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ORIGINAL ARTICLE

Insights into fungal communities colonizing the acarosphere in a forest soil habitat

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Abstract

Knowledge on the diversity and ecology of microfungi associated with soil-dwelling mites is rather limited. To get insights into associations between the two highly diverse groups, we studied composition and potential function of mite-associated fungal communities occurring in soil. Two different mite species living in temperate region pine forest soil were screened for associated fungi. The fungal community was assessed by restriction fragment length polymorphism (RFLP) analyses in a predatory (*Leptogamasus obesus*) and a predominantly saprobic (*Oppiella subpectinata*) mite species as well as in the organic soil layer. Key fungi were identified by sequencing, and community composition was exemplarily compared between the RFLP and a 454 metabarcoding approach. Composition of the fungal communities differed between mite species and between mites and organic soil layer. The mites were predominantly associated with Zygomycota, less frequently with Ascomycota, and rarely with Basidiomycota. The bulk soil was colonized by roughly equal proportions of the three phyla. Fungal taxa being known to exhibit chitinolytic activity were predominantly restricted to mites. Compositional and functional differences between the communities suggest that mites represent a particular microhabitat for fungi, the "acarosphere." This mobile habitat may contribute to nutrient cycling by combining fungal and animal decomposition activities and serve as vector for soil-inhabiting fungi.

Keywords Fungi · Mites · Micro-compartment · ITS rRNA gene · *Leptogamasus obesus* · *Oppiella subpectinata*

Introduction

Organic layers covering the mineral soil constitute a complex environment with a multitude of biotic interactions. Elementary processes of phosphorous, nitrogen, and carbon cycling are predominantly accomplished by bacteria and fungi (Smith et al. 1993; Dijkstra et al. 1998; Romaní et al. 2006). These processes mostly occur in the proximity of plant roots and soil-inhabiting animals, which facilitates decomposition processes of organic matter (Coleman 1986). Specific structures and compartments in the rhizosphere such as mycorrhiza or plant root tubercles facilitate nitrogen and/or phosphorus uptake (Spratt 1919; George et al. 1995).

The bulk soil may also be subdivided into specific micro-compartments, which differ in terms of nutrient availability and composition, structure, pore volume, acidity, and other physiochemical properties. The specific nature of each of these compartments entails colonization by specific soil biota communities (Nazir et al. 2010). Indeed, distinct or even compartment-specific microbial communities have already been identified for different litter layers (Lindahl et al. 2007; Clemmensen et al. 2013; Peršoh et al. 2013), soil horizons (Uroz et al. 2013; Weig et al. 2013; Gabor et al. 2014; Peršoh et al. 2018), the rhizosphere of different plant species (Marschner et al. 2004), and the drilosphere, i.e., burrows resulting from earthworm activities (Stromberger et al. 2012).

Generally, the combined activities of soil micro- and mesofauna and of bacterial and fungal microorganisms are one of the key factors enabling the successful establishment

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of new compartments with a significant impact on nutrient flux (Eisenbeis 2006). Emerging and altering microhabitats may attract further organisms resulting in microbial communities that change over time (Effmert et al. 2012; Kuzyakov and Blagodatskaya 2015). The activity of epigeic earthworms in forests soils, for instance, affects the composition of whole fungal communities (McLean and Parkinson 2000). Furthermore, the galleries of wood-inhabiting ambrosia beetles are obligately associated with auxiliary ambrosia fungi (Batra 1963), which differ between beetle species (Nakashima et al. 1987; Gebhardt et al. 2005). And finally, arthropods themselves may act as fungal microhabitats of very specific character. *Cordyceps* spp. from tropical forests are known for their narrow host spectra, particularly in ant-fungal associations, where they constitute primary pathogens of these insects (Evans 1982). Other host-specific interactions with flies or beetles are described for obligate parasitic fungi from the Laboulbeniales (e.g., Blackwell 1994).

Soil-dwelling mites are a rather prominent element of the mesofauna, as they constitute the most abundant and species-rich group of arthropods in the pedosphere (Wallwork 1983; Moore et al. 1988; Lavelle 1997). Comprising parasites, predators, herbivores, detritivores, and fungal and bacterial grazers, they play different roles in the food web, but also serve as host animals for microorganisms (Walter and Proctor 1999; Weigmann and Miko 2006). Mite activities influence the formation of new compartments and the establishment of distinct microbial communities. One of the most apparent effects caused by soil-inhabiting mites is the scrunching and feeding on organic matter that increases the relative particle surface, thus facilitating efficient microbial colonization (Swift et al. 1979; Walter and Proctor 1999) and in consequence, accelerating the decomposition process (Kendrick 1962). Resulting spatially and temporally varying cavities promote respiration and biomass production of soil-dwelling fungi (Maraun et al. 1998). In return, mites depend on microbial degradation activities, since they, as most soil animals, are unable to digest the particular organic matter without involvement of associated microorganisms (Eisenbeis 2006). In particular, yeast-like fungi are known to support intra- and extraintestinal digestion of arthropods (Vega and Blackwell 2005).

Interdependencies between mites and fungi may therefore significantly contribute to an ecological balance that might be necessary to preserve the major soil functions (Thomsen et al. 2012). For instance, fungal recolonization of contaminated or depauperate soils is facilitated by mite-mediated phoresy (Coleman 1985; Maraun et al. 1998). Many fungi are known as being primarily entomopathogens, but also playing additional roles during their life cycle. They may act as endophytes and antagonists of plant pathogens, or be associated with the rhizosphere, and therefore possibly promote plant growth (O'Brien et al. 2005). The mites themselves are mobile "micro-compartments" of the soil, with specific communities of associated microorganisms colonizing the cuticle, digestive tract, and other parts of their animal vectors (Poinar and Poinar 1998; Hoy and Jeyaprakash 2005; Renker et al. 2005).

This study provides first insights into the diversity of mite-associated fungi, i.e., fungi with occurring in close physical contact to mite species, irrespective of the nature of interaction (e.g., antagonistic or mutualistic) and its relevance (obligate or facultative) for thriving of the species. In order to assess the mite-associated fungal communities, fungi in two ecologically distinct mite species frequently found in European temperate forest soils were compared. One of those was the obligate predatory (Manu 2010) gamasid mite *Leptogamasus obesus*. Representatives of the genus are known to feed on arthropods as springtails and dipteran larvae or on other soil invertebrates like nematodes (Buryn 2008; Manu et al. 2013), but not on fungal hyphae or debris. The other mite in focus, *Oppiella subpectinata*, belongs to the Oribatida. The genus *Oppiella* has been described to comprise litter feeders (McMinn and Crossley 1993) and fungal grazers (Ponge 1991; Kaneko et al. 1995; Schneider and Maraun 2005) with a potential preference for ectomycorrhizal fungi (Remén 2010). And also, algae or even nematodes are described as food (Moore and de Ruiter 2012). Current findings indicate a more diverse role in the food web, where *Oppiella* spp. are additionally considered to act as mesofauna predators (Klarner 2014; Lehmitz and Maraun 2016; Pausch et al. 2016). Overall, the genus seems to exhibit omnivorous feeding habits being typical for scavengers. The fungal communities found in connection with these mites were also compared to those colonizing the surrounding habitat, i.e., the organic layer of soil, to ascertain microhabitat preferences of the fungi. We hypothesized that fungal communities differ between mites and soil, as well as between the two mite species. We further assumed that traits differ between fungi preferring mites and soil.

Materials and methods

Sampling site and sample collection

The investigation site of about 4 m^2 in size is located in a mixed forest with predominant *Pinus sylvestris* on the hill Hohe Warte close to the city of Bayreuth, Upper Franconia, Germany (49° 58′ 16″ N, 11° 34′ 51″ E, 460 m alt.). The understory is dominated by *Vaccinium myrtillus*, *Calluna vulgaris*, and two bryophyte species (*Polytrichum formosum* and *Pleurozium schreberi*). The soil is a podsolized ranker, covered by an organic layer of 5–10 cm in depth.

Over a period of 18 months, four replicates of samples (250 cm^3 each) were taken every second month from the uppermost 5 cm of the organic Oe subhorizon, consisting of fragmented litter. The covering layer of fresh and

undecomposed litter was removed before sampling. The sampling area itself was a small clearance still comprising a more or less homogenous forest ground vegetation. Sampling points for each sampling event were randomly chosen. Thereby, the four replicates were sampled spatially as close as possible. Three samples were used for the extraction of mite individuals and a fourth one to analyze the bulk soil-inhabiting fungal communities. Mites were extracted using a Berlese funnel (Berlese 1905). Gamasid mites were identified using the key of Karg (1993), and oribatid mites determined by F. Horak (Karlsruhe). *Leptogamasus obesus* Holzmann (Gamasina) and *Oppiella subpectinata* Oudemans (Oribatida) were the only dominating mite species occurring at the sampling site throughout the whole sampling period. Individuals of the two species were superficially washed in a water drop to remove adhering soil particles and subsequently pooled into samples of five and ten individuals, respectively. The different sample sizes compensated the different body sizes of the species and thus the amount of potentially enclosed fungal material. Figure 1 illustrates the whole sampling procedure as well as the preparation and analysis steps described in the following, which were needed for primary data achievement.

