

Ecology and Distribution of Lepiotaceous Fungi (Agaricaceae) – A Review –

by

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Abstract: Lepiotaceous fungi form relatively fragile basidiocarps with white, rarely coloured, spores. Most are saprotrophic forest-floor dwellers that grow in the lower litter layers of the soil, and probably decompose lignin and cellulose. They occur worldwide, with many representatives in tropical and temperate regions, and a few species in arctic-alpine areas and in deserts. Most taxa are agaricoid, though a relatively small number of secotioid variants exist. Because of their relative rarity, the clustering together of many species in limited habitats, and the differences in species composition along latitudinal transects, lepiotaceous fungi may be vulnerable to changes in the environment, both on a local (habitat destruction) and on a global scale (climate change). Sister taxa occur in different parts of the temperate zones of the Northern Hemisphere, indicating that vicariance events might have played a role in speciation. A few species have a very extended distribution, and those species occur either in man-made habitats or else in cooler habitats. Many ecological features of the lepiotaceous fungi are unknown, including the survival rates and colonization success of spores, nutrient and temperature requirements, longevity and size of genets. Conservation of existing diversity calls for policies underpinned by new ecological research, more taxonomical studies, and more recording projects.

Introduction

Scope

This paper reviews the present state of knowledge of the ecology and distribution of the lepiotaceous fungi, based on the literature, and supplemented with field observations. Information pertaining to other members of the Agaricaceae is presented to contrast or to supplement knowledge about lepiotaceous fungi.

The objective is not only to present an overview of what is known, but also to illuminate what is not known, in order to stimulate further research. Despite the important roles fungi play in nature, they are still poorly known; even the number of 1.5 million species in total is a crude estimate based on extrapolation from only a few case studies (Hawksworth 1991; 2001). Insights in the ecology and distribution of lepiotaceous fungi are prerequisites for decisions concerning the conservation of the present diversity. Distribution data alone, such as collected in recording projects in various European countries, are not sufficient to make such decisions.

Lepiotaceous fungi comprise the white- and green-spored members of the Agaricaceae belonging to the genera *Chamaemyces*, *Chlorophyllum*, *Cystolepiota*, *Endoptychum*, *Lepiota*, *Leucoagaricus*, *Leucocoprinus*, *Macrolepiota* and *Melanophyllum*¹. They have been fairly well-inventoried in Europe, but elsewhere, even in North America, knowledge is rudimentary.

The data presented here are based almost exclusively on ecological and geographical observations of basidiocarps. These observations are partly based on the author's experience in the Netherlands and in central coastal California (U.S.A.). Comprehensive information is especially rich in the Netherlands where the mycological society (Nederlandse Mycologische Vereniging) has long maintained a data base, with information on the distribution and ecology of all macrofungal taxa found there (see e.g. Vellinga 2000). A checklist (Arnolds et al. 1995) gives an overview of these data, now surpassing a million records, and an atlas (Nauta & Vellinga 1995), maps the distribution of selected taxa and analyses the ecology and changes in fructification times and places. Extensive ecological information on lepiotaceous fungi is also available from France (Bon 1993) and from Germany (e.g. Saarland: Derbsch & Schmitt 1987).

Current constraints on knowledge

As stated above, our knowledge of ecology and distribution of lepiotaceous species, and indeed saprotrophic Agaricales in general, is extremely incomplete. Several factors play a role:

i. Our present knowledge is geographically biased. The taxonomy has been studied mostly in Europe; lepiotaceous diversity in other regions is poorly known, and the tropics in particular are woefully under-sampled and under-studied. Courtecuisse et al. (1996) listed only two species of the entire family Agaricaceae for French Guiana, viz. *Chl. molybdites* (G. Mey.: Fr.) Masee and *Lc. squamulosus* (Montagne) Pegler. The situation for Venezuela is better, as Dennis (1970) listed 52 lepiotaceous species in his flora of that region. One reason tropical lepiotaceous species are under-studied is that they tend to fruit solitarily. Taxonomists do not like to study species from a

¹The following abbreviations of the genus names are used throughout the paper: *Chl.* = *Chlorophyllum*; *C.* = *Cystolepiota*; *E.* = *Endoptychum*; *L.* = *Lepiota*; *La.* = *Leucoagaricus*; *Lc.* = *Leucocoprinus*; *M.* = *Macrolepiota*, and *Me.* = *Melanophyllum*.

single basidiocarp. Furthermore, foreign collectors are often required to split their collections into two parts to obtain a collection permit. In contrast, in temperate regions many lepiotaceous species grow gregariously.

ii. Misapplication of names is common. European names have, often mistakenly, been used for taxa in other regions. An example is *M. procera* (Scop.: Fr.) Singer, which occurs definitively in Europe, although its eastern extent is not known. Records from eastern North America refer to a different, as yet undescribed, species complex. The Australian '*M. procera*' has been described recently as the new species, *M. clelandii* Grgur. (Grgurinovic 1997). Similarly, in Colombia, Franco-Molano (1999) has described *M. colombiana* for the South American '*M. procera*'. Japanese '*M. procera*' may well represent a fourth species (Vellinga et al. 2003). Careful morphological comparisons, as well as molecular research, will certainly bring other differences to light.

iii. The extent of, and correlation between, molecular and morphological variation is hardly known. Molecular investigations have shown that distinct ITS-types occur in morphologically almost identical collections from different regions of the world. Examples from the Agaricaceae include *Me. haematospermum* (Bull.: Fr.) Kreisel and *L. cristata* (Bolt.: Fr.) P. Kumm. (Vellinga 2001b), and *Coprinus comatus* (O.F. Müll.: Fr.) Pers. (Ko et al. 2001). These different ITS-types may represent different biological species, but more research is needed before this can be established. It has been shown that closely related taxa, differing in ITS-sequences, may have different ecological requirements, e.g. different hosts in the case of *Sarcodon* taxa (Johannesson et al. 1999). As a result some species, formerly considered widespread, now appear to have quite limited distributions, while some ecological ranges may be narrower than hitherto supposed.

iv. Most studies focus on the above-ground part of the fungal organism. While sporocarps are an important part of the fungal life cycle, the majority of the fungal organism is under-ground, in the form of a mycelium made up of thin hyaline colourless hyphae. These hyphae are extremely hard to trace and to study. The available data on the ecology of most saprotrophic fungi are entirely based on the occurrence of basidiocarps, with a few notable exceptions. Warcup (1959) showed that the diversity of basidiomycetous fungi growing in soil of a wheat field and a pasture did not reflect the above-ground diversity; the below-ground community of the wheat field was much species richer than above-ground. The non-fruiting stage of leucoagaricoid fungi has also been investigated in connection with studies of the attine ants and their cultivars. Attine ants, an American ant family to which the leaf cutting ants belong, suppress the basidiocarp formation of their fungi. Currently, a wealth of information is emerging about this highly interesting ecology and the phylogeny of these taxa and their mutualists (Bot et al. 2001; Chapela et al. 1994; Currie et al. 1999; Fisher et al. 1994; Fisher & Stradling 2002; Green et al. 2002; Mueller 2002; Mueller et al. 1998, 2001).

v. Autoecological studies are extremely rare. Ohasi (1977 and 1978) conducted a unique study of the physical and chemical properties of the soil in which *Chl. molybdites* was growing and compared it with the soil supporting other mushroom

species, such as *La. americanus* (Peck) Vellinga (as *L. bresadolae*), *Amanita fuliginea* Hongo, and *Agaricus placomyces* Peck.

vi. Experimental and cultivation studies are lacking or treat only a very limited number of species. The situation for cultivated species, like *Agaricus bisporus* (J.E. Lange) Imbach, is totally different (e.g. Van Griensven 1987; Stamets 2000; Vedder 1978). However, Manz (1971) investigated the cultivation of *La. leucothites* (Vittad.) Singer and *M. procera* from spores. Several studies have focused on cultivation of *Chl. rachodes* (Vittad.) Vellinga (e.g. Eger 1964), and of *M. zeyheri* (Berk. & Singer) Heinem. (Coetzee et al. 1980; Eicker et al. 1989), though in these cases tissue cultures were made from the basidiocarps. Some studies have looked into the presence of oxidative enzymes in basidiocarps, including laccases, which play a role in lignin degradation, and tyrosinases (Gramss et al. 1998; Marr et al. 1986), but these studies focused on the systematic value of the presence of these enzymes, not on their role in nature.

