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ORIGINAL PAPER

Diversity of saprobic microfungi

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Abstract The data needed to derive an accurate estimate of saprobic microfungi are insufficient, incomplete and contradictory. We therefore address issues that will ultimately reveal whether there are 1.5 million global fungal species, which is the generally accepted working estimate. Our data indicates that large numbers of fungi occur on host families, such as *Musaceae*, host genera such as *Nothofagus* and individual host species such as *Eucalyptus globulus*, and that fungi may be specific or recurrent on different plant groups. Recent studies have shown that fungal numbers on hosts may be larger than originally thought as saprobes are organ-specific/-recurrent and changes in fungal communities occur as substrata decays. Other issues,

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such as the impact of geography, of methodology and of taxonomy are also addressed. There is evidence that fungi on the same host at different locations also differs; site-specific factors and geographic distance may be more important than host/substrate in shaping fungal assemblages. Methodology impacts on estimates of species diversity with many more taxa observed using indirect isolation protocols as compared to direct isolations from leaves. Our understanding of fungal species numbers in speciose genera is important. In some fungal groups accepted species have been reduced to a few species, while in other groups many cryptic species are being uncovered. While we make a number of generalisations from the studies reported here, this review also highlights some of the limitations mycologists currently have to contend with. A large body of knowledge exists for certain groups of microfungi or for microfungi occurring on certain substrata/hosts. However, it is likely that we are drawing conclusions from data that are somewhat biased toward fungi and host/substrata that are of interest to human endeavours. The discrepancy between the numbers of fungi described from only one economically important genus, *Eucalyptus*, and all the other members of the *Myrtaceae* is but one example of this bias. By incorporating the large body of work that is already available and adding appropriate complementary studies, we can accelerate our understanding of microfungal diversity and this will eventually lead us to a realistic estimate of global fungal species numbers.

Keywords Biodiversity estimates · Litter fungi · Saprobes · Speciose genera

Numbers of saprobic microfungi

The figure of 1.5 million global fungal species is a generally accepted working estimate (Hawksworth 2001; Hyde 2001; Crous et al. 2006d). It is based on some relatively robust figures involving certain groups of fungi (e.g. basidiomycetes) and rather conservative extrapolations from other data, e.g. fungus to host ratios, fungi on insects (Hawksworth 1998, 2001). In this paper we set out to discuss the numbers of saprobic microfungi, but have included data on pathogens and endophytes. This is because fungi are capable of switching their modes of nutrition i.e. many endophytic and pathogenic fungi may persist as saprobes once the plant organ, on which they reside, senesces (Zhou and Hyde 2001; Photita et al. 2004, 2005; Promputtha et al. 2005). The data needed to derive numbers of saprobic microfungi are insufficient, incomplete and contradictory. We have therefore chosen to address issues that will ultimately reveal whether there are 1.5 million global fungal species. Our present understanding of the relationships between microfungi and their hosts (species, genera and families), plant tissues and organs, and biogeographical distribution will be discussed. We will also include case studies from recent work exemplifying saprobic microfungal diversity. We will not estimate saprobic microfungi numbers as there is insufficient data for such an exercise. We will however, highlight areas that need further research in order for the scientific community to obtain a better understanding of exactly how many saprobic microfungi there are.

Fungal specificity at the plant host level?

The numbers of fungi occurring on a single host and in particular whether they are specific to that host are extremely important indicators of microfungi numbers.

Below we report on some host species for which considerable fungal data is known.

Agathis australis—Kauri

The endemic New Zealand kauri (*Agathis australis*) belongs to the small, mainly Southern Hemisphere gymnosperm family, *Araucariaceae*. A total of 189 named fungal species and 75 species identified only to genus, distributed within 199 genera, have been recorded on this host (McKenzie et al. 2002). At least half of these are microfungi, mainly saprobes on dead and fallen wood and litter. Many of the fungi are commonly found on other plant substrates within New Zealand, or elsewhere. However, seven hyphomycetes and three ascomycetes were described from *A. australis*. All 10 species are considered to be endemic to New Zealand, and seven of these are known only on *A. australis*.

Eucalyptus globulus

Eucalyptus has more than 700 species, ranging from those adapted to semi-arid areas, to those occurring in cooler, wetter environments. One species *E. globulus* is commonly planted in most countries that grow eucalypts for timber. Sankaran et al. (1995) listed approximately 313 fungal species from *E. globulus*, while a further 34 species were described between 1995 and 2003. Currently the USDA database in Beltsville (http://www.nt.ars-grin.gov) lists 696 species of fungi from *E. globulus*. While the majority of these species are thought to be specific to *Eucalyptus*, most are known from only a few collections, and thus it is not possible to obtain a realistic figure of how many would be specific to *E. globulus*. Of the 180 species described on *Eucalyptus* species between 1995 and 2003, 34 are known only from *E. globulus*. Within *Eucalyptus* there are examples of host-specificity concerning the plant pathogenic fungi, which will occur in certain subgenera, or on specific species (Gryzenhout et al. 2004, 2006; de Beer et al. 2006). The saprobic microfungi occurring on eucalypts are, for the most part, also highly specific to eucalypts (Gryzenhout et al. 2005; Crous et al. 2006g), although insufficient data is available as to specificity to species level.

Nypa fruticans

Nypa is an interesting host for fungal colonisation, as it is a palm that grows in the intertidal region along marine shorelines in the tropics. As with most palms it has been found that petioles of *Nypa* support a high diversity of fungi (Hyde and Alias 2000; Yanna et al. 2001a, b). To-date, 63 fungi have been identified from this host, of which 40 are thought to be unique to this host (Hyde and Alias 2000). The fungi on *Nypa* include common marine species (e.g. *Halocyphina villosa, Lignincola laevis, Lulworthia* spp.), marine species which appear to be unique to this host (e.g. *Aniptodera nypae*, *Helicascus nypae*), and species from palm-inhabiting fungal genera (e.g. *Oxydothis nypicola, Linocarpon nipae*), most of which also appear to be unique to this host (Hyde and Alias 2000). *Nypa fruticans* therefore appears to support large numbers of unique fungi, which do not overlap with those occurring on terrestrial palms (Yanna et al. 2001a, b, 2002). There are two other intertidal mangrove palms (i.e. *Calamus erinaceus, Oncosperma tigillarum*) and it would be

revealing to examine the fungi on these hosts in order to establish if there is overlap in fungal communities.

Grasses, sedges and rushes

Wong and Hyde (2001) studied the diversity of microfungi on six species of *Poaceae* and one species of *Cyperaceae* in Hong Kong. They found that different grasses were host to different fungal communities. They concluded that no single saprobe identified was unique to any grass species, however, certain taxa were recurrent (Wong and Hyde 2001) on specific grass species. One very important finding was that grasses with more durable, strongly sclerenchymatic (woody) stems supported a higher diversity of fungi than those with more herbaceous stems.