Molecular analyses

DNA isolation and amplification

Total DNA was extracted from mite samples (*L. obesus*: 40 samples; *O. subpectinata*: 31 samples) using the Charge Switch® gDNA Plant Kit (Invitrogen) as recommended by the manufacturer, but using 0.2 μl tubes and with all volumes reduced to 10%. DNA from soil (0.5 g of well-mixed material per soil core) was isolated from 12 samples according to Peršoh et al. (2008). The internal transcribed spacer (ITS) rRNA gene (ITS1, 5.8S, and ITS2 regions) was amplified in a total volume of 25 μl containing 0.1 μl Taq polymerase (5 U/μl, Invitrogen), 2.5 μl 10× PCR buffer, 0.75 μl $MgCl_2$ (50 mM), 2.5 μl dNTP mix (2 mM), and 1.25 μl forward and reverse primers (10 μM) each as well as 1 μl DNA extract. The primer pair SSUh35-F/LSUh11-F (Werner et al. 2012) was applied to selectively amplify fungal DNA from soil and mite DNA extracts. Following an initial denaturation step for 2 min at 95 °C, 35 cycles (20 s at 94 °C, 1 min at 58 °C, and 2 min at 72 °C) were conducted. The PCR ended with an elongation step for 15 min at 72 °C.

Sub-cloning, restriction digest, and DNA sequencing of PCR products

The TOPO TA Cloning Kit for Sequencing (Invitrogen) was used for sub-cloning the fungal PCR products (900–1200 bp) according to the manufacturer's instructions. Twenty-four and 96 clones from each mite and soil sample, respectively, were subjected to colony PCR for subsequent analysis. The inserts within the plasmids were amplified using the M13 primers enclosed in the cloning kit.

The restriction enzymes MspI and AluI (Fermentas) were used to digest the 1514 amplified inserts. Restriction fragment length polymorphism (RFLP) patterns were visualized by analysis of ethidium bromide-stained agarose gels (3% agarose in TBE, separation by 90 V). A low molecular weight DNA ladder (New England BioLabs) with a range from 25 to 766 bp served as length standard. Identical RFLP patterns were treated as belonging to one RFLP type (see below). For each non-unique RFLP type—i.e., those detected in at least two different samples—two clones were sequenced. The ITS sequences were deposited in GenBank (www.ncbi.nlm.nih.gov) under the accession numbers LN680553–LN680623.

DNA extracts of five randomly chosen soil samples already screened by the RFLP approach were additionally analyzed by 454 pyrosequencing. Amplicon libraries were prepared as detailed by Peršoh et al. (2013) and shipped to Beckman Coulter Genomics for sequencing. Further processing of the obtained sequence data and the generation of reference sequences (operational taxonomic units (OTUs)) was accomplished using Genomics Workbench (CLC bio), as detailed by Peršoh et al. (2013). The reference sequences were deposited under the accession numbers LN736269–LN736301.

Cluster analysis, taxonomic assignment, and phylogenetic tree calculation

The fragment lengths resulting from the enzymatic digestion were digitally quantified using the software GeneProfiler (Meyer Instruments). Fragments below 50 bp were excluded from the analysis. The RFLP patterns were further analyzed in R (R Development Core Team 2011) using the package RFLPtools (Flessa et al. 2010), which provides a set of functions facilitating the grouping of restriction patterns by similarities calculated from the enclosed fragment numbers and their sizes. Thresholds for grouping RFLP patterns were adjusted to the number of RFLP fragments per clone, to assure consistent resolution. Finally, the resulting clusters of restriction patterns, hence termed as "RFLP types," were manually revised to eliminate falsely grouped elements and unique patterns.

Consistency of this classification with RFLP types was verified by sequence data obtained from clones representing each RFLP type. For this purpose, pairwise similarities between all sequences were determined by conducting a local BLAST search (Altschul et al. 1990) with the settings -m 8 -r 2 -G 5 -E 2. The resulting similarity matrix was subjected to a hierarchical cluster analysis using the R package RFLPtools. Clusters with minimal similarities of 90%, recognized

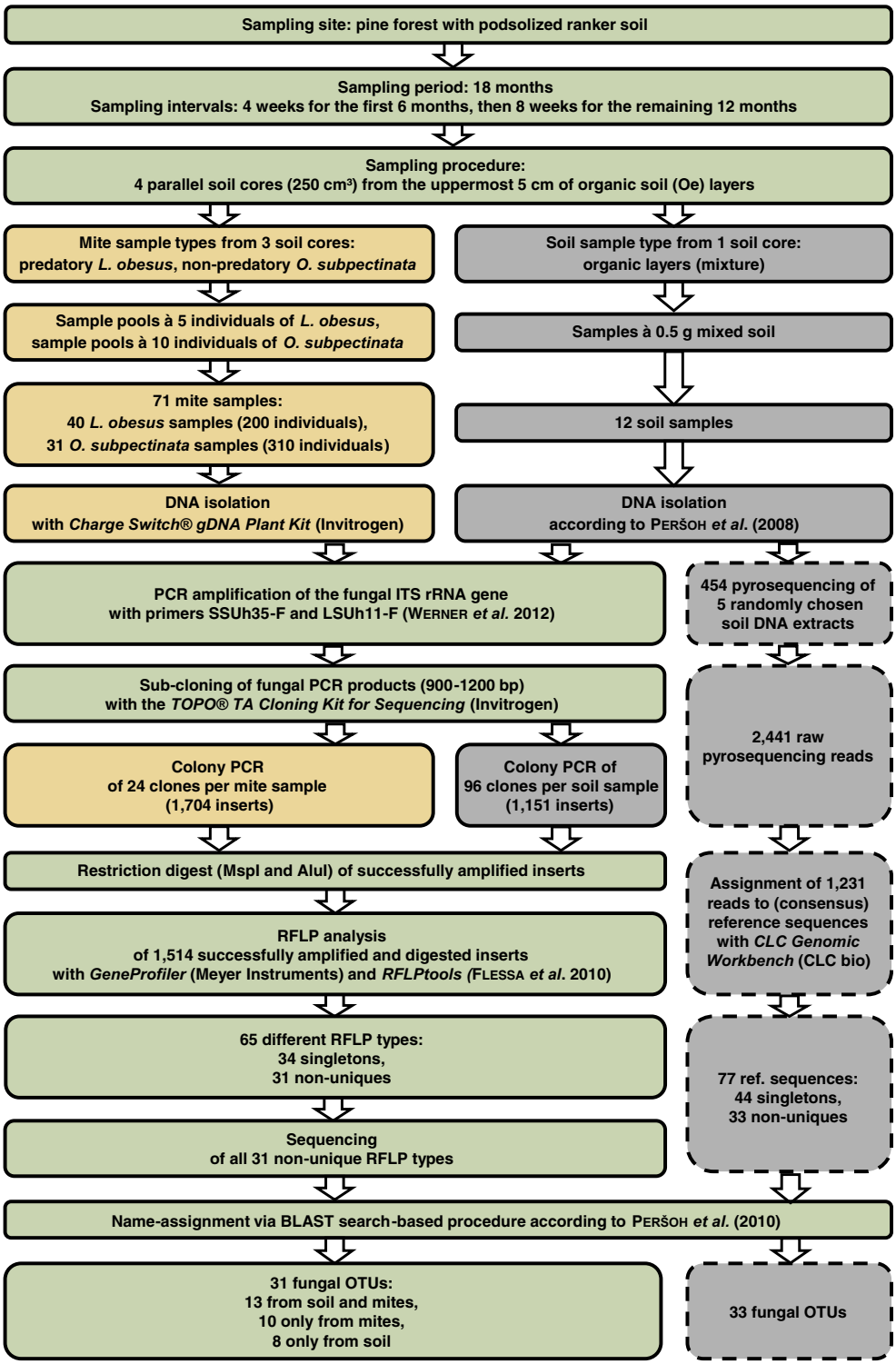


Fig. 1 Primary data achievement of this study. Described are sampling procedure as well as subsequent sample preparation and analysis steps being necessary for fungal OTU generation

according to the average linkage (AL) option, were defined as initial cluster groups. The sequences of each initial cluster group were aligned and the ends of the sequences were truncated to the length of the respective shortest sequence. Sequences covering less than 90% of the ITS region were discarded. Subsequently, a second similarity matrix was calculated based on the length-adapted sequences, and clusters with at least 97% AL similarity (cf. Quince et al. 2009) were assumed to represent one genotype.

