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Article

Diversity of the *Capnocheirides rhododendri*-dominated fungal community in the phyllosphere of *Rhododendron ferrugineum* L.

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With 3 figures and 3 tables

Abstract: Individuals of *Rhododendron ferrugineum* at natural sites within the mountain ranges and valleys Flüela, Julier, Monstein and Grimsel (in the cantons of Graubünden and Bern, Switzerland) were analysed to determine the occurrence of pigmented epifoliar fungi in their phyllosphere. Molecular data from the fungal isolates revealed a wide range of species to be present, forming a well characterized oligospecific community, with *Capnocheirides rhododendri* (Mycosphaerellaceae, Capnodiales, Ascomycota) being the most frequently occurring taxon. One group of fungi was exclusively isolated from the leaf surfaces and recognized as being residential epifoliar. A second ecological group was absolutely restricted to the inner leaf tissues and considered as truly endofoliar. Members of a third group occurring in both the epifoliar and endofoliar habitats were considered to have an intermediate life habit. Members of this latter group are likely to invade the inner leaf tissues from the outside after having established a mycelium on the leaf surface. Comparison of the degree of pigmentation between cultivated strains of the strictly epifoliar and strictly endofoliar community members provided some indication that epifoliar growth is to a certain degree correlated with the ability of the fungi to develop hyphal pigmentation. The endofoliar growth is assumed to entail a complete lack or presence of a more or less weak hyphal pigmentation.

Key words: Ascomycota, succession, epifoliar, endofoliar, sooty moulds, alpine zone, dark pigmentation.

Introduction

Filamentose fungi with darkly pigmented hyphe in the vegetative part are typical colonizers of plant surfaces in various habitats of the world (Schoulties 1980). They are commonly referred to as 'sooty moulds' when found covering living leaves with a mat of more or less dense hyphal layers in the tropics (Kirk et al. 2008), or in a wider sense of all dark pigmented filamentose fungal taxa living on exudates of aphids and scale

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insects (Hughes 1976, Parbery & Brown 1986, Perez et al. 2009), on plant secretions (Weyman-Kaczmarkowa & Pedziwilk 2001), or on deposited pollen grains (Fokkema 1984). The circumscription of the group of sooty moulds has been sometimes restricted to certain taxonomic groups (Hughes 1976). Earlier studies on the composition of sooty patch-forming fungal communities on leaves of Central European deciduous and evergreen plants revealed a lack of any significant interdependence between the fungal taxonomic spectrum and the host plant taxa (Flessa et al. 2012), in contrast to what is known about various phytopathogenic fungal groups (O'Kane 1910, Hasan 1974, Hughes 1976, Goos 1978, Francis 2002). Recently, dependency on the life spans of colonized leaves has become apparent with regard to community composition (Flessa et al. 2012). Fungal taxa that are well known as epifoliar fungi (e.g. *Aureobasidium pullulans*, *Alternaria*, *Cladosporium* and *Phoma*) (Webb and Mundt 1978, Fenn et al. 1989, Yang et al. 2001, Osono 2002) are also reported as regular endophytic fungi (Suryanarayanan et al. 2005, Osono & Masuya 2012).

The present study is focused on the leaf-associated fungal communities of *Rhododendron ferrugineum* L. (Ericaceae). This plant is one of nine species of the genus with a natural occurrence in Europe (Crane et al. 2004) and is distributed from the European Alps to the Pyrenees (Ozenda 1985). This evergreen shrub is known regularly to host dark-pigmented, leaf surface-colonizing fungi (Corda 1829, Crane & Hughes 1982) and dominates several plant communities in the northern European Alps at altitudes from 1600 to 2200 m (Escaravage et al. 1998). *Rh. ferrugineum* is characterized by rather conspicuous glands on the lower leaf surface (Kratzmann 1910), the exudates of which may provide a nutritive source for various kinds of microbial organisms.

Sooty mould symptoms on the lower leaf surfaces of *Rh. ferrugineum* and *Rh. hirsutum* L. were first described by Kunze in Corda (1829) for the species *Torula rhododendri* Kunze. The taxon was subsequently recognized as not being congeneric with the generic type of *Torula* Pers., *T. herbarum* (Pers.) Link, and was transferred into the monospecific genus, *Capnocheirides* J.L.Crane & S.Hughes (Crane & Hughes 1982). Given their status as among the most popular ornamental plants, cultivars of *Rhododendron* were objects of quite a number of extensive studies concerning morphology and ecology of their leaf pathogens, such as the rust fungus *Caeoma tsukubaens* (Crane et al. 2004) and members of the genus *Chrysomyxa* (Hiratsuka & Sato 1969, Crane 2001, Nierhaus-Wunderwald 2002). However, there is still a lack of detailed studies with a focus on the community composition of *Rhododendron* leaf-associated, non-phytopathogenic fungi.

In the present study, *Rh. ferrugineum* leaf-colonizing epifoliar and endofoliar fungi were analysed to determine the community composition and possible life strategies of their members. Furthermore we addressed how far there was an overlap between the compositions of fungal communities found in and on the leaves, based on the assumption that several of the mostly pigmented epifoliar taxa are likely to invade the leaf interior from the outer surface during leaf development. Such behaviour of direct ingression into the leaves has been discussed in detail for endophytic fungi of *Viscum album* ssp. *austriacum* (Wiesb.) Vollm. and associated ascomycetes by Peršoh et al. (2010). The opposite behaviour observed in primarily endophytic fungi, where epifoliar growth takes place at later stages of development (e.g. Tanaka 2010). It is also to be expected that there are certain differences in morphological traits between the

Rh. ferrugineum-colonizing fungal groups with an obligately epifoliar and obligately endofoliar life habit such as, for instance, the intensity of hyphal pigmentation in response to different degrees of UV radiation (Rangel et al. 2006).

The objective of the present study was to test the following hypotheses: A) *Rh. ferrugineum* leaf-associated fungal communities represent multipartite associations; B) epifoliar pigmented fungi on *Rh. ferrugineum* build up an oligospecific community that is different in composition from fungal sooty mould associations colonizing other plants at lower altitudes in Central Europe; C) differences in *Rh. ferrugineum*-associated fungal leaf community compositions in their natural habitats are mainly due to age of the host leaves and the altitudinal vegetation zones, respectively; and D) parts of the endofoliar fungal community in *Rh. ferrugineum* pertain to primarily epifoliar (pigmented) fungi and access their habitat by invasion from the plant surface.

Material and methods

Collections: In order to screen for epifoliar fungal taxa, host plant individuals of *Rh. ferrugineum* were sampled in August 2007 at four separate natural sites in the Alps of Switzerland: Grimsel Valley, Flüela Mountain Pass, Julier Mountain Pass, and the surroundings of Monstein. To screen for endofoliar taxa, additional host plant samples from three sites were also collected in August 2007 (Julier and Monstein surroundings) and in August 2008 (Flüela). All host plants occurred in open populations, as defined by Pornon et al. (1996), having a coverage of ≤25% of the area. In each geographic area samples were taken at the following three altitudinal vegetation zones. 1) European larch forest zone with *Larix decidua* Mill. at 1770–1980 m alt. In the region of the Julier mountain pass, *Rh. ferrugineum* was lacking in this forest type and individuals in the Albula Valley, parallel to Julier Valley, were sampled instead. 2) Mountain pine zone with *Pinus mugo* Turra at 2000–2200 m alt. 3) Alpine zone at 2100–2300 m alt.

Switzerland, Bern, Grimsel Valley: **G1.** 46°33'43.11"N, 8°20'6.45"E, 2150 m alt. *Vaccinium myrtillus* L. shrubs in open situation (M-0126011). **G2.** 46°34'23.64"N, 8°20'11.00"E, 1870 m alt. (M-0126006; M-0126007). **G3.** 46°35'32.59"N, 8°19'32.62"E, 1750 m alt. Slope with dominant *Pinus mugo* (M-0126009; M-0126010). **G4.** 46°35'48.50"N, 8°19'33.55"E, alt. 1620 m. Slope behind small creek with *Larix decidua* (M-0126004; M-0126005). Graubünden, Monstein surroundings: **M1.** 46°40'57.96"N, 9°45'57.29"E, 2150 m alt. Alpine grassland with dominant *Vaccinium myrtillus* (M-0125984, M-0125985). **M2.** Alp Mäschenboden. 46°41'5.31"N, 9°47'2.32"E, 2090 m alt. Alpine grassland with dominant *Vaccinium myrtillus* (M-0125990, M-0125991). **M3.** 46°41'23.67"N, 9°47'7.35"E, 1980 m alt. Slope with dominant *Larix decidua* in the surroundings (M-0126001). Graubünden, Bever, Julier Mountain Pass: **J1.** 46°27'43.42"N, 9°40'54.73"E, 1850 m alt. Farmed grassland, without *Larix* (M-0125982; M-0126003). **J2.** 46°27'54.51"N, 9°42'28.96"E, 2080 m alt. Predominant *Pinus mugo*, no *Larix* (M-0125993, M-0125992). **J3.** 46°28'16.18"N, 9°43'19.1"E, 2233 m alt. *Vaccinium myrtillus* shrubs, without *Pinus mugo* and *Larix* (M-0125998, M-0125999). Graubünden, Flüela Mountain Pass: **F1**. 46°44'46.48"N, 9°57'18.55"E, 2300 m alt. Slope with *Vaccinium myrtillus* in open situation (2007: M-0126020, M-0126021; 2008: M-0126014, M-0126015). **F2.** 46°44'34.41"N, 9°58'32.45"E. 2200 m alt. Slope with dominant *Pinus mugo* (2007: M-0126016, M-0126017; 2008: M-0125977, M-0125976). **F3.** 46°44'40.24"N, 9°59'01.20" E, 2000 m alt. Slope with predominant *Pinus mugo* (2007: M-0126018; 2008: M-0125981). **F4.** 46°45'03.49"N, 10°02'57.59"E, 1770 m alt. with dominant *Larix europaea* (2007: M-0126019; 2008: M-0125983). Graubünden, Palpuogna: **P1.** 46°34'52.92"N, 9°47'03.03"E, 1920 m alt., with dominant *L. decidua* (M-0126012, M-0126013).

Isolation and cultivation of the fungi: Two leaved twigs per *Rh. ferrugineum* individual and collecting site were sampled. Leaves covered by macroscopically recognizable dark pigmented mycelia were collected twice per plant individual at the same time, and fungi were isolated from three segments of

the mycelium of two different leaves from the current year (cyl, 5–6 months) and previous year (pyl, 17–18 months). The plant material was stored at <10°C and was processed immediately after being transported to the laboratory. Leaf glands of *Rh. ferrugineum* are restricted to lower leaf surfaces. In order to obtain epifoliar fungi, the mycelium was dissected from the leaf and washed in sterile tap water to remove the majority of the adhering airborne fungal spore material. For isolation of endofoliar fungi, the plant parts were surface-sterilized in 70% ethanol for 1 min, in 1.2% sodium hypochlorite for 3 min, rinsed three times in sterile water for 1 min, and subsequently wrapped in sterile paper towels for about 15 min to remove water from the surface (Peršoh et al. 2010). Disc-shaped segments (20 mm^2) were cut from the leaf centre of two surface-sterilized leaves per maturity stage, twig and plant individual. Three discs were cut from each leaf, one from the basal end, one from the middle and one from the tip of the leaf. In order to obtain individual fungal strains, the pieces of washed mycelium (epifoliar fungi) and the punched discs (endofoliar fungi) were subsequently transferred to Petri dishes of 5.5 cm diam. containing yeast-malt medium (4 g glucose, 10 g malt extract, 4 g yeast extract, and 12 g agar per litre) with 0.1% tetracycline to suppress bacterial growth. The Petri dishes were incubated at 15°C and observed daily to record emergence of hyphae. Emerging colonies were separated and transferred onto new plates. One fungal strain of each operational taxonomic unit (OTU), with at least three isolates in total, and an assortment of OTUs with two isolates and singletons were deposited in the collection of the Jena Microbial Research Collection (JMRC). Accession numbers are listed in the appendix. The OTUs (n = 3) were examined and compared for consistency with morpho-anatomical concepts using a light microscope.

Pigmentation tests: The fungal strains were classified based on hyphal pigmentation using cultures grown on three different growth media: yeast-malt medium (4 g glucose, 10 g malt extract, 4 g yeast extract, and 12 g agar per litre), carrot-agar (4 ml carrot juice, 12 g agar per litre) and agar containing *Rhododendron* crushed leaves (20.75 g crushed fresh leaves from *Rh. ferrugineum*, 12 g agar per litre, with fresh twigs cut in the field, and the cut surfaces wrapped in a damp towel and kept in a plastic bag, stored at 5°C until usage). The Petri dishes were incubated at 15°C and fungal cultures were examined after one month for macroscopically recognizable pigmentation. In order to demonstrate coherence between obligately endofoliar life habit and pigmentation, the hyphal pigmentation was tested for mycelia on yeast-malt-agar, carrot-agar and agar containing *Rhododendron* crushed leaves. One piece of every dark coloured mycelium was placed in tubes with acetone or methanol. Pigmentation not soluble in either solvent was considered to be hyphal pigmentation. CMYK-values for pigmentation classified as 'dark' were: C: 39–73%; M: 50–75%; Y: 51–94%; K: 21–83%. CMYK-values for pigmentation classified as 'light' or 'lacking' were: C: 28–49%; M: 32–48%; Y: 33–61%; K: 0–10%.

