well as amounts of sampled wood sometimes differed strongly. Nevertheless the gathered data on diversity and substratum preferences could be regarded as representative of the investigation plot and allowed for statistical analyses. Because of the multivariate nature of our data we decided to apply the multivariate statistics explained in the method section to extract main environmental gradients.

The storage of samples in open boxes and the temporary spraying with water prevented permanent moist conditions and minimized the occurrence of superficially fast growing imperfect fungi such as *Penicillium* Link, *Botrytis* P. Micheli ex Pers. or *Cladosporium* Link. The only frequently found species of this group was *Trichoderma lignorum* (Tode) Harz. It appeared mostly on wood of *Q. robur* and grew on the surface of old basidiomes of *V. comedens* in more than 80 % of cases. Few of these samples were stored for more than two weeks and occasionally the teleomorphic state *Hypocrea rufa* (Pers.) Fr. appeared between the *Trichoderma* mycelia. Our method of storing wood in high humidity after sampling seems appropriate to stimulate fructification especially if sampling occurred during unfavourable conditions (drought, frost). Fruitbodies of *P. chioneus*, *R. applicatus*, *R. trichotis*, *E.fraxinicola*, *Orbilia spp.* and *Lachnella spp*. for instance often were

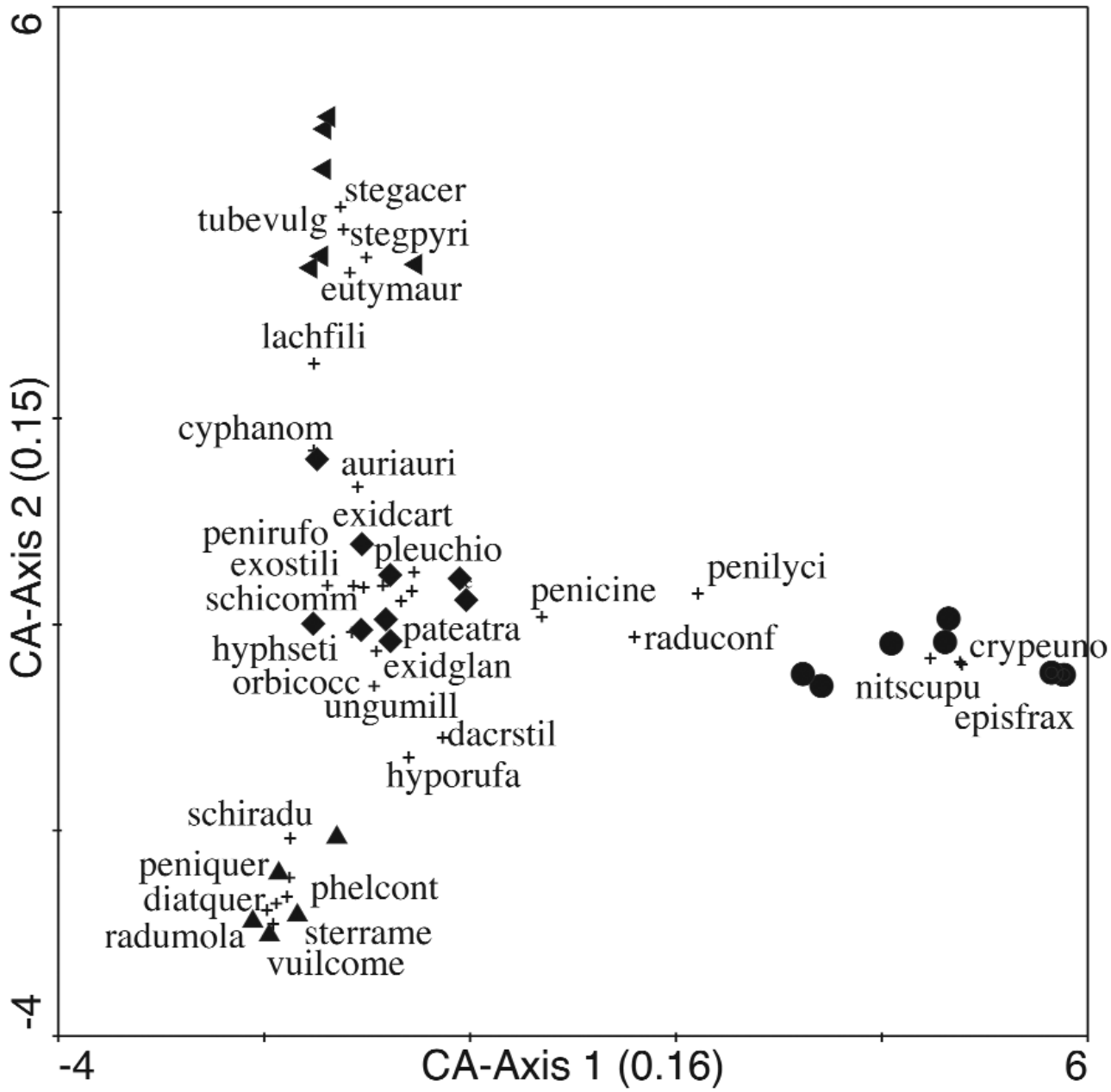