Juncus roemarianus (needlerush, *Juncaceae*) and *Phragmites australis* (*Poaceae*) have been particularly well-studied with respect to saprobes (Kohlmeyer and Kohlmeyer 2001). *Phragmites* is a cosmopolitan grass that occurs in intertidal, freshwater and terrestrial habitats and is woody. More than 170 fungal taxa have been described with their type specimen from this host (Wong and Hyde 2001). There have also been several reports on the saprobes of this host (Apinis et al. 1972a, b; Farr et al. 1989; Shearer 1993; Poon and Hyde 1998a, b; Wong and Hyde 2001, 2002; van Ryckegem and Verbeken, 2005ab) and Wong and Hyde (2001) suggested that the fungi presently known from *Phragmites australis* is well over 300. *Juncus roemarianus* is an example of a herbaceous substrate that is host to a surprisingly large number of fungi (118), many of which appear to be adapted to the intertidal habitat of the host (Kohlmeyer and Kohlmeyer 2001; Wong and Hyde 2001).

Pandanus furcatus and *P. tectorius*

Two species of *Pandanus* occurring in Hong Kong, have been relatively well-studied for associated microfungi (Whitton 1999; Whitton et al. 2001a, b, 2002). Of the 45 microfungi recorded from *P. furcatus*, a coastal species, and 35 taxa on *P. tectorius*, a rainforest species, in Hong Kong, only ten species overlap. In the rest of the world, no other fungal species are known from *P. furcatus*, but 88 taxa are known from *P. tectorius*, with 18 species overlapping. The degree of overlap is low and this may be due to the distinct habitats of these hosts. Further work is required to establish the amount of host-specificity in the genus *Pandanus*.

Concluding remarks

The above discussion provides evidence that some plants accommodate large numbers of saprobic taxa, particularly microfungi. These examples have been selected as they are particularly well-studied plants or support diverse communities of fungi. Most of these plants offer large surface areas for fungal colonisation. They are also woody and persistent, characters that appear to favour high fungal diversity (Wong and Hyde 2001). It is unlikely that the smaller short-lived herbaceous plants will accommodate anything like the fungal diversity referred to above. These aspects, however, need studying in order to confirm such assumptions.

Fungal specificity at the host genus level?

The plant species discussed above have generally been studied in isolation to other species of the same genus. If fungal occurrence is genus-specific as compared to host-specific, this would have important implication for estimates of fungal numbers. Below we report on some genera for which considerable fungal data is known.

Agathis, Metrosideros, Nothofagus–southern beech

The genus *Nothofagus* (*Fagaceae*), or southern beech, is restricted to the Southern Hemisphere. The genus, with five taxa in New Zealand, is ectomycorrhizal, so that many macroscopic mushrooms are associated with it. Over 900 taxa of fungi have been recorded on *Nothofagus* species in New Zealand, including 35% of the known New Zealand *Agaricales* and 50% of the known polypore species. However, more than 350 microfungi are known from *Nothofagus*, and the ascomycetes recorded by McKenzie et al. (2000) are thought to be only a small proportion of these fungi associated with *Nothofagus*. There are also several undescribed hyphomycete species deposited in Herbarium PDD.

When the numbers of fungi recorded in New Zealand on *Nothofagus* are compared with those recorded on *Agathis australis* (McKenzie et al. 2002) and on *Metrosideros* (McKenzie et al. 1999), which is represented by 13 endemic taxa in New Zealand, the overlap in species is low (Table 1).

Eucalyptus

Sankaran et al. (1995) collated the data of fungal species occurring on *Eucalyptus* and reported 1,350 species in more than 630 genera and 120 families. For the period 1995–2002, a further 180 species have been described from *Eucalyptus*, with many more microfungi (including genera) awaiting description. Since 1993, P.W. Crous and co-workers have described nearly 80 new species of *Mycosphaerella* and associated anamorphs from *Eucalyptus* (Crous 1998; Crous et al. 2004a, b, 2006h; Summerell et al. 2006), which appear to be highly specific to this host. Similarly though, during this same period a further 20 new species were described in *Calonectria* (*Cylindrocladium*), of which only one appears to occur on *Eucalyptus* alone (Crous 2002; Crous et al. 2004c, 2006b). There are more than 700 species in *Eucalyptus*, and currently more than 1400 species of fungi are associated with 150 of these species or subspecies. Many of these eucalypts have, therefore, never been studied, and thus far more work is required to enable us to make any prediction about how many species are host or genus-specific.

Table 1 Number (and percentage) of identified fungal species found in common between three substrata (*Agathis australis*, *Metrosideros* spp. and *Nothofagus* spp.) in New Zealand

	Agathis australis	*Metrosideros* spp.	*Nothofagus* spp.
Agathis australis	189		
Metrosideros spp.	15 (4.4%)	155	
Nothofagus spp.	65 (6.7%)	29 (3.1%)	776

Palm genera *Arenga, Livistona, Oraniopsis, Oncosperma* and *Salacca*

Yanna et al. (2001a) have studied the microfungi on *Livistona australis* and *Oraniopsis appendiculata* in north Queensland, Australia, *Arenga engleri* and *L. chinensis* in Hong Kong, and *Arenga undulatifolia*, *Oncosperma horridum* and *Salacca affinis* in Brunei. Host genera affected fungal species compositions. In Australia only 6–9% of fungi were common to palms of different genera. Similarly, in Brunei and Hong Kong only low numbers of fungi were common to palms of different genera. Yanna et al. (2002) have studied fungal succession of *Phoenix hanceana* and Taylor and Hyde (2003) have also studied the fungi on *Archontophoenix alexandrae* in Hong Kong where it is an introduced species. Fungi overlapping with those on other palm hosts in Hong Kong was very low. Pinnoi et al. (2006) studied the fungi on a peat swamp palm in Thailand and there was very low overlap with a common palm in the same stand. Most of the palms studied above were only one species in the genus and it is unclear whether these results are the result of host- or genus-specificity.

Concluding statements

The above examples serve to illustrate cases where fungi may be genus-specific. These data are, however, derived from limited data sets. In most cases a plant species (or in the case of palms, several plant species) from a habitat have been well-studied. Plants from other families growing with these plants however, have not generally been studied, and one could argue that some fungi may be ubiquitous on other non related hosts. The level of host-specificity differs according to the fungal genera studied, which will seriously affect any conclusion concerning species numbers.

Fungal specificity at the host family level

Myrtaceae

Between 1995 and 2003, 180 new taxa were described on *Eucalyptus*. This is chiefly due to the worldwide commercial interest being placed on eucalypts for timber, pulp, fibre, poles and firewood. During the same period, only 82 new taxa were described for the whole remainder of the *Myrtaceae*. The latter number is just more than double the 34 new taxa described from *Eucalyptus globulus* alone. Due to the lower commercial interest placed in the other 129 genera of *Myrtaceae*, no in-depth study has been made to establish which fungi occur on them, and thus these numbers remain largely unknown. However, a recent compilation of fungi occurring on *Kunzea ericoides* and *Leptospermum scoparium* in New Zealand listed 125 species of ascomycetes and anamorphs from these two plants, including 19 species with either *K. ericoides* or *L. scoparium* as the host substrate (McKenzie et al. 2007). Preliminary collections of foliar fungi from genera such as *Syzygium* and *Eugenia* (MJ Wingfield, FABI, South Africa), have suggested that as for *Eucalyptus*, they also have a rich mycota of largely unknown, and undescribed species (Pavlic et al. 2004; Van Wyk et al. 2004). In a study of the *Mycosphaerella* species, Crous (1999)

listed 30 species from *Myrtaceae* other than *Eucalyptus*. Although U. Braun and co-workers have since described several additional taxa on *Myrtaceae*, these numbers represent only half of the estimated 80 species presently described, or soon to be described from eucalypts. In trying to explain the high number of microfungal species occurring on eucalypts, Crous (1999) was unable to provide evidence of taxa with wider host ranges within the *Myrtaceae*, which suggests that these species are for the large part highly host specific.