Clusters of ITS genotypes were checked for consistency with the corresponding RFLP types. In case of different RFLP types representing the same genotype, the corresponding

RFLP types were unified. Operational taxonomic units (OTUs) represent these final RFLP types (Table 1). The assignment of taxonomic names to RFLP types and sequence data obtained by pyrosequencing was achieved by a BLAST search-based procedure relying on the lowest common taxonomic level of the best matching publicly available sequence data from GenBank, as detailed by Peršoh et al. (2010). OTUs being not assignable to any known fungal group were referred to as "Mycota."

The most likely phylogenetic tree was reconstructed from the ITS1 sequences using the software package MEGA 6 (Tamura et al. 2013) and applying the Tamura three-parameter model with gamma distribution. To assess support of the respective branches, 1000 bootstrap replicates were calculated. Only unambiguously alignable positions were included in the phylogenetic analyses, corresponding to base pairs 1–35, 37–55, 81–83, 157–166, 167–170, and 187–241 of sequence **LN680591**. Six sequences (**LN680571** and

Table 1 RFLP types (OTUs) and corresponding sequences detected. Each most similar sequence found in GenBank is given together with the total number of sequences considered for name assignment, i.e., sequences obtaining "Bit Scores" which are at least 0.9 times as high as the "Bit Score" the best matching sequence obtained. The range of bit scores for the best matching considered sequences is also listed. Finally, the number of ambiguously assigned sequences among them is given, followed by the number of outliers, i.e., sequences deposited under names deviating from the assigned name

RFLP type [OTU]	Corresponding ITS sequences	Best match [GenBank acc. no.]	Considered sequences	Bit score [min/max]	Ambiguities	Outliers
Acremonium-1	LN680575	FJ770373	4	383/407	0	0
	LN680573	FJ770373	4	374/398	0	0
Arxula adeninivorans-1	LN680564	JN013959	6	145/159	2	0
	LN680570	JN013959	5	156/165	1	0
Basidiobolus-1	LN680598	EF392524	12	425/472	3	0
	LN680607	EF392524	12	420/466	3	0
Basidiobolus haptosporus-1	LN680587	FJ780318	7	462/503	3	0
	LN680597	FJ780318	7	462/503	3	0
Cladosporium-1	LN680602	JX984700	100	436/477	88	0
	LN680599	JX984700	100	436/477	88	0
Cladosporium-2	LN680616	KC525568	100	468/475	71	0
	LN680618	KC525568	100	468/475	71	0
Coemansia-1	LN680611	JN942676	4	104/11	0	0
	LN680590	JN942676	4	104/11	0	0
Dactylella oxyspora-1	LN680592	JX901425	100	108/110	99	0
	LN680593	JX901425	100	108/110	99	0
	LN680589	JX901425	100	108/110	99	0
Kickxellaceae-1	LN680594	JN942679	14	87.9/97.1	0	0
	LN680595	JN942679	14	87.9/97.1	0	0
Mortierella alliacea-1	LN680617	FJ475794	58	416/462	56	0
	LN680620	FJ475794	58	422/468	56	0
	LN680622	FJ475794	58	422/468	56	0
Mortierella formicicola-1	LN680557	JX975933	1	340/340	0	0
	LN680596	JX975933	1	340/340	0	0
Mortierella parvispora-1	LN680610	HQ335301	32	348/385	28	0
	LN680601	HQ335301	32	339/375	28	0
Paecilomyces-1	LN680591	FJ475815	46	401/440	42	2
	LN680614	FJ475815	46	401/440	42	2
	LN680621	FJ475815	46	401/440	42	2
Phialocephala fortinii-1	LN680565	HF947849	100	494/508	97	1
	LN680612	HF947849	100	494/508	97	1
Pochonia bulbillosa-1	LN680604	HM030580	17	453/501	12	0
	LN680600	HM030580	17	453/501	12	0
Pochonia bulbillosa-2	LN680603	HM030580	17	453/501	9	0
	LN680605	HM030580	17	433/481	9	0
Ramicandelaber-1	LN680562	JX043214	99	93.5/104	6	80
	LN680586	JX043214	99	93.5/104	6	80

Table 1 (continued)

RFLP type [OTU]	Corresponding ITS sequences	Best match [GenBank acc. no.]	Considered sequences	Bit score [min/max]	Ambiguities	Outliers
Rhizoscyphus ericae-1	LN680576	FJ475745	28	475/527	25	0
	LN680613	FJ475745	28	475/527	25	0
	LN680563	FJ475745	34	466/516	31	0
Russula paludosa-1	LN680572	JX029923	22	466/514	19	0
	LN680583	JX029923	21	479/525	18	0
	LN680584	JX029923	21	484/531	18	0
Tylospora fibrillosa-1	LN680556	FN610897	19	424/470	18	0
	LN680609	FN610897	19	424/470	18	0
Mycota-1	LN680553	JQ666716	100	449/466	100	0
	LN680588	JQ666716	100	453/470	100	0
	LN680561	JQ666716	100	460/477	100	0
Mycota-2	LN680566	JN032553	44	342/379	44	0
	LN680623	JN032553	40	363/401	40	0
	LN680619	JN032553	39	355/390	39	0
Mycota-3	LN680615	JN032553	37	418/460	37	0
	LN680579	JN032553	37	418/460	37	0
	LN680582	JN032553	37	418/460	37	0
Mycota-4	LN680581	EF521256	1	527/527	1	0
	LN680574	EF521256	1	527/527	1	0
Mycota-5	LN680569	JN847504	17	425/472	17	0
	LN680608	JN847504	17	425/472	17	0
Mycota-6	LN680558	JN032553	40	368/407	40	0
	LN680568	JN032553	40	368/407	40	0
Mycota-7	LN680585	JX270447	100	414/448	100	0
	LN680555	JX270447	100	414/448	100	0
Mycota-8	LN680571	AM260799	2	481/756	2	0
	LN680606	AM260799	2	481/756	2	0
Mycota-9	LN680554	JQ272445	100	440/451	100	0
	LN680559	JQ666716	100	424/440	100	0
Mycota-10	LN680560	AM260799	1	246/246	1	0
	LN680567	AM260799	1	233/233	1	0
Mycota-11	LN680577	HF947868	7	494/527	7	0
	LN680578	HF947868	7	488/532	7	0
	LN680580	HF947868	7	488/532	7	0

LN680606, **LN680560** and **LN680567**, **LN680562** and **LN680586**) representing three different OTUs (Mycota-8, Mycota-10, Ramicandelaber-1, cf. Table 1) were not alignable and were therefore excluded from the analysis.

Fungal traits

Data of spectra of selected extracellular enzymes, namely chitinases, amylases, cellulases, peroxidases and polyphenol oxidases, lipases, and esterases as well as proteinases, were compiled from literature (Abdulla and Taj-Aldeen 1989; Bonants et al 1995; Böer et al. 2005; Büttner et al. 1991; Caldwell et al. 2000; Chambers et al. 1999; Esteves et al. 2009; Fenice et al. 1997; Friedrich et al. 2002; Fujii et al. 2009; Gopinath and Hilda 2005; Gradišar et al. 2005; Gramss et al. 1998; Gupta et al. 1992; Ikeda et al. 2008; Khan et al. 2004; Kluczek-Turpeinen et al. 2003; Lin et al. 2011; Manning et al. 2007; Marshall 1975; Marlida et al. 2000; Mase et al. 1996; Middelhoven et al. 1991; Mishra et al. 2011; Okafor et al. 1987; Okeke and Okolo 1990; Peberdy and Turner 1967; Quigley et al. 1998; Saparrat et al. 2000; Seigle-Murandi et al. 1992; Skare et al. 2006; Stirling and Mankau 1979; Takó et al. 2012; Terashita et al. 1993; Wang et al. 2006; Wilson et al. 2004; Yan-Hong et al. 2013; Zenin and Park 1983) and assigned on a taxonomic basis to fungal OTUs. Data concerning spore sizes were also retrieved from literature (Baral and Krieglsteiner 2006; Beaton and Weste 1980; Cannon and Kirk 2007; Chen et al. 2007; Chuang and Ho 2011; Domsch et al. 2007; Drechsler 1947, 1956; Gams 1977; Kowalski and Kehr 1994; Shaffer 1962; Young 1968). For statistical evaluation, spore lengths were grouped into the categories "shorter than 10 μm," "10–20 μm," and "longer

than 20 μm." Metadata concerning the isolation sources of sequences in GenBank being next related to the sequence data obtained in this study were gathered from the same set of sequences, which served for the assignment of OTU names.