Fig. 5: Ordination biplot of a CA with axis 2 plotted against axis 1. Values in brackets are the percentage of total explained variation of species data (see Tab. 2) The data matrix used contained presence-absence data of species with 3 or more counts per sample unit (tree individual). Only *Acer pseudoplatanus* (◀), *Fraxinus excelsior* (●), *Quercus robur* (▲) and *Tilia cordata* (◆) are considered. Program settings: CA, interspecies distance, Hill-scaling, no transformation, no weighting.

not present in the field but emerged within several days after keeping the samples in boxes at high humidity.

Many phaneroplasmodia and sporocarps of Myxomycetes emerged rapidly on the branches after a few days of storage in the laboratory. Together with the observation of many sporocarps in the field (eg. *Stemonitis* Gled., *Arcyria* Hill ex F.H. Wigg) this indicates that the canopy might be an ideal habitat for slime molds (SCHNITTLER pers. comm. [a publication on this topic is in preparation]).

Species richness

Without doubt the detected richness of 118 fungal species is preliminary. One can clearly see that species-accumulation curves rise almost linearly and obviously more samples will have to be collected before species saturation can be approached and inferred (Fig. 4). About 10 % of the collected material could not be identified at species or generic level because fructifications were in conditions lacking spores or other morphological features important for determination. With the