Arecaceae

Much data on the saprobic fungi occurring on palms has recently been published (Yanna 2001a, b, 2002) with descriptions of numerous new species (Frohlich and Hyde 2000; Smith and Hyde 2001; Yanna et al. 2001c). Palms, in particular their petioles, support a high diversity of fungi, many species of which are unique to palms. Many genera (e.g. *Myelosperma*, *Palmicola* and *Pemphidium*) comprise species known only from palms, while speciose genera such as *Linocarpon* and *Oxydothis*are predominantly found on palms (Hyde et al. 1997; Pinnoi et al. 2006).

Musaceae

Several taxonomic studies have assessed the microfungal diversity on banana. These include studies of both endophytic fungi (Brown et al. 1998; Photita et al. 2001b) and saprobic fungi (e.g. Matsushima 1971, Photita et al. 2001a). Photita et al. (2001a, 2003) examined microfungi on *Musa acuminata* in Hong Kong and Thailand. In Hong Kong, 46 fungal taxa were identified from 1125 samples, while 80 fungal species were identified from 900 samples in Thailand. Photita et al. (2002) also provided a checklist of 252 fungi with their type specimen described from *Musaceae*. Brown et al. (1998) listed 46 pathogens while Photita et al. (2001b) listed five endophytes, all of which are probably unique to *Musa* species. Six of the 46 saprobes observed on *Musa* species in Hong Kong (Photita et al. 2001a) are most probably unique to this plant genus. In a list of fungi on plants in the USA (Farr et al. 1989), 47 fungi are recorded on *Musa* species. As a conservative estimate, probably more than 300 fungi are presently known from 37 *Musa* species (Farr et al. 1989; Brown et al. 1998; Photita et al. 2001a, b, 2002, 2003).

Pandanaceae

This host family has been studied by several workers including McKenzie (e.g. 1995), Dulymamode et al. (e.g. 2001) and Whitton (1999). Approximately 450 species of fungi are known to occur on the *Pandanaceae*, more than 90% of these are microscopic. McKenzie et al. (2002) noted that 171 species of ascomycetes and anamorphic fungi had been described from the *Pandanaceae*, and that at least another 58 were awaiting description. Of these 229 species, 175 are known on only a single member of the *Pandanaceae*. With 800–900 species in the *Pandanaceae*, these 'unique' fungi give a fungus:host ratio of 0.2:1. This is a long way short of the 5000 species, which would be required by the 6:1 ratio suggested by Hawksworth (1991). However, every collection taken by Whitton (1999) revealed fungi that previously had not been known from the *Pandanaceae*.

Zingiberaceae

The *Zingiberaceae* is a monocotyledonous family of tropical plants with medicinal, agricultural, and horticultural uses. The family comprises about 53 genera, with about 1200 species (Mabberley 1987; Griffiths 1992). More than 170 fungal species have been described from 17 genera (about 80 species) of zingiberaceous plants, most being pathogens on ornamental or spicy genera (Bussaban et al. 2002, 2003a,b). An in-depth study for saprobes of *Zingiberaceae* have yet to be carried out. Preliminary studies of microfungi from *Alpinia malaccensis* and *Amomum siamense*, indicate that both plants have a rich mycota of undescribed species. Three new anamorphic fungi, *Berkleasmium nigroapicale*, *B. sutheppuiense* and *Xenosporium amomi*, described from both plants, are probably unique to this host family (Bussaban et al., 2001, 2003a).

Concluding statements

The examples given above illustrate that plant families may harbour distinct microfungal assemblages. Whether a small or large proportion of any of these fungal taxa occur on other plant families deserves further attention.

Are fungi organ-specific or-recurrent

A further question to be answered is whether fungi show a specificity or recurrence on particular tissue types.

Fungi on palm organs

Palms comprise several different parts, including trunks, petiole bases, rachides, leaves and flowers, which are quire different in texture and presumably chemistry. Yanna et al. (2001a) investigated the effect of different palm frond parts on fungal communities. Distinct fungal communities occurred on the leaves, rachis-tips, mid-rachides and rachis-bases of most species examined. The exception was *Livistona chinensis* in which fungal communities on the rachis-tips, mid-rachides and rachis-bases were more similar, probably because of their similar structures. The fungi on the leaves however, were distinct.

The above results indicate that the fungi occurring on different palm parts are distinct. This difference is probably due to substrate structure. However, fungi on the same structure on different hosts (e.g. rachis-bases) also tend to differ (Yanna et al. 2001a). Similar results were found on a palm in a peat swamp (Pinnoi et al. 2006).

Organ-specificity in the *Mycosphaerellaceae*

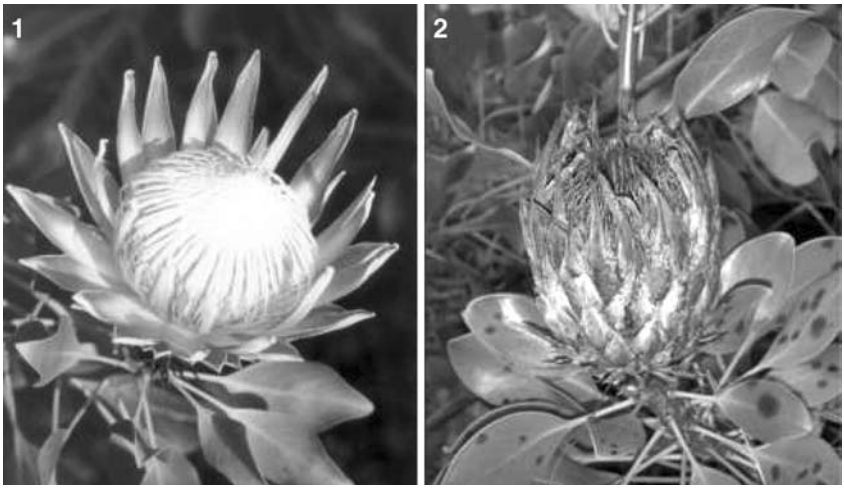
Species of *Mycosphaerella* (and their anamorphs) are commonly associated with leaf spots, or stem cankers (Crous 1998; Barnes et al. 2004; Crous et al. 2004a, b, 2006a, b, c; Cortinas et al. 2006; den Breeÿen et al. 2006). As well as being host-specific, most of these taxa are also highly tissue-specific, to the degree that some cercosporoids will sporulate on either the upper or lower leaf surface. This feature, together with symptomatology, and their ability to infect juvenile or mature foliage, can also be used

to differentiate some taxa (Crous 1998). An exception to the rule is the *Davidiella allicina* (*Mycosphaerella tassiana*) complex, as well as other species with *Cladosporium* anamorphs. Although some of these *Cladosporium* species have wider host ranges, and occur on more than one tissue type, this is not true for the whole complex, as some are not only highly specific to certain hosts but also to certain tissue types (Ellis 1971, 1976; Crous et al. 2006e). Tissue-specificity may also not necessarily play a role in all phases of the fungal life-cycle, as these fungi develop a saprobic teleomorph stage on various parts of leaf and twig litter in the colder winter months.