DNA extraction, amplification, sequencing of the ITS rDNA and grouping of the ITS nrDNA: Pure cultures of the fungal isolates were preselected according to the following phenotypic traits: presence/absence and type of aerial mycelia, growth form, and type of pigmentation. For every leaf sample, representatives of each morphotype were chosen for sequencing. Consistency between molecular name assignments and the morpho-anatomical concepts was confirmed for multiton taxa using light microscopic examination (Peršoh et al. 2010, Flessa et al. 2012).

The Charge Switch® gDNA Plant Kit (Invitrogen, Life Technologies Corporation, Carlsbad, California, USA) was used to isolate DNA from the culture material. Cell disruption was accomplished using the Fast Prep FP120 (Bio101, Thermo Fisher Scientific Inc., Waltham, Massachusetts, USA) at a speed of 6.0 ms^{-1} for 2 × 40 s. Polymerase chain reaction (PCR) was performed using a MWG Biotech Primus 96 plus thermocycler. Double-stranded sequences of the ITS rRNA gene were obtained and further processed according to the method of Triebel et al. (2005). Sequences were deposited in the NCBI GenBank under accession numbers as listed in detail in the table in the appendix.

For statistical analysis, fungal isolates were grouped according to their ITS rDNA sequence similarities as described by Peršoh et al. (2010). Briefly, pairwise similarities among length-adjusted sequences were calculated using the BLAST application 'blastall' (v. 2.2.18). The resulting tabular output dataset was transformed using the function 'simMatrix', package 'RFLPtools' (Flessa et al. 2010) in R (R Development Core Team 2010). A cluster analysis was conducted using the function 'hclust' with the clustering method 'average linkage' in R, and clusters with minimal similarities of 96% were grouped into OTUs (Flessa et al. 2012).

Sequence-based assignment of names to similarity groups: Taxon names were assigned to the clusters to allow comparison with the results of other studies, but all data were exclusively analysed on the basis of sequence clusters, independent of the assigned names. The nomenclature followed the Index Fungorum (http://www.indexfungorum.org) and the higher classification MYCONET (http://www.fieldmuseum.org/myconet).

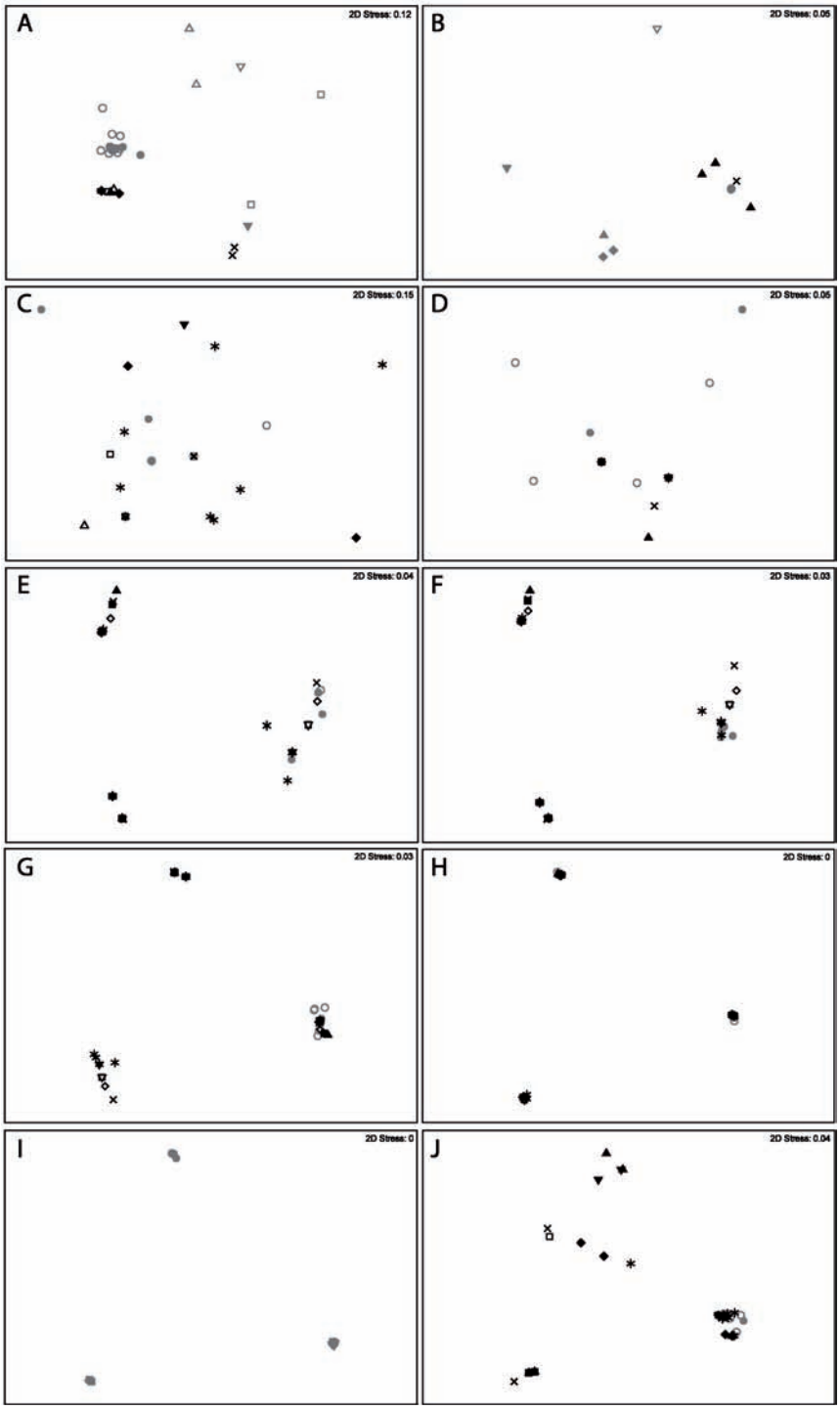
Names were assigned to the sequences, and correspondingly to the isolates, based on the nearest relatives determined by the 'Mega BLAST' (Zhang et al. 2000) results in the NCBI database (http://www.ncbi.nlm.nih.gov; status: January 2010). A consensus taxonomic assignment was compiled from the names of deposited sequences with a 'bitscore' of at least 90% of the best matching sequences, following the approach of Peršoh et al. (2010). The reliability of the assigned name may be assessed considering the number of best matching sequences obtained, the maximal and minimal 'bit scores' their alignment obtained with the query sequence, and the number of outliers and environmental samples are included in the appendix. Groups, i.e. clusters, were named according to the sequences they included, with consecutive numbering of groups that would otherwise have identical names. An analysis of similarity (ANOSIM; as defined by Chapman & Underwood 1999) served further to assess the reliability of the assigned names by analysing the sequence similarity matrix (see above) against the classification linked to the assigned names.

Separate BLAST searches for each group with n=5 in GenBank were conducted to obtain all sequences sharing at least 90% for any query sequence of each group. Similarity matrices were calculated as described above, and imported into Primer 6 (Plymouth Routines, v. 6.1.6) in order to conduct non-metric multidimensional scaling (NMDS) analyses. Following Peršoh & Rambold (2011), substrate data of all isolated strains, including published reference data, were mapped onto the NMDS graphs (Fig. 1 Table 1). The assigned taxon names, as well as reliability estimates of the sequence-based name assignments, are provided in the appendix.

Data analysis of fungal community trends: The binary matrix coding for the presence or absence of the fungi of each cluster in each sample was transformed into a similarity matrix, based on Jaccard distances using PRIMER 6 (Plymouth Routines, v. 6.1.6). The occurrence of fungal OTUs (singletons were excluded) was noted for the samples of each host plant. The respective isolation source, i.e. current year's leaves ('cyl', i. e. 5–6 months old) or previous year's leaves ('pyl', i. e. 17–18 months old), the geographical location and also the altitudinal vegetation zone, were each coded as grouping factors. Analysis of similarity (ANOSIM) was conducted to assess the impact of each factor on the sample grouping. ANOSIM calculates the p-value, which is considered to indicate significant differences when below 0.05. The R-value was used to indicate to what degree the respective factors explained groupings among samples. R-values >0.75 were interpreted as indicating clearly separate groups, R >0.5 overlapping, but clearly different, and R <0.25 barely separate groups (Chapman & Underwood 1999). The similarity of epifoliar fungi forming sooty patches and endofoliar fungal assemblages was compared using the Sørensen Similarity Index (QS) as follows: $QS = 2a/(2a + b + c)$, where a is the number of OTUs occurring in both communities, while b and c are the numbers of OTUs exclusively epifoliar and endofoliar fungi, respectively (Osono & Mori 2004, Kharwar et al. 2010).

Results

Grouping of the isolates and assignment of taxon names: In total, 323 sequences were gained from 153 epifoliar and 106 endofoliar fungal isolates, originating from the study sites together with sequences from an additional 64 isolates of epifoliar fungi from the Grimsel region. By using cluster analysis, 253 of the 323 sequences were grouped into 111 clusters and 70 singletons. ANOSIM revealed the factor 'taxonomy', i.e. name assignment according to the BLAST search results, in order to explain the significance ($p<0.05$) of genetic dissimilarities among the sequences at the various taxonomic levels, i.e. at species (p=0.01, R=1, n=119), genus (p=0.01, R=1, n=240), order (p=0.01, R=0.978, n=231), family (p=0.01, R=1, n=140), and subclass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C
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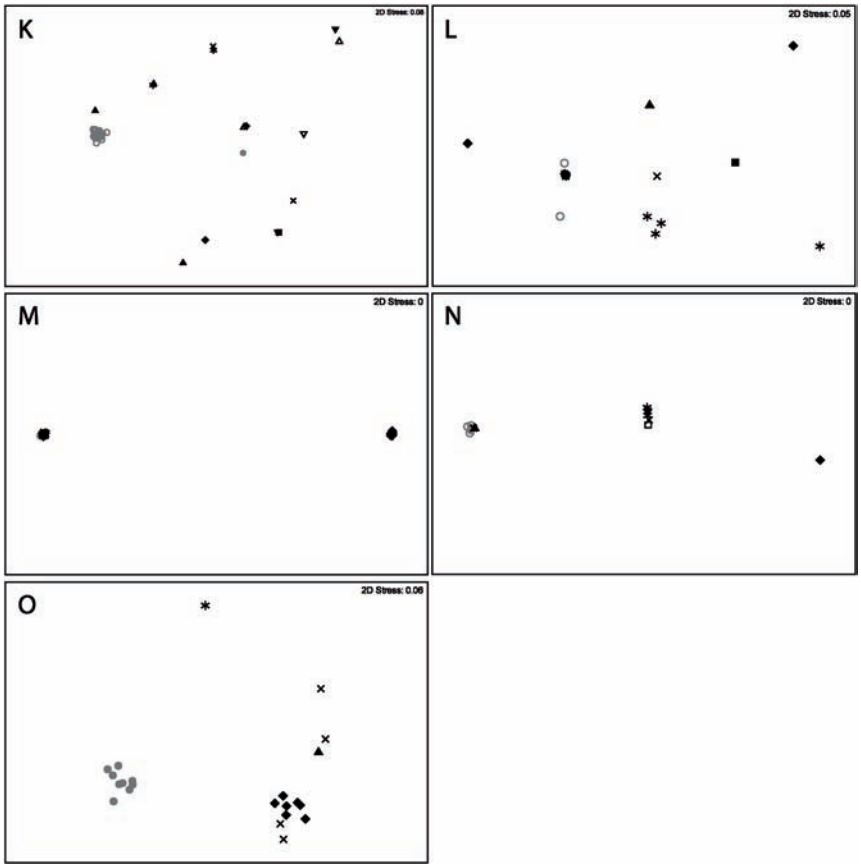

Fig. 1 A.–O. Sequence similarities among groups of *Rhododendron ferrugineum*-associated fungal strains, and all published sequences showing at least 90% similarity to the respective group. Similarities among ITS rRNA gene sequences are visualized by non-metric multidimensional scaling (NMDS). Symbols code the origin of the corresponding strains: fungi associated with *Rh. ferrugineum*: [●] non-surface sterilized leaves of *Rh. ferrugineum*, [○] surface sterilized leaves of *Rh. ferrugineum*, [✳] surface sterilized living plant leaves or steams, [×] non-surface sterilized living plant material, [▼] leaf litter, [■] plant roots, [▲] soils, [△] rocks, [▽] air, [◇] water, [□] dust, [+] dung. Undifferentiated substrates [◆] include ants, lichens, wood, cheese, sea sediment and fungal fruit bodies. Other symbols in grey indicate related sequences with less than 90% similarity to the isolates. Letters indicate the different clusters according to the names of clusters used in the text. The groups include sequences deposited as members of the taxa *Sarcinomyces* (cluster A), Mycota (B), Dothideomycetes (C), *Herpotrichia juniperi* (D), *Cladosporium* (E–H), Vibrisseaceae (I), Leotiomycetes (J), *Capnocheirides rhododendri* (K), *Aureobasidium pullulans* (L), *Penicillium* (M), *Dothichiza pityophila* (N), *Hypoderma rubi* (O).