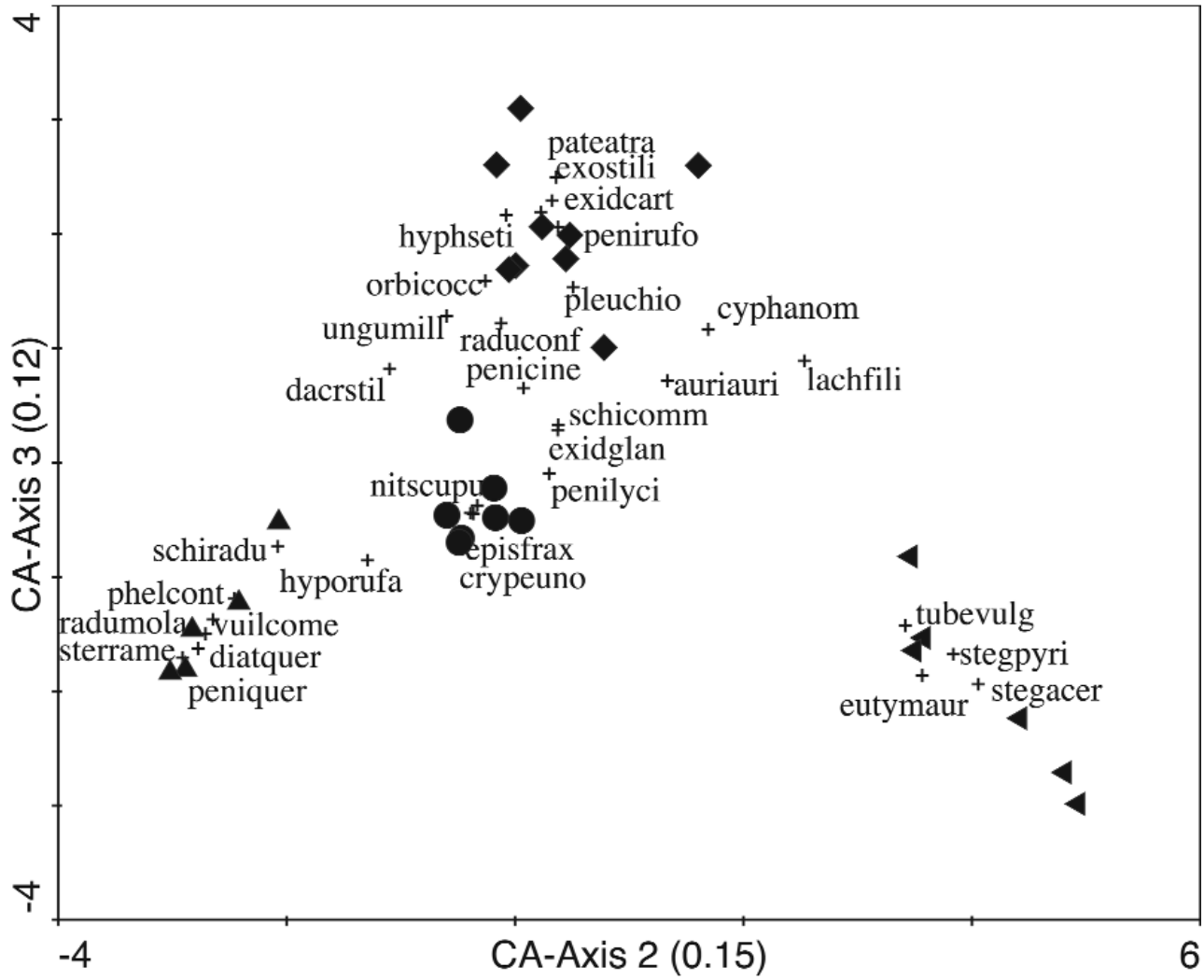

Fig. 6: Ordination biplot of a CA with axis 3 plotted against axis 2. Values in brackets are the percentage of total explained variation of species data (see Tab. 2) The data matrix used contained presence-absence data of species with 3 or more counts per sample unit (tree individual). Only *Acer pseudoplatanus* (◀), *Fraxinus excelsior* (●), *Quercus robur* (▲) and *Tilia cordata* (◆) are considered. Program settings: CA, interspecies distance, Hill-scaling, no transformation, no weighting.

identification of fungi restricted to morphological-chemical characters only data on the diversity of morphospecies were captured. We are aware of the fact that only the additional application of molecular methods allows us to define biological species and to estimate the effective species diversity of a study site (HAWKSWORTH 2001; KÜFFER & HALLENBERG 2000; HALLENBERG & LARSSON 1991; HALLENBERG 1991). Isolating DNA samples from the species and analysing fungal DNA sequences was not possible within the framework of this research. To clarify the problem of defining biological species for wood inhabiting fungi a few examples are given for corticioid species found in the crane site. Following NILSSON et al. ([2003] for *Hyphoderma setigerum*), HALLENBERG, LARSSON & LARSSON ([1994] for *Hyphoderma praetermissum* [P. Karst.] J. Erikss. & Å. Strid) and CHAMURIS (1991), HALLENBERG & LARSSON (1992) (both for *Peniophora cinerea*), many members of corticioid fungi form cryptic species or species complexes with populations being physiological and genetically different. NILSSON et al. (2003) hypothesise that due to high spore dispersal capacities of corticioid fungi, allopatric speciation probably played an important role in the diversification processes of this group. CHAMURIS (1991) supposed, that changes in host and substratum preferences may also be involved in the formation of European sibling species in the *P. cinerea* complex. Therefore, molecular analyses have to be done with the corticioid fungi we collected, to decide for instance if *P. cinerea* found on *F. excelsior* is a different biological species from that found on *T. cordata*. A similar taxonomical situation has to be assumed for other systematical groups that were typical for the investigated forest canopy such as pyrenomycete fungi. Aside from problems concerning the delimitation and recognition of fungal species there are ad-