Ecology

Lifestyle

All taxa in the family Agaricaceae have a saprotrophic lifestyle, and most taxa grow terrestrially in the litter layer. Most lepiotaceous species tend to grow in the F horizon of the soil, below the Aoo layer that contains mostly fresh leaves. Many form short rhizomorphs (see also Agerer 2002), and several also form a mycelial mat (e.g. *L. spheniscispora* Vellinga). In temperate regions, lepiotaceous fungi often grow on mull soils, which are characterized by a relatively high pH and a rapid decomposition of litter. Only a few lepiotaceous species are known to grow directly on decaying plant material, such as sawdust, woodchips, decomposing stumps or dung. Among them are *La. meleagris* (Sow.) Singer on wood chips (Van den Berg & Vellinga 1998; Hemmes & Desjardin 2002a) and occasionally on horse droppings (J.F. Ammirati, pers. comm.; identification by the author), *L. calcicola* Knudsen on decaying sawdust (Lohmeyer et al. 1993), and *Lc. cygneus* (J.E. Lange) Bon on the inside of stumps (Boisselet & Migliozi 1995). *Chlorophyllum hortense* (Murrill) Vellinga has been recorded on dung in Australia (as *La. fimetarius*; Aberdeen 1992). However, many lepiotaceous fungi do fruit on decaying wood in the tropics (e.g. Dennis 1970).

In growth experiments on sterilized leaves of *Fagus sylvatica*, it was shown that *M. procera* decomposes both lignin and cellulose (Lindeberg 1947). *Agaricus bisporus* is able to degrade lignin and utilize the holocellulose while growing on fermented straw (Ten Have et al. 2003). Siqueira et al. (1998) grew the attine ant associated *La. gongylophorus* (A.F.H. Möller) Singer on several carbon sources to determine the metabolism of the fungus; they showed that polysaccharides are taken up while cellulose is digested at a low rate, perhaps too low for it to be the main source of carbon for these fungi as was earlier suggested (Bacci et al. 1995).

Most lepiotaceous taxa grow in shaded places under scrub and trees. Only a few are found in open habitats, such as dune grasslands, alpine meadows (*L. erminea* (Fr.: Fr.) P. Kumm., *M. excoriata* (Schaeff.: Fr) Wasser), lawns, grasslands or fields (e.g.

L. cristata, *La. leucothites* and *La. barssii* (Zeller) Vellinga). This pattern contrasts strikingly with the genus *Agaricus*, whose representatives are frequently found in open habitats (Fig. 1).

Lepiota (s.l.) species occur both in deciduous and in coniferous forests, but typically shun very wet and very dry conditions. In his study of the peat bogs of the French Jura, Favre (1948) listed only a single species, *L. clypeolaria* (Bull.: Fr.) P. Kumm.,

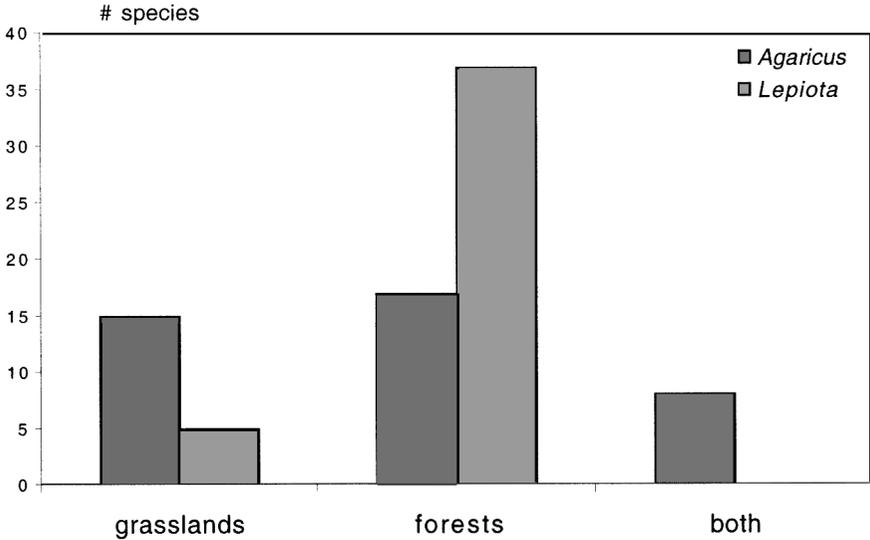


Fig. 1. Number of *Agaricus* and *Lepiota* species in grasslands and in woods or in both in the Netherlands. Data taken from Nauta (2001) and Vellinga (2001a).

though recently a second species, *L. jacquieri* Fillion, was described from peat moss bordering a lake in the same area (Fillion 1995). Likewise, the very dry coniferous forests of the Sierra Nevada in western America are very poor in *Lepiota* species; Sundberg (1967) listed only *L. magnispora* Murrill (as *L. clypeolaria*). Lepiotaceous fungi are dominant in some forest types, especially those with a low number of ectomycorrhizal trees, e.g. stands of *Cupressus macrocarpa* (Guinberteau et al. 1998; Sundberg 1967). *Juniperus communis*-scrub in Europe commonly harbours at least one species of *Lepiota*, *L. ochraceofulva* P.D. Orton.

Some taxa display a wide ecological range: *L. decorata* Zeller was described from a *Pseudotsuga* old growth forest in central Oregon (U.S.A.) (Zeller 1922), but was recently found in *Eucalyptus* plantations in central coastal California (pers. obs.). This seems to be a recurrent trend for the lepiotaceous fungi: they are substrate generalists, but confine themselves to the litter layer.

In general, the group is often found in nutrient-rich situations with a certain degree of disturbance, but there are gradations. In a natural setting, Ohasi (1978) showed that *Chl. molybdites* grows under relatively nutrient-rich conditions. *Chl. molybdites* was, with *Podaxis pistillaris* (Pers.) Fr., the most commonly encountered species (out of 32) in the urban setting of the Mexican town of Hermosillo (Esqueda-Valle et al. 1995). Actually, most *Chlorophyllum* species exhibit this pattern and are found in man-made enriched and ruderal habitats. For example, *Chl. rachodes* was found on old ant nests in England (Sagara 1992). Examples from other genera are the neotropical *L. spiculata* Pegler on abandoned termite and ant nests (Pegler 1983; Singer & Garcia 1989), and *L. aspera* (Pers.: Fr.) Quél. in a wide variety of disturbed more or less natural habitats. Notwithstanding the occurrence of lepiotaceous species in ruderal habitats, it should be noted that the mycelia of *La. leucothites*, *Chl. rachodes* and *M. zeyheri* grow well on standard agar media, such as potato dextrose agar, malt agar and glucose agar (Coetzee et al. 1980; Eger 1964; Manz 1971).

Mor soils, with their low pH, and high litter contents are in general avoided by lepiotaceous fungi. The nutrient-poor habitats, like the *Pinus* plantations on dry sandy Pleistocene soils in the central parts of the Netherlands, are poor in *Lepiota* species. When species such as *L. cristata* (Fig. 9) and *L. castanea* Quél. do occur in these areas, they are found on compost, piles of leaves, or beside the bicycle trails, which are typically surfaced with seashells.

In reports on the occurrence of fungal species on contaminated soils, the two edible species *M. procera* and *Chl. rachodes* are often mentioned; both species accumulate heavy metals like chromium, copper, lead and mercury (Kalac et al. 1996; Kalac & Svoboda 2000).

