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The Importance and Conservation of Ectomycorrhizal Fungal Diversity in Forest Ecosystems: Lessons From Europe and the Pacific Northwest

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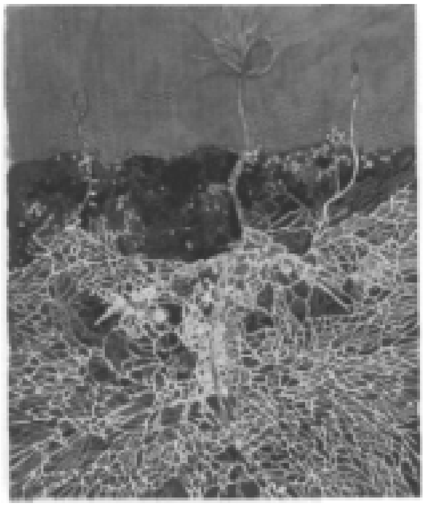

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Cover Artwork	Cover drawings show a range of ectomycorrhizal fungi function and issues surrounding management.

Abstract

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Ectomycorrhizal fungi (EMF) consist of about 5,000 species and profoundly affect forest ecosystems by mediating nutrient and water uptake, protecting roots from pathogens and environmental extremes, and maintaining soil structure and forest food webs. Diversity of EMF likely aids forest ecosystem resilience in the face of changing environmental factors such as pollution and global climate change. Many EMF are increasing in commercial value and gathered both as edible fruiting bodies and for production of metabolites in an emerging biotechnical industry. Concerns over decline of EMF have centered on pollution effects, habitat alteration, and effects of overharvest. In many areas of Europe, a large percentage of EMF are in decline or threatened. Various atmospheric pollutants have had serious direct effects by acidifying and nitrifying soils and indirect effects by decreasing the vitality of EMF-dependent host trees. In addition, a reduction in EMF diversity has been documented where the distribution of host plants have been reduced, intensively used, or simplified. Strategies for the conservation of EMF include decreasing levels of environmental pollutants and retaining diverse assemblages of native host species, habitats, and structures across a landscape. In the Pacific Northwestern United States, high levels of diversity and habitat still exist for conserving, monitoring, and understanding EMF ecology and function. Ectomycorrhizal conservation is an important issue with mycologists, naturalists or conservationists; however, a wider appreciation of the EMF is needed because of their far-reaching influence on the functioning of ecosystems.

Keywords: Conservation, diversity, ectomycorrhizal fungi, forest productivity, forest ecosystem, mushrooms, pollution, truffles.

Introduction

Mycorrhizal fungi, a major functional group of soil organisms, are symbiotic and form mycorrhizal associations with most vascular plants. The most common mycorrhizal types form with arbuscular mycorrhizal fungi, which penetrate the host cells, but do not modify the external appearance of the root. This type of mycorrhiza forms with several hundred species in the family Endogonaceae and predominates in grasses, forbs, bryophytes, pteridophytes, and most tropical tree genera and is associated with many agricultural crops. This paper concentrates on the much more diverse ectomycorrhizal fungi (EMF), which form the mycorrhizal relation with members of the *Pinaceae, Fagaceae, Betulaceae* and *Ericaceae* (see Harley and Smith 1983 for a more exhaustive list). The EMF consist of about 5,000 species that colonize roots, modify root color, shape, and function and often are characterized by extensive external hyphal development (fig. 1).

Importance

Fungal diversity usually is overlooked during consideration of management of forest ecosystems. Foresters, ecologists, and managers are recognizing now that forest productivity, recovery, and stability depend on organisms and processes belowground. The EMF are essential for host plant nutrient uptake and play important roles in nutrient cycling and host productivity in many forests (Cromack and others 1979, Read and others 1992). An estimated 50 to 70 percent of the net annual productivity may be translocated to roots and associated mycorrhizal fungi (Fogel and Hunt 1979, Norton and others 1990, Vogt and others 1982). Through the ectomycorrhizal association, the plant provides carbohydrates to the fungus while the fungus facilitates the uptake of nitrogen, phosphorus, other minerals, and water to the plant. The ectomycorrhizal association promotes fine root development, and produces antibiotics, hormones, and vitamins useful to the plant (see Harley and Smith 1983, Trappe and Fogel 1977 for reviews). Ectomycorrhizal fungi participate in various other important roles, including protecting plant roots from pathogens, moderating the effects of heavy metal toxins, and promoting soil structure (Harley and Smith 1983, Perry and others 1989).

The vital role of EMF forest establishment and recovery is well established (Castellano 1994; Amaranthus and Perry 1987, 1989). Rapid mycorrhiza formation with EMF is essential for reforestation success on harsh sites (Amaranthus and Perry 1987, 1989; Park 1984) (fig. 2) and plant colonization of new soils in glacial moraines, fresh volcanic deposits, and mine spoils (Trappe and Luoma 1992). The EMF also are used to detoxify soils contaminated with heavy metals (Rizzo and others 1992). Some EMF, notably *Pisolithus tinctorius,* are grown commercially as nursery inoculum, or for use in mine spoil reforestation (Castellano 1994, Marx 1980). The role of the large array of EMF, however, is still unknown. For example, Douglas-fir *(Pseudotsuga menziesii* (Mirb.) Franco) can form mycorrhizae with an estimated 2,000 species of fungi (Trappe 1977), but few data exist on the diversity, abundance, synecology, or autecology of these fungi. Although much is known about the role of EMF in plant nutrition and their importance in establishment of conifers on harsh sites, the functional role of EMF diversity is largely unexplored. The EMF species differ in their ability to provide particular benefits to their hosts, and presence and abundance of EMF species may change during forest development (Trappe 1977).