Statistics

Using the software package Primer 6 (Primer-E), a Jaccard similarity matrix was calculated according to the presence or absence of RFLP types in samples. Differences between groups of samples were assessed by analysis of similarity (ANOSIM), with respect to the grouping factors "compartment class" (soil, mite) and "compartment subclass" (soil, *L. obesus*, *O. subpectinata*). Similarities among sample groups according to the RFLP-type composition were analyzed and visualized by canonical analysis of principle coordinates (CAP). Correlation coefficients of fungal RFLP type (OTU) distributions with the CAP axes (CAP1/CAP2) were calculated by the Spearman rank-order correlation. Species richness was estimated on the basis of all RFLP types (including the singletons) using the abundance- and incidence-based Chao2 algorithm (Chao 1984, 1987). The Spearman rank-order correlations among fungal traits and habitat preferences were calculated in STATISTICA 7 (StatSoft) based on a presence-absence data matrix providing the trait categories described above.

Results

Fungal OTU occurrences and spectra

Altogether, 184 different fungal RFLP types were obtained from the samples, including 40 and 31 samples from *L. obesus* (corresponding to 200 individuals) and *O. subpectinata* (310 individuals), respectively, and 12 soil samples. Thereof, 31 RFLP types were non-unique, i.e., occurred in at least two different samples (Table 1). Ten (32% of non-uniques) originated exclusively from mite and eight (26%) exclusively from soil samples. The remaining 13 RFLP types (42%) occurred in both sample types. Of the ten mite-associated RFLP types, none occurred exclusively in *O. subpectinata*, but only three in *L. obesus* (Fig. 2). On average, soil and mites yielded five and two different non-unique RFLP types per sample, respectively.

Estimation of species diversity (i.e., different RFLP types, singletons included) in soil resulted in 614 calculated RFLP types, 113 of which were actually observed (Fig. 3a). This accounts for a theoretical diversity coverage of 18%. Three hundred and fifty RFLP types were calculated for the mites; 86 were actually observed (Fig. 3b), resulting in a diversity coverage of 25%.

OTUs assignable to the Zygomycetes are clustered in three distinct clades comprising the fungal families Kickxellaceae [*Coemansia*-1, Kickxellaceae-1], Mortierellaceae [*Mortierella alliacea*-1, *Mortierella formicicola*-1, *Mortierella parvispora*-1, Mycota-1, Mycota-2, Mycota-3, Mycota-6, Mycota-7], and Basidiobolaceae [*Basidiobolus*-1, *Basidiobolus haptosporus*-1]. The OTUs assignable as Basidiomycota are *Tylospora fibrillosa*-1, clustering in the family Atheliaceae as well as *Russula paludosa*-1 and Mycota-4 in the Russulaceae (all Agaricomycetes). Ascomycota OTUs are clustered within the Hypocreales [*Acremonium*-1, *Paecilomyces*-1, *Pochonia bulbillosa*-1, *Pochonia bulbillosa*-2], Cladosporiaceae [*Cladosporium*-1, *Cladosporium*-2, Mycota-5], Vibrisseaceae [*Phialocephala fortinii*-1], Lachnaceae [*Rhizoscyphus ericae*-1], Trichomonascaceae [*Arxula adeninivorans*-1], and Orbiliaceae [*Dactylella oxyspora*-1].

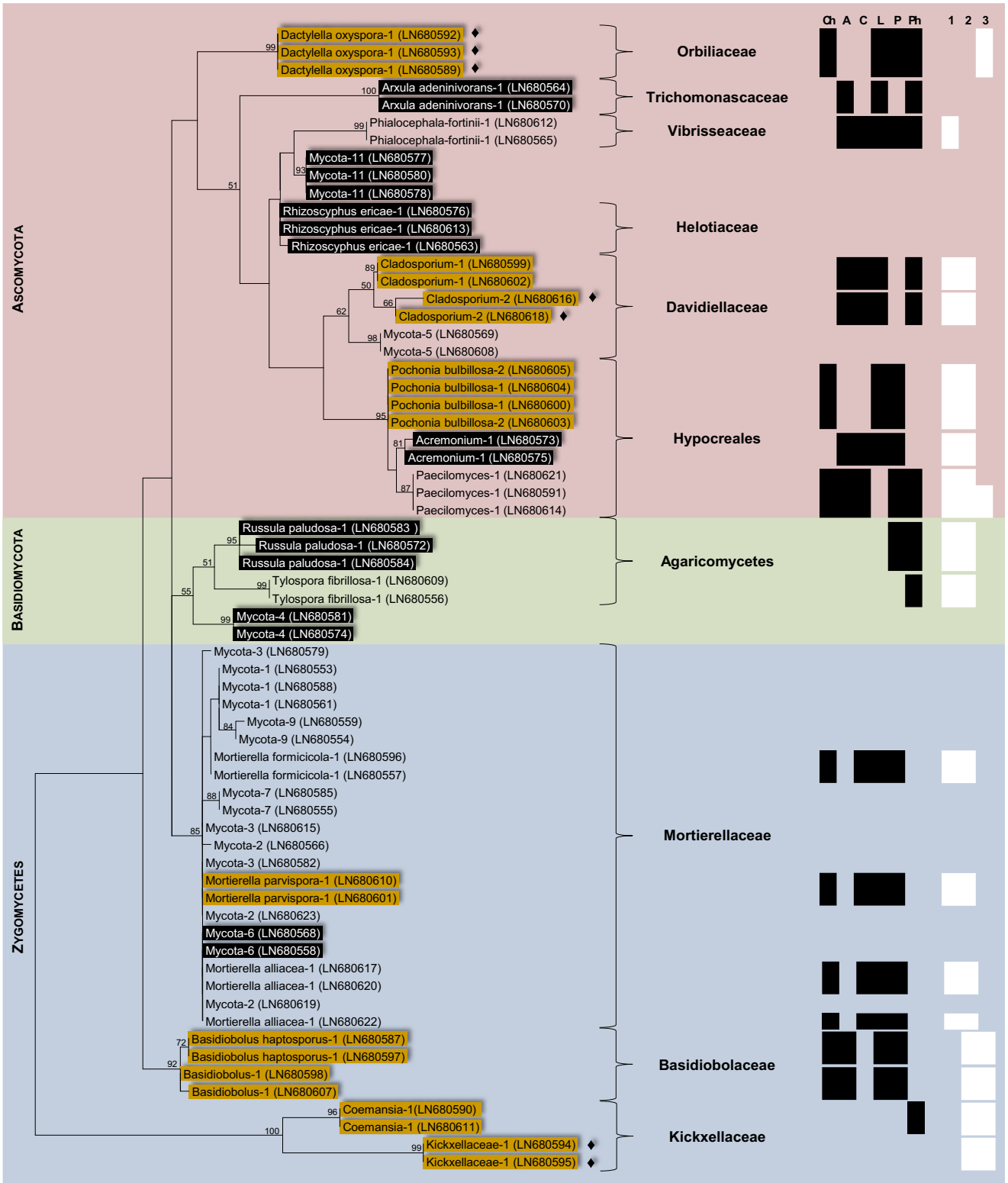
Most OTUs in mite samples (Fig. 4a) were assignable to Zygomycetes (78%), followed by Ascomycota (18%), and Basidiomycota (3%). A negligible part (1%) of the enclosed OTUs was not assignable to any phylum. Soil samples (Fig. 4a) mainly comprised fungi of the basal lineages (38%) and Ascomycota (30%), whereas Basidiomycota accounted for 25% and unassignable OTUs for 7%. The part of the community restricted to mites comprised Zygomycetes (73%) and Ascomycota (27%) (Fig. 4b). The part exclusively found in soil included similar proportions of Ascomycota (39%) and Basidiomycota (39%), followed by Zygomycetes (15%) and unassignable OTUs (7%).

Differences among fungal communities

ANOSIM revealed a significant difference ($p = 0.001$; $R = 0.22$) between the fungal communities in mite and soil samples. Each mite species separately also differed from soil significantly (*O. subpectinata* $p = 0.002$, $R = 0.227$; *L. obesus* $p = 0.001$; $R = 0.310$) and the communities associated with the two mite species significantly differed in composition ($p = 0.005$, $R = 0.093$). Distinctiveness of the fungal communities was supported by the CAP analysis results (Fig. 5). Distribution of *Basidiobolus haptosporus*-1 was most strongly correlated to the CAP axes (CAP1/CAP2 0.388/0.647) (Fig. 5). Additional OTUs with the Spearman correlations > 0.3 for CAP2 were Mycota-2 (0.128/0.357) as well as *Coemansia*-1 (− 0.002/− 0.404) and *Paecilomyces*-1 (− 0.204/− 0.434) separating the mite species. Among those correlating with CAP1, thus separating soil from the mites were *Rhizoscyphus ericae*-1 (− 0.396/0.110), *Russula paludosa*-1 (− 0.455/0.120), *Tylospora fibrillosa*-1 (− 0.321/0.131), Mycota-3 (− 0.389/0.093), Mycota-4 (− 0.371/0.096), and Mycota-9 (− 0.417/− 0.014).