(p=0.01, R=0.811, n=241) levels. Comprising 287 sequences, OTUs assigned to Ascomycota were the predominant group, whereas only nine OTUs were assignable to Basidiomycota, and four OTUs to Zygomycota. Among the Ascomycota, the most abundant groups represented Dothideomycetes with 167 OTUs (133 epifoliar, 34

Table 1. Substrates from which closely related sequences of the most frequent fungal OTUs (n=5) were isolated, with reference to ecological data from GenBank.

OTU	Non-surface sterilized leaves of *Rh. ferrugineum*	Surface sterilized leaves of *Rh. ferrugineum*	Surface sterilized living plant leaves or steams	Non-surface sterilized living plant material	Leaf litter	Plant roots	Soils	Rocks	Air	Water	Dust	Dung	Undifferentiated substrates include ants, lichens, wood, cheese, sea sediment and fungal fruit bodies	Total
Aureobasidium pullulans-1	6	0	6	8	4	1	1	0	0	0	1	0	5	32
Capnocheirides rhododendri-1	60	2	2	2	3	1	3	3	1	0	0	0	3	82
Cladosporium-1	1	5	9	7	4	5	5	0	4	19	4	2	1	66
Cladosporium-2	0	5	9	7	4	5	5	0	4	19	4	2	1	65
Cladosporium-3	16	2	9	7	4	5	5	0	4	19	4	2	1	79
Cladosporium-4	8	3	9	7	4	5	5	0	4	19	4	2	1	72
Dothichiza pityophila-1	5	1	2	3	2	0	1	0	0	0	1	0	1	17
Dothideomycetes-1	3	4	8	1	1	0	0	2	0	0	2	0	2	23
Herpotrichia juniperi-1	4	2	0	19	2	1	1	0	0	0	0	0	2	31
Hypoderma rubi-1	0	9	1	5	0	0	3	0	0	0	0	0	10	28
Leotiomycetes-1	7	1	22	4	8	4	11	0	0	0	1	0	6	64
Mycota-2	4	1	0	1	3	0	4	0	1	0	0	0	2	16
Penicillium-1	3	10	3	3	2	0	1	0	3	1	1	0	13	40
Sarcinomyces-1	17	6	1	2	1	0	1	3	1	0	3	0	2	37
Vibrisseaceae-1	3	5	1	2	0	11	0	0	4	0	0	0	2	28

endofoliar), followed by Leotiomycetes with 53 OTUs (30 epifoliar, 23 endofoliar), Eurotiomycetes with 38 OTUs (22 epifoliar, 16 endofoliar), Sordariomycetes with 19 OTUs (nine epifoliar, 10 endofoliar), and 10 OTUs (four epifoliar, six endofoliar) of unknown relationships. The distribution of fungal genotypes (n=3) according to their epifoliar and endofoliar occurrences are displayed in Fig. 2.

Sequence similarities between groups of *Rh. ferrugineum*-associated fungal strains and all published sequences showing at least 90% similarity to the respective group revealed the following results: Published sequences with a high similarity to the group of OTUs comprising *Sarcinomyces*-1 and *Capnocheirides rhododendri*-1 (Fig. 1, graphs **A**, **K**) originated from heterogeneous substrate types. Clusters comprising *Cladosporium*-1 to -4 (**E**–**H**) corresponded to sequences of OTUs derived from water samples and surface-sterilized or non-surface-sterilized living plant material. Sequences of the *Penicillium*-1 cluster (**M**) mainly corresponded to sequences of OTUs isolated from surface-sterilized living plant tissues and air samples. Results for smaller OTUs are displayed in Fig. 1.

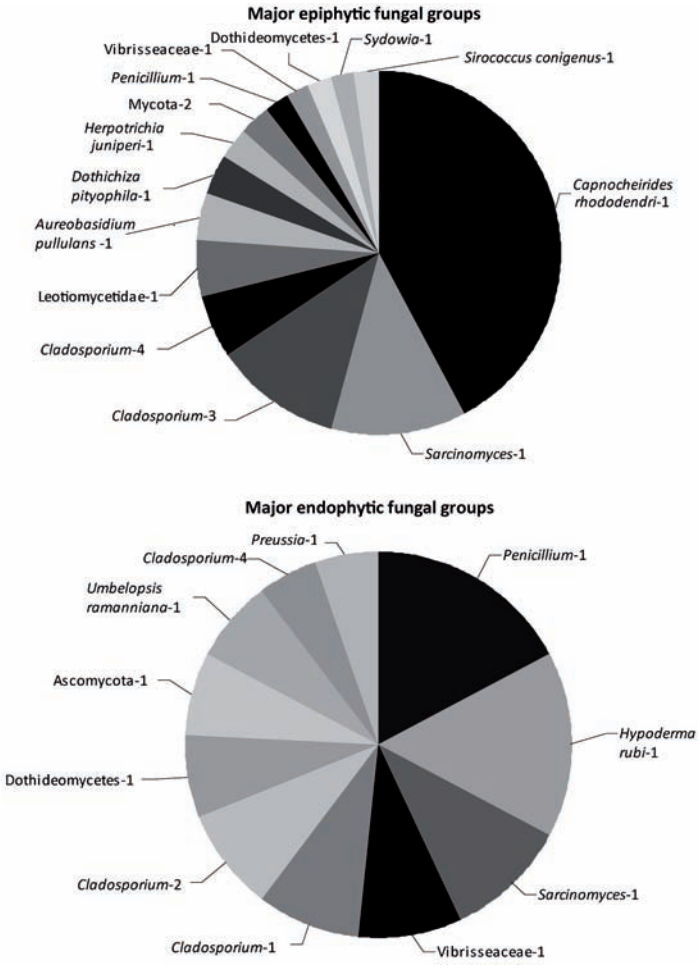

Fig. 2. Epifoliar and endofoliar fungal OTUs (n=3) on *Rhododendron ferrugineum.*

This analysis also revealed that the best matching sequences corresponded to those of surface-sterilized or non-surface-sterilized living plant organs, or leaf litter, and, to a much lower degree, to sequences from plant root and soil-derived OTUs.

Observations on the life habit of *Capnocheirides rhododendri*: *Capnocheirides rhododendri*-1 was predominant on the current and previous year's leaves (82.9% and 50%, respectively). The decrease of this value is probably because of the lower secretion activity of the previous year's leaves. Sooty patches due to *C. rhododendri* occurred on the lower surface of *Rh. ferrugineum* leaves. On the current year's lower leaf surfaces the fungus always formed a considerable number of small and dispersed sooty patches. Their distribution is likely to have coincided with leaf glands. These

glands were observed to start as green, and covering the leaf surface of the current year's leaves rather densely, but protruding and turning to brown on the previous year's leaves. The gland activity was observed on leaves from fresh twigs which were cut in the field and stored at 5°C until use. On the lower leaf surfaces of the current year's leaves, drops of a viscous, yellowish brown secretion were detected, whereas the glands of the previous year's leaves were non-functional and remained dry. Sooty patches caused by *C. rhododendri*-1 on the previous year's leaves were observed to fuse together, forming a contiguous layer more or less covering the whole lower leaf surface. Observations on *C. rhododendri*-1 in culture showed that growth is rather slow on all tested media when compared, for example, to *Cladosporium* spp.

Alpha-diversity of epifoliar fungi: In the present study, 93 visibly infected leaves (cyl/pyl) were investigated. Sooty patches were only observed on the lower leaf surface, correlated to occurrence of leaf glands in the host plant, these also being restricted to lower leaf surfaces. Samples with only one OTU were obtained from 35 leaves (30 cyl, 5 pyl). However, oligospecific communities mainly occurred: two OTUs were present on 24 leaves (cyl/pyl: 7/17), three on 16 (cyl/pyl: 4/12), four on 10 (cyl/pyl: 0/10), five taxa on five (pyl), and communities with six to eight OTUs in one sample (pyl). As result of the ANOSIM, differences in fungal community compositions of parallel samples from corresponding plants from the same sampling sites could be ignored.

According to the ANOSIM analysis, the factor 'leaf age' was significant (p=0.008) but the rather low *R* value (*R* = 0.068) indicated that the leaf age groups largely overlap. No fungal OTU was found to occur on all leaves. Aside from the predominant *C. rhododendri*-1 (82.9% cyl, 50% pyl), the fungal OTUs with overall frequencies >10% were *Cladosporium*-3 and *Sarcinomyces*-1. While *C. rhododendri*-1 was more frequent on cyl, the frequency of *Cladosporium*-3 was higher on pyl, and *Sarcinomyces*-1 exhibited similar frequencies on leaves of both stages. Among the OTUs found in more than 5% of the samples, Leotiomycetidae-1 and *A. pullulans*-1 preferentially occurred on older leaves, whereas *Cladosporium*-4 and *D. pityophila*-1 had a balanced distribution between both leaf stages (Table 2). The factor 'sampling site' was significant (p=0.009), but the very low *R*-value (*R*=0.084) indicated that the groups largely overlapped according to sampling site.

Alpha-diversity of endofoliar fungi: In 56% of cyl and pyl leaves, fungal occurrence was observed, with 25% in the cyl, and 88% in the pyl. In 14 leaves (four in cyl, 10 in pyl) one single fungal species was detected. Oligospecific communities were most commonly observed: two species were present in 16 leaves (five cyl, 11 pyl), three species in seven leaves (one cyl, six pyl), four species in three leaves (pyl), five species in three leaves (pyl), and six species were present in two leaves (pyl).

The factor 'leaf age' was not significant (*p*=0.137, *R*=0.045). Predominant fungal OTUs, colonizing >10% of the cyl or pyl (>10% of the leaves), were *Cladosporium*-1 and 2, *Hypoderma rubi*-1, *Penicillium*-1, *Sarcinomyces*-1 and Vibrisseaceae-1. More than one third of the cyl leaves was inhabited by *Penicillium*-1, showing lower frequencies on old leaves. *Cladosporium*-4, Ascomycota-1, *Cladosporium*-3 and *Preussia*-1 were less common, but showed a similar trend. *Sarcinomyces*-1 and *Cladosporium*-2 exhibited an opposite tendency. Fungi occurring in >10% of pyl and lacking in cyl were *Cladosporium*-1, Dothideomycetes-1, *Hypoderma rubi*-1 and Vibrisseaceae-1.

Table 2. Relative abundance of fungal OTUs (epifoliar and endofoliar fungi) isolated from *Rhododendron ferrugineum* in all (total) leaves, current year's leaves (cyl) and previous year's leaves (pyl).

OTU	Epifoliar OTUs			Endofoliar OTUs		
	total %	cyl %	pyl %	total %	cyl %	Pyl %
Amphisphaeriaceae-1	2.2	0.0	3.8	0.0	0.0	0.0
Ascomycota-1	0.0	0.0	0.0	8.9	20.0	5.7
Ascomycota-3	2.2	2.4	1.9	0.0	0.0	0.0
Aureobasidium pullulans-1	6.5	0.0	11.5	0.0	0.0	0.0
Botryotinia-1	1.1	0.0	1.9	2.2	0.0	2.9
Capnocheirides rhododendri-1	64.5	82.9	50.0	4.4	0.0	5.7
Capnodiales-1	1.1	0.0	1.9	2.2	0.0	2.9
Cladosporium-1	1.1	0.0	1.9	11.1	0.0	14.3
Cladosporium-2	0.0	0.0	0.0	11.1	10.0	11.4
Cladosporium-3	17.2	2.4	28.8	4.4	10.0	2.9
Cladosporium-4	8.6	9.8	7.7	6.7	10.0	5.7
Coleophoma empetri-1	0.0	0.0	0.0	4.4	0.0	5.7
Dothichiza pityophila-1	5.4	4.9	5.8	2.2	0.0	2.9
Dothideomycetes-1	3.2	2.4	3.8	8.9	0.0	11.4
Dothioraceae-1	2.2	0.0	3.8	0.0	0.0	0.0
Geomyces-1	0.0	0.0	0.0	4.4	0.0	5.7
Herpotrichia juniperi-1	4.3	0.0	7.7	4.4	0.0	5.7
Hyaloscyphaceae-1	1.1	0.0	1.9	2.2	10.0	0.0
Hypocrea-1	2.2	0.0	3.8	0.0	0.0	0.0
Hypoderma rubi-1	0.0	0.0	0.0	20.0	0.0	25.7
Leotiomycetidae-1	7.5	2.4	11.5	2.2	0.0	2.9
Leotiomycetidae-2	2.2	0.0	3.8	0.0	0.0	0.0
Lewia infectoria-1	1.1	0.0	1.9	2.2	10.0	0.0
Mycota-2	4.3	0.0	7.7	2.2	0.0	2.9
Mycota-3	0.0	0.0	0.0	4.4	0.0	5.7
Mycota-4	1.1	0.0	1.9	2.2	0.0	2.9
Penicillium-1	3.2	2.4	3.8	22.2	40.0	17.1
Phaeosphaeria-2	2.2	0.0	3.8	0.0	0.0	0.0
Phialocephala-1	1.1	0.0	1.9	4.4	0.0	5.7
Phoma-1	2.2	0.0	3.8	0.0	0.0	0.0
Physalospora-1	0.0	0.0	0.0	4.4	0.0	5.7
Physalospora-2	0.0	0.0	0.0	4.4	0.0	5.7
Pleosporales-1	2.2	0.0	3.8	0.0	0.0	0.0
Pleosporales-3	2.2	0.0	3.8	0.0	0.0	0.0
Preussia-1	0.0	0.0	0.0	6.7	10.0	5.7
Preussia-2	0.0	0.0	0.0	4.4	0.0	5.7
Sarcinomyces-1	18.3	17.1	19.2	13.3	10.0	14.3
Sirococcus conigenus-1	3.2	0.0	5.8	0.0	0.0	0.0
Sydowia-1	3.2	0.0	5.8	0.0	0.0	0.0
Umbelopsis ramanniana-1	0.0	0.0	0.0	8.9	10.0	8.6
Vibrisseaceae-1	3.2	0.0	5.8	11.1	0.0	14.3