Tab. 3: IndVal output showing substrate preferences. The values are the sums of occurrences of fungi per sample. Ranks and significance values are also displayed to allow definition of indicator species (written with bold). Program settings: 499 permutations, significance level: p=0.01, random number =5, no wheighting of species or samples. AcPs: *Acer pseudoplatanus*, CaBe: *Carpinus betulus*, FrEx: *Fraxinus excelsior*, QuRo: *Quercus robur*, TiCo: *Tilia cordata*, CeAv: *Cerasus avium*, PoCa: *Populus* x *canadensis*, QuRu: *Quercus rubra*, RoPs: *Robinia pseudacacia*. Sign.: ** = significant as to define indicator species, NS = not significant, ?? = undecided because of small number of samples.

Number of sampled trees	**7**	**2**	**8**	**5**	**9**	**2**	**1**	**1**	**2**		
Fungal Species	**AcPs**	**CaBe**	**FrEx**	**QuRo**	**TiCo**	**CeAv**	**PoCa**	**QuRu**	**RoPs**	**Rank**	**Sign.**
Eutypa maura	**16**	0	0	0	0	0	0	0	0	**1**	**
Stegonsporium pyriforme	**8**	0	0	0	0	0	0	0	0	**1**	**
Stegonsporium acerinum	**7**	0	0	0	0	0	0	0	0	6	??
Tubercularia vulgaris	**5**	0	0	0	**1**	0	0	0	0	17	NS
Massaria pupula	**4**	0	0	0	0	0	0	0	0	7	NS
Peniophora laeta	0	**6**	0	0	0	0	**1**	0	0	**4**	**
Schizopora radula	0	**4**	0	**7**	**1**	0	0	**1**	0	91	NS
Cryptosphaeria eunomia	0	0	**22**	0	0	0	0	0	0	**1**	**
Nitschkia cupularis	**2**	0	**15**	0	0	0	0	0	0	**1**	**
Episphaeria fraxinicola	0	0	**12**	0	0	0	0	0	0	**1**	**
Lachnella cf. villosa	0	0	**3**	0	0	0	0	0	0	147	NS
Lachnella sp.	**1**	0	**2**	0	**1**	0	0	0	0	415	NS
Vuilleminia comedens	0	0	0	**14**	0	0	0	0	0	**2**	**
Diatrypella quercina	0	0	0	**11**	0	0	0	**2**	0	11	??
Peniophora quercina	0	0	0	**5**	0	0	0	0	0	13	NS
Phellinus contiguus	0	0	0	**5**	0	0	0	0	0	12	NS
Stereum rameale	0	**1**	0	**6**	0	0	0	0	0	23	NS
Hypocrea rufa	**1**	0	**1**	**6**	**1**	0	0	0	0	55	NS
Colpoma quercinum	0	0	0	**3**	0	0	0	0	0	130	NS
Peniophora rufomarginata	0	0	0	0	**19**	0	0	0	0	**1**	**
Exosporium tiliae	0	0	0	0	**5**	0	0	0	0	23	NS
Patellaria atrata	0	0	0	0	**5**	0	0	0	0	23	NS
Exidia cartilaginea	0	0	0	0	**4**	0	0	0	0	157	NS
Rabenhorstia tilia	0	0	0	0	**4**	0	0	0	0	136	NS
Coniochaeta sp.	0	0	0	0	**3**	0	0	0	0	151	NS
Orbilia cf. *coccinella*	0	**1**	0	**1**	**5**	0	0	0	0	234	NS
Unguicullaria cf. millepunctata	0	0	0	**1**	**3**	0	0	0	0	241	NS
Schizophyllum commune	**1**	0	0	**2**	**3**	0	0	0	0	397	NS
Hyphoderma radula	0	**1**	0	0	0	**2**	0	**1**	0	7	??
Radulomyces molaris	0	**2**	0	**4**	0	**2**	0	**1**	0	33	NS
Hyphoderma setigerum	0	0	0	0	**2**	**1**	0	0	0	12	NS
Pleurotellus chioneus	0	0	0	0	**3**	**1**	0	0	0	14	NS
Peniophora lycii	**1**	0	**2**	0	0	**1**	**1**	0	0	224	NS
Phellinus sp.	0	0	0	**5**	**1**	**1**	0	0	**1**	208	NS
Merismodes anomalus	**1**	0	0	0	**2**	0	**1**	0	0	33	NS
Lachnella cf. fillicana	**1**	0	0	0	**2**	0	**1**	0	0	37	NS
Auricularia auricula-judae	**1**	0	0	0	**2**	0	**1**	0	**1**	151	NS
Peniophora cinerea	**1**	0	**7**	**1**	**5**	**1**	**1**	**2**	0	71	NS
Exidia glandulosa	**1**	0	0	**1**	**4**	0	0	**1**	0	63	NS
Dacrymyces stillatus	0	**2**	**1**	**2**	**2**	0	0	**1**	**1**	286	NS
Massaria anomia	0	0	0	0	0	0	0	0	**4**	**1**	**
Diaporthe oncostoma	0	0	0	0	0	0	0	0	**3**	**2**	**
Radulomyces confluens	0	**2**	**1**	0	**1**	0	**1**	0	**3**	41	NS