Trait occurrences among fungal OTUs

Of the 975 published sequences related to those in our study, sequences assigned as Basidiomycota consistently originated from environmental samples (mostly soil; data not shown) but not from living organisms (Fig. 6). The isolation sources of Ascomycota comprised more living organisms, in particular



plants. Zygomycetes were isolated more often from animals than Ascomycota and Basidiomycota.

Preference of fungal OTUs for mites correlated significantly ($p < 0.05$, $R^2 = 0.284$) with the ability of the respective taxa to produce extracellular chitinases, as inferred from literature (Abdulla and Taj-Aldeen 1989; Bonants et al 1995; Böer et al. 2005; Büttner et al. 1991; Caldwell et al. 2000; Chambers et al. 1999; Esteves et al. 2009; Fenice et al. 1997; Friedrich et al. 2002; Fujii et al. 2009; Gopinath and Hilda 2005; Gradišar et al. 2005; Gramss et al. 1998; Gupta et al. 1992; Ikeda et al. 2008;

◀ **Fig. 2** Phylogenetic relationships among fungal OTUs associated with soil and mite samples as inferred from ITS sequence data. Maximum likelihood phylogeny calculated by MEGA 6, applying the Tamura three-parameter model with gamma distribution. GenBank accession numbers of the sequences are preceded by the OTU names. Support values from 1000 bootstrap replicates are noted above the respective branches. Sequences representing OTUs, which are restricted to soil samples, are highlighted in black. Sequences of OTUs occurring exclusively in mite samples are highlighted in yellow; those restricted to *L. obesus* are additionally marked by ♦. Black bars on the right indicate the potential within the respective genus to express certain kinds of extracellular enzymes. Ch chitinases, A amylases, C cellulases, L lipases/esterases, P proteinases, Ph peroxidases/polyphenol oxidases. White bars label the spore size categories in congeneric taxa (1: < 10 μm; 2: 10–20 μm; 3: > 20 μm)

Khan et al. 2004; Kluczek-Turpeinen et al. 2003; Lin et al. 2011; Manning et al. 2007; Marshall 1975; Marlida et al. 2000; Mase et al. 1996; Middelhoven et al. 1991; Mishra et al. 2011; Okafor et al. 1987; Okeke and Okolo 1990; Peberdy and Turner 1967; Quigley et al. 1998; Saparrat et al. 2000; Seigle-Murandi et al. 1992; Skare et al. 2006; Stirling and Mankau 1979; Takó et al. 2012; Terashita et al. 1993; Wang et al. 2006; Wilson et al. 2004; Yan-Hong et al. 2013; Zenin and Park 1983). Actually, production of extracellular chitinase was completely absent in taxa to which OTUs restricted to soil were assigned (Fig. 7). The capability to produce other exoenzymes (amylases, cellulases, proteases, lipases/esterases, and peroxidases/polyphenol oxidases) was not correlated to substrate preferences and appeared similar in all compartment classes.

Deduced spore sizes partially correlated significantly to the habitat preferences of fungal OTUs. Spores longer than 20 μm negatively correlated with OTUs appearing only in soil, whereas spores shorter than 10 μm were positively correlated to soil-restricted OTUs ($p < 0.05$, $R^2 = 0.267$ in both cases). Indeed, fungal spores measuring more than 20 μm in length were completely absent from soil (Fig. 8). However, no further significant correlations were found for mite-restricted OTUs or those occurring in both sample types.

Comparison between 454 pyrosequencing and RFLP approach

The 454 pyrosequencing data provided 2441 reads, 1231 of which could be clustered to 77 operational taxonomic units (OTUs). The remaining reads were discarded being either too short, of poor quality or representing singletons. Thirty-three OTUs (Table 2) occurred in at least two samples (non-uniques). Regarding only soil samples, RFLP analysis accounted for five OTUs assignable to the Ascomycota, two from the Basidiomycota, and three belonging to the Zygomycetes. Pyrosequencing revealed seven ascomycete OTUs in the soil samples, whereas sequence-derived RFLP pattern analysis detected five. With five OTUs, three more basidiomycete OTUs were detected by pyrosequencing, whereas both approaches yielded three OTU records of the Zygomycetes. The RFLP approach yielded 11 of taxonomically unassignable fungal OTUs, pyrosequencing 18.

The fungal families Helotiaceae, Hypocreaceae, Trichocomaceae, Vibrisseaceae (all Ascomycota), Atheliaceae (Basidiomycota), and Mortierellaceae (Zygomycetes) were found by both approaches. Trichomonascaceae (Ascomycota) and Kickxellaceae (Zygomycetes) exclusively occurred in the RFLP analysis, whereas Gloniaceae, Xylariaceae (both Ascomycota), and Thelephoraceae (Basidiomycota) were detected only in the pyrosequencing data. OTUs referred as *Phialocephala fortinii*-1, *Rhizoscyphus ericae*-1 (both Ascomycota), *Russula paludosa*-1, (Basidiomycota), and *Mortierella alliacea*-1 (Zygomycetes) were detected by both techniques. By contrast, *Acremonium*-1, *Arxula adeninivorans*-1, *Paecilomyces*-1 (both Ascomycota), *Tylospora fibrillosa*-1 (Basidiomycota), *Mortierella fomicicola*-1, and Ramicancelaber-1 (both Zygomycetes) were found only by the RFLP approach. Pyrosequencing exclusively revealed *Cenococcum geophilum*-1, *Hypocrea*-1, *Meliniomyces variabilis*-1, *Hypoxylon rubiginosum*-1, *Penicillium*-1 (all Ascomycota), *Thelephora terrestris*-1, *Piloderma*-1,

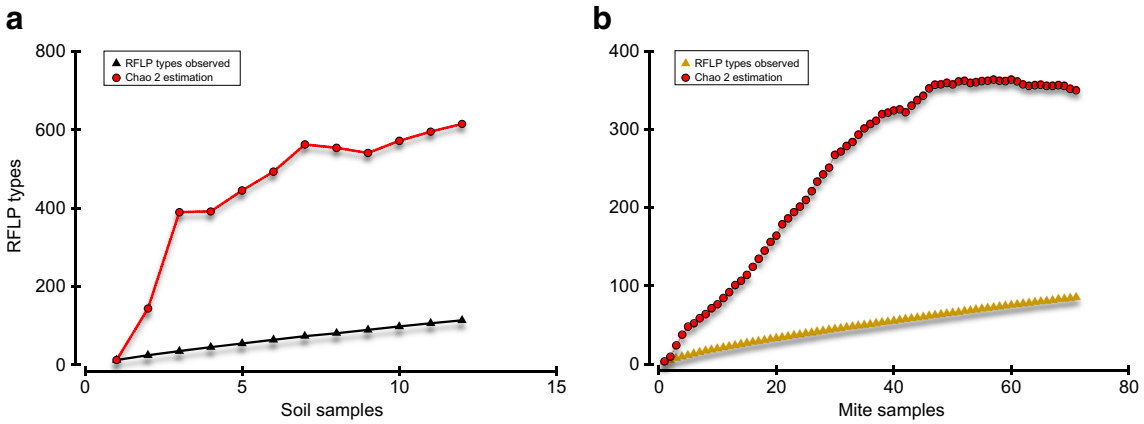


Fig. 3 Species (=RFLP type) accumulation curves for **a** soil samples and **b** mite samples. The numbers of different RFLP types observed in dependency of the respective sample counts are compared to the diversity estimated by the Chao 2 algorithm

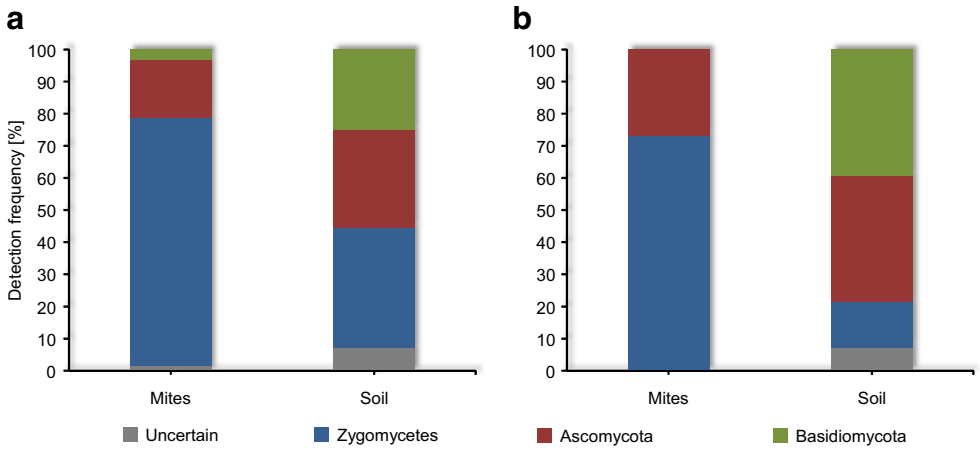


Fig. 4 Detection frequencies of major taxa in samples of mites and soil on phylum level. **a** All OTUs. **b** OTUs restricted to the respective sample type

Piloderma spaerosporum-1 (all Basidiomycota), *Mortierella*-1, and *Mortierella sossauensis*-1 (both Zygomycetes).