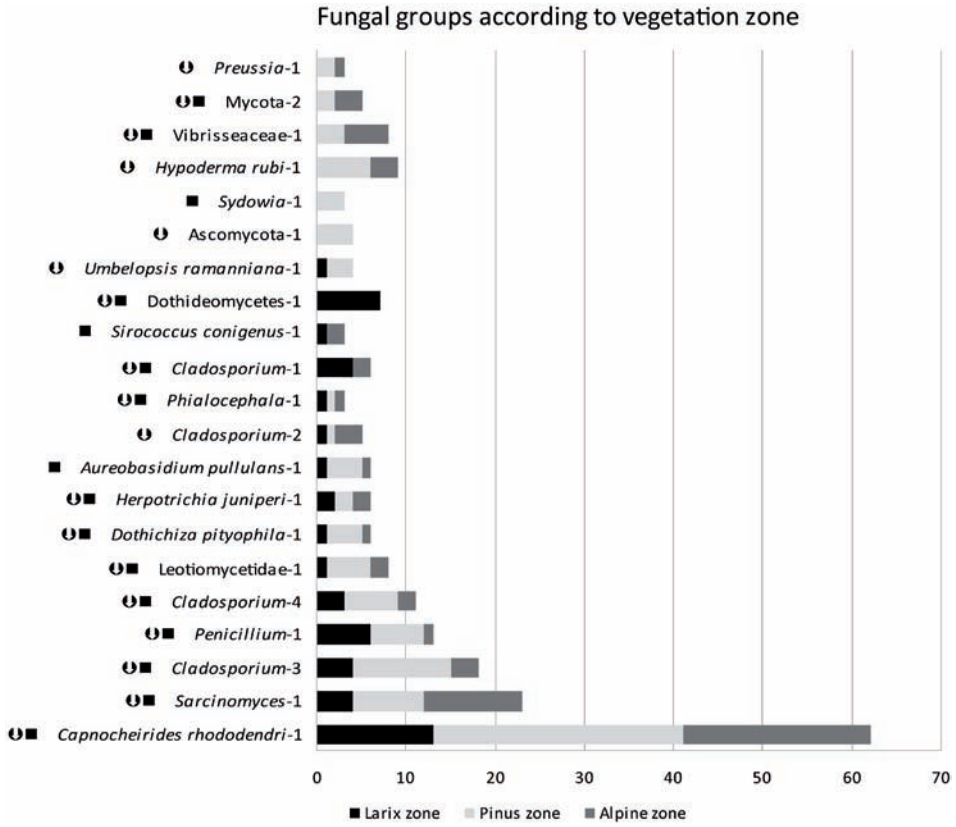

Fig. 3. Absolute abundance of the most abundant (n=3) fungal OTUs associated with the leaves of *Rhododendron ferrugineum* in the different altitudinal vegetation zones. ■: OTUs exclusively occurring on the leaf surfaces (epifoliar fungi). Ʊ: OTUs restricted to the leaf interior (endofoliar fungi) are underlined. ■Ʊ: OTUs occurring as both epifoliar and endofoliar.

Although most members of the endofoliar fungal community were not significantly influenced by leaf age, *Penicillium*-1 and Ascomycota-1 tended to prefer the younger leaves. Global ANOSIM was significant for the factor 'geographical region' (p=0.001, R=0.131), and for the factor 'sampling sites' over all geographical regions (p=0.001, R=0.248).

The effect of altitudinal zonation: OTUs either occurred in all of the three altitudinal vegetation zones (AVZ), in two adjacent AVZs, or were restricted to a single zone (Fig. 3) (zones are characterized in the Material and Methods). OTUs occurring in all of the three AVZs apparently formed a community with obligately associated fungal species on *Rh. ferrugineum*. Such a community contains *A. pullulans*-1, *C. rhododendri*-1, *Cladosporium*-2, *Cladosporium*-3, *Cladosporium*-4, *D. pityophila*-1,

H. juniperi-1, *Leotiomycetidae*-1, *Penicillium*-1, *Phialocephala*-1, and *Sarcinomyces*-1. Records from two adjacent AVZs exist for *Hypoderma rubi*-1, Vibrisseaceae-1, Mycota-2 and *Preussia*-1 for the two upper zones (*Pinus* and alpine zones), and *Cladosporium*-1 and *S. conigenus*-1 were found in the two lower zones (*Larix* and *Pinus* zones). While none of the fungal OTUs was restricted to the alpine zone, Dothideomycetes-1 exclusively occurred in the *Larix* zone, and Ascomycota-1 and *Sydowia*-1 were only recorded from the *Pinus* zone.

AVZs had no significant effect on the composition of epifoliar fungi (p=0.578, R=0.009), and had only a minimal effect on the endofoliar one (p = 0.016, R = 0.063). Significant (p=0.018) but slight (R=0.112) differences were found between the *Larix* and alpine zones, the *Pinus* and *Larix* zones (p=0.02, R=0.119), and between the *Larix* and *Pinus* zones (p=0.043, R=0.083). Differences in fungal community compositions between the *Pinus* and the alpine zone were insignificant (p=0.19, R=0.024).

Examination of the epifoliar and endofoliar fungal communities: The parallel examination of the communities of epifoliar and endofoliar fungi on *Rh. ferrugineum* leaves was motivated by the hypothesis that some of the mostly pigmented phyllosphere fungi may have different life strategies. A considerable number of OTUs was restricted to the leaf surface (Amphisphaeriaceae-1, Ascomycota-3, *A. pullulans*-1, Dothioraceae-1, *Hypocrea*-1, Leotiomycetidae-2, *Phoma*-1, Pleosporales-1 and 2, *S. conigenus*-1, *Phaeosphaeria*-2 and *Sydowia*-1) and are therefore considered to have an exclusively epifoliar life strategy. A similar number of OTUs was found to have a strictly endofoliar occurrence (Ascomycota-1, *Cladosporium*-2, *C. empetri*-1, *Geomyces*-1, *H. rubi*-1, Mycota-3, *Physalospora*-1 and -2, *Preussia*-1 and -2 and *U. ramanniana*-1). A third group of OTUs occurred in both habitats (*Botryotinia*-1, *C. rhododendri*-1, Capnodiales-1, *Cladosporium-1*, -3 and -4, *D. pityophila*-1, Dothideomycetes-1, *H. juniperi*-1, Hyaloscyphaceae-1, Leotiomycetidae-1, *L. infectoria*-1, Mycota-2 and -4, *Penicillium*-1, *Phialocephala*-1, *Sarcinomyces*-1 and Vibrisseaceae-1). The Sørensen Index of Similarity gave a result of 0.83 (n=3). The Sørensen Index of Similarity enables comparisons with the data of other studies regarding to the common sooty moulds and endophytic fungi. It is indicated that epifoliar and endofoliar fungal communities overlap in their species spectra.

Pigmentation was considered to be dark if it was not soluble in solvents, and CMYK-values for pigmentation were detected. Fungi exhibiting brown pigmented cells on all three culture media were considered as obligately pigmented taxa, while those pigmented on just one or two culture media were considered to exhibit pigmentation facultatively. The lack of pigments in strains on all three culture media was considered indicative for the inability to produce any dark pigments. Two epifoliar fungi (*Phoma*-1 and *Sydowia*-1) were recognized to be obligately pigmented, and all others belonged to the facultative pigmented group (Table 3). Additionally, *C. rhododendri*-1, which has been considered as only an occasional invader, was found to be 'obligately pigmented'. Among the endofoliar taxa, only three were obligately pigmented (Ascomycota-1, *Cladosporium*-2, and *U. ramanniana*-1), but two were completely lacking pigmentation (*Physalospora*-1 and *Preussia*-1). The remaining taxa belonged to the group of facultatively pigmented group. *Penicillium*-1, which has been considered to occur

Table 3. Pigmentation of fungal OTUs isolated from *Rhododendron ferrugineum*. Symbols indicate whether pigmentation is absent (○) or present (●) on malt yeast agar (MYA), carrot agar (C) and agar with *Rh. ferrugineum* leaves. Strains were isolated from the leaf surface (■, epifoliar) or from the leaf interior (◒, endofoliar).

Names Cluster	**Ep/En**	**MYA**	**C**	**Rfer**
Ascomycota-3	■	○	●	●
Aureobasidium pullulans-1	■	○	●	●
Leotiomycetidae-2	■	○	●	●
Phoma-1	■	●	●	●
Sirococcus conigenus-1	■	○	○	●
Sydowia-1	■	●	●	●
Ascomycota-1	◒	●	●	●
Cladosporium-2	◒	●	●	●
Coleophoma empetri-1	◒	○	●	●
Physalospora-1	◒	○	○	○
Physalospora-2	◒	○	○	●
Preussia-1	◒	○	○	○
Umbelopsis ramanniana-1	◒	●	●	●
Capnocheirides rhododendri-1	■ ◒	●	●	●
Cladosporium-1	■ ◒	●	●	●
Cladosporium-3	■ ◒	○	●	●
Cladosporium-4	■ ◒	●	●	●
Dothichiza pityophila-1	■ ◒	●	●	●
Dothideomycetes-1	■ ◒	●	●	●
Herpotrichia juniperi-1	■ ◒	●	●	●
Leotiomycetidae-1	■ ◒	●	●	●
Mycota-2	■ ◒	●	●	●
Penicillium-1	■ ◒	○	○	○
Sarcinomyces-1	■ ◒	●	●	●
Vibrisseaceae-1	■ ◒	○	●	●

occasionally on leaf surfaces, also lacked any pigmentation. When considering all OTUs occurring in both habitats, the obligate pigmentation type in culture was the most frequently found.

Discussion

Methodology: The observed colonization frequency (56%) of the leaves by endofoliar fungi in this study is within the range of comparable cultivation-based studies (Fisher et al. 1994, Arnold & Lutzoni 2007). Despite only a fraction of microbial populations being assessed by culture-based methods (Yang et al. 2001), this method was evidently sufficient for detecting the majority of fungal strains causing symptoms of sooty mould, because even *C. rhododendri*, a slowly growing fungus with a very narrow host

spectrum and occurring on the leaves of *Rh. ferrugineum* (Kunze in Corda 1829, Crane & Hughes 1982, Hughes 2007), could be regularly recognized. Common taxa described in other studies of dark pigmented epifoliar communities, i.e. *A. pullulans*, *Chaetomium* sp., *Cladosporium* spp., *Lewia* sp., and *Phoma* spp. (Webb & Mundt 1978, Fenn et al. 1989, Yang et al. 2001, Osono & Takeda 2002), as well as taxa such as *Penicillium* spp. and *H. rubi*, common on plant genera other than *Rhododendron* (Hou et al. 2007, Egorova et al. 2008), were also detected. Furthermore, substrate durability-dependent shifts in epifoliar fungal community composition were detected, which indicates that the fungal spectrum isolated was sufficient for addressing the hypotheses focused on in this study, despite fungi being not regularly part of the epifoliar community (i.e. adhering airborne spores) may be added to this group, due to the isolation method, which did not exclude airborne spores.

Therefore, cultivation-based studies can be considered to be adequate for observing potential compositional shifts in communities of isolated and presumably most of the characteristic taxa. Cultivation was also a precondition for testing the capability of the isolates to develop hyphal wall pigmentation, an assumed indicator for their natural life habit, as discussed below. Due to possible multi-factorial environmental impacts on the fungal community composition, re-inoculation experiments in a glasshouse with the isolated fungal strains were considered unfeasible and therefore not undertaken.

Names were assigned to groups and sequences to ensure that the obtained data may be comparatively discussed with the results of similar studies, which are not necessarily based on molecular data. It is primarily complicated by the fact that a considerable number of sequence data in public databases is not deposited under the correct name (Bridge et al. 2003). Hence, due to misidentified reference sequences, an assignment solely based on the best matching sequence is unreliable. In this study, 'consensus names', based on a defined fraction of all best matching sequences were assigned. Furthermore, the exclusion of sequences obviously deposited under incorrect names, i.e. 'outliers', allowed for an improved assignment of names. The comprehensive data noted for each name assignment (Table 1, appendix) to easily judge its reliability.