ditional difficulties in respect to their biology and ontogeny. Many fungi grow vegetatively most of the time and fructificate only sporadically or exist symptomless as endophytes in living or dead parts of a tree (WILSON 1995, 1993). Such fungi probably await death of the branch or suitable microclimatic conditions to expand into the wood (BODDY & RAYNER 1983). The discovery of such species therefore may require several years of investigation and additional cultivation techniques. Many species of the pyrenomycetes, Coelomycetes or the Helotiales produce scattered, minute and short living fruitings. Especially cup fungi like *Orbilia* Fr. or *Mollisia* (Fr.) P. Karst., but also members of the Auriculariales/Tremellales possess sporomes that are nearly invisible in desiccated conditions. Hence, such species are easily overlooked.

Fungal richness and composition on host trees

Our results show clearly that tree species differ with respect to their mycota. Lignicolous fungi that grow during initial stages of decay are often known to be highly specific to their hosts. This specificity is probably due to secondary compounds in bark and wood and to specific defense mechanisms that follow fungal infection (PEARCE 1996). In our studies *T. cordata* possessed the richest mycota with 47 fungal species. This high diversity is probably due to the lack of phenolic compounds and the softness of the wood that facilitates the invasion of insects. MALLOCH & BLACKWELL (1992) speculated that insects most probably play an important role in the dispersal of fungal diaspores. Preliminary results of entomological studies within the LAK project demonstrate a high diversity of insects on lime trees, especially xylotrophic beetles and mycetophagous flies (SCHMIDT, pers. comm.). This diversity seems to be positively correlated with the fungal richness and supports the idea that insects act as potent vectors of lignicolous fungi within the observed part of the forest.

Another probable reason for the high beta diversity and the differences in fungal richness on the tree species is the high structural complexity of the investigated part of the forest. PAR measurements in summer 2003 resulted in the division of canopy trees into three distinct vertical zones. Furthermore the conditions in ash crowns seemed to be more uniform than in oak crowns (HORCHLER 2004). The more heterogeneous conditions with respect to solar radiation, and, to a large extent, to temperature possibly result in the availability of more ecological niches in oak trees. Indeed, they are populated by a higher number of fungal species. Additionally, some of the oak trees accessible with the crane are more than 200 years old. They possess a large amount of dead branches as potential substrate for lignicolous fungi. Sycamore and ash are mostly younger than 100 years and enjoy sound health compared with oak and lime trees.

