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Biodiversity of soil-inhabiting fungi

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Abstract This survey is concerned only with filamentous fungi living in the soil layer. The observed diversity of soil fungi largely depends on the method used and the numbers of isolates obtained. Particle-plating usually yields higher numbers of taxa than dilution plating. The Centraalbureau voor Schimmelcultures (CBS) preserves a great diversity of soil fungi. The CBS database contained 2,210 species of soil fungi in 2001, an estimated 70% of the known species available in culture. Thus, the current estimate for described culturable soil fungi is approximately 3,150 species, many of which have a cosmopolitan distribution. Adding the ca. 150 spp. of nonculturable *Glomerales* results in 3,300 species of currently known soil fungi. Molecular studies in such groups as *Fusarium*, *Trichoderma*, *Penicillium*, and *Aspergillus* are finding a number of more narrowly distributed cryptic species. Thus the number of species of soil fungi is expected to be considerably higher than the 3300 species currently known.

Keywords Filamentous fungi · Particle filtration · Culturing · *Aspergillus* · *Fusarium*

When Domsch and I compiled ecological data on some 400 common soil fungi 25 years ago (Domsch et al. 1980), we were of the opinion that most of these fungi were cosmopolitan and that species at a particular site were only selected by various soil parameters, the action of which are still hardly understood. We were also of the opinion that most fungal species would potentially spend part of their life in the soil. Since I moved to CBS in 1967, these views have been modified considerably as very many plant-parasitic species (except root parasites) are never isolated from the soil.

For the purpose of this survey, I take into account only filamentous fungi living in soil layers. The diverse fungi living in the litter layer are not treated, being dealt with by Hyde et al. (this volume). The delimitation between litter and soil is admittedly vague! Basidiomycetes often account for more than half of the fungal biomass and activity in a soil, but are usually not recovered in soil-fungal inventories. Their diversity is much

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better assessed in the context of inventories of mycorrhizal and wood/litter-decomposing fungi and recently with molecular methods, and therefore basidiomycetes are also excluded from the present survey, which is confined to culturable soil fungi.

The observed diversity of soil fungi largely depends on the method of isolation used and the numbers of isolates obtained. Particle-plating usually yields higher numbers of taxa than dilution plating (Gams 1992) and the curve of numbers of species versus numbers of isolates is initially steeper with the former technique. But when some 20,000 isolates have been made from a particular soil, both curves approach each other, without, however, ever-reaching complete saturation. When you make some thousands of isolates from any handful of soil, you are likely to find some taxonomic novelties.

Bills et al. (2004) emphasized the high rate at which new taxa are described from soil. These authors gave some estimates of the diversity of fungi in different soils, with maxima of more than 200 species in a single soil when approximately 20,000 isolates, obtained at different times, are critically examined (the highest numbers were reported for deserts of northern Arizona and southern Utah, and in north upland conifer-hardwood forests of Wisconsin). In that beautiful compilation the reader will also find many qualitative details about the fungal diversity in different kinds of soils.

Soil fungi spread easily and most of them are regarded as having a cosmopolitan distribution. Even in tropical forests many taxa are similar to taxa found in temperate latitudes, and the numbers of species for a particular tropical soil are normally the same or even lower than those observed for soils in temperate regions (Pfenning 1997; Bettucci and Roquebert 1995). Needless to say that the species diversity in the litter layer is considerably higher and many novelties have resulted, e.g., from voluminous studies carried out in Ivory Coast (Rambelli et al. 1984, 2004).

Thermophilic and heat-resistant species are largely cosmopolitan. The numbers of known species have roughly doubled within the last 25 years. In desert soils (Mouchacca 1995), these fungi can reach high proportions among the isolates. Among the 246 new fungal taxa described in the last 60 years from the Middle East, mainly desert and salt marsh soils, 53 species are soil fungi (Mouchacca 2005), many of which are adapted to high temperatures or high salt concentrations. Alkaliphilic and alkalitolerant fungi form another ecological group that is adapted to unusual substrata. In highly alkaline soils a range of fungi that grow well on agar media with pH 9.8, particularly of acremonium-like and *Fusarium* species, has been found in Indonesia (Nagai et al. 1995). Unusual habitats also include deposits of burying rodents which have yielded several new *Penicillium* species (Frisvad et al. 1987).