Proteaceae senescent flowerheads vs leaf or twig litter

In a study undertaken in the Western Cape Province of South Africa, a total of 535 fungi were obtained from leaf and twig litter and senescent inflorescences of *Proteaceae* (e.g. Lee et al. 2004). Analysis of collections on tissue types demonstrates that dead twigs supported the highest number of taxa (264 taxa or 49%) followed by dead leaves (188 taxa, 35%) and senescent flowerheads (83 taxa, 16%). Of this number, 254 taxa (48%) were teleomorphs (ascomycetes), while 270 taxa (51%) were anamorphic ascomycetes, i.e. coelomycetes and hyphomycetes.

Senescent flowerheads supported the lowest number of taxa, but revealed a unique composition of fungi, which was completely different to those obtained from leaf and twig litters. *Protea* flowerheads (Figs. 1–2) are open only a few weeks, and then close and remain intact for several years, which creates a unique niche for insects and microorganisms (Rebelo, 1995). Ascomycetes with long ostiolar necks such as *Gondwanamyces*, *Ophiostoma* and *Rhynchostoma* were exclusively isolated from flowers (Lee et al. 2003; Roets et al. 2006). A sticky mass of spores is present at the tips of perithecial necks, thus indicating that these fungi are ideally suited for insect dispersal. Ascomycetes such as *Chaetomium*, *Sordaria* and a hyphomycete *Phaeoisaria* were also confined to the flowers. Woody bracts, which comprise the most outer layer of the flower heads, shared some fungal species with the twig litter, for example some species of *Lophiostoma*, *Hysterium* and some coelomycete species.



Figs. 1–2 Live and senescent flowerheads of *Protea cynaroides* on the same tree

Dead twigs had the highest diversity of fungi and harboured more teleomorphic rather than anamorphic stages, while the opposite was true for senescent leaves. The most commonly encountered fungi on both tissue types were members of *Xylariaceae*, *Hysteriaceae* and *Lophiostomataceae*. Although some fungi such as *Botryosphaeria*, *Fusicoccum* (anamorphic *Botryosphaeria*; Crous et al. 2006f) and *Coniothyrium* were found equally on both dead leaf and twig litter, there were other fungi isolated only from one tissue type. With the exception of *Anthostomella cynaroides* which was isolated from dead twigs, and is thus far known only from *Protea*, four *Anthostomella* (*Xylariaceae*) taxa were identified from dead leaves (Lee and Crous 2003a). *Pestalosphaeria* and its *Pestalotiopsis* anamorph (Lee et al. 2006), and *Conoplea* sp., were found on both tissue types. The same was also true for a species of *Leptosphaeria*. The *Coniothyrium* anamorph of this *Leptosphaeria* species, however, was found to occur only on senescent leaves, raising the possibility that different fungal morphs of the same species could show differences in tissue recurrence. *Lophiostoma* was found exclusively on dead twigs, while another common member of the family, a species of *Massarina*, was found both on dead leaves and twigs. *Hysterium* was identified only on dead twigs, while *Gloniopsis* and *Glonium* were mostly found on dead twigs but some taxa were also found on dead leaves and senescent flowerheads (Lee and Crous, 2003c).

Although most taxa could be identified to generic level, the taxonomic position of a further 91 taxa (17%) is still uncertain, and probably harbour a high percentage of new species, and probably also genera.

Tissue specificity in litter fungi

Examples of tissue-specificity were found in a study of saprobic microfungi of an Australian tropical rainforest (Paulus et al. 2003a, b). Two new species of *Gnomonia* dominated the majority of decaying *Elaeocarpus angustifolius* leaves examined (72% of leaves for *Gnomonia queenslandica* and 86% for *G. elaeocarpa*). Both species were never observed on other leaf types examined during this study. Ascomata of *Gnomonia elaeocarpa* occupied the abaxial surface of the leaf lamina (Figs. 4, 5, 7) while those of *Gnomonia queenslandica* were invariably restricted to petioles, the abaxial surface of midribs and domatia on the adaxial leaf surface (Figs. 3, 4, 6, 8).

A similar observation was made for leaves of *Ficus pleurocarpa* and *F. destruens*. An undescribed discomycete was found on 86% of examined *F. pleurocarpa* and 70% of *F. destruens* leaves at early to moderate stages of decay. In most instances ascomata of this fungus were restricted to petioles and midribs and were only rarely observed on minor leaf veins or on the leaf lamina (see Fig. 4). The underlying reasons for the apparent tissue recurrence remains unclear, however, petioles and midribs of freshly fallen *F. pleurocarpa* and *F. destruens* leaves contain latex, which may provide the primary substrate for this particular ascomycete.

Concluding remarks

The above examples illustrate organ-specificity amongst saprobic fungi and similar examples are available for endophytes (e.g. Kumar and Hyde 2004). Taken together with host-specificity, it indicates the potential that numerous fungi may be specific to some hosts.

Fig. 3 *Elaeocarpus angustifolius* leaf. Adaxial surface

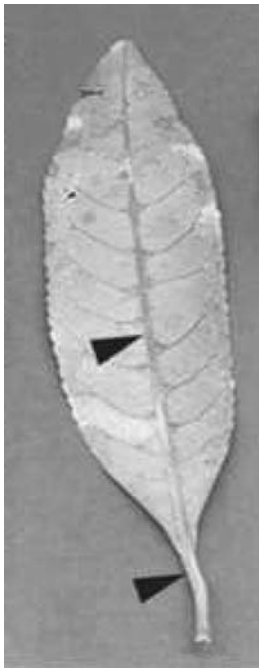


Fig. 4 *Elaeocarpus angustifolius* leaf. Abaxial surface (arrowheads indicate sites which are usually colonised by *Gnomonia queenslandica*)

Fig. 5 Ascus of *G. elaeocarpa*

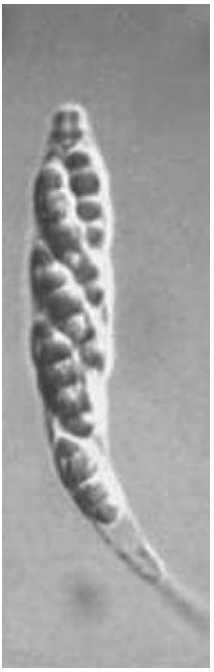


Fig. 6 Ascus of *G. queenslandica*

Fig. 7 Semisubmerged ascomata of *G. elaeocarpa* on leaf lamina

Effect of site and country on fungal communities on hosts?