Many taxa fruit year after year at the same location, but in most cases it is not known whether the same individual mycelium is responsible, or whether these basidiocarps originate from separate germination events. Some species form fairy rings; *Chl. molybdites* can grow in rings of more than 200 m in diameter, which must be decades old (Hemmes & Desjardin 2002).

How long spores can survive in the soil is an open question. Miller et al. (1994) showed that the coloured spores of the ectomycorrhizal genera *Rhizopogon* and *Suillus*, can survive several winters in the soil, but comparable data on spores of lepiotaceous fungi are lacking. The melanins present in the spore wall of *Agaricus bisporus* (Rast & Hollenstein 1977), are considered to delay enzymatic lysis of the cell wall (Butler & Day 1998) so the generally unpigmented spores of lepiotaceous fungi may be shorter-lived.

When do they fruit?

The factors determining the appearance of basidiocarps for individual species are not known, despite many reports on the fruiting of fungi in general (Straatsma et al. 2001; Vogt et al. 1992; but compare Kües & Liu (2000) for cultivated species). Temperature, moisture and to a lesser extent light, seem to be the principal factors. Typically, the mushrooms appear in temperate parts of Europe after rains and

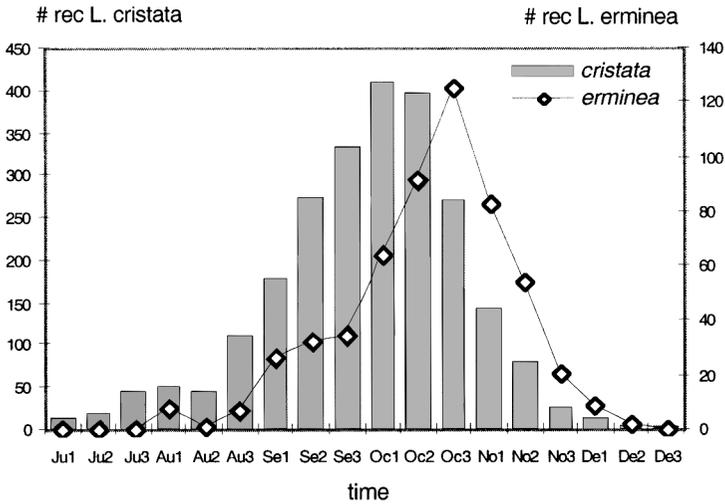


Fig. 2. Fruiting pattern of *Lepiota erminea* compared with that of *L. cristata* in the Netherlands. Only the period July-December is shown. Data from the Dutch data base from 30 Sept. 2002.

number of records

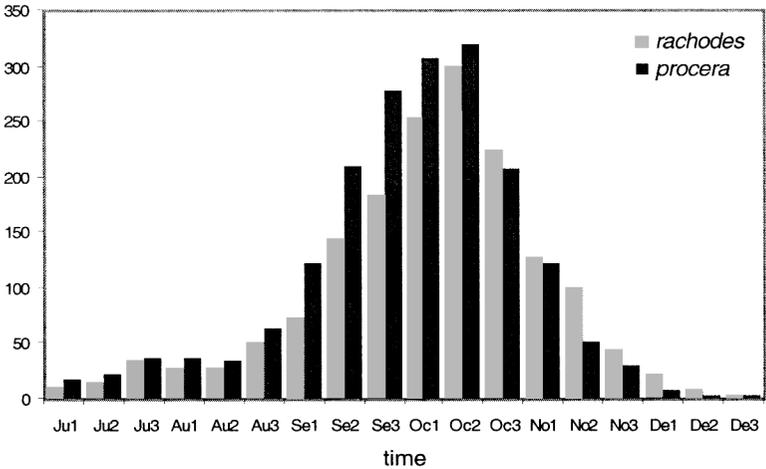


Fig. 3. Fruiting patterns of *Chlorophyllum rachodes* and *Macrolepiota procera* in the Netherlands. Only the period July-December is shown. Data from the Dutch database from 30 Sept. 2002.

thunderstorms at the end of summer and during the autumn rains. Most taxa cease to fruit when night frosts hit, and day-time temperatures drop. An exception is *L. erminea*, which in the Netherlands has its peak fruiting later in the year than other *Lepiota* species (Figs 2 and 3); this species is also able to grow at high altitudes (Peintner & Horak 1999). In the Mediterranean climate of central coastal California

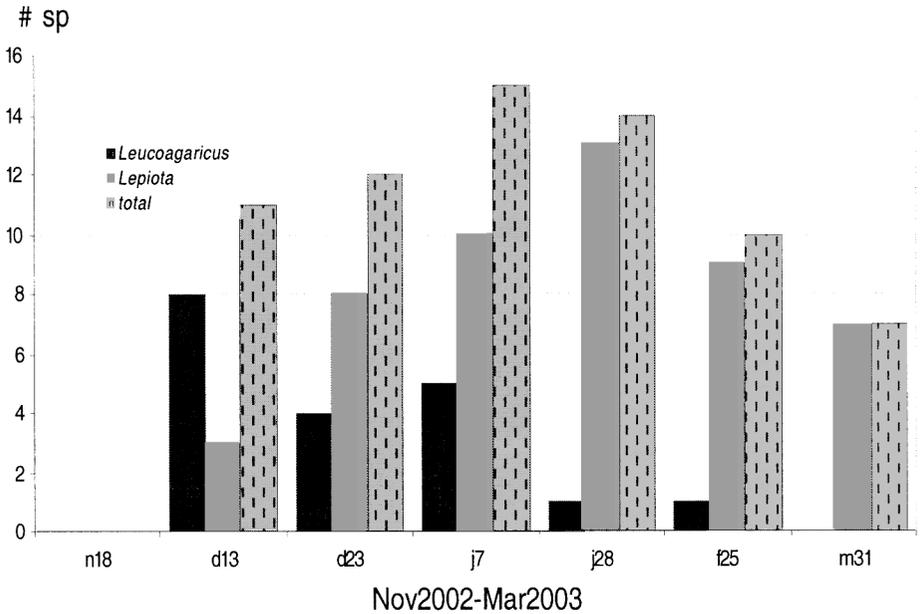
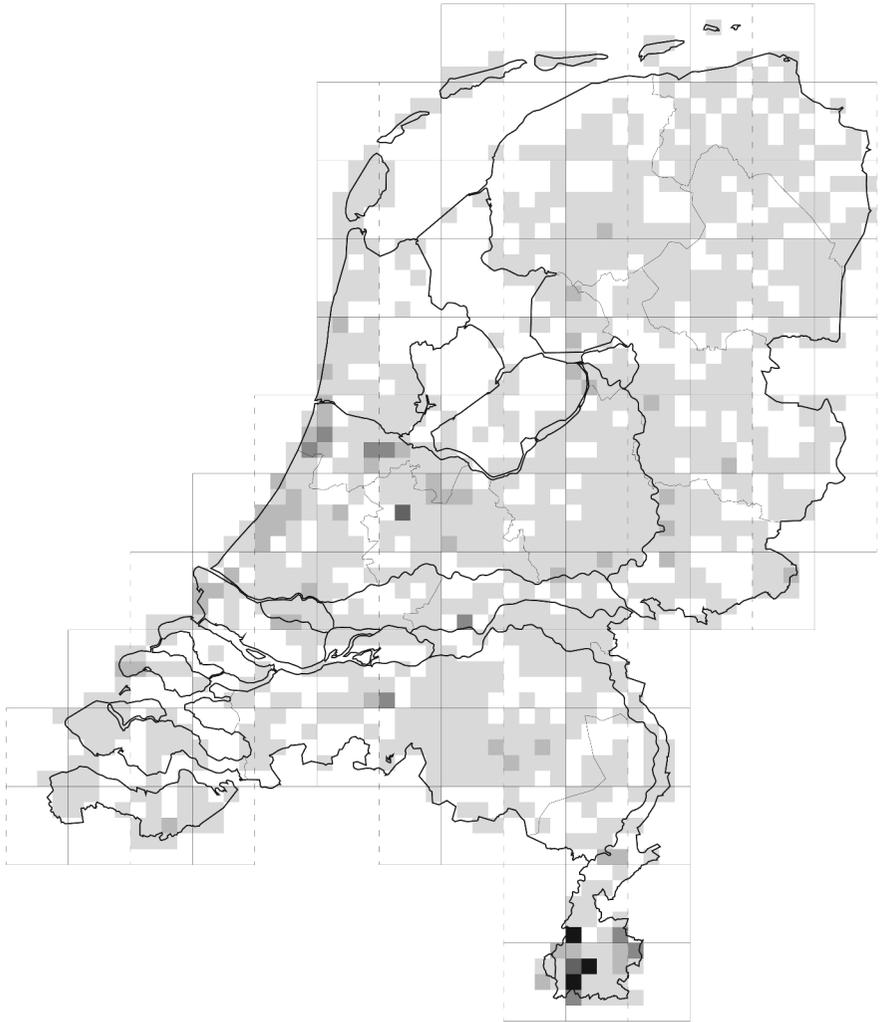