Discussion

Methodology

Similarity between fungal and mite rRNA gene sequences was observed while preparing samples for this study (Werner et al. 2012). For this reason, a new set of PCR primers was designed to meet the special requirements needed for the amplification of fungal DNA from mite samples. The primers SSUh-35F and LSUh-11F (Werner et al. 2012) strictly discriminated between fungal and animal DNA templates while covering a broad range of fungi from the Eumycota. These new primers were evaluated with mixed DNA from very different samples (mites, insects, soil, plants, fungal cultures). In every case, they reliably delivered fungal PCR products (data not shown).

Reliability of the RFLP-based grouping was confirmed by sequencing of PCR products. The applied approach and data analysis workflow was even shown to reliably discriminate at species level. Significant differences in the distribution of certain fungal groups among sample types could be demonstrated, while others were ubiquitously distributed. Nevertheless, the OTU spectra obtained from soil samples differed to some degree between the RFLP and the 454 pyrosequencing approach. Pyrosequencing revealed a higher number of OTUs than RFLP, which may be explained by the detection of rare genotypes due to a nearly 60 times higher sequencing depth. Most important for the reliability of this study is the fact that both approaches concertedly detected certain OTUs in soil

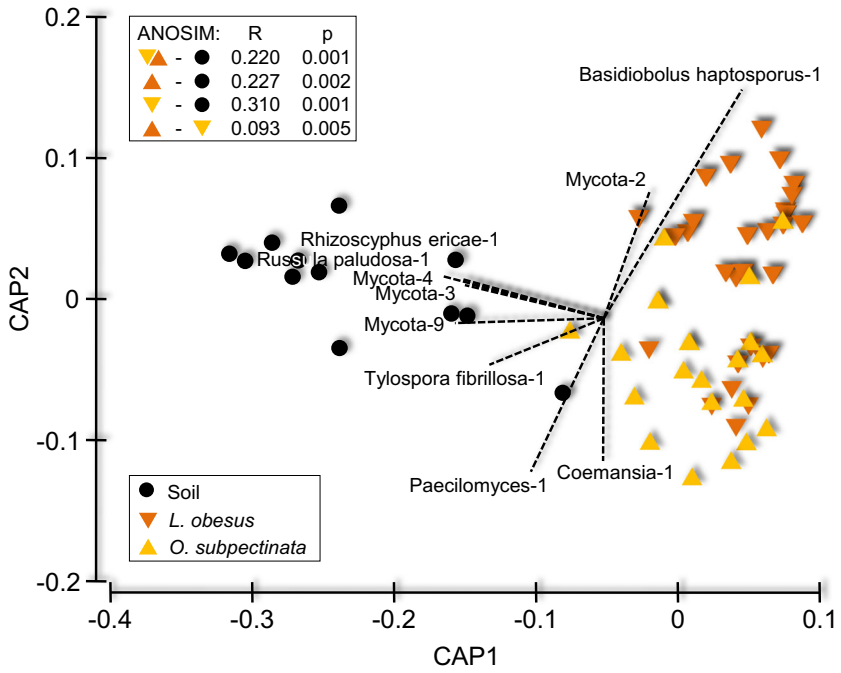


Fig. 5 Similarity among samples according to fungal OTU composition. Canonical analysis of principal coordinates (CAP) based on the grouping factor "compartment subclass" with the integrated Spearman rank-order correlation (—) of fungal OTU occurrences. Only correlation coefficients > 0.3 were considered. ANOSIM R values and significance levels are given in addition. The underlying calculations were performed on a Jaccard similarity matrix generated from presence-absence data

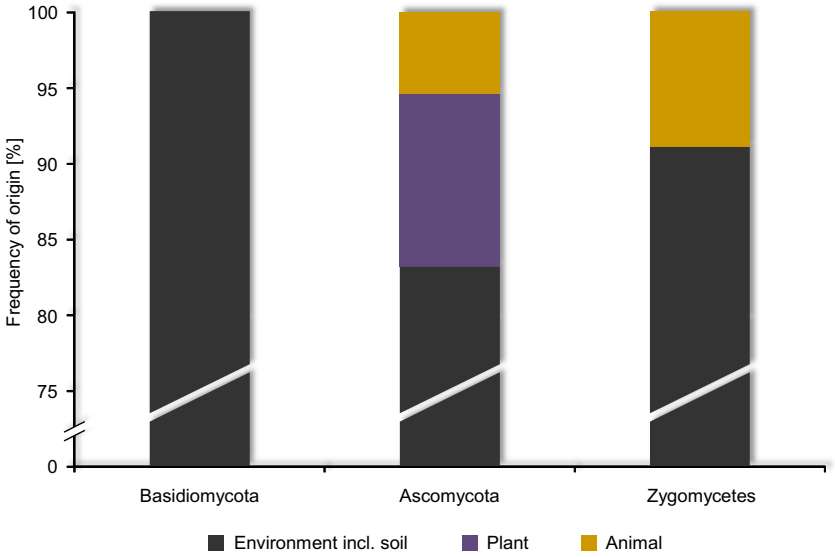


Fig. 6 Isolation sources of published sequences related to those obtained in this study

and that none of the OTUs classified as being mite-specific by the RFLP approach were among those rare OTUs in the organic soil layer according to the NGS approach. While both spectra were largely comparable, at least at a higher taxonomic level, the RFLP approach interestingly also detected OTUs that were absent from the pyrosequencing data. The combined application of both approaches therefore revealed a wider spectrum of relevant fungal OTUs and the primary goal of the present study was sufficiently reached by highlighting differences in OTU and thereof inferred trait composition spectra between the communities in soil and soil mites.

The numbers obtained by the estimation of species richness suggest that a higher amount of samples may have led to higher coverage rates. Nevertheless, dominant fungal OTUs seem to have been covered to a sufficient extent, and the achieved results proved to be suitable to reveal significant differences in traits among the fungi of the compartments in focus. In case of the mites, the number of clones detected by 454 pyrosequencing was 12 times higher than the average RFLP-type richness and five times higher than the maximum. Against this background, the number of analyzed soil and mite samples is considered sufficient to cover at least that part of fungal associates, which regularly occurs in the respective sample type.

Since soil fungal spores adherent to mite individuals (c.f. Lilleskov and Bruns 2005) were not distinguished from physiologically active hyphae, it is rather likely that the active units of the communities might differ even more. We assume that particularly, the soil-specific fraction might considerably increase compared to the mite-specific one. Ingestion of fungal particles, fungal material enclosed in detritus serving as food, as well as fungal residues taken up along with prey organisms, may be considered as further an additional factor blurring differences to the soil body environment.

Some limitations preventing the inquiry of quantitative data are based on the necessary differences in DNA isolation for the

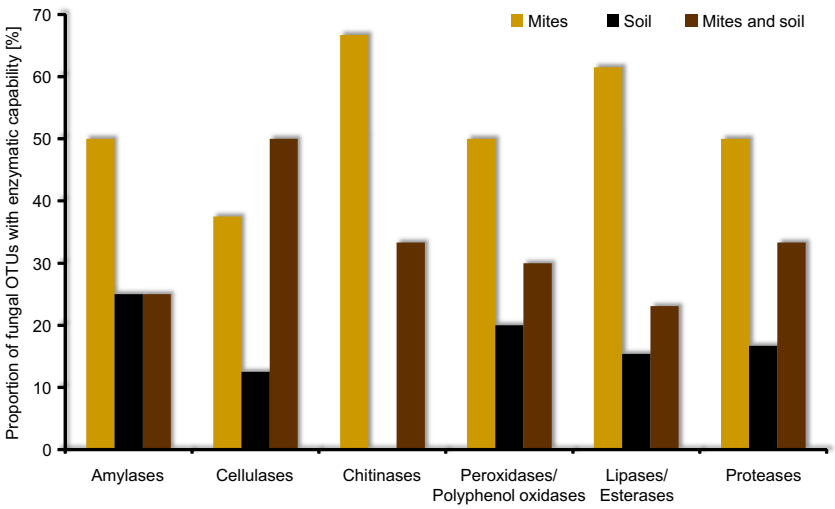


Fig. 7 Proportion of OTUs with certain exoenzymatic capabilities among all OTUs preferring a certain habitat, or not