One important aspect requiring discussion is the effect of geography on fungal presence. Whether the same host taxa occurring in different countries support similar or different fungal assemblages, this will have important implications for fungal estimates.

Eucalyptus

There has been some focused attempt to obtain worldwide collections of the *Mycosphaerella* complex on *Eucalyptus* and some interesting patterns have begun to emerge. *Eucalyptus* originate in Australia, Papua New Guinea and Indonesia, from

Fig. 8 Superficial ascomata of *G. queenslandica* on midrib

where seeds (and recently also cuttings) were dispersed to Africa, Asia, Europe and the Americas. This crop has been cultivated for nearly 200 years and more than 8 million hectares of commercial plantations have been established (Turnbull 1991). Several species of *Mycosphaerella* seem to have migrated with their host to these new continents. For example, *Mycosphaerella suberosa*, described from eucalypts in South America, has been also found in the centre of origin of *Eucalyptus*, Australasia (Carnegie et al. 1997; Crous et al. 2006h). In Madagascar, eucalypt forestry was initiated with material obtained from Indonesia. *Mycosphaerella heimii*, which was described from Madagascar (Crous and Swart 1995), has also been found in Indonesia, and is now known to occur in Brazil and Hawaii (Crous et al. 2004a). *Mycosphaerella grandis*, and *M. marksii*, two species recently described from Australia, are now known from South America and Africa. *Mycosphaerella nubilosa*, which is a serious pathogen of eucalypts in Australia and New Zealand, has also been discovered in Africa and Europe (Crous et al. 2004a). Most early reports cited the cercosporoid leaf spots of eucalypts as *Cercospora eucalypti* or *C. epicoccoides* (Chupp, 1954). Since this complex has been revised, these taxa have been treated as *Pseudocercospora eucalyptorum* (Crous et al. 1989). However, a recent revision has shown that this is, in fact, a complex of numerous taxa (Crous 1998), with many more species discovered in the centre of origin of eucalypts (Braun and Dick, 2002). Some species such as *M. parkii*, *M. juvenis*, *M. endophytica* and *M. molleriana* are, however, known only on eucalypts outside of its native range (Crous et al. 2006h; Hunter et al. 2006b). If these taxa are as host-specific as is commonly accepted, they should in future also be found in the centre of origin of *Eucalyptus*.

Arecaceae

Yanna et al. (2001a) showed that fungal species composition was significantly affected by the site of collection. There were few fungi in common among palms from different sites, and fungal compositions on palms from different sites were less closely coherent than those from the same sites. Taylor et al. (1999, 2000) have also shown variation between geographically separated communities of endophytic fungi in *Trachycarpus fortunei* and saprobes on other palms.

Concluding remarks

Pathogens such as *Mycosphaerella* spp. appear to be highly host specific, as is evident from the data provided here for *Eucalyptus* spp. However, when one looks at the saprobes on this host, it is more difficult to draw conclusions, as different sampling methods result in different saprobic components being isolated. Isolates encountered via endophytic isolations (Fisher et al. 1993), represent common species that would also be isolated from most agricultural crops in the area. This has also been found when comparing endophytes from crops such as grapevines, apples, wheat and *Eucalyptus* using similar isolation protocols (Crous unpublished). However, when litter of these hosts are collected and incubated in moist chambers a different, and generally more host-specific component of saprobic fungi is encountered sporulating on these tissues. Saprobes succeed one another on dead tissue, and different techniques, therefore, generally isolate a specific component of saprobic fungi. To

get a clear impression of all saprobic fungi, therefore, more robust and thorough techniques will have to be developed.

Selected studies in microfungal diversity

Litter fungi, a case study for diversity

A study was undertaken to assess the diversity of microfungal communities in decaying leaves of four tree species in a rainforest of the wet tropics of Australia. The selected tree species represent four common plant families of the region i.e. *Lauraceae* (*Cryptocarya mackinnoniana*), *Elaeocarpaceae* (*Elaeocarpus angustifolius*), *Moraceae* (*Ficus pleurocarpa*) and *Proteaceae* (*Opisthiolepis heterophylla*). Two isolation methods were used, designed to complement each other. Microfungal fruiting bodies were isolated directly from leaves of six individual trees for each tree species following incubation in humid chambers and cultures were obtained using a particle filtration protocol (Kirby and Webster 1990; Bills and Polishook 1994; Paulus et al. 2003a, b).

Direct isolations yielded 103 taxa and particle filtrations 392 morphogroups. A comparison of the number of taxa isolated by the two methods and Shannon's indices for each of the four tree species is provided in Table 2. A pairwise comparison of the four tree species indicated an overlap of between 3.9% and 23.3% of microfungal taxa isolated directly from leaves and between 12% to 22% of morphogroups isolated by particle filtration (Figs. 9, 10). Among direct isolations, seven (6.8%) species were shared between three tree species and three (2.9%) between four tree species. Similarly, among particle filtration isolations, 24 (6.1%) of morphogroups were shared between three and 15 (3.8%) between four tree species.

Of the microfungal species, which occurred on more than two tree species, a number are 'soil fungi', for example *Acremonium* sp., *Ochroconis humicola* and *Gliocladium* sp. Other shared species appear to have a wide distribution and seem to be adaptable in terms of substrate. These include *Beltrania rhombica*, *Beltraniella portoricensis*, *Gliocladiopsis tenuis*, *Hansfordia pulvinata* and *Zygosporium mansonii*. In addition, several shared species are in large and taxonomically difficult genera, for example *Phoma, Phomopsis* and *Pestalotiopsis* and more than one species may have been inadvertently grouped together.

The large number of fungi, which occurred solely on one leaf type may indicate a certain 'recurrence' of microfungi on a particular substrata. However, it is unlikely

Table 2 Comparison of species, morphotypes and Shannon's diversity index for fungi isolated by direct method and by particle filtration

	Direct isolations		Particle filtration isolations	
	Number of species	Shannon's diversity index (H')	Number of morphogroups	Shannon's diversity index (H')
Elaeocarpus angustifolius	24	2.6	129	4.52
Cryptocarya mackinnoniana	55	3.6	171	4.52
Ficus pleurocarpa	35	3.0	98	4.0
Opisthiolepis heterophylla	39	3.4	141	4.64

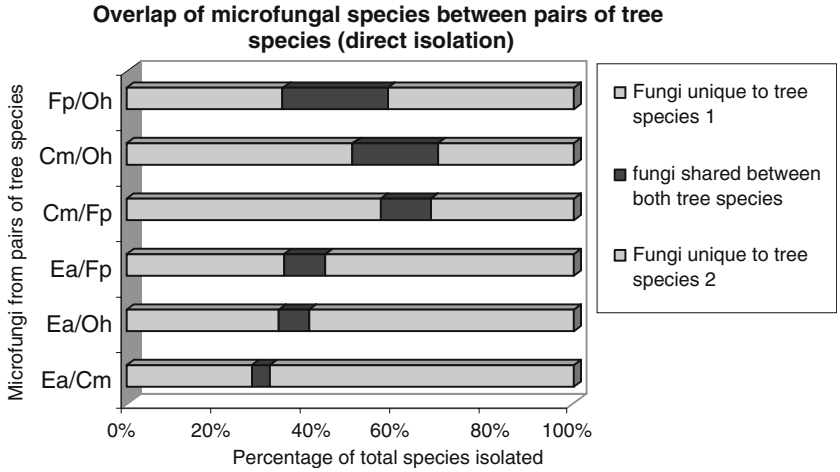


Fig. 9 Overlap of microfungal species between pairs of tree species (direct isolation)