Fig. 4. Number of species of *Lepiota* and *Leucoagaricus* and in total in one grove of *Cupressus macrocarpa* south of San Francisco (California, U.S.A.) during the period November 2002 – March 2003; 25 different species were found. No lepiotaceous fungi were found in November.

moisture, rather than frost, is the limiting factor for fruiting, resulting in a prolonged fruiting season from late autumn to spring. *Leucoagaricus* species (especially belonging to sections *Rubrotincti* and *Sericeomyces*) are the first to appear after the start of the rains in the autumn, followed by *Lepiota* species (Fig. 4). For *Chl. molybdites* both moisture and temperature are the limiting factors, and irrigation in locations with suitable daily minimum temperatures ($> 15^{\circ}\text{C}$) has expanded the possible habitat considerably (e.g. Avizohar-Herschenson 1967). The occurrence of compost heaps in which the temperature is much higher than in the surrounding environment, make fruiting in temperate regions (in summer) of tropical species possible (e.g. *Lc. cretaceus* (Bull.: Fr.) Locq.). The tropical species *Lc. birnbaumii* (Corda) Singer and *Lc. ianthinus* (Cooke \rightarrow Sacc.) Locq. fruit throughout the year in flowerpots indoors in temperate areas.

Hotspots of lepiotaceous diversity

An interesting phenomenon is the ability of many lepiotaceous species to grow together in small geographic areas. Such hotspots occur in the Netherlands in southern Limburg (Bunderbos; Örenberg; Kelderman, 1994), near Breukelen and in Amsterdam (Amsterdamse Bos and Amstelpark; Chrispijn 1999) (Figs 5 and 6). They are also known in other countries (e.g. Bon 1976; Guinberteau et al. 1998; Henrici 2001; Nitare 2000; Rald et al. 1992; Sundberg 1967; Winterhoff & Bon 1994).



■ 1-11 (967) ■ 12-23 (56) ■ 24-34 (9) ■ 35-51 (2) ■ 52-56 (3)

Fig. 5. Map of the Netherlands with number of lepiotaceous species per grid unit of 5 × 5 sq. km. Lepiotaceous fungi have been recorded from 1037 grid units. In total 1682 grid units are on Dutch territory, and from 1609 of these mushrooms have been recorded. 812 Grid units harbour five or fewer lepiotaceous species, and 305 only one. The maximum number of species per grid unit is 57 (one grid unit); two grid units harbour 52 species; these three are situated in southern Limburg. Estate Nijenrode near Breukelen is also very rich in *Lepiota* species (39). Data of 30 Sept. 2002.

Thus, despite the fact that many lepiotaceous seem to grow in nutrient-rich or enriched habitats, there are not that many localities which meet these requirements.

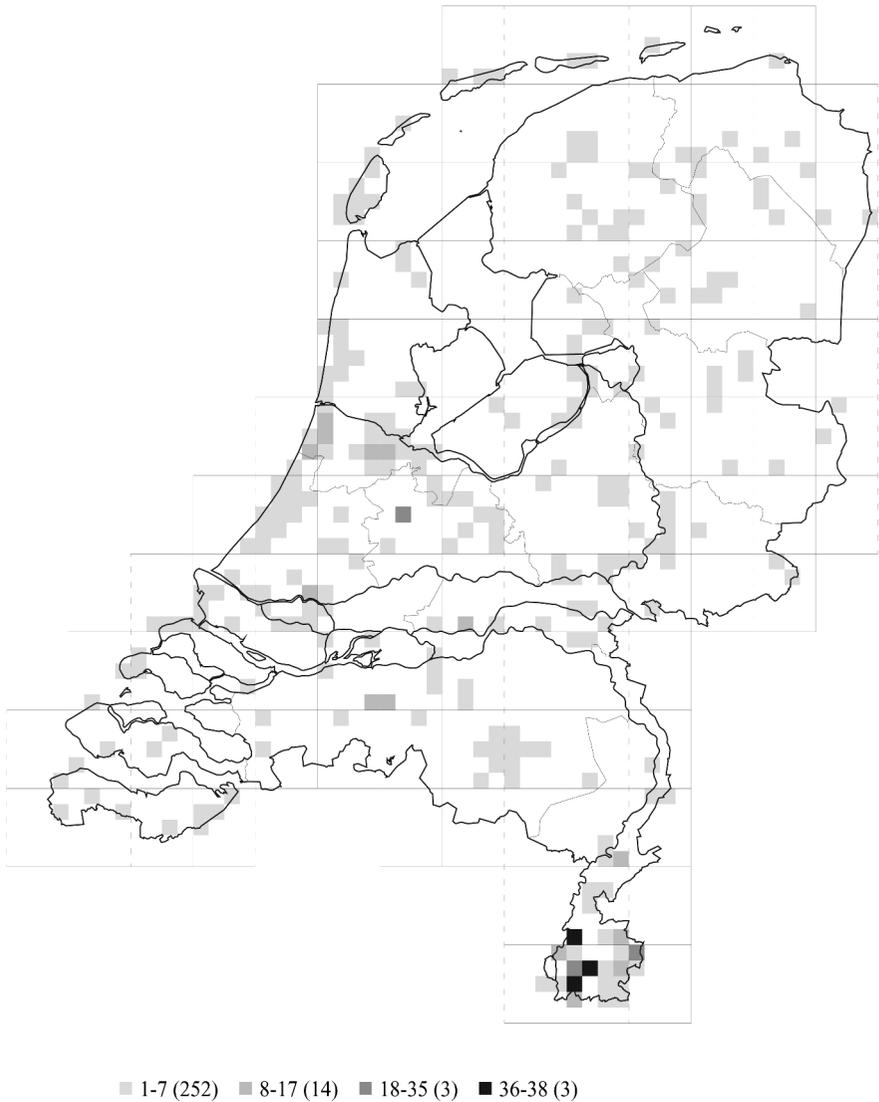


Fig. 6. Map of the Netherlands with the number of rare lepiotaceous species per grid unit of 5×5 sq. km. 61 Species occurring outdoors (i.e. not restricted to flowerpots and greenhouses) reported from less than 50 grid units are included. Southern Limburg plots harbour the highest numbers of rare species. Data of 30 Sept. 2002.

This pattern of co-existence in small geographic areas has also been observed in several groups of grassland fungi, including *Hygrocybe* and *Entoloma* species (e.g. Newton et al. 2003). The most famous example of the coexistence of closely related species, in this case trees, is the tropical rain forest. Despite the many theories that

have been put forward to explain this phenomenon (e.g. Chesson & Warner 1981; Wright 2002), no single all-encompassing explanation has been found.