From sampling in remote areas, particularly near the centres of diversification of particular fungal groups, considerable numbers of novelties are expected. By assiduous search in remote locations of Australia, Burgess et al. (1996) and Summerell et al. (1995) found several well-known and a few new species of *Fusarium* that had not yet been known from elsewhere.

Progress in classification

With the advent of refined molecular methods, species can be delimited more accurately, and previously distinguished taxa often turn out to comprise more than one species. This phenomenon of cryptic speciation is probably the most important source of the increase in numbers of soil fungal species. Also among the glomeralean

fungi the numbers of extant species appear to be twice as high as recognized when morphology is used alone (Redecker et al. 2003). While previously most soil fungal species had been thought to be cosmopolitan, molecular studies by O'Donnell, Samuels and co-workers (O'Donnell et al. 1998; Samuels et al. 1998, and later publications) document that continental barriers coincide with phylogeographical patterns for slimy-spored species of *Fusarium* (now about 110 recognized species in CBS) and *Hypocrea*/*Trichoderma* (now 62 recognized species in CBS, not all strictly soil-borne); thus sharply defined species sometimes have a narrower range of distribution than hitherto supposed. Some of these distributional patterns have faded away due to human interference and the worldwide cultivation of many crops. However, even for these two important genera it is predicted that numbers of known taxa will hardly increase by more than 100%; the greatest increase in species numbers has already taken place in recent revisions. The same level of increase in species, 100% or less, is predicted for the more ubiquitous genera *Penicillium* and *Aspergillus* (now ca. 300 and 200 spp. known, respectively) (R.A. Samson and J.C. Frisvad, personal communication). Among the 58 rather sharply delimited species of *Penicillium* subgen. *Penicillium* recognized by Samson and Frisvad (2004), 30 have been described in the last 20 years. In this thoroughly studied group fewer novelties are to be expected than in the remaining subgenera that still await revision. A molecular revision of many other relevant soil fungal genera with an associated increase of numbers is still to come.

Statistics from the CBS culture collection

The Centraalbureau voor Schimmelcultures (CBS) preserves a great diversity of soil-inhabiting fungi (Anon. 2001). The CBS database in 2001 contained 5,768 isolates originating from soil or roots, distributed over approximately 2,430 species, including some unpublished names and a few double counts for anamorph and teleomorph names. When the 131 species of zoosporic fungi and 89 species of macromycete basidiomycetes are subtracted from this number, we get 2,210 spp. of soil fungi now preserved in CBS. We estimate that this database includes roughly 70% of the known culturable species. This would amount to approximately 3,150 spp. of described culturable soil fungi. Adding another ca. 150 spp. of the unculturable *Glomerales* (fungi that form arbuscular mycorrhizas) yields an estimate of 3,300 currently known species of soil fungi.

The rate of increase in the numbers of soil fungi has accelerated only slightly since the broadening of CBS' accession policy and the advent of molecular taxonomic tools. Among the CBS accessions for the years 1991–1996 were 114 new species records for soil fungi (incl. six oomycetes). New accessions during 1997–2002 included 108 new soil-inhabiting species (incl. 12 oomycetes), i.e., ca. 20 species per year. Generally, these were newly described species and the numbers since 1991 do not include new combinations. Many of these new species are classified in poorly defined genera.

Conclusion

While a steady increase in the numbers of species of soil fungi is expected for the coming years, it is likely that we currently know at least 30% of the total diversity of

soil fungi. This is a much higher percentage than the estimated 5% suggested by Hawksworth (1991) for fungi in general.

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