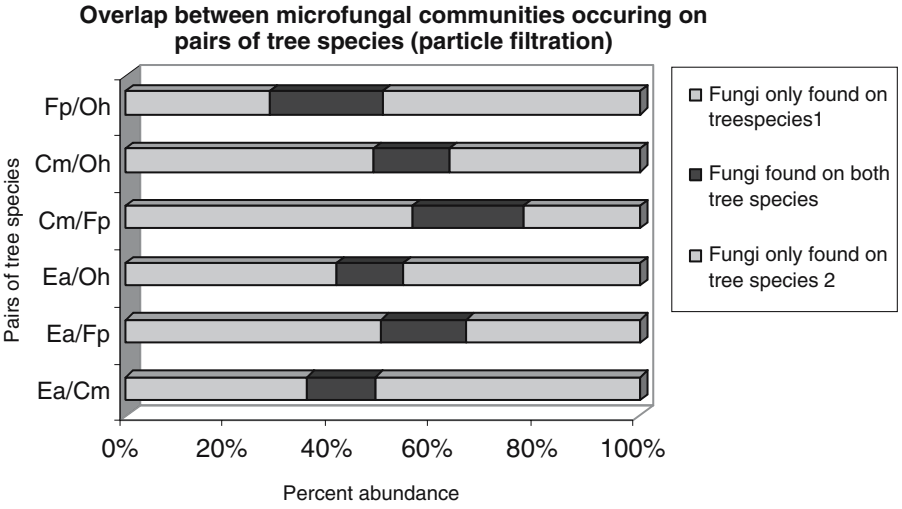


Fig. 10 Overlap between microfungal communities occuring on pairs of tree species (particle filtration)

that many of these fungal taxa are strictly 'host-specific' since they have been previously reported from different substrata, e.g. *Bahusutrabeeja dwaya, Subulispora procurvata* and *Thozetella tocklaiensis*,to name a few. Some species new to science were recorded, for example two species of *Gnomonia* on *Elaeocarpus angustifolius* and five species of *Thozetella* on *Cryptocarya mackinnoniana* (Paulus et al. 2003a, b, 2004). Species in this group had a relatively high abundance (i.e. they were present on many of the examined leaves) and frequently occurred in high densities (i.e. they covered a large area of the available leaf surface). These taxa may be specific to a particular tree species or at least to a group of closely related tree species. Further work is needed to clarify their host range.

Fungi on *Proteaceae* and *Restionaceae* in South Africa

A survey of saprobic fungi on two Southern Hemisphere plant families, dicotyledenous *Proteaceae* (proteas) and monocotyledonous *Restionaceae* (restios), have been carried out over 3 years (2000–2002). Both plant families are the major vegetation types in the fynbos biome which is defined by moderate to high amount of winter rain and a predominance of low to medium-height shrubs, comprising 80% of the Cape Floral Kingdom (Cowling and Richardson 1995). The specimens were either inspected immediately for fungal structures or air-dried for further study. Air-dried samples were incubated in moisture chambers for 2–3 d before examination. Restios produced more coelomycetes (43%, 234 isolates) than proteas (32%, 151 isolates), whereas more teleomorphic ascomycetes were isolated from proteas (52%, 248 isolates) than restios (40%, 218 isolates) (Crous et al. 2006d; Lee et al. 2006). This may result from the nature of tissue structures of host plants: proteas have more diverse tissue types favoured by fungi such as twigs, leaves and flowerheads than restios, which have herbaceous culms only (Lee et al. 2004, 2005).

Anthostomella species occurred both on proteas and restios, however, *A. clypeata* was found only from restios and *A. conorum* only from proteas (Lee and Crous 2003a). The ascomycetes with hysterothecioid ascomata, *Gloniopsis* and *Hysterium* were found indiscriminately from both genera on various tissue types. *Glonium* also occurred on both families but showed host-specificity in some species: *G. compactum* was isolated only from restios and *G. lineare* only from a protea (Lee and Crous 2003c). The hyphomycetes, *Arthrinium* and *Gyrothrix* and an anamorphic ascomycete *Dinemasporium* were found only on restios, whereas an ascomycete *Pleospora* occurred on both families. The study also showed the high possibility of restios harbouring exclusive members of coelomycetes (Lee and Crous 2003b).

Concluding remarks

A number of separate studies have provided an indication that microfungal assemblages on substrata from phylogenetically distant hosts have a low degree of overlap, even if they occur in same ecosystem. The number and kind of taxa discovered on a particular substrate appears to depend on the sampling and isolation protocols, that are applied.

Other data useful in estimating fungal diversity

How many fungi can occur on a single tree?

An interesting exercise would be to study the numbers of fungi on a single plant. Aptroot (2001) sampled the lichenized and saprobic fungi on a single *Elaeocarpus* tree in Papua New Guinea and identified over 200 associated ascomycetes. Fröhlich and Hyde (1999) examined the saprobes, pathogens and endophytes on three individual plants of *Licuala* sp. in a Brunei forest. They estimated that there were at least 240 distinct taxa on these three plants. There study excluded numerous groups of fungi including lichens, phylloplane fungi and rhizosphere fungi. Promputtha et al. (pers. comm.) examined the fungi on five *Manglietia garrettii*trees in a forest at Doi Suthep National Park, northern Thailand. Promputtha et al. (2002) identified 22 taxa

from these trees in a study of fungal succession on the leaves. In ongoing research, endophytes, saprobes on wood, lichens and pathogens have been identified from these five plants and more than 100 taxa are presently recorded (Promputtha et al., pers. comm.).

Fungal succession

Several studies on fungal succession on various substrata (Sivichai et al. 2002; Somrithipol et al. 2002; Zhou and Hyde 2002) have indicated that there is a sequential order in which fungi appear on substrata as it decays. There is evidence that some of the early colonisers are derived from endophytes and therefore likely to be host-specific (Hyde 2001; Zhou and Hyde 2002; Photita et al. 2004). Further work is required to test this hypothesis. However, as different fungi colonise substrata at different stages of decay, this has important implications for fungi numbers.

Advances in taxonomy will affect fungal species numbers

Many saprobic genera are ubiquitous and contain numerous species, which may also be pathogens or endophytes. Some genera contain a large number of taxa because species concepts in these genera were previously based on the host of the fungus rather than morphological characteristics (e.g. *Pestalotiopsis*; Jeewon et al. 2004; Wei and Xu 2004; Lee et al. 2006). There have been several recent monographs based on morphological characters that have reduced the numbers of some genera drastically. Aptroot (1997) reduced the 550 *Didymosphaeria* names to 7 taxa, while Lu and Hyde (2000) reduced more than 300 *Anthostomella* epithets to 86 taxa.