Observations on *Capnocheirides rhododendri*: In the context of community changes, *C. rhododendri* (being present in >80% of the cyl) clearly plays an important role in establishing initial fungal sooty patch communities. The observation that this taxon only grew on or in close vicinity to the leaf glands of the host plant indicated that growth and predominance of *C. rhododendri* on the lower leaf surface is favoured by its effective use of leave gland secretions, these being of high nutritive value for the fungus. Evidence of this assumption is deduced from the observation that not only contiguous fungal layers were formed to some degree on the leaf surface, such as by pigmented epifoliar fungi at lower altitudes (Flessa et al. 2012), but also considerable numbers of incoherent, small sooty patches. This is also supported by the observation that the appearance and activity of the glands changed dramatically during ageing of the leaves. Once they turned brown and protruded on the previous year's leaves, possibly even stopping their secretion, so this nutritional source for *C. rhododendri* was no longer available and the fungus lost its advantage over other epifoliar, less specialized fungi. As its speed of growth is relatively low it was soon outperformed and exhibited a dramatic decrease to an occurrence of only 50% on the pyl.

Alpha-diversity and changes in community structure in relation to the geographic distribution and altitudinal range of the host plant: The 323 fungal isolates gained from the host plant were assigned to 181 OTUs, which indicated that *Rh. ferrugineum* hosts a broad variety of endofoliar and epifoliar fungal species.

C. rhododendri, which was present on >80% of cyl, appeared unable to suppress the growth of other epifoliar fungal groups, because the sooty patch symptoms were mostly caused by an association of various fungal taxa (58 samples) rather than by only one species (30 samples).

In the cyl, the frequency of occurrence of oligospecific endofoliar communities was considerable, but was still higher on the pyl. This indicated that, even when colonization frequency is relatively low, once an endofoliar fungus has colonized the leaf, it is followed by additional fungi and an oligospecific community is established.

In sooty patches on pyl, *C. rhododendri*-1 was less frequent (50% of pyl samples) than on cyl. However, in contrast to findings in other dark pigmented epifoliar fungal communities (Flessa et al. 2012), there was no transition towards a community being dominated by another fungal species. Only in four samples was a transition to a more complex, i.e. oligo-specific aggregate observed with a tendency towards co-dominance with *Cladosporium*-3 on pyl.

Some of the isolated epifoliar strains appeared to belong to ubiquitous taxa, and several others to obligately alpine ones. Taxa from the genus *Sarcinomyces* were, for instance, also found on marble in the Mediterranean region (Wollenzien et al. 1997, Sert et al. 2007). *A. pullulans* and *Cladosporium* sp. are very common fungal taxa on plants in habitats of lower altitudes (Flessa et al. 2012). *S. conigenus* was found on sugar maple and white oak leaf samples from streams (Das et al. 2006). Besides these ubiquitous taxa, obligately alpine sooty mould symptom-causing OTUs could also be recognized (*C. rhododendri*-1, *H. juniperi*-1 and *Sydowia*-1). Analysis of published sequences showing 90% similarity to OTUs in this study indicated that Vibrisseaceae-1 may represent an alpine fungus that is exclusively associated with *Rh. ferrugineum*. The most frequent fungal taxa (*Penicillium* sp. and *H. rubi*) do not exclusively occur in alpine habitats. *Penicillium* spp. are common in *Rhododendron* (Egorova et al. 2008), and also in other Ericaceae (Stohr & Dighton 2004), and are assumed to inhibit pathogens (Nix-Stohr et al. 2008). *H. rubi* is also a typical fungus colonizing *Rhododendron* (Hou et al. 2007).

Surprisingly, composition of epifoliar fungi was not affected by the altitudinal vegetation zones, the most abundant groups being isolated from all three zones. Therefore, we assume that the community of the epiphyllous, sooty patch-forming fungi on *Rh. ferrugineum* are not influenced by fungal taxa derived from the surrounding vegetation. In contrast, significant differences among the *Larix*, *Pinus* and alpine vegetation zones existed with regard to the community composition of endofoliar growing fungi. These differences with respect to the predominant surrounding vegetation indicated that there may be a direct or indirect exchange of leaf-inhabiting fungi between *Rh. ferrugineum* and certain other plant species typical of the respective vegetation zone. In the absence of studies of leaf samples from *Larix* and *Pinus* and other plant species of montane to alpine habitats, we were unable to verify the assumption of a possible

Table 4. Effects of *Rhododendron ferrugineum* leaf age, alpine vegetation zone, sampling site and geographic location, as revealed by ANOSIM.

Factors	Epifoliar OTUs	Endofoliar OTUs
Leaf age	$p = 0.008$, $R = 0.068$	$p = 0.137$, $R = 0.045$
Alpine vegetation zone	$p = 0.578$, $R = –0.009$	$p = 0.016$, $R = 0.063$
Geographical region	$p = 0.362$, $R = 0.005$	$p = 0.001$, $R = 0.131$
Sampling site	$p = 0.009$, $R = 0.084$	$p = 0.001$, $R = 0.248$

horizontal distribution of certain endofoliar strains. Another possibility is the existence of differences in microclimate (e.g. temperature and precipitation) between the three zones, which may be influenced by the vegetation (i.e. alpine zone has the lowest neighbouring plants, the *Pinus* zone has an intermediate height of plants compared with the *Larix* zone, which exhibits the highest plants of the three vegetation zones), and also abiotic factors.

The 'leaf age' factor has instead of show no or minimal effect on the composition of the endofoliar fungi. The significant shifts of epifoliar fungal communities between cyl and pyl were probably due to the changing availability of certain cell compounds in the host plant. Studies on cell compound shifts correlated with leaf age were undertaken in earlier studies using the leaves of *Rh. ferrugineum* (Pisek 1950; Namibar & Fife 1991; Helmisaari 1995; Pornon et al. 1996; Lamaze et al. 2003; Marty et al. 2009, 2010). We therefore consider that a higher concentration of sugars, starch, nitrogen and a higher photosynthetic activity may favour the presence or predominance of fungi in cyl, whereas in pyl the same is favoured by a decrease in nutrients and photosynthetic activity. In contrast, the latter may be capable of destroying complex polymer cell wall compounds. Leaching substances in plants mostly include compounds of low molecular weight, sugars and amino acids (Tukey 1970), leading to a significant loss of nutritives (Wallace 1930, Schoch 1955), which are available on the leaf surface and may influence the epifoliar fungal community.

Generally, young and old leaves differ in their surface structure (Mechaber et al. 1996). While younger leaves are mostly strongly hydrophobic, this property may be lost in older leaves (Fogg 1947). Therefore leaching substances may have accumulated onto the surface of old leaves or already have disappeared. Nevertheless, different leaf age has been recognized as a factor of low relevance for fungal community composition (R=0.068 in epifoliar communities) in this study. For subalpine and alpine plant species, snow cover is a requirement for survival in harsh environments (Körner & Larcher 1988). Due to its low thermal conductivity (Aulitzky et al. 1982, Rango & Martinec 1994), snow cover prevents temperature extremes exceeding frost tolerance levels, and snow-covered plants may therefore be exposed to temperatures close to 0°C (Cernusca 1976). Winter desiccation is therefore not observed to occur (Sakai & Larcher 1987). The factor 'snow cover' probably explains to some degree the minimal impact of the factor 'leaf age' on the overall composition of the fungal assemblages on *Rh. ferrugineum*.

Based on the results of this study, we conclude that the epifoliar fungal community on *Rh. ferrugineum* is influenced by leaf age and sampling site, whereas the endofoliar fungal community is influenced by the vegetation zone, geographic region and sampling site.

Conclusion: residual and invading taxa: In the endofoliar habitat, two ecological groups were assumed to occur: a) those exhibiting a 'systemic' growth, combined with a presumably mutualistic relationship to the host plant, named 'residual endofoliar taxa' in the present study; and b) such groups, originating from the exterior of the leaf, named here 'invading endofoliar taxa'. *Rh. ferrugineum* is characterized by rather conspicuous glands on the lower leaf surface (Kratzmann 1910). The green-coloured glands closely cover the lower leaf surface of cyl and become physiologically inoperable in pyl. For some fungal species, they probably function as 'gateways' to the endofoliar habitat. Among these taxa, *C. rhododendri*-1 may simply behave as an occasional invading endofoliar taxon, much more frequently remaining on the leaf surface. As we observed significant differences between the composition of the endofoliar fungal community in the three altitudinal vegetation zones, the possibility of occasional infections of the leaf interior by *C. rhododendri*-1 is considered rather likely (Table 4). In contrast to *C. rhododendri*-1, *Cladosporium*-1 is regarded to be only an occasionally epifoliar fungus, more frequently occurring in the inner leaf tissues of *Rh. ferrugineum*. In summary, three types of fungi could be recognized. A group of epifoliar fungi exhibited the ability to form pigments (at least, in two of three culture media), and can be classified as 'residual epifoliar taxa'. A second group of endofoliar taxa may have colonized the leaf interior from the outer surface and accordingly obligately and facultatively exhibits hyphal wall pigmentation. They can be classified as 'invading endofoliar taxa'. A third group of strictly unpigmented taxa probably belongs to a group of 'residual endofoliar' taxa.

Due to the observed significant positive correlation between the properties of the leaf and hyphal pigmentation of the colonizing fungi, the potential to develop hyphal pigments is likely to have an indicative value for assigning these fungal taxa to major life strategies.

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Appendix

Appendix: Details of deposition, assignment and grouping of the isolated fungal strains and the corresponding ITS nrDNA sequences. The first columns list the GenBank accession numbers for the ITS sequences and the ID of the corresponding strains deposited at the "Pilz-Referenz-Zentrum Jena" ('FSU'). Details of the most similar sequences found in GenBank are given in the following column. The assigned name is listed in the following column, together with details of the least well matched sequence for the name assignment. The total number of sequences considered (i.e. sequences obtaining "Bit Scores" which are at least 0.9 times as high as the "Bit Score" for the best matching sequence obtained), the number of environmental samples among them, and the number of outliers (i.e. sequences deposited under names not considered for the name assignment) are also given. The final column lists the name of the cluster in which the sequence is grouped in.

Best matching sequence					Name assignment						
Sequence ID	Culture ID	GenBank Acc.	Bit-Score	Deposited as	Number of sequences considered	Matches	Outliers	Environmental samples	Lowest Bit-Score	Highest e-value	Cluster name (assigned consensus name)
HQ228246		FJ791155.1	990	*Thanatephorus cucumeris*	50	26	0	24	963	0	Agaricomycetes-1
FR773218	FSU8682	EF619630.1	715	Amphisphaeriaceae sp.	22	19	1	2	680	0	Amphisphaeriaceae-1
FR773220	FSU10193	EF619630.1	688	Amphisphaeriaceae sp.	16	15	0	1	654	0	Amphisphaeriaceae-1
FR773329	FSU10381	GU062284.1	905	*Annulohypoxylon multiforme*	10	6	0	4	863	0	*Annulohypoxylon multiforme-1*
FR773221	FSU8681	FJ820752.1	874	Fungi sp.	4	3	0	1	789	0	*Ascochyta-1*
FR773212	FSU10412	AM084763.1	907	Ascomycete sp.	10	10	0	0	878	0	Ascomycete-2
HQ228238		AM999660.1	693	Fungi sp.	2	1	0	1	684	0	Ascomycota-1
HQ228244		AM999660.1	678	Fungi sp.	2	1	0	1	656	0	Ascomycota-1
HQ228322	FSU10440	AM999660.1	758	Fungi sp.	2	1	0	1	737	0	Ascomycota-1
HQ228343	FSU10394	AM999660.1	750	Fungi sp.	2	1	0	1	736	0	Ascomycota-1
FR773245		FJ553299.1	865	Ascomycota sp.	1	1	0	0	865	0	Ascomycota-3
FR773250		FJ903364.1	904	Ascomycota sp.	1	1	0	0	904	0	Ascomycota-3