Likewise, various hypotheses can be formulated to explain why so many lepiotaceous species can occupy one area. Hutchinson (1957 and 1959) stated that sympatric species must differ in niche preference to be able to live together, and an example from the basidiomycetes is the host specificity of *Sarcodon squamosus* (Schaeff.) Quél. and *S. imbricatus* (L.: Fr.) P. Karst. (Johannesson et al. 1999). Niche partitioning for sympatric lepiotaceous fungi can either be spatial or temporal, and forests provide many different microhabitats for relatively small organisms like the non-cord-forming basidiomycetes. For example, some species may grow close to a creek or low on a slope, where the soil is relatively moist and nutrient-rich, while others prefer slightly dryer conditions that may occur a few metres away. It is not known whether different species occupy different layers of the A-horizon in the soil. A distinct seasonality, as shown for one stand of *Cupressus macrocarpa* in California (Fig. 4), provides an example of temporal differentiation, assuming that the activities of the mycelium are reflected by basidiocarp formation. But, competitive dynamics within the lepiotaceous fungi is not known.

The absence of ectomycorrhizal competitors may also contribute to the high diversity of saprotrophic fungi (Gadgil & Gadgil 1971 and 1975; Leake et al. 2002). In forests with nutrient-rich and moist soil, whatever ectomycorrhizal trees are present may be less dependent on their associated fungi, making these fungi vulnerable to competition (compare Harley & Smith 1983 and Last et al. 1984). However, studies on competition between saprotrophic and ectomycorrhizal fungi have all been done from the perspective of the plant or the ectomycorrhizal fungi (e.g. Leake et al 2002), so how the saprotrophic fungi are affected is not clear. A study in Mexico found that the growth of *Pinus pseudostrobus* seedlings was more enhanced by inoculation with both the ectomycorrhizal *Pisolithus arrhizus* (Scop.) Rauschert (as *P. tinctorius*) and *Lc. birnbaumii* (as *L. lutea*) than with *P. arrhizus* on its own (Valdés 1986).

The presence of monoterpenes and sesquiterpenes in *Sequoia sempervirens* needles inhibits growth in many fungal species; however, lepiotaceous fungi are common and often dominant in groves of this tree species. As mentioned above, lepiotaceous fungi have also been found growing on sites contaminated with heavy metals (Kalac & Svoboda 2000).

Life forms

Most species in the family Agaricaceae form agaricoid basidiocarps. However, in dry and open habitats, secotiation has occurred several times in different lineages within the Agaricaceae. Examples are *Agaricus inapertus* Vellinga, *Gyrophragmium dunalii* (Fr.) Zeller, and *Longula texensis* (Berk. & M.A. Curtis) Zeller within *Agaricus*, and *Endoptychum agaricoides* Czern., a relative of *Chl. molybdites* (Vellinga et al. 2003). All lycoperdaceous and tulostomataceous fungi are gasteroid, and form separate lineages in the Agaricaceae (Krüger et al. 2001; Moncalvo et al. 2002).

Hypogeous basidiocarps do not occur within the family; as far as known, all truly hypogeous fungi are ectomycorrhizal.

All the secotioid and gasteroid taxa in the Agaricaceae have dark coloured spores, possibly as an adaptation to drought and exposure to UV-light (see also Butler & Day 1998). Coloured spores are not restricted to secotioid and gasteroid taxa, but are also found in *Agaricus*, *Allopsalliota* and *Micropsalliota*, and in several isolated taxa of other lineages within the family (*Chl. molybdites* and *Chl. globosum* (Mossebo) Vellinga, *Heinemannomyces*, *Melanophyllum*, *Termiticola*, and *Coprinus comatus* and allies).

Food source

Basidiocarps of lepiotaceous fungi are eaten by various animals. In one study, in Finland, larvae of several taxa of Diptera were found in *M. procera*, *Chl. rachodes*, *La. nymphaeum* (Kalchbr.) Bon, and in *L. clypeolaria*. The species with big basidiocarps harboured more fly taxa than the smaller ones, such as *L. clypeolaria* (Hackman & Meinander 1979).

Adult specimens of *Oxyporus major*, a staphylinid beetle and obligate inhabitant of fleshy fungi, have been found in relatively high numbers in the basidiocarps of *L. aspera* (as *L. acutesquamosa*) in Illinois (U.S.A.) (though they were found more often in *Stropharia hardii* G.F. Atk.) (Hanley & Goodrich 1994).

Collembola, slugs, and sow bugs are commonly encountered on basidiocarps of lepiotaceous fungi. Interestingly, Greenslade et al. (2002) reported on the occurrence of introduced Collembola species on non-native *Leucoagaricus* species in Australia. Mammalian *Lepiota*-eaters are much rarer; tooth marks are extremely uncommon, even on large, fleshy basidiocarps. Predation by humans leaves little trace.

Distribution

Dispersal, establishment and persistence

It is perhaps surprising that not all lepiotaceous species have a world-wide distribution. Their spores are small, and global air circulation patterns are such that Sahara sand ends up in North America, and dust from volcanic eruptions can be distributed around the world. The spores which do rise to levels where the wind can transport them, face cold, drought and UV radiation. If dispersal is nonetheless followed by germination, an encounter with a second compatible mycelium must typically follow in order to form a heterokaryon.

Yet spores of important crop rusts, appear to be able to span oceans and pass from one side of a continent to another (Brown & Hovmøller 2002). These authors pointed out that rust fungi have several characteristics which assist dispersal and colonization: their spores are brown, the host species are widely available plants, and the species are able to reproduce clonally.

Basidiospores are present in air columns, but their sources are considered to be overwhelmingly local (Burge 1986; Williams et al. 1984). James & Vilgalys (2001) studied *Schizophyllum commune* Fr., a lignicolous species of exposed situations, and found that spore dispersal over long distances was a very rare event, though the number of spores within air columns was higher than expected. When long-distance dispersal of basidiospores does occur its role is considered to be minor (Malloch & Blackwell 1992). It has been reported that living spores of *Pleurotus djamor* (Rumph. ex Fr.) Boedijn, a species with a wide tropical distribution, can reach temperate areas, in this case Canada and Switzerland (Vilgalys & Sun 1994).

Dark coloured spores seem to be protected against both UV and temperature extremes, due to the presence of melanins (Butler & Day 1998); they also resist desiccation. Watling (1963) demonstrated that the brown and thick-walled spores of several taxa in the Bolbitiaceae were able to germinate after spending three years in a dry herbarium. Most lepiotaceous fungi have non-pigmented spores and seem poorly adapted to long-range dispersal. In the Hawaiian islands where about 40 taxa of lepiotaceous fungi have been found (Hemmes, pers. comm.), only a few, occurring in native forests, are considered to predate the arrival of man (Hemmes & Desjardin 2002b). It is not clear whether the other lepiotaceous species arrived with imported plant material, or whether the newly created habitats facilitated the establishment of wind-dispersed spores.

Dispersal of mycelium and spores by man, inadvertently in most cases, but purposefully for cultivated species like *Agaricus bisporus* and *Chl. brunneum* (Farlow & Burt) Vellinga, clearly influences the present distribution. This is shown by the occurrence of tropical lepiotaceous taxa in temperate regions in such managed habitats as tropical greenhouses, flowerpots and the planted areas of indoor recreation areas, swimming pools and the like (Pidlich-Aigner & Hausknecht 2001; Vellinga 1990 & 1999; Watling 1991, etc.). However it has not been proven, that the fungi came with the soil or plant material.

Insects may play a minor role in dispersal by feeding on basidiocarps and inadvertently transport their spores. In the attine ants, a queen who is going to establish a new colony, transfers a small pellet of hyphae from the fungus in her infrabuccal pocket and uses this to initiate her own culture (Bailey 1920; U.G. Mueller et al. 2001). Fungal spores and hyphae in general are transported in these pockets by worker-ants of the so-called lower attine ants, which gather plant material from the forest floor, and do not bring fresh leaf material to the nest like the leaf cutting ants (Mueller et al. 2001).

Experiments on the germination of spores have only been executed for *La. leucothites* and *M. procera* (Manz 1971). Spores of the former germinated easily on a wide range of substrates, whereas *M. procera* spores only germinated on agar with *Rhodotorula* colonies, and even then in very low numbers.