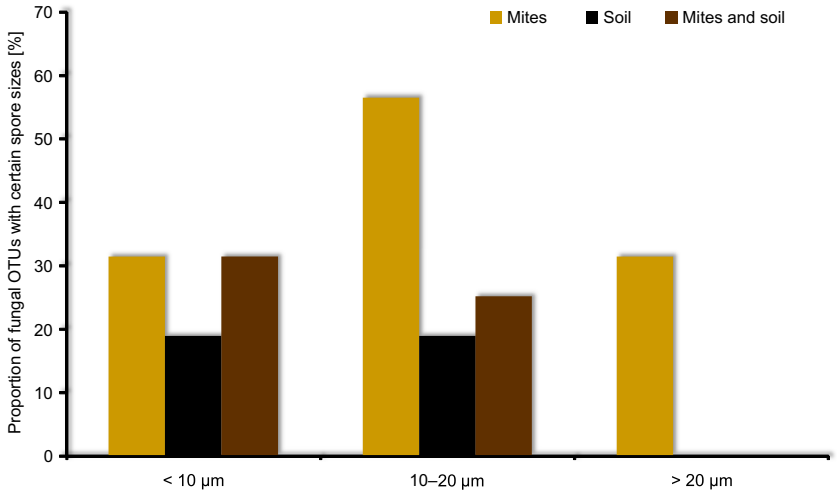


Fig. 8 Proportion of OTUs producing spore types of certain size categories among all OTUs preferring a certain habitat, or not

different substrate types. The soil approach demanded considerably more material compared to the mite approach. The yield of DNA was also different between the samples. Against this background, quantitative data are comparable between soil and mite samples to a certain degree. Therefore, the statistical part of the study relied on qualitative presence-absence data only.

Fungal colonization of different compartments correlated with functional traits like degradation capabilities, i.e., the spectra of actively produced extracellular enzymes. For providing a preferably comprehensive profile of the exoenzymatic potential of each fungal group, we compiled data from respective literature. It is known that production of mycotoxins, antibiotics, and other secondary metabolic compounds under laboratory conditions differs from that in nature (Jarvis 1971; Ciegler 1978; Brakhage and Schroeckh 2011). However, combined results from studies using different methodical approaches should provide sufficiently reliable information. Enzymatic tests with isolates from *Basidiobolus haptosporus* (Werner et al. 2012) and *Mortierella alliacea* (Werner et al. 2016), two dominant fungal species of the sampling site, were conducted in two spin-off studies.

Substrate preferences of major fungal groups were deduced from substrate information of next-related sequence data in GenBank. This approach may be biased by depositors' preferences for certain research targets. However, the vast number of available DNA sequences originating from a broad spectrum of environmental samples ensures a reliable statistical background.

Fungal diversity

The number of OTUs recovered from soil seems to be quite low in comparison to other studies on soil-inhabiting fungi (e.g., Jumpponen and Johnson 2005; Lindahl et al. 2007; Poll et al. 2009; Peršoh et al. 2018). Despite limited sequencing depth (with an OTU coverage rate of approximately one fifth of the calculated diversity), comparatively low species richness might also be due to specific environmental conditions. Ranker soils as well as podsols and the transitional stages are known to be acidic and nutrient-poor (Horn et al. 2010), thereby representing an unfavorable environment for many microorganisms. Furthermore, species of *Calluna* and *Vaccinium* (both Ericaceae) accumulate and segregate polyphenolic substances into the soil (Jalal and Read 1983; Jäderlund et al. 1996), which act as potent enzyme inhibitors (Freeman et al. 2004) and therefore have a growth-inhibiting impact on most organisms (Jalal and Read 1983; Gallet 1993; Northup et al. 1998). While such conditions may results in species-poor fungal communities, pine forest soils in general considerably differ with regard to fungal community composition (e.g., O'Brien et al. 2005; Lindahl et al. 2007; Buee et al. 2009). Such heterogeneity is due to soil chemical properties, and nutrient availability, differences in precipitation, and soil physical properties (c.f. Högberg et al. 2007; Christ et al. 2011; Gomez-Hernandez and Williams-Linera 2011; Brockett et al. 2012). The roughly equal proportion of Zygomycetes, Ascomycota, and Basidiomycota in the organic layer (Fig. 4a) is comparable to the spectrum reported from 1-year-old litter in coniferous forest sites with Ericacean understory in the Bohemian Forest National Park (Haňáčková et al. 2015), whereas the fungal litter community at a site in central Sweden with a vegetation even more similar to the one in focus of the present study was clearly dominated by Ascomycota and comprised only few Zygomycetes (Lindahl et al. 2007). Accordingly, community composition in coniferous forest appears to be influenced also by factors other than vegetation structure.

Mites and the surrounding organic layer as distinct compartments for soil fungi

Fungal communities in mites were clearly enriched in OTUs of the Zygomycetes and depleted in Basidiomycota, compared to the decaying litter (Fig. 4a). This finding is consistent with the limited number of known associations between arthropods and Basidiomycota (Bałazy et al. 2008; Humber

Table 2 OTUs and corresponding sequence IDs detected by 454 pyrosequencing of soil samples. Each most similar sequence found in GenBank is given together with the total number of sequences considered for name assignment, i.e., sequences obtaining "Bit Scores" which are at least 0.9 times as high as the "Bit Score" the best matching sequence obtained. The range of bit scores for the best matching considered sequences is also listed. Finally, the number of ambiguously assigned sequences among them is given, followed by the number of outliers, i.e., sequences deposited under names deviating from the assigned name

OTU	Corresponding ITS sequence ID	Best match [GenBank acc. no.]	Considered sequences	Bit score [min/max]	Ambiguities	Outliers
Cenococcum geophilum-1	LN736300	KM576406	78	230/255	73	0
Hypocrea-1	LN736274	KF856962	100	322/326	25	0
Hypoxylon rubiginosum-1	LN736277	DQ223759	2	329/329	0	0
Meliniomyces variabilis-1	LN736294	KM068383	100	265/289	73	1
Mortierella alliacea-1	LN736284	JF300658	77	255/281	75	0
Mortierella-1	LN736272	KM504403	100	291/291	77	1
Mortierellla sossauensis-1	LN736285	JN032553	44	235/259	41	0
Penicillium-1	LN736297	JN905350	100	298/320	46	1
Phialocephala fortinii-1	LN736292	KM504500	100	318/322	79	0
Piloderma sphaerosporum-1	LN736270	JF300826	100	313/316	86	0
Piloderma-1	LN736271	DQ233782	100	285/305	85	0
Rhizoscyphus ericae-1	LN736282	HQ873698	100	278/300	66	2
Russula paludosa-1	LN736288	LM992857	43	311/344	32	2
Thelephora terrestris-1	LN736301	KM504490	100	363/370	81	0
Tomentella sublilacina-1	LN736278	JN905183	100	324/340	59	1
Mycota-1	LN736273	JF300603	6	246/252	6	0
Mycota-2	LN736275	HM069467	2	292/298	2	0
Mycota-3	LN736276	JN904185	2	217/239	2	0
Mycota-4	LN736279	KF617286	2	302/357	2	0
Mycota-5	LN736280	AB476540	19	272/300	19	0
Mycota-6	LN736281	HF947868	10	313/329	10	0
Mycota-7	LN736283	HQ154358	10	344/361	10	0
Mycota-8	LN736286	JQ711781	13	187/207	13	0
Mycota-9	LN736287	JX030882	58	267/294	58	0
Mycota-10	LN736289	KF617349	3	281/292	3	0
Mycota-11	LN736290	KM504438	2	311/311	2	0
Mycota-12	LN736291	DQ672274	100	213/219	100	0
Mycota-13	LN736293	JX030594	2	340/340	2	0
Mycota-14	LN736295	GU366726	1	228/228	1	0
Mycota-15	LN736296	GU973772	20	267/281	20	0
Mycota-16	LN736298	JX860490	1	318/318	1	0
Mycota-17	LN736299	KM504464	35	228/252	35	0
Mycota-18	LN736269	HM036653	6	305/333	6	0

2008; Roy et al. 2010). Soil-preferring Basidiomycota mostly mediate the adaption of vegetation to soil via root associations (Giri et al. 2005) but are also important agents in the context of final stages of litter decomposition due to their ability to degrade lignin (Frankland 1998).