FR773197		GQ376094.1	896	*Aureobasidium pullulans*	50	28	4	18	885	0	*Aureobasidium pullulans-1*
FR773204		EF690466.1	837	*Aureobasidium pullulans*	50	30	4	16	830	0	*Aureobasidium pullulans-1*
FR871187	FSU10198	EF690466.1	815	*Aureobasidium pullulans*	50	33	3	14	813	0	*Aureobasidium pullulans-1*
FR773317	FSU6491	GQ376094.1	920	*Aureobasidium pullulans*	50	25	4	21	905	0	*Aureobasidium pullulans-1*
FR773331		GQ376094.1	920	*Aureobasidium pullulans*	50	25	4	21	905	0	*Aureobasidium pullulans-1*
FR773411		EF690466.1	911	*Aureobasidium pullulans*	50	25	4	21	900	0	*Aureobasidium pullulans-1*
FR773400	FSU10611	FJ169673.1	837	*Botrytis* sp.	50	44	2	4	837	0	*Botryotinia-1*
HQ228335	FSU10393	FJ169667.2	850	*Botryotinia fuckeliana*	50	39	8	3	839	0	*Botryotinia-1*
FR773176	FSU8620	FJ553155.1	713	Mycosphaerellaceae	1	1	0	0	713	0	*Capnocheirides rhododendri-1*
FR773264		FJ553155.1	763	Mycosphaerellaceae	1	1	0	0	763	0	*Capnocheirides rhododendri-1*
FR773271		FJ553155.1	771	Mycosphaerellaceae	1	1	0	0	771	0	*Capnocheirides rhododendri-1*
FR773273		FJ553155.1	778	Mycosphaerellaceae	1	1	0	0	778	0	*Capnocheirides rhododendri-1*
FR773274		FJ553155.1	769	Mycosphaerellaceae	1	1	0	0	769	0	*Capnocheirides rhododendri-1*
FR773275		FJ553155.1	765	Mycosphaerellaceae	1	1	0	0	765	0	*Capnocheirides rhododendri-1*
FR871178		FJ553155.1	760	Mycosphaerellaceae	1	1	0	0	760	0	*Capnocheirides rhododendri-1*
FR773281	FSU10264	FJ553155.1	778	Mycosphaerellaceae	1	1	0	0	778	0	*Capnocheirides rhododendri-1*
FR773282		FJ553155.1	765	Mycosphaerellaceae	1	1	0	0	765	0	*Capnocheirides rhododendri-1*
FR773287		FJ553155.1	760	Mycosphaerellaceae	1	1	0	0	760	0	*Capnocheirides rhododendri-1*
FR773288		FJ553155.1	793	Mycosphaerellaceae	1	1	0	0	793	0	*Capnocheirides rhododendri-1*
FR773296		FJ553155.1	739	Mycosphaerellaceae	1	1	0	0	739	0	*Capnocheirides rhododendri-1*
FR773297		FJ553155.1	758	Mycosphaerellaceae	1	1	0	0	758	0	*Capnocheirides rhododendri-1*
FR773300	FSU8610	FJ553155.1	784	Mycosphaerellaceae	1	1	0	0	784	0	*Capnocheirides rhododendri-1*
FR871180		FJ553155.1	795	Mycosphaerellaceae	1	1	0	0	795	0	*Capnocheirides rhododendri-1*
FR871181		FJ553155.1	767	Mycosphaerellaceae	1	1	0	0	767	0	*Capnocheirides rhododendri-1*
FR871182		FJ553155.1	763	Mycosphaerellaceae	1	1	0	0	763	0	*Capnocheirides rhododendri-1*
FR871183	FSU10377	FJ553155.1	754	Mycosphaerellaceae	1	1	0	0	754	0	*Capnocheirides rhododendri-1*

FR871188	FSU10265	FJ553155.1	795	Mycosphaerellaceae	1	1	0	0	795	0	*Capnocheirides rhododendri-1*
FR871191	FSU10378	FJ553155.1	761	Mycosphaerellaceae	1	1	0	0	761	0	*Capnocheirides rhododendri-1*
FR773304		FJ553155.1	776	Mycosphaerellaceae	1	1	0	0	776	0	*Capnocheirides rhododendri-1*
HQ228273	FSU10289	FJ553155.1	767	Mycosphaerellaceae	1	1	0	0	767	0	*Capnocheirides rhododendri-1*
FR773308		FJ553155.1	747	Mycosphaerellaceae	1	1	0	0	747	0	*Capnocheirides rhododendri-1*
FR773309		FJ553155.1	726	Mycosphaerellaceae	1	1	0	0	726	0	*Capnocheirides rhododendri-1*
FR773310	FSU8607	FJ553155.1	787	Mycosphaerellaceae	1	1	0	0	787	0	*Capnocheirides rhododendri-1*
FR773311	FSU8608	FJ553155.1	774	Mycosphaerellaceae	1	1	0	0	774	0	*Capnocheirides rhododendri-1*
FR773324	FSU8571	FJ553155.1	741	Mycosphaerellaceae	1	1	0	0	741	0	*Capnocheirides rhododendri-1*
FR773325		FJ553155.1	750	Mycosphaerellaceae	1	1	0	0	750	0	*Capnocheirides rhododendri-1*
FR773326	FSU10267	FJ553155.1	728	Mycosphaerellaceae	1	1	0	0	728	0	*Capnocheirides rhododendri-1*
FR773332		FJ553155.1	795	Mycosphaerellaceae	1	1	0	0	795	0	*Capnocheirides rhododendri-1*
FR773333		FJ553155.1	795	Mycosphaerellaceae	1	1	0	0	795	0	*Capnocheirides rhododendri-1*
FR773334		FJ553155.1	785	Mycosphaerellaceae	1	1	0	0	785	0	*Capnocheirides rhododendri-1*
FR773335		FJ553155.1	795	Mycosphaerellaceae	1	1	0	0	795	0	*Capnocheirides rhododendri-1*
FR773337		FJ553155.1	785	Mycosphaerellaceae	1	1	0	0	785	0	*Capnocheirides rhododendri-1*
FR773361		FJ553155.1	795	Mycosphaerellaceae	1	1	0	0	795	0	*Capnocheirides rhododendri-1*
FR773362		FJ553155.1	791	Mycosphaerellaceae	1	1	0	0	791	0	*Capnocheirides rhododendri-1*
FR773363		FJ553155.1	715	Mycosphaerellaceae	1	1	0	0	715	0	*Capnocheirides rhododendri-1*
FR773364		FJ553155.1	760	Mycosphaerellaceae	1	1	0	0	760	0	*Capnocheirides rhododendri-1*
FR773379	FSU8574	FJ553155.1	745	Mycosphaerellaceae	1	1	0	0	745	0	*Capnocheirides rhododendri-1*
FR773380		FJ553155.1	761	Mycosphaerellaceae	1	1	0	0	761	0	*Capnocheirides rhododendri-1*
FR773381	FSU10269	FJ553155.1	752	Mycosphaerellaceae	1	1	0	0	752	0	*Capnocheirides rhododendri-1*
FR773383		FJ553155.1	791	Mycosphaerellaceae	1	1	0	0	791	0	*Capnocheirides rhododendri-1*
FR773389	FSU8575	FJ553155.1	773	Mycosphaerellaceae	1	1	0	0	773	0	*Capnocheirides rhododendri-1*
FR773390		FJ553155.1	806	Mycosphaerellaceae	1	1	0	0	806	0	*Capnocheirides rhododendri-1*
FR773393	FSU8603	FJ553155.1	704	Mycosphaerellaceae	1	1	0	0	704	0	*Capnocheirides rhododendri-1*
FR773394		FJ553155.1	795	Mycosphaerellaceae	1	1	0	0	795	0	*Capnocheirides rhododendri-1*
FR773395		FJ553155.1	793	Mycosphaerellaceae	1	1	0	0	793	0	*Capnocheirides rhododendri-1*
FR773396		FJ553155.1	765	Mycosphaerellaceae	1	1	0	0	765	0	*Capnocheirides rhododendri-1*
FR773405		FJ553155.1	758	Mycosphaerellaceae	1	1	0	0	758	0	*Capnocheirides rhododendri-1*

FR773442		FJ553155.1	784	Mycosphaerellaceae	1	1	0	0	784	0	*Capnocheirides rhododendri-1*
FR773443		FJ553155.1	795	Mycosphaerellaceae	1	1	0	0	795	0	*Capnocheirides rhododendri-1*
FR773444	FSU10274	FJ553155.1	773	Mycosphaerellaceae	1	1	0	0	773	0	*Capnocheirides rhododendri-1*
FR773461		FJ553155.1	704	Mycosphaerellaceae	1	1	0	0	704	0	*Capnocheirides rhododendri-1*
FR773462		FJ553155.1	773	Mycosphaerellaceae	1	1	0	0	773	0	*Capnocheirides rhododendri-1*
FR773464		FJ553155.1	765	Mycosphaerellaceae	1	1	0	0	765	0	*Capnocheirides rhododendri-1*
FR773466		FJ553155.1	769	Mycosphaerellaceae	1	1	0	0	769	0	*Capnocheirides rhododendri-1*
FR773467		FJ553155.1	758	Mycosphaerellaceae	1	1	0	0	758	0	*Capnocheirides rhododendri-1*
FR773468		FJ553155.1	721	Mycosphaerellaceae	1	1	0	0	721	0	*Capnocheirides rhododendri-1*
FR773470		FJ553155.1	739	Mycosphaerellaceae	1	1	0	0	739	0	*Capnocheirides rhododendri-1*
FR773473		FJ553155.1	778	Mycosphaerellaceae	1	1	0	0	778	0	*Capnocheirides rhododendri-1*
FR773481		FJ553155.1	708	Mycosphaerellaceae	1	1	0	0	708	0	*Capnocheirides rhododendri-1*
HQ228306		FJ553155.1	760	Mycosphaerellaceae	1	1	0	0	760	0	*Capnocheirides rhododendri-1*
FR773295	FSU8566	EU167586.1	579	*Cladosporium* sp.	9	7	0	2	551	6.00E-162	*Capnodialea-2*
HQ228268	FSU10374	AM992158.2	752	Capnodiales sp.	4	3	0	1	737	0	*Capnodiales-1*
FR773213		AM992160.1	813	Capnodiales sp.	4	3	0	1	778	0	*Capnodiales-1*
FR773398		AM992160.1	686	Capnodiales sp.	4	3	0	1	656	0	*Capnodiales-3*
HQ228270		GQ996574.1	937	*Chaetomium funicola*	15	9	0	6	894	0	*Chaetomium-1*
FR773313	FSU10420	FJ820813.1	881	Fungi sp.	5	2	1	2	843	0	*Chalara microchona-1*
HQ228251		FJ266012.1	813	Fungi sp.	50	50	0	0	813	0	*Cladosporium-1*
HQ228291	FSU10211	FJ266011.1	791	Fungi sp.	50	50	0	0	791	0	*Cladosporium-1*
FR773477		FJ266011.1	809	Fungi sp.	50	50	0	0	809	0	*Cladosporium-1*
HQ228323	FSU10282	FJ266011.1	869	Fungi sp.	50	50	0	0	869	0	*Cladosporium-1*
FR773492		EU977278.1	869	Fungi sp.	3	3	0	0	869	0	*Cladosporium-1*
HQ228334	FSU10391	FJ266011.1	857	Fungi sp.	50	50	0	0	857	0	*Cladosporium-1*
HQ228254		EU977278.1	789	Fungi sp.	3	3	0	0	789	0	*Cladosporium-2*
FR773174		EU977278.1	791	Fungi sp.	3	3	0	0	791	0	*Cladosporium-2*
HQ228260		EU977278.1	791	Fungi sp.	3	3	0	0	791	0	*Cladosporium-2*
HQ228261		EU977278.1	876	Fungi sp.	3	3	0	0	876	0	*Cladosporium-2*
HQ228321	FSU10204	EU977278.1	869	Fungi sp.	3	3	0	0	869	0	*Cladosporium-2*

FR773178		EU715666.1	678	*Cladosporium sp.*	50	42	3	0	678	0	*Cladosporium-3*
FR773179		EU715666.1	837	*Cladosporium sp.*	50	43	2	5	837	0	*Cladosporium-3*
FR773194		EU715666.1	881	*Cladosporium sp.*	50	43	2	5	881	0	*Cladosporium-3*
FR773217		EU715666.1	865	*Cladosporium sp.*	50	43	2	5	865	0	*Cladosporium-3*
FR773228		EU715666.1	854	*Cladosporium sp.*	50	43	2	5	854	0	*Cladosporium-3*
FR773236		EU715666.1	880	*Cladosporium sp.*	50	44	2	4	880	0	*Cladosporium-3*
FR773247		EU715666.1	885	*Cladosporium sp.*	50	44	2	4	885	0	*Cladosporium-3*
FR773265	FSU10209	EU715666.1	802	*Cladosporium sp.*	50	43	2	5	802	0	*Cladosporium-3*
FR773291		EU715666.1	752	*Cladosporium sp.*	50	39	2	9	752	0	*Cladosporium-3*
FR773344		EU715666.1	850	*Cladosporium sp.*	50	43	2	5	850	0	*Cladosporium-3*
FR773387		EU715666.1	874	*Cladosporium sp.*	50	43	2	5	874	0	*Cladosporium-3*
FR773419		EU715666.1	845	*Cladosporium sp.*	50	43	2	5	845	0	*Cladosporium-3*
FR773420		EU715666.1	833	*Cladosporium sp.*	50	43	2	5	833	0	*Cladosporium-3*
FR773425	FSU8555	EU715666.1	881	*Cladosporium sp.*	50	43	2	5	881	0	*Cladosporium-3*
FR773428	FSU10271	EU715666.1	867	*Cladosporium sp.*	50	43	2	5	867	0	*Cladosporium-3*
FR773483		AY251077.2	784	*Cladosporium sphaerospermum*	50	43	2	5	780	0	*Cladosporium-3*
HQ228312	FSU10214	EU715666.1	874	*Cladosporium sp.*	50	43	2	5	874	0	*Cladosporium-3*
HQ228332		EF504369.1	863	Fungi sp.	50	42	2	6	861	0	*Cladosporium-3*
FR773195	FSU8559	FJ556911.1	802	*Cladosporium cladosporioides*	50	29	5	16	802	0	*Cladosporium-4*
FR773199		GQ370370.1	846	*Cladosporium* sp.	50	29	5	16	846	0	*Cladosporium-4*
FR773216		GQ370370.1	852	*Cladosporium* sp.	50	29	6	15	852	0	*Cladosporium-4*
FR773227		EU715666.1	837	*Cladosporium* sp.	50	43	2	5	837	0	*Cladosporium-4*
FR773244		AY251071.2	878	*Cladosporium uredinicola*	50	26	7	17	878	0	*Cladosporium-4*
FR773343	FSU8549	GU212392.1	872	*Cladosporium* sp.	50	21	8	21	872	0	*Cladosporium-4*
FR773386	FSU10270	AY251071.2	850	*Cladosporium uredinicola*	50	28	5	17	845	0	*Cladosporium-4*
FR773410	FSU8554	EF672315.1	887	*Cladosporium* sp.	50	22	8	20	881	0	*Cladosporium-4*
HQ228285	FSU8557	GU214631.1	887	*Cladosporium* sp.	50	24	7	19	887	0	*Cladosporium-4*
HQ228308	FSU10213	GU214631.1	894	*Cladosporium* sp.	50	24	7	19	894	0	*Cladosporium-4*
HQ228328		GU214631.1	852	*Cladosporium* sp.	50	24	7	19	852	0	*Cladosporium-4*