Spores of most taxa of lepiotaceous fungi have two, identical, nuclei, but the species are outcrossing, as Manz (1971) demonstrated for *La. leucothites* and *M. procera*. It is not known whether 2-spored taxa, which have 4-nucleate spores, are homothallic, which would be advantageous in the colonization of new areas (Tommerup et al.

1991). *Macrolepiota clelandii*, a 2-spored species, is as far as known limited to Australia and New Zealand; on the other hand, *Chl. hortense*, also a 2-spored taxon, has been found in many (sub)tropical areas.

Distribution patterns

The family Agaricaceae occurs world-wide, but the numbers of taxa and the species composition per region differ considerably. For lepiotaceous fungi, there is a significant decrease in the numbers of taxa with increasing latitude, and only a few species are recorded for arctic and alpine habitats (Favre 1955; Knudsen & Borgen 1987; Kühner 1983; Peintner & Horak 1999). Temperature and nutrient availability seem to be the decisive factors for this pattern.

There are no records of *Leucoagaricus* or *Leucocoprinus* species from higher altitudes and latitudes (Peintner & Horak 1999). Significant differences are evident even over quite short distances. Within north-western Europe, Lange (1995) listed nine *Leucoagaricus* species in Denmark, while Vellinga (2001a) found 21 taxa in the more southerly situated Netherlands (the species concepts of these two authors are comparable, and the areas of the two countries are almost equal, Denmark being slightly the larger). In central coastal California (pers. obs.) and in the Lesser Antilles (Pegler 1983, data interpreted by the present author) there are almost twice as many *Leucoagaricus* species as *Lepiota* species (Fig. 7).

Ten taxa were listed for arctic and alpine habitats, nine of them in *Lepiota*, one in *Cystolepiota*. Only *L. cortinarius* var. *dryadicola* (Kühner) Bon, which grows with

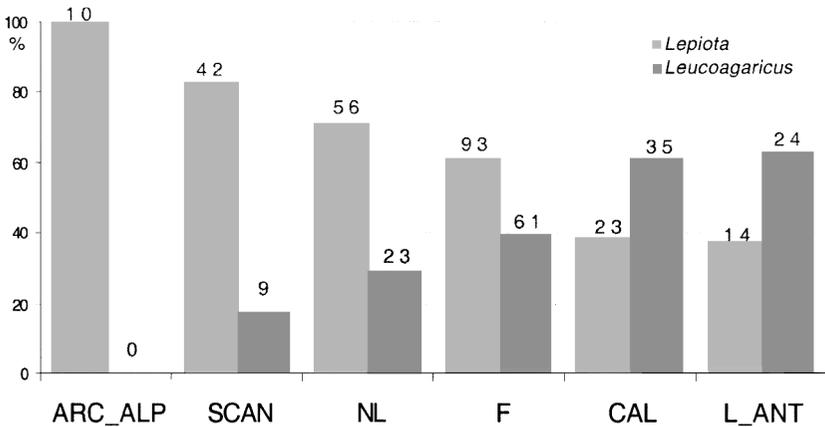


Fig. 7. Percentages and numbers species in the genera *Lepiota* (including *Cystolepiota* and *Melanophyllum*) and *Leucoagaricus* (including *Leucocoprinus*) in different regions on a north south transect. Greenhouse species have not been included. ARC_ALP: arctic and alpine regions after Peintner & Horak (1999); SCAN: Scandinavia after Lange (1995) and Hansen & Knudsen (1992); NL: the Netherlands (Vellinga 2001a); F: France after Bon (1993); CAL: coastal central California (pers. obs.); LA: Lesser Antilles (after Pegler 1983).

Dryas octopetala, is restricted to arctic-alpine areas (Peintner 1998; Peintner & Horak 1999). In subalpine zones of the Alps, *Macrolepiota* and *Chlorophyllum* taxa do occur (Favre 1960). *Lepiota* species are also known from tropical areas (Horak 1981), but *Leucocoprinus* and *Leucoagaricus* taxa are probably more common there than in temperate regions, although data to prove this are scarce, as most authors (e.g. Dennis 1970; Pegler 1983) treat many *Leucoagaricus* species under the genus *Lepiota* (see also Fig. 4).

The fruiting patterns of *Leucoagaricus* and *Lepiota* species in one area (Fig. 4) already demonstrate a difference in abiotic requirements for the formation of basidiocarps. The fact that *Lepiota* species are able to grow at higher altitudes than *Leucoagaricus* species might be an indication that these species are not only able to survive at lower temperatures but also under situations with a lower nutrient availability. However, the differences and trends also suggest that *Leucoagaricus* and *Leucocoprinus* taxa may be good indicators for climate change.

Deserts, steppes, and other dry habitats harbour mostly secotioid and gasteroid taxa, like *Endoptychum agaricoides*, *Podaxis*, *Tulostoma* and secotioid *Agaricus* species.

Species distribution

There is a wide variation in distribution areas among the species, ranging from pan(sub)tropical to a single localized region, but for many, even conspicuous, common and widespread species, the exact distribution is not known.

As already mentioned, most *Chlorophyllum* species have wide distribution areas; the relatively thick-walled spores, the sturdy basidiocarps and the ability to grow on disturbed places may be advantageous characters in this respect. One example is *Chl. hortense*, growing in lawns, on compost- and dung-heaps and in other man-made habitats throughout the (sub)tropics. It has been recorded (under various names) from the south-eastern parts of the U.S.A. (e.g. Murrill, 1914), the Lesser Antilles (Pegler 1983), Venezuela (Dennis 1970), Bolivia (E. Boa, pers. comm., identification by the author), the state of Paraná in Brazil (A.A.R. de Meyer, pers. comm.), Japan (as *M. alborubescens*; Imazeki et al. 1988), Queensland in Australia (as *La. fimetarius*; Aberdeen 1992), Hawai'i (Hemmes & Desjardin 2002a), and from Africa (Cameroon, 4-spored variant (identification by the author), Congo, as *L. bisporus* (Heinemann 1973), and South Africa (Reid & Eicker 1993)). This species is one of the few in the family with 2-spored basidia, and 4-nucleate spores.

Several species with a northern, temperate distribution are widespread, without evidence of human intervention. For example, *L. subincarnata* J.E. Lange and *L. clypeolaria* occur in Europe and in North America.

A species known from both the Northern and the Southern Hemispheres is *La. leucothites*. It flourishes in man-made habitats, and is known from Australia (e.g. Grgurinovic 1997, as *La. naucinus*), North America (e.g. Arora 1986; as *L. naucina*) and Europe (e.g. Vellinga 2001a), South Africa (Reid & Eicker 1993), Hawai'i (Hemmes & Desjardin 2002a), and China (Z.L. Yang, pers. comm.). The fact that

La. leucothites spores germinate easily, and on a wide range of substrates (including water) (Manz 1971), may explain why this species is able to colonize man-created areas world-wide. *Macrolepiota procera*, whose spores do not easily germinate on artificial substrates, has a much smaller distribution area.

The most widespread species in the Netherlands (i.e. the one recorded from the greatest number of 5×5 sq. km grid units) is *Chl. rachodes*, in the broad sense that includes *Chl. olivieri* (Barla) Vellinga and *Chl. brunneum* (Fig. 8). All three taxa are widely distributed in the Northern Hemisphere, and *Chl. brunneum* is also known from Australia (Vellinga 2003). The second most common species is *Lepiota cristata* (Fig. 9), which is widespread in the Northern Hemisphere.

At the other extreme are taxa with a very localized distribution, like *L. spheniscispora* Vellinga, which is only known so far from various woody habitats in a small area in central California (Vellinga 2001b), and *L. castaneidisca* Murrill, which occurs in *Sequoia sempervirens* forests in northern California (Vellinga 2001c).