The genera of *Phomopsis* and *Phyllosticta* contain thousands of names, which are associated with different host genera (Uecker 1988; van der Aa and Vanev 2002). For species of *Phomopsis*, recent molecular work has shown, however, that although some taxa are highly host-specific, others can infect a wide range of hosts as weak pathogens, or as endophytes (Mostert et al. 2001; Van Rensburg et al. 2006). In another study focused on the taxa occurring in grapevines, several isolates were obtained that were similar to species occurring in fruit trees, roses, and sunflowers. These findings imply that host substrate is not a good character to distinguish taxa in *Phomopsis*.

Likewise recent molecular work has shown that most of the *Phyllosticta* isolated as endophytes from a diverse range of host plants in South Africa was one commonly occurring species (Baayen et al. 2002). This will no doubt have serious implications for the species presently acknowledged in *Phyllosticta* (van der Aa and Vanev 2002).

Similarly, pioneering work in the 1950s reduced numerous species of *Colletotrichum* (von Arx 1957) and *Botryosphaeria* (von Arx and Müller 1954; Phillips et al. 2006) to synonymy. Molecular techniques, however, have provided an indication that there are numerous species of *Colletotrichum*, and that most of the commonly acknowledged species are in fact species complexes (Photita et al. 2005). A similar situation exists in *Botryosphaeria*, where numerous new taxa are being discovered, which seem to have their own host ranges and geographic distributions (Slippers et al. 2004; Crous et al. 2006f; Phillips et al. 2006).

Recent molecular analyses of the *Fusarium* and *Trichoderma* species complexes, in the Hypocreales have also indicated that there are many more taxa than presently accepted in these genera (O'Donnell 2000, Phan et al. 2004: Bogale et al. 2006).

Within the *Fusarium solani* complex, O'Donnell (2000) recognized 26 phylogenetic groups, and also concluded that many *formae speciales* were also not monophyletic, possibly representing yet additional species. Summerbell and Schroers (2002) also estimated that *F. solani* could well represent more than 50 groups or taxa. Using molecular data sets, O'Donnell et al. (2000) also recognized 44 species to exist within the *F. fujikuroi* species complex. Whether all these groups represent biological species, however, remains to be determined. The use of a combination of phenotypic and genotypic characteristics, determined from morphological and molecular studies, together with anamorph-teleomorph connections has resulted in the recognition and description of many new species of *Trichoderma* and *Hypocrea* within the past 15 years (e.g., Bissett 1991; Chaverri et al. 2003; Chaverri and Samuels 2003). This contrasts to only nine ''species aggregates'' recognized from a by Rifai (1969).

Within the genus *Alternaria*, approximately 400–450 epithets, variants thereof, and named varieties are known from the literature (Simmons 1992, 2004). The classification of these species, especially the small-spored species of *Alternaria*, is often confusing due to the overlap in conidial size ranges. Simmons and Roberts (1993) pointed out the critical value of the three-dimensional sporulation patterns at 50 × magnification to help separate these species. The production of mycotoxins and other secondary metabolites has also been shown to be of major importance in separating species, not only for those species producing host-specific toxins, but also for non-host-specific toxin producers. Andersen and Thrane (1996) showed that metabolite production together with the more traditional morphological and physiological characteristics can provide a much better picture of the species and species-groups within this genus. By employing these techniques, it has been shown that the pathogen identified as *A. alternata* causing dry core rot of apples was in fact a complex of several small-spored *Alternaria* species, which are each still seen as species groups (Serdani et al. 2002). The same species diversity was also observed for *A. citri*, the name commonly used for the organism associated with black rot of citrus (Kang et al. 2002). Within *Alternaria* thus, it appears that many well established species could consist of larger species complexes, which could again influence any estimates based on these species numbers (Guo et al. 2004).

The genus *Mycosphaerella* is one of the largest genera of ascomycetes. It includes more than 2000 described species, most of which have been distinguished based on the host (Aptroot 2006). The host substrate has also played a prominent role in distinguishing species of the anamorphs linked to *Mycosphaerella* (Chupp 1954). Kendrick and DiCosmo (1979) calculated that *Mycosphaerella* had been linked to more than 27 different anamorph genera, while Crous et al. (2000, 2006a, b, c) recognized 23 anamorph genera based on links established between *Mycosphaerella* and their anamorphs in culture. Since the papers published by Crous et al. (2000, 2001), numerous additional taxonomic changes have been undertaken in *Mycosphaerella*. If we were to accept the morphological species concept and ignore the host range in *Mycosphaerella*, the large number of teleomorph taxa could be reduced to only a few taxa, which would include a small number of common species with a wide host range, and a large number of highly host-specific taxa.

Looking at specific host genera such as *Protea* and *Eucalyptus*, where some concerted effort has been made to collect, culture and sequence fungal taxa, an exponential increase in species numbers has been observed. Within but a few years, the species occurring on *Eucalyptus* have grown from ten to around 80, while those

occurring on South African *Proteaceae* have also increased from less than 10 to close to 40 taxa.

In addressing the anamorph states of *Mycosphaerella* for which no teleomorph is known, several thousand species have to be dealt with in genera such as *Cladosporium*, *Cercospora*, *Pseudocercospora, Septoria* and *Stenella* alone (Kirschner et al. 2004; Schubert and Braun 2005; Ayala-Escobar et al. 2006; Braun and Schubert 2006; Hunter et al. 2006a, b). In a recent revision of the genus *Cercospora* (Crous and Braun 2003), 5720 names were treated, of which more than 3000 were published in *Cercospora*. The conclusion from this study was that for the majority, host-specificity still appears to be the norm within the various anamorph genera of *Mycosphaerella*. It was clear, however, from morphology and ITS sequence data, that the weak secondary plant pathogen, *Cercospora apii*, had been described as new from numerous host plants. Recent findings however, have revealed that ITS data is acceptable to show relationships among species, but is frequently insufficient to reveal differences between closely related taxa, and that in many fungal genera, ITS data alone is not sufficient to support the synonymy of species. Thus, when a multi-allelic molecular dataset was obtained for the *Cercospora apii* complex (Groenewald et al. 2005, 2006), most of these synonymous names were again revealed to be closely related, but are distinct clades within the *Cercospora apii* complex. Further work is needed to resolve if these clades are also biologically and ecologically isolated taxa and thus represent cryptic species. This may have serious implications for our species estimates to date, as it may show that host plants could harbour morphologically similar, but genetically and ecologically quite diverse taxa.

Fungi on invertebrates and on other fungi

While there is some data available addressing fungal numbers on plants, there have been fewer studies addressing fungal numbers on invertebrates or on other fungi. The use of fungi in biological control against fungal plant pathogens has become a popular research trend (Anon. 2003; El-Morsy 2004; El-Morsy et al. 2006). Deighton (1969) and Deighton and Pirozynski (1972) described 13 new genera and many new species of hyphomycetes that are hyperparasitic on other fungi. There has, however, been little recent research concerning biodiversity of fungi colonising other fungi, although Johnston (1999) described a new genus parasitising *Meliolina*, while Grunden et al. (2001) investigated the fungi colonizing microsclerotia of *Verticillium dahliae* in urban environments. Although they did not identify any species new to science they identified a high diversity of 27 species. Further studies of this type are needed.