Accordingly, among the fungi that significantly separate soil from the mites were the basidomycete genera *Rhizoscyphus* and *Russula* beside the ascomycete *Tylospora* species. The occurrence of *Rhizoscyphus* at the sampling site fits to the family's (Lachnaceae) preference for nutrient-poor soils of high acidity (Webster and Weber 2007), where these fungi live saprotrophically in herbaceous and woody tissues (Cannon and Kirk 2007) or—like *Rhizoscyphus* spp.—form mycorrhizae with Ericaceous plants (Webster and Weber 2007), just like the genus *Tylospora* (Atheliaceae), which exclusively comprises ectomycorrhizal fungi (Domsch et al. 2007). Further members of this family include facultative plant pathogens with a wide host range, several saprobes,

and active decomposers and many ectomycorrhizal species, mostly favoring acidic soils (Cannon and Kirk 2007). In contrast, the mite-restricted fungal communities exclusively consisted of Zygomycetes and Ascomycota (Fig. 4b). Zygomycetes comprised the genera *Basidiobolus* (Basidiobolaceae), *Coemansia* (Kickxellaceae), and *Mortierella* (Mortierellaceae) and another representative of the Kickxellaceae. Ascomycete fungi were represented by *Cladosporium* spp. (Cladosporiaceae), *Dactylella* (Orbiliaceae), and *Pochonia* (Hypocreaceae).

Thus, mites form a clearly distinct pedosphere compartment with regard to fungal occurrence, taxonomic affiliation, and diversity. Only 35% of the recorded fungi were observed in both soil and mites. Particularly, Zygomycetes, in the first instance, Mortierellaceae, caused an overlap between the fungal communities of both habitats. In comparison, a significantly different spectrum of fungi was recorded from oribatid mites from the litter layer of a temperate oak-beech forest (Renker et al. 2005). In the present study, mites were also dominated by Ascomycota and Zygomycetes, but only with little overlap of the proven genera, with the exception of *Basidiobolus* spp., *Cladosporium* spp., and *Mortierella* species. The absolute or relative restriction of certain fungi to mites is considered being indicative for more or less intimate fungus-arthropod relationships, i.e., some kind of symbiosis.

Such associations certainly may differ with regard to host specificity. In the present case, significant differences existed between the fungal communities of the two examined mite species. There, occurrence frequencies of *Basidiobolus*, *Coemansia*, and *Paecilomyces* (Trichocomaceae) were quite different. With regard to fungal diversity, *L. obesus* was distinguished from *O. subpectinata* primarily by some additional species, while they had most of the rest in common.

In terms of functional traits, significant differences between the soil-dwelling and mite-associated fungi could be demonstrated. Despite slight differences of the two fungal communities with regard to their potential of producing certain extracellular enzymes, there was an increased potential for producing exochitinases observed in mite-associated fungi. This is in line with a concentrated localization of chitinases in soil areas where fungal mycelia are grazed by soil invertebrates (Crowther et al. 2011) and also with the fact that arthropod-associated fungi, particularly pathogens, join the trait of producing extracellular chitinases (Humber 2008). Interestingly, known mite-pathogenic fungi (e.g., van der Geest 1985; Poinar and Poinar 1998; Chandler et al. 2000; van der Van der Geest et al. 2000) were not detected in the present study, aside from the genus *Cladosporium*, whose potential pathogenicity has yet been documented weakly (Bałazy et al. 2008).

Spore size seems to be less decisive in terms of functional differentiation of the fungal communities. Despite a significant negative correlation of large spores with exclusively soil-associated fungi, a positive correlation of significantly smaller spore types existed for the same fungal group. However, both correlations are rather weak which entails that spore sizes cannot be connected with a decisive influence on the compartmentalization due to known functional aspects. As the transport of fungal spores by mites may occur inside the gut as well as on the body surface (Behan and Hill 1978; Lilleskov and Bruns 2005), spore volumes seem to play a minor role in the context of phoresy.

Potential roles of fungus-mite associations in soil ecology

The Zygomycota showed a stronger affiliation to animals than the other fungal phyla (Fig. 6), which is in line with the existence of many arthropod-associated pathogens in this group. The ability to secrete exochitinases being restricted to mite-specific taxa (Fig. 7) indicates that this family of enzymes may play a certain role in the life habit of these arthropod-associated fungi. However, since no pathogenic fungi were found in the present study, but exclusively saprobic Zygomycetes, it is more likely that the extracellular chitinases are needed for the degradation of dead fungal hyphae (Brabcová et al. 2016) or remnants of arthropods.

Accordingly, arthropod-mediated phoresy is likely to underlay these associations. Most species of Mortierellaceae have comparatively limited degradation capability (Terashita et al. 1993; Schmidt et al. 2008) and depend on access to readily utilizable carbon sources in form of simple soluble substrates (Kjøller and Struwe 2002), which are present in certain freshly fallen plant matter, in particular in fruits, or in root exudates (Schmidt et al. 2008). Small conidia, like those of *Mortierella* spp., can be easily ingested by most grazing mites without the need for crushing. They often pass the guts without taking visible damage (authors' personal observation, data not shown) and remain germinable to a considerable degree after their excretion (Harinikumar and Bagyaraj 1994; Dromph 2001). Phoresy may also underlay the association with another group of Zygomycetes, the Basidiobolaceae. These are known to be present in decaying plant matter (Drechsler 1947; Cannon and Kirk 2007) and are regularly isolated from guts and feces of a wide range of mostly insectivorous animals (Benjamin 1962; Coremans-Pelseneer 1974; Cannon and Kirk 2007). They produce adhesive capilliconidia (Drechsler 1956), which are suspected of being vectored by mites (Blackwell and Malloch 1989; Werner et al. 2012). A further important aspect in the context of phoresy is the functional co-evolution of fungi and mites resulting in specialized morphological structures like sporothecae (Moser 1985), which are somehow comparable to the mycetangia found in ambrosia beetles (Batra 1963). Several different mite species (e.g., Moser 1985; Ebermann and Hall 2004; Ebermann et al. 2013) are known to possess such sporothecae, saccular invaginations of the cuticles harboring fungal spores that cannot be easily peeled or washed off the

body surface. However, even though the mites examined in this study are not among those possessing sporothecae, *Mortierella* spores were already isolated from mite species having such (Hofstetter and Moser 2014).

Ascomycete OTUs and relatives seem to be associated more frequently with living plants than the other groups (Fig. 6). This may be ascribed to their frequent life habit as plant pathogens or endophytic fungi (Porras-Alfaro and Bayman 2011), inhabiting plant litter before reaching the ground (Guerreiro et al. 2017). These ascomycetes may act as initial destruents but are also capable to degrade recalcitrant substrates like cellulose (Dix 1985) or lignin (Kirk and Farrell 1987). As the prevailing vegetation at the study site mainly consists of Pinaceae and Ericaceae, the detrital matter is rich in polyphenolic compounds like tannins (Iason et al. 1993; Suominen et al. 2003; Ho et al. 2010), which may be toxic for some arthropods (Poinsot-Balaguer et al. 1993; Barbehenn et al. 2008). Thus, the high potential of certain ascomycete fungi to segregate extracellular peroxidases and polyphenol oxidases (Fig. 2, Abdulla and Taj-Aldeen 1989; Bonants et al 1995; Böer et al. 2005; Büttner et al. 1991; Caldwell et al. 2000; Chambers et al. 1999; Esteves et al. 2009; Fenice et al. 1997; Friedrich et al. 2002; Fujii et al. 2009; Gopinath and Hilda 2005; Gradišar et al. 2005; Gramss et al. 1998; Gupta et al. 1992; Ikeda et al. 2008; Khan et al. 2004; Kluczek-Turpeinen et al. 2003; Lin et al. 2011; Manning et al. 2007; Marshall 1975; Marlida et al. 2000; Mase et al. 1996; Middelhoven et al. 1991; Mishra et al. 2011; Okafor et al. 1987; Okeke and Okolo 1990; Peberdy and Turner 1967; Quigley et al. 1998; Saparrat et al. 2000; Seigle-Murandi et al. 1992; Skare et al. 2006; Stirling and Mankau 1979; Takó et al. 2012; Terashita et al. 1993; Wang et al. 2006; Wilson et al. 2004; Yan-Hong et al. 2013; Zenin and Park 1983) could facilitate ingestion by making these plant remains easier digestible for the mites. Similar associations of yeasts and arthropods are described by Vega and Blackwell (2005).

Conclusion

The study revealed even single mite species as a discrete microhabitat for ecologically variable fungi of the pedosphere. Due to the vast density and diversity of mites there and the high number of potentially associated fungi, it seems to be justifiable to coin the term "acarosphere." This compartment hosts a species-rich assemblage of ecologically and taxonomically diverse fungi, which benefit in some form from their association with mites. The mobile and temporary condition of the acarosphere predestines it as a vector for fungal propagules. Distinct microhabitats in soil are interlinked by this acarosphere. Regarding their activities related to the degradation of organic matter, soil mites and fungi may be complementary and may therefore constitute a combined agent in the nutrient recycling processes. Assessing distribution pattern of mite-associated fungi in a broader host spectrum, locating them inside the arthropods, and assessing their enzymatic spectra and biochemical traits are certainly fruitful approaches towards a better understanding of the probably manifold associations.

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