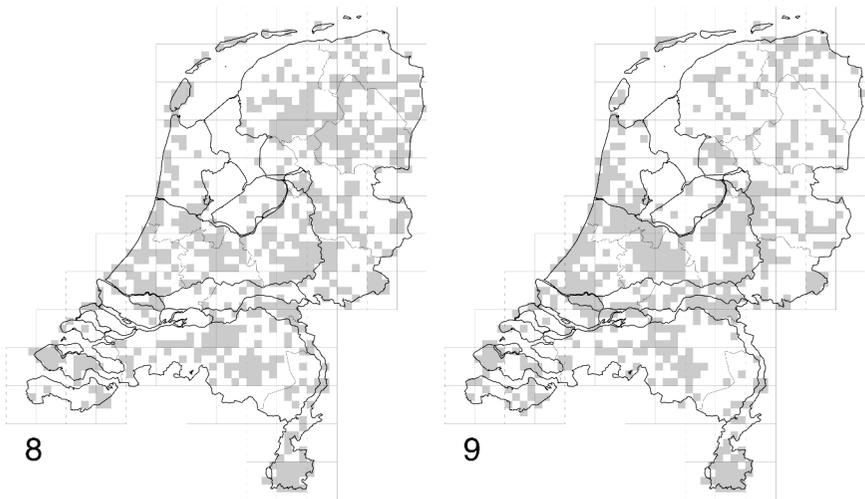


Fig. 8. Distribution map of *Chl. rachodes* (including *Chl. olivieri* and *Chl. brunneum*) in the Netherlands. *Chlorophyllum rachodes* is the species which has been recorded from more grid units of 5×5 sq. km in the Netherlands than any other lepiotaceous species. This species complex has been recorded 1980 times from 590 grid units. Data as of 30 Sept. 2002.

Fig. 9. Distribution map of *L. cristata* in the Netherlands. *Lepiota cristata* is the second most common species in the Netherlands, and is known from 555 grid units, and 2851 records. Data of 30 Sept. 2002.

Distribution and biogeography

Several processes act to obscure the historical pathways of distribution and the means of speciation. Among them, i. former distribution patterns may be upset by human intervention, both in the introduction of species, and in the creation of new habitats,

ii. sampling for phylogenetic analyses is biased to taxa from temperate and subtropical regions, although even there the sampling is by no means complete, and iii. dispersal mechanisms, survival rates of spores under diverse circumstances, and colonization success rates are all unknown.

Nonetheless, some data hint at a tropical origin for the group as a whole or for some of its genera. For instance, the basal clade of the genus *Macrolepiota* is only found in the tropics (it was formerly considered a separate genus, *Volvolepiota*; Vellinga & Yang 2003; Vellinga et al. 2003).

Several species-pairs exist with one representative in Europe, and another in western North America, suggesting a common origin, followed by vicariance and speciation. Examples of such species-pairs are *L. cystophoroides* Joss. & Rioussset and *L. scaberula* Vellinga (Vellinga 2001b); *C. pulverulenta* (Huijsman) Vellinga and *L. petasiformis* Murrill (Vellinga 2001b); *La. marriagei* D.A. Reid and *L. roseolivida* Murrill; and *La. croceovelutinus* (Bon & Boiffard) Bon & Boiffard and *L. carmineobasidia* Sundberg (see Sundberg 1967) (Fig. 10). It is plausible that glaciation events and the presence of the north-south oriented mountain ranges in North America could have played a role, though repeated long distance dispersal followed by speciation cannot be ruled out. These species are not found in alpine, or arctic regions, but appear to grow in regions with warmer climates. A similar pattern has not been found in *L. clypeolaria*, a species that grows in cooler regions. It is unknown whether these species-pairs or other closely related taxa occur in intermediate locations, notably eastern North America and Asia, or in other parts of the world.

The recently discovered *La. cupresseus* (Burlingham) Boisselet & Guinberteau in France under *Cupressus macrocarpa* (Boisselet & Guinberteau 2001) and the Californian taxon known under the same name may furnish another example, since their ITS sequences differ, while morphologically they are indistinguishable (Fig. 10). It would be natural to suppose that the fungus was introduced when the trees were brought to France (probably at the end of the 19th century), but in fact the trees were grown there from seed (Ph. Callac, pers. comm.). Several *Cupressus* species existed in Europe before the Pleistocene but the only one extant today is *C. sempervirens*, which occurs in natural stands in Greece, and harbours a slightly different species in that same group of *Leucoagaricus* sect. *Piloselli* (Fig. 10).

Rarity and vulnerability

Many lepiotaceous fungi are confined to a few areas in a certain country or state. Because of this relative rarity, many taxa are included in European Red Data Lists. The Dutch Red Data List (Arnolds & Van Ommering 1996) contained 52 lepiotaceous species, most of them in the category 'susceptible', which covers rare species. Examples in this category are *C. bucknallii* (Berk. & Broome) Singer & Cléménçon, *L. lilacea* Bres., *La. americanus*, and *La. serenus* (Fr.) Bon & Boiffard. A few species are listed as 'vulnerable' or 'endangered', among them are *M. excoriata* and *L. oreadiformis* Velen. whose habitat of semi-natural grasslands without artificial fertilizers is becoming increasingly rare. The percentages of records of *M. excoriata*,

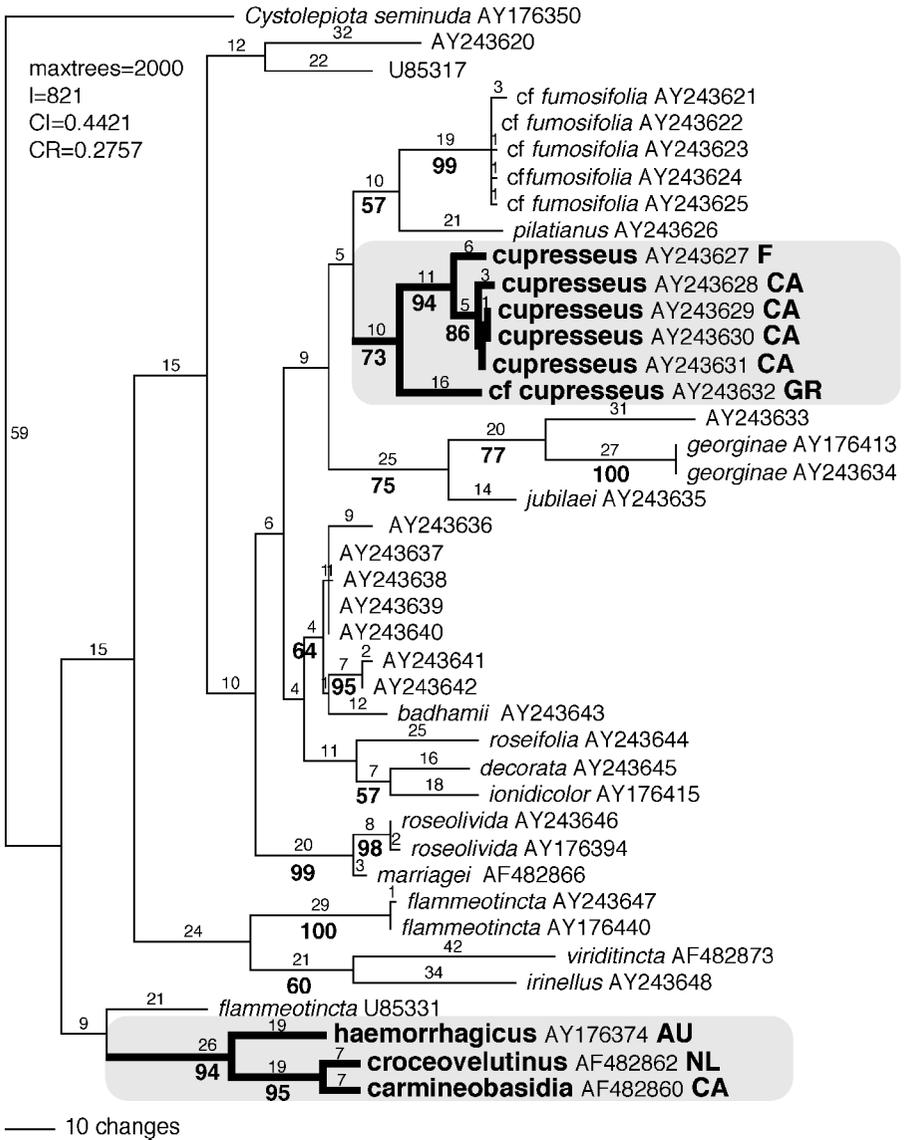


Fig. 10. Phylogram of selected *Leucoagaricus* species, belonging to sect. *Piloselli*, showing *L. cupresseus*, *L. croceovelutinus*, and *L. marriagei* and their respective sister taxa, based on ITS sequences. The GenBank accession numbers are given for each sequence. AU = Australia; CA = California, U.S.A.; F = France; GR = Greece; NL = the Netherlands.