Since the important paper of Weir and Hammond (1997) there have been relatively little data on biodiversity of parasitic invertebrate fungi, although new species have been described (e.g. *Cordyceps campsosterna*, Zhang et al. 2004). If invertebrate fungi were host-specific and occurred in most fungi this would have extreme implications for fungal numbers. Although not saprobes, these fungi are discussed here because of their potential importance. Weir and Hammond (1997) suggest that between 5 and 7% of beetle species may act as hosts for *Laboulbeniales* (ascomycetous obligate ectoparasites of Arthropoda) and speculated that at least 20,000 and possibly 50,000 species of *Laboulbeniales* await description. Trichomycetes (symbiotic gut fungi) numbers were also shown to be dependent on host diversity and host-specificity was shown to be a crucial factor in trichomycete diversity

(Nelder et al. 2006). Much work is still needed to address fungal numbers in this area.

Future

From these data it is obvious that we need to develop a more complete inventory of microfungi in various ecological niches if we are ever hopeful to preserve a representative collection of these organisms for future research, society and prosperity. This will, however, only be achievable through strong international collaborative efforts, and the development of appropriate protocols and methods to detect and utilise this diversity. Molecular data from numerous phylogenetic studies have elucidated countless additional cryptic taxa in well-known, established species, suggesting that our species estimates, which are morphology based, may be a huge underestimate. It has reached a point, therefore, where molecular data sets suggest vast species richness to exist within the aggregate morpho-species commonly recognized by mycologists. The current trend into genomics and bioinformatics is short sighted if done in isolation without a similar impulse into field work, collection and culturing, as even by conservative estimates, at the current rate of species description, it would take more than 1,000 years to describe the estimated remainder of the fungal kingdom. Mycological research has also reached the crossroads, and genomics initiatives should realise that they have no future without a similar impulse into taxonomy and collection-based research. Furthermore, this also means that culture collections, both private and international, are the cornerstone of all future research, and that molecular or ecological data are worthless without accompanying specimens, that should also be linked to cultures. A further point to consider is how to manage these data, and how to link the various data sets, and make it all freely available. The latter is certainly possible via the internet, but calls for better integration, standardisation and collaboration.

To conclude, the world has a huge wealth of undiscovered and untapped microfungi that could hold vast potential for mankind. To successfully study, collect and preserve this resource, however, a major investment is required in basic systematics, collection, culturing and storage. In most cases this calls for the development of new collection, culturing and preserving protocols. Only then, will we set the stage for a future in which we will be able to fully integrate genomic data sets with ecology and systematics, which will enable us to fully understand and interpret the advantages to be gained from the world's fungal biodiversity.

Conclusions

In this paper, we have sought to address some issues, which will ultimately influence estimates of fungal species numbers. We have reviewed a large but by no means comprehensive body of literature as well as discussed some current projects. Host specificity or substratum recurrence may be an important factor in estimating global fungal species numbers and was, therefore, examined at different levels ranging from host family, host genera, host species to tissue specificity and recurrence. A number of other factors, which might impact on fungal diversity estimates, such as the effect

of methodology, of geographic distance between host plants and selected issues in taxonomy were also assessed.

Diversity data from host families such as *Musaceae*, host genera such as *Nothofagus* and individual host species such as *Eucalyptus globulus* provide an indication of the large numbers of fungal taxa that can be attributed to one plant taxon. Sampling remains necessarily incomplete, both in terms of the full distributional range of the host taxon and of the range of taxa examined within those plant genera and families. It is, therefore, likely that the numbers provided in this paper represent only a small proportion of the total number of fungi occurring on members of those plant taxa.

Some tentative conclusions can be drawn from the data on host-specificity and substratum-recurrence. Fungal specificity for plant pathogens has been reported at the host species and genus level, for example in the well-studied genus *Eucalyptus* and for species within *Eucalyptus*. A body of literature is already focused on the underlying causes for host-specificity in fungal pathogens and, therefore, this does not need to be further discussed here. Surprisingly, numerous separate studies of saprobic microfungi have also suggested a degree of fungal recurrence as indicated by the low degree of overlap between fungal assemblages on different species, genera and families or by the occurrence of presumably unique fungal taxa not reported from other substrata. Tissue-specificity and -recurrence have also been observed both for fungal assemblages and for individual fungal taxa in pathogenic and saprobic microfungi. We however, currently lack knowledge of the full extent of fungal specificity or recurrence because of incomplete sampling and because no systematically collected data is available for microfungal assemblages on other closely related plant taxa. The underlying causes for the apparent recurrence of saprobic microfungi on certain plant tissues or plant taxa have also not been elucidated and deserve further investigation. Developing an understanding of microfungal distribution patterns in relation to host chemistry may provide not only an answer to the question of tissue recurrence but also to recurrence patterns at higher taxonomic levels.

A number of other issues, such as the impact of geography, of methodology and of taxonomy have also been addressed. For example, there is evidence that pathogenic fungi spread to distant locations with their hosts, while separate studies on saprobic and endophytic palm fungi have provided an indication that site-specific factors and geographic distance may be more important in shaping fungal assemblages. Methodology was shown to impact on estimates of species diversity with many more taxa observed using an indirect isolation protocol compared to direct isolations from leaves in a case study from Australia. These issues are of vital importance in planning future research projects. It is, yet, too early to say how ongoing advances in taxonomic understanding will impact on fungal diversity estimates. However, in some groups of fungi, many taxa are in the process of being reduced to one or few species while in other groups cryptic species are uncovered.

While we have attempted to make a number of generalisations from the studies reported here, this review has also highlighted some of the limitations mycologists currently have to contend with. A large body of knowledge exists for certain groups of microfungi or microfungi occurring on certain substrata/hosts. However, it is likely that we are drawing conclusions from data that is somewhat biased toward fungi and host/substrata that are of interest to human endeavours. The discrepancy between the numbers of fungi described from only one economically important

genus, *Eucalyptus*, and all the other members of the *Myrtaceae* is but one example of this bias.

The majority of studies we discussed were undertaken for reasons other than assessing host-specificity or -recurrence patterns and have employed different sampling designs and methodologies. Therefore comparisons between various data may not be applicable. For example, when comparing microfungal assemblages on plant taxa that do not co-occur in the same habitat, it becomes difficult to disentangle the effect of host-specificity or -recurrence from other factors that may impact on fungal assemblages. These may include climate or microclimate or other yet unknown site-specific factors. Although indications exist that some fungal saprobes show recurrent patterns, evidence of their exclusivity on one plant taxon is lacking. This aspect needs to be further addressed. By incorporating the large body of work that is already available and adding appropriate complementary studies, we can accelerate our understanding of microfungal diversity and this will eventually lead us to a realistic estimate of global fungal species numbers.

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