Canopy mycoflora

Species richness and composition in the canopy cannot be compared with that on the forest floor of the plot for the lack of comprehensive data (a comparative study is planned for the near future). However, there are some indications from the Leipzig crane site both from this study as well as from the literature that the fungal associations of the canopy strongly differ from those of the forest floor. HALLENBERG & PARMASTO (1998) mentioned that dead attached branches constitute a specific niche in nature for wood-inhabiting fungi. Such branches are often dry for long periods of time and fungal growth is limited to recurrent periods of humid weather. A characteristic flora of basidiomycetes of the orders Russulales, Polyporales and Hymenochaetales is found as primary occupiers in this habitat. This view is supported by our observation in which members of corticioid fungi (eg. of Corticiaceae, Stereaceae, Hymenochaetaceae, Schizoporaceae) comprise about one third of the total species richness. NUÑEZ (1996) describes also several corticioid fungi growing frequently on dead hanging branches. INGOLD (1954) mentioned pyrenomycete fungi as a group which is also able to outlast long periods of aridity. In our studies they were the second most abundant group in the canopy with 15 % of total species richness. BARAL, BARAL & MARSON (2003) and SHERWOOD (1981) mentioned that xerotolerant or xeroresistant taxa of the Helotiales are frequent. In some genera and families xerotolerant species even outnumber the intolerant (BARAL, pers. comm.). These are important factors to explain the majority of ascomycetes in the species list (Tab. 2). The high number of heterobasidiomycetes can also be explained by the special climatic conditions that occur in the canopy. Draught can do no harm to species like *Exidia* spp. because the sporomes are able to desiccate in dry periods. This process is reversible, the fungi start growing again if conditions change to higher humidity.

Taking into account the origin of decay in living deciduous trees as proposed by BODDY & RAYNER (1983) it becomes understandable why fungal communities on dead attached branches differ from that of dead wood lying on the forest floor. CHAPELA & BODDY (1988c) reported on the disappearence of early colonisers that emerged in branches still attached to the tree after falling to the ground. BODDY & RAYNER (1984) stated that communities established on attached twigs can be regarded as the starting point for subsequent development on the woodland floor. In their review, LODGE & CANTRELL (1995) cited the studies of NUÑEZ & RYVARDEN (1992) and RYVARDEN & NUÑEZ (1992), who investigated wood-decaying fungi from understorey and canopy of a rain forest in Cameroon, Africa. They found that the extreme moisture and temperature regimes of the canopy are apparently more selective, resulting in a lower species richness and different species composition.

The almost complete lack of fungi with ephemeral fructifications in the canopy of our plot was apparent. LODGE & CANTRELL (1995) think that fruiting of agaric fungi may be rare and confined to the wet season. In our study basidiomes of *Pluteus cervinus*, *Mycena galericulata* and *Gymnopilus hybridus* were found only once. They emerged exclusively in shaded areas after extensive rainfall and high relative humidity on thick branches (UNTERSEHER, OTTO & MORAWETZ 2003). Other Agaricales were represented by *Episphaeria fraxinicola*, *Crepidotus subtilis*, *Pleurotellus chioneus*, *Resupinatus spp*. and *Lachnella spp. Episphaeria fraxinicola* and *Lachnella spp*. belong to the cyphelloid basidiomycetes, whose minute, cup shaped basidiomes are plastic. Under humid conditions they emerge quickly on the upper side of branches. They take a spheroidal shape when their tissues dry up thus enclosing the hymenium. This probably results in a slower desiccation of the inner fertile, damageable structures. *C. subtilis* and *P. chioneus* possess small basidiomes of about 1cm diameter. They develop well protected in clefts of branches and under partly detached bark.

The great number of available environments and substrata in old growth, species rich, temperate deciduous forests like the study area in Leipzig most likely leads to high local diversity but also makes sufficient sampling difficult. With the use of construction cranes in long-term canopy projects it be-

comes easier to investigate fungal richness at all vertical levels of a forest. Considering the fact that fungi play a very important role in nutrient cycling on both the temporal and spatial scales, and that various associations with other organisms exist, more attention should be given to fungi in all canopy projects worldwide.

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