M. procera and *Chl. rachodes* in relation to all records during the second half of the 20th century show neither increase nor decrease, though they greatly fluctuate (Fig. 11). Arnolds & Veerkamp (1999) speculated that *Lc. brebissonii* (Godey) Locq.

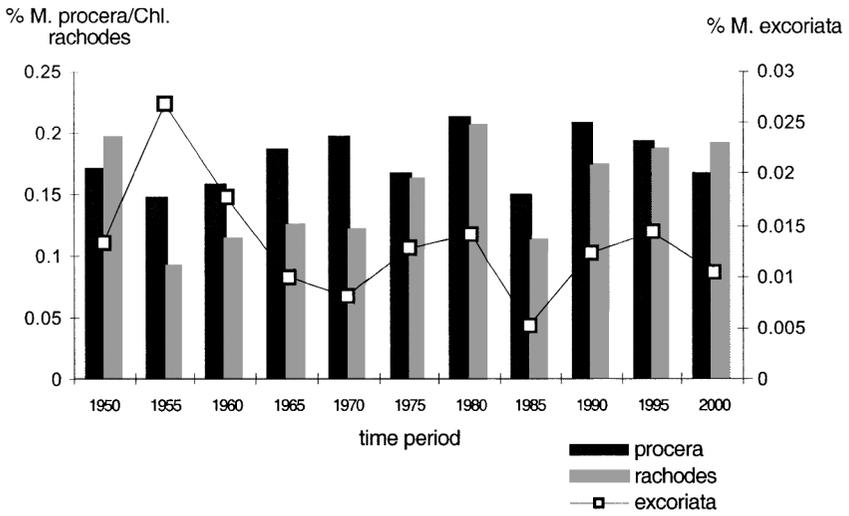


Fig. 11. Percentages of records of *Macrolepiota excoriata* in comparison to those of *M. procera* and *Chl. rachodes* s.l. in the Netherlands. The percentages of numbers of the species are in relation to the total number of records during the time periods of 5 years (methodology after Nauta & Vellinga 1993). Compare with Fig. 1. Data as of 30 Sept. 2002.

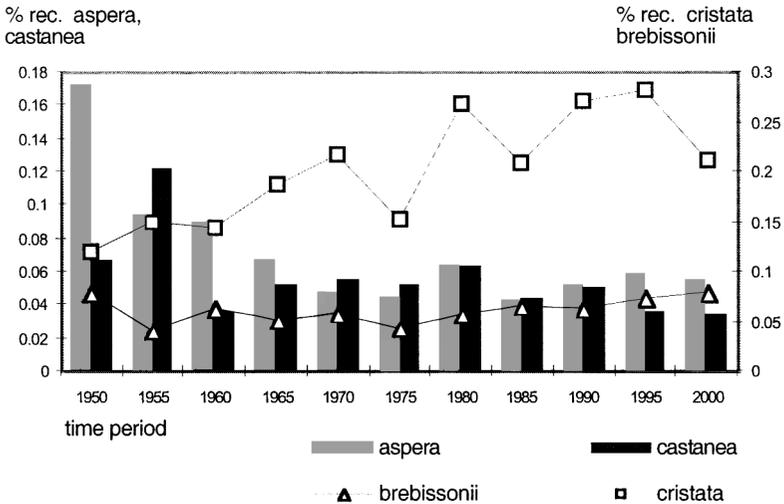


Fig. 12. Percentages of records of *Lepiota cristata* and *Leucocoprinus brebissonii* in comparison to those of *L. aspera* and *L. castanea* in the Netherlands. The percentages of numbers of the species are in relation to the total number of records during the time periods of 5 years (see Nauta & Vellinga 1993 for methodology). Data as of 30 Sept. 2002.

percentage

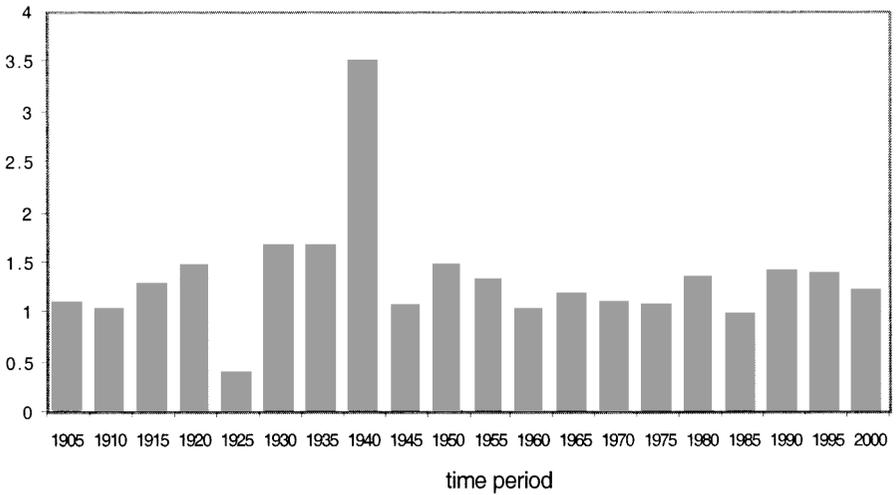


Fig. 13. Percentages of numbers of records of all lepiotaceous fungi in relation to all records in the Netherlands, in the period 1900-2000. Data of 30 Sept. 2002.

is increasing in the Netherlands, in response to elevated nitrogen deposition during the second half of the twentieth century. However, the percentages of records of *Lc. brebissonii* have been rather stable since 1950 (Fig. 12). In contrast, *L. cristata* does show an increase in percentage of records (Fig. 12; compare also with Fig. 11; the distribution of this species is given in Fig. 9). Overall, the percentage of records of all lepiotaceous taxa in the Netherlands in relation to the total number of records has been rather stable for the last 50 years (Fig. 13), despite the greater attention this group has received recently. The number of lepiotaceous species observed has significantly increased in this period.

The clustering of many different lepiotaceous species in small geographic areas, makes this group especially vulnerable to habitat destruction. A map of the rare Dutch species, occurring in natural habitats coincides with the locations of the species-rich areas which are in need of conservation (Fig. 8). Unfortunately, this type of information is lacking for most regions elsewhere. Deforestation in many areas, in particular in the tropics, may eliminate many habitats for these fungi.

Conclusions

Much more extensive observation, sampling, recording, inventorying, and analysis are necessary before we can determine the origins of the lepiotaceous fungi, and understand their history and their ecological roles. Especially useful would be field observations on fruiting patterns throughout the year linked to meteorological data from the fruiting areas in order to shed light on some of the requirements for

basidiocarp formation (compare Ayer (1990) and Strandberg & Rald (1995) for *Cortinarius caperatus* (Pers.) Fr.; as *Rozites caperata*). Experiments concerning spore germination and durability, nutrient requirements of the mycelia, and competition among saprotrophic species or with ectomycorrhizal species are quite feasible. Observations in a species-rich setting on the spatial distributions of individuals within the soil, both horizontally and vertically, might reveal the mechanisms underlying this ability of many species to co-exist (compare with the exemplary research done by Griffith et al. (2002) on *Hygrocybe* species in a Welsh grassland). This knowledge is also indispensable for conservation planning, but unless this research begins quickly much fungal diversity will be lost.

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