HQ228266	FSU8616	EU686928.1	614	Fungi sp.	4	1	0	3	612	2.00E-172	*Clypeosphaeria mamillana-1*
HQ228265	FSU8617	DQ979647.1	795	Fungi sp.	37	33	2	2	758	0	*Coleophoma empetri-1*
HQ228278	FSU8553	FJ480139.1	750	*Coleophoma empetri*	41	36	2	3	723	0	*Coleophoma empetri-1*
FR773341		AJ244242.1	902	*Dothichiza pityophila*	2	1	1	0	885	0	*Dothichiza pityophila-1*
FR773423		FJ553079.1	1007	*Dothioraceae sp.*	2	1	1	0	959	0	*Dothichiza pityophila-1*
FR773427		AJ244242.1	963	*Dothichiza pityophila*	2	1	1	0	961	0	*Dothichiza pityophila-1*
FR773434	FSU10386	AJ244242.1	957	*Dothichiza pityophila*	2	1	1	0	946	0	*Dothichiza pityophila-1*
HQ228284	FSU8576	AJ244242.1	952	*Dothichiza pityophila*	2	1	1	0	946	0	*Dothichiza pityophila-1*
FR773482		AJ244242.1	911	*Dothichiza pityophila*	2	1	1	0	900	0	*Dothichiza pityophila-1*
HQ228239	FSU10191	AM901920.1	891	Fungi sp.	10	3	0	7	850	0	Dothideomycetes-1
HQ228241		AM901920.1	872	Fungi sp.	14	4	0	10	830	0	Dothideomycetes-1
HQ228271		FJ997287.1	926	Dothideales sp.	6	3	0	3	880	0	Dothideomycetes-1
FR773237		FJ997287.1	926	Dothideales sp.	6	3	0	3	880	0	Dothideomycetes-1
FR773399	FSU10383	AM901920.1	880	Fungi sp.	13	4	0	9	837	0	Dothideomycetes-1
FR773407	FSU10384	FJ997287.1	902	Dothideales sp.	8	4	0	4	857	0	Dothideomycetes-1
HQ228277		AM901920.1	941	Fungi sp.	7	2	0	5	894	0	Dothideomycetes-1
FR773202	FSU10409	FJ150873.1	595	*Kabatiella microsticta*	28	9	0	19	568	6.00E-167	Dothioraceae-1
FR773415		FJ612670.1	734	Fungi sp.	24	4	0	20	701	0	Dothioraceae-1
FR871179	FSU8609	DQ667153.1	835	*Exobasidium rhododendri*	2	2	0	0	822	0	*Exobasidium rhododendri-1*
HQ228236		EF540755.1	837	*Geomyces pannorum*	32	16	0	16	798	0	*Geomyces-1*
HQ228252		EF540755.1	769	*Geomyces pannorum*	32	16	0	16	736	0	*Geomyces-1*
HQ228295	FSU10348	AY465448.1	832	Helotiaceae sp.	2	2	0	0	822	0	Helotiaceae-1
FR773312	FSU10419	AY969380.1	732	Fungi sp.	10	2	2	6	697	0	Helotiales-1
HQ228240	FSU10295	FJ904465.1	798	*Herpotrichia juniperi*	45	34	1	10	760	0	*Herpotrichia juniperi-1*
FR773198	FSU10263	FJ904461.1	800	*Herpotrichia juniperi*	45	34	1	10	767	0	*Herpotrichia juniperi-1*
FR773205	FSU8561	GQ203759.1	730	*Herpotrichia juniperi*	50	38	1	11	702	0	*Herpotrichia juniperi-1*
FR773286	FSU10197	FJ904454.1	826	*Herpotrichia juniperi*	50	41	1	8	787	0	*Herpotrichia juniperi-1*
FR871184		FJ904484.1	806	*Herpotrichia juniperi*	50	41	1	8	784	0	*Herpotrichia juniperi-1*
HQ228327		GQ203759.1	761	*Herpotrichia juniperi*	50	40	1	9	739	0	*Herpotrichia juniperi-1*

FR773203	FSU8560	X74923.1	937	*Heterobasidion annosum*	50	50	0	0	928	0	*Heterobasidion-1*
FR773231	FSU8684	FJ379833.1	745	*Hyalodendriella* sp.	3	1	1	0	721	0	*Hyalodendriella-1*
FR773330	FSU8548	U59145.1	841	*Lachnellula calyciformis*	3	2	1	0	802	0	Hyaloscyphaceae-1
HQ228303	FSU10435	U59145.1	856	*Lachnellula calyciformis*	2	2	0	0	837	0	Hyaloscyphaceae-1
FR773201	FSU8619	AM504125.1	1051	*Hypholoma fasciculare*	10	10	0	0	1013	0	*Hypholoma fasciculare-1*
FR773185	FSU10338	EU294196.1	780	*Hypocrea* sp.	24	16	2	6	741	0	*Hypocrea-1*
FR773222	FSU8544	DQ083026.1	1000	*Trichoderma croceum*	40	28	8	4	950	0	*Hypocrea-1*
HQ228287	FSU10429	GU367895.1	628	*Hypoderma rubi*	32	15	11	6	597	6.00E-177	*Hypoderma rubi-1*
FR773456		GU367895.1	651	*Hypoderma rubi*	31	14	11	6	619	0	*Hypoderma rubi-1*
FR773484		GU367895.1	656	*Hypoderma rubi*	30	14	10	6	625	0	*Hypoderma rubi-1*
HQ228316		GU367895.1	612	*Hypoderma rubi*	33	15	12	6	584	6.00E-172	*Hypoderma rubi-1*
FR773493		GU367898.1	612	*Hypoderma rubi*	32	15	11	6	584	6.00E-172	*Hypoderma rubi-1*
HQ228336		GU367895.1	601	*Hypoderma rubi*	37	15	15	6	573	1.00E-168	*Hypoderma rubi-1*
HQ228337		GU367895.1	612	*Hypoderma rubi*	27	15	9	3	586	6.00E-172	*Hypoderma rubi-1*
HQ228340		GU367895.1	597	*Hypoderma rubi*	39	15	18	6	568	2.00E-167	*Hypoderma rubi-1*
HQ228344		GU367895.1	641	*Hypoderma rubi*	32	14	12	6	612	0	*Hypoderma rubi-1*
FR773232	FSU10375	FJ612670.1	734	Fungi sp.	3	1	0	2	704	0	*Kabatiella caulivora-1*
HQ228297	FSU10432	FJ528692.1	1271	Fungi sp.	21	17	0	4	1212	0	*Leohumicola-1*
FR773370	FSU10422	FJ553685.1	839	Leotiomycetes sp.	7	5	1	0	821	0	Leotiomycetes-3
FR773314	FSU8606	DQ273332.1	536	Pezizomycotina sp.	13	9	1	3	510	4.00E-149	Leotiomycetes-4
FR773182		EU625294.1	865	Fungi sp.	30	15	4	11	822	0	Leotiomycetidae-1
FR773184	FSU8558	AY183372.1	832	Cf. *Phoma* sp.	11	1	3	7	795	0	Leotiomycetidae-1
FR773188	FSU10261	FJ904499.1	826	*Allantophomopsis* sp.	28	15	4	9	787	0	Leotiomycetidae-1
FR773257	FSU10195	AY969742.1	856	Fungi sp.	30	15	5	10	821	0	Leotiomycetidae-1

FR773267		EU625294.1	856	Fungi sp.	29	14	5	10	817	0	Leotiomycetidae-1
FR773277		AY969742.1	880	Fungi sp.	29	15	5	9	839	0	Leotiomycetidae-1
FR773435	FSU10272	EU625294.1	833	Fungi sp.	30	15	6	9	793	0	Leotiomycetidae-1
HQ228310		FJ904499.1	773	*Allantophomopsis* sp.	35	16	6	13	739	0	Leotiomycetidae-1
FR773457	FSU10291	FJ904499.1	806	*Allantophomopsis* sp.	36	18	6	12	767	0	Leotiomycetidae-10
FR773193		FJ904499.1	789	*Allantophomopsis* sp.	33	15	5	13	761	0	Leotiomycetidae-2
FR773200	FSU10288	AY608648.1	846	*Phacidiopycnis washingtonensis*	35	18	4	13	811	0	Leotiomycetidae-2
FR773206	FSU8562	FJ904499.1	747	*Allantophomopsis* sp.	36	16	6	14	713	0	Leotiomycetidae-3
FR773226		FJ904499.1	815	*Allantophomopsis* sp.	33	15	6	12	782	0	Leotiomycetidae-4
FR773251		AY969742.1	856	Fungi sp.	35	18	5	12	821	0	Leotiomycetidae-5
FR871186		AY969742.1	854	Fungi sp.	35	18	5	12	819	0	Leotiomycetidae-6
FR773436		FJ904499.1	800	*Allantophomopsis* sp.	33	15	6	12	767	0	Leotiomycetidae-8
FR773438		FJ904499.1	826	*Allantophomopsis* sp.	36	18	6	12	785	0	Leotiomycetidae-9
HQ228245	FSU10207	GQ376103.1	918	*Lewia infectoria*	50	33	13	4	907	0	*Lewia infectoria-1*
FR773302	FSU6492	GQ376103.1	846	*Lewia infectoria*	50	29	11	10	839	0	*Lewia infectoria-1*
FR773375	FSU8680	DQ491498.1	1029	*Mollisia cinerea*	1	1	0	0	1029	0	*Mollisia cinerea-1*
HQ228313	FSU10438	AF439461.1	776	*Leptosphaeria dryadis*	4	3	1	0	745	0	*Monodictys arctica-1*
FR773283	FSU10341	DQ068346.1	817	Fungi sp.	18	17	0	1	778	0	*Mycosphaerella-1*
HQ228253	FSU10407	EF619925.1	856	*Mycosphaerella* sp.	4	2	1	0	845	0	*Mycosphaerella-2*
FR773319		EF434011.1	856	Fungi sp.	1	1	0	0	856	0	Mycota-1
FR773397	FSU8602	FJ612953.1	303	Fungi sp.	4	4	0	0	303	4.00E-79	Mycota-10
HQ228279	FSU10426	AM901933.1	869	Fungi sp.	11	11	0	0	832	0	Mycota-11
HQ228280	FSU10427	AM999755.1	1315	Fungi sp.	2	2	0	0	1308	0	Mycota-12
HQ228281	FSU10346	EF619862.1	444	Fungi sp.	1	1	0	0	444	2.00E-121	Mycota-13
FR773451	FSU10428	AM999599.1	702	Fungi sp.	1	1	0	0	702	0	Mycota-14
HQ228255	FSU10586	FJ820750.1	920	Fungi sp.	1	1	0	0	920	0	Mycota-15
FR871193	FSU10347	EU516950.1	734	Fungi sp.	2	2	0	0	710	0	Mycota-19
FR773269		AM999660.1	773	Fungi sp.	2	2	0	0	741	0	Mycota-2
FR773316	FSU8569	AM999660.1	743	Fungi sp.	2	2	0	0	773	0	Mycota-2
FR773371		AM999660.1	765	Fungi sp.	2	2	0	0	728	0	Mycota-2

FR773421	FSU10385	AM999660.1	774	Fungi sp.	2	2	0	0	774	0	Mycota-2
HQ228298		AM999660.1	732	Fungi sp.	2	2	0	0	710	0	Mycota-2
HQ228307	FSU10436	FJ235861.1	809	Fungi sp.	4	4	0	0	778	0	Mycota-20
HQ228339	FSU10205	AY561199.1	641	Fungi sp.	1	1	0	0	641	1.00E-180	Mycota-3
HQ228345	FSU10613	AY561199.1	612	Fungi sp.	1	1	0	0	612	8.00E-172	Mycota-3
FR773219	FSU10414	FJ820775.1	778	Fungi sp.	2	2	0	0	778	0	Mycota-4
HQ228346	FSU10423	EU686068.1	715	Fungi sp.	2	2	0	0	713	0	Mycota-4
FR773223	FSU10415	EU517039.1	848	Fungi sp.	2	2	0	0	846	0	Mycota-6
HQ228272	FSU10417	FJ820826.1	963	Fungi sp.	1	1	0	0	963	0	Mycota-7
FR773292	FSU10608	AM262385.1	691	Fungi sp.	1	1	0	0	691	0	Mycota-8
FR773360	FSU10609	DQ884464.1	512	Fungi sp.	1	1	0	0	512	6.00E-142	Mycota-9
FR773214	FSU10413	AY969346.1	507	Fungi sp.	50	17	16	17	483	3.00E-140	*Neofabraea alba-1*
HQ228309	FSU10437	AF201751.1	1064	*Nodulisporium* sp.	3	3	0	0	1062	0	*Nodulisporium-1*
HQ228311		EU781661.1	466	*Nodulisporium* sp.	2	2	0	0	466	7.00E-128	*Nodulisporium-2*
FR773229		EU128597.1	900	*Penicillium glabrum*	50	30	14	6	881	0	*Penicillium glabrum-1*
FR773211		EU729705.1	880	*Penicillium citreonigrum*	46	43	0	3	837	0	*Penicillium-1*
FR773225		EU729705.1	902	*Penicillium citreonigrum*	45	42	0	3	857	0	*Penicillium-1*
FR773385		EU729705.1	900	*Penicillium citreonigrum*	43	40	0	3	869	0	*Penicillium-1*
HQ228290	FSU10275	EU729705.1	854	*Penicillium citreonigrum*	47	43	1	3	813	0	*Penicillium-1*
HQ228317		EU128641.1	850	*Penicillium citreonigrum*	50	46	1	3	808	0	*Penicillium-1*
HQ228318	FSU10281	EU128641.1	929	*Penicillium citreonigrum*	50	46	1	3	887	0	*Penicillium-1*
HQ228319		EU128641.1	848	*Penicillium citreonigrum*	50	46	1	3	806	0	*Penicillium-1*

HQ228320		EU128641.1	920	*Penicillium citreonigrum*	50	46	1	3	878	0	*Penicillium-1*
HQ228325	FSU10283	EU128641.1	904	*Penicillium citreonigrum*	50	46	1	3	861	0	*Penicillium-1*
HQ228329		EU128641.1	887	*Penicillium citreonigrum*	50	46	1	3	845	0	*Penicillium-1*
FR773497		EU128641.1	826	*Penicillium citreonigrum*	46	43	0	3	789	0	*Penicillium-1*
HQ228333	FSU10286	EU128641.1	898	*Penicillium citreonigrum*	50	46	1	3	856	0	*Penicillium-1*
HQ228338		EU128641.1	878	*Penicillium citreonigrum*	50	46	1	3	835	0	*Penicillium-1*
FR773315	FSU8547	FJ820605.1	994	Fungi sp.	7	3	0	4	963	0	*Peniophora incarnata-1*
FR773368	FSU10610	GU433224.1	963	*Peniophora* sp.	20	8	1	11	915	0	*Peniophora-1*
FR773422	FSU10612	AM901741.1	920	Fungi sp.	2	1	0	1	918	0	*Phaeococcomyces nigricans-1*
FR773278	FSU10418	FJ609291.1	833	Fungi sp.	40	20	3	17	793	0	*Phaeosphaeria-1*
FR773369	FSU8552	AF439478.1	828	*Phaeosphaeria dennisiana*	5	5	0	0	797	0	*Phaeosphaeria-2*
FR773418		AF439496.1	865	*Phaeosphaeria padellana*	4	4	0	0	826	0	*Phaeosphaeria-2*
HQ228242		FJ903314.1	652	*Phialocephala* sp.	18	14	0	4	623	0	*Phialocephala-1*
FR773376	FSU10345	DQ309109.1	706	Fungi sp.	18	13	0	5	673	0	*Phialocephala-1*
FR773488	FSU10216	FJ903314.1	658	*Phialocephala* sp.	19	14	0	5	632	0	*Phialocephala-1*
FR773189	FSU10339	AB465199.1	774	*Phoma* sp.	18	16	0	2	736	0	*Phoma complanata-1*
FR773328	FSU10344	FJ515608.1	553	*Phoma complanata*	1	1	0	0	553	4.00E-154	*Phoma complanata-1*
FR773412		EF589893.1	856	*Phoma* sp.	1	1	0	0	856	0	*Phoma-1*
FR773414	FSU6494	EF589893.1	833	*Phoma* sp.	1	1	0	0	833	0	*Phoma-1*
FR773192	FSU10605	AJ279473.1	830	Ascomycete sp.	8	3	0	5	795	0	*Phoma-2*
FR773165	FSU10192	FJ603599.1	374	*Physalospora vaccinii*	21	20	1	0	357	2.00E-97	*Physalospora-1*
HQ228283		FJ603599.1	372	*Physalospora vaccinii*	21	20	1	0	357	3.00E-100	*Physalospora-1*
HQ228248		FJ603599.1	388	*Physalospora vaccinii*	6	6	0	0	372	1.00E-99	*Physalospora-2*
HQ228275	FSU8573	FJ603610.1	364	*Physalospora vaccinii*	20	20	0	0	350	1.00E-99	*Physalospora-2*

HQ228282		FJ603599.1	292	*Physalospora vaccinii*	20	19	1	0	278	8.00E-76	*Physalospora-3*
FR773180		EU852362.1	898	*Leptosphaeria* sp.	4	2	2	0	854	0	Pleosporales-1
FR773224	FSU8685	EU852362.1	939	*Leptosphaeria* sp.	2	2	0	0	922	0	Pleosporales-1
FR773215	FSU8678	U04207.1	771	*Leptosphaeria doliolum*	2	2	0	0	754	0	Pleosporales-2
FR773230	FSU8685	FJ427022.1	848	*Phoma herbarum*	29	14	4	11	806	0	Pleosporales-3
FR773252	FSU8563	FJ554029.1	874	Fungi sp.	50	34	10	6	833	0	Pleosporales-3
FR773186	FSU10604	FJ515608.1	776	*Phoma complanata*	50	28	5	17	739	0	Pleosporales-4
HQ228247		FJ210518.1	743	*Preussia* sp.	21	6	12	3	710	0	*Preussia-1*
HQ228267	FSU10208	AY510415.1	863	*Preussia intermedia*	8	6	2	0	828	0	*Preussia-1*
HQ228326		AY510415.1	848	*Preussia intermedia*	8	6	2	0	821	0	*Preussia-1*
HQ228269		GQ203775.1	725	*Preussia borealis*	9	6	3	0	697	0	*Preussia-2*
HQ228296	FSU10212	GQ203775.1	778	*Preussia borealis*	9	6	3	0	756	0	*Preussia-2*
HQ228262	FSU10408	DQ068995.1	870	*Pseudeurotium bakeri*	13	8	0	5	833	0	*Pseudeurotium-1*
HQ228292		AY128700.1	647	*Pseudotaeniolina globosa*	1	1	0	0	647	0	*Pseudotaeniolina globosa-1*
FR773246	FSU8614	GU328618.1	959	*Basidiomycota* sp.	2	1	0	1	941	0	*Psilocybe montana-1*
FR773301	FSU8568	EF151248.1	957	*Rhodotorula psychrophenolica*	3	3	0	0	941	0	*Rhodotorula psychrophenolica-1*
HQ228342	FSU10442	EF040837.1	394	Fungi sp.	16	7	3	6	375	3.00E-106	*Rhodotorula-1*
FR773303	FSU10343	AF384681.1	1042	*Rhynchosporium secalis*	6	6	0	0	1037	0	*Rhynchosporium secalis-1*
FR773290	FSU10342	AY744286.1	603	Leptosphaeriaceae sp.	12	5	1	6	573	4.00E-169	*Saccharicola-1*
FR773431		U04203.1	540	*Saccharicola bicolor*	15	6	1	8	514	3.00E-150	*Saccharicola-2*
HQ228237		AY843045.1	518	*Stigmina* sp.	9	2	1	6	494	1.00E-143	*Sarcinomyces-1*
HQ228258		AY843192.1	621	Fungi sp.	4	2	0	2	604	8.00E-175	*Sarcinomyces-1*
HQ228263		AY843192.1	606	Fungi sp.	4	2	0	0	623	0	*Sarcinomyces-1*
FR773272	FSU8613	FJ553309.1	621	Fungi sp.	4	2	0	2	608	8.00E-175	*Sarcinomyces-1*

FR773276		FJ553309.1	638	Fungi sp.	4	2	0	2	625	8.00E-180	*Sarcinomyces-1*
FR773298		AY843192.1	599	Fungi sp.	4	2	0	2	582	4.00E-168	*Sarcinomyces-1*
FR773299	FSU8611	AY843192.1	630	Fungi sp.	4	2	0	2	617	1.00E-177	*Sarcinomyces-1*
FR871189		AY843192.1	582	Fungi sp.	4	2	0	2	566	4.00E-163	*Sarcinomyces-1*
FR871190		AY843192.1	590	Fungi sp.	4	2	0	2	573	2.00E-165	*Sarcinomyces-1*
FR773307	FSU10379	AY843192.1	636	Fungi sp.	4	2	0	2	619	3.00E-179	*Sarcinomyces-1*
FR773322	FSU10380	AY843192.1	630	Fungi sp.	4	2	0	2	619	1.00E-177	*Sarcinomyces-1*
FR773339		AY843192.1	577	Fungi sp.	5	2	1	0	544	2.00E-161	*Sarcinomyces-1*
FR773377		FJ553309.1	651	Fungi sp.	4	2	0	2	636	0	*Sarcinomyces-1*
FR773378		AY843192.1	625	Fungi sp.	4	2	0	2	608	6.00E-176	*Sarcinomyces-1*
FR773391	FSU10382	AY843192.1	630	Fungi sp.	4	2	0	2	619	1.00E-177	*Sarcinomyces-1*
FR773392		AY843192.1	636	Fungi sp.	4	2	0	2	625	3.00E-179	*Sarcinomyces-1*
FR773406		AY843192.1	628	Fungi sp.	4	2	0	2	612	5.00E-177	*Sarcinomyces-1*
FR773408		AY843192.1	628	Fungi sp.	4	2	0	2	617	5.00E-177	*Sarcinomyces-1*
FR773441		FJ553309.1	651	Fungi sp.	4	2	0	2	630	0	*Sarcinomyces-1*
FR773472		AY843192.1	630	Fungi sp.	4	2	0	2	619	1.00E-177	*Sarcinomyces-1*
HQ228293	FSU10430	AY843192.1	634	Fungi sp.	4	2	0	2	623	1.00E-178	*Sarcinomyces-1*
HQ228304	FSU10585	AY843192.1	636	Fungi sp.	4	2	0	2	625	3.00E-179	*Sarcinomyces-1*

HQ228305		AY843192.1	636	Fungi sp.	4	2	0	2	619	3.00E-179	*Sarcinomyces-1*
FR773359	FSU10584	AJ292393.1	708	*Simplicillium lamellicola*	10	6	4	0	686	0	*Simplicillium lamellicola-1*
FR773268		AM992154.1	828	*Sirococcus* aff. *conigenus*	10	6	2	2	787	0	*Sirococcus conigenus-1*
FR773280	FSU8565	FM172748.1	800	Fungi sp.	10	7	1	2	769	0	*Sirococcus conigenus-1*
FR871185		FM172748.1	813	Fungi sp.	10	7	1	2	782	0	*Sirococcus conigenus-1*
HQ228294	FSU10388	GQ153162.1	802	Sordariomycetes sp.	9	8	0	1	765	0	*Sordariomycetes-1*
FR773234		GQ153122.1	889	Dothideomycetes sp.	50	31	10	9	856	0	*Sydowia-1*
FR773293	FSU8645	GQ412728.1	948	Sydowia polyspora	50	33	10	7	909	0	*Sydowia-1*
FR773346	FSU10199	AY465454.1	931	*Hormonema* sp.	50	31	11	8	889	0	*Sydowia-1*
FR773409	FSU10425	GQ153122.1	880	Dothideomycetes sp.	50	32	10	8	846	0	*Sydowia-2*
FR773294	FSU8612	FJ000374.1	821	Tetracladium setigerum	50	38	0	12	793	0	*Tetracladium-1*
HQ228250		EU113211.1	968	Fungi sp.	19	13	0	6	920	0	*Umbelopsis ramanniana-1*
HQ228331	FSU10293	EU715662.1	965	*Umbelopsis ramanniana*	15	9	0	6	918	0	*Umbelopsis ramanniana-1*
HQ228341	FSU10294	EU715662.1	977	*Umbelopsis ramanniana*	10	5	0	5	931	0	*Umbelopsis ramanniana-1*
FR773500	FSU10217	EU113211.1	981	Fungi sp.	13	7	0	6	933	0	*Umbelopsis ramanniana-1*
FR773285	FSU8546	EF029203.1	880	*Helicoon fuscosporum*	4	2	1	0	850	0	*Venturia-1*
HQ228256		EU434823.1	612	*Acephala* sp.	50	39	1	10	590	6.00E-172	Vibrisseaceae-1
HQ228257		EU434823.1	588	*Acephala* sp.	50	38	5	7	566	1.00E-164	Vibrisseaceae-1
HQ228274	FSU8550	EU434823.1	608	*Acephala* sp.	50	36	5	9	590	8.00E-171	Vibrisseaceae-1
HQ228276		EU434823.1	603	*Acephala* sp.	50	37	5	8	579	4.00E-169	Vibrisseaceae-1
FR773372		EU434823.1	617	*Acephala* sp.	50	37	1	12	588	1.00E-173	Vibrisseaceae-1
FR773373	FSU8605	EU434823.1	627	*Acephala* sp.	50	32	1	17	597	2.00E-176	Vibrisseaceae-1
FR773453	FSU10202	EU434823.1	619	*Acephala* sp.	50	37	1	12	593	4.00E-174	Vibrisseaceae-1
HQ228288		EU434823.1	610	*Acephala* sp.	49	37	1	11	582	2.00E-171	Vibrisseaceae-1