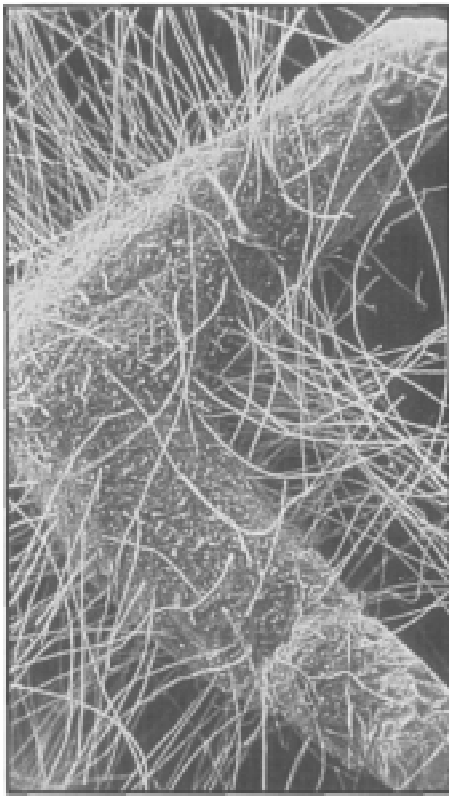

Figure 1—Scanning electron micrograph of pine ectomycorrhiza showing mycorrhizal branching, mantle covering, and abundant external hyphae. (Photo courtesy of Huges Massicote.)

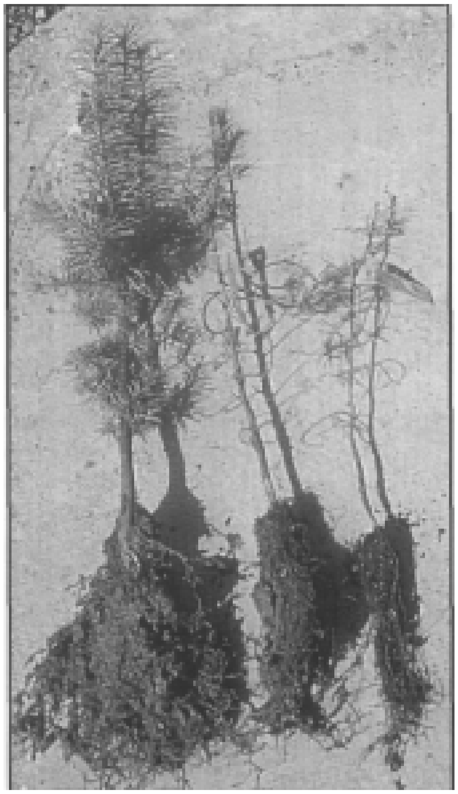

Figure 2—Seedling on the left was rapidly colonized with the EMF Rhizopogon; the two seedlings on the right were not colonized.

Information is needed regarding the role of EMF diversity in maintaining forest health and resilience in the face of environmental challenges. Ectomycorrhizal fungi diversity may equip both tree and forest to functionally adapt to changes in season and habitats or assaults by pollution, degrading soil, or changing climate. In Europe, many authors have observed a direct causal relation between the decline of ectomycorrhizal fungi and tree vitality (Arnolds 1988, Meyer 1984).

Ectomycorrhizal fungi are potentially excellent bioindicators due to their large number of species, specialization, and important ecological functions. Because each EMF species has its own set of physiological characteristics (Trappe 1977), none can be said to be strictly redundant to any other. Some may be active at cool or moist times of year, others at warm or dry times. Some may be particularly effective at extracting phosphorus or nitrogen from mineral soil, others more effective at releasing bound nutrients from organic matter. Some may thrive in coarse woody debris, others in humus or other substrate components. Even individual small trees may have many ectomycorrhizal fungal associates (Amaranthus and Perry 1987), and healthy forests typically have a highly diverse ectomycorrhizal flora (Arnolds 1991, Fogel 1976, Hunt and Trappe 1987, Luoma and others 1991, Menge and Grand 1978). The ecology and distribution of most EMF species, however, are largely unknown and ecological research and monitoring of EMF incomplete.

Ectomycorrhizal fungi are essential in many forest food webs. Exudates and hyphae of EMF form a major link between aboveground producers and soil food webs, while providing photosynthetically fixed carbon to rhizosphere consumers such as bacteria, protozoa, arthropods, and microfungi. Ectomycorrhizal fungi produce, with few exceptions, macroscopic sporocarps (mushrooms and truffles) that are essential in wildlife food webs in temperate forest ecosystems worldwide (Maser and Maser 1988). As opposed to other EMF that fruit as mushrooms or crusts or wafts in the soil, truffles depend on being eaten by animals for their spore dispersal (Maser and others 1978, Maser and Maser 1988). Many animals, in turn, have evolved a dependence on truffles; some rodent species rely on them for over 90 percent of their food supply (Maser and others 1988). In Pacific Northwestern coniferous forests, both the northern flying squirrel *(Glaucomys sabrinus)* (color plate 1)[1] and California red-backed vole *(Clethronomys californicus)* use truffles as their primary food source (Maser and others 1988, Ure and Maser 1982). The northern flying squirrel is of recent special interest as the primary prey of the threatened northern spotted owl *(Strix occidentalis)* in much of its range in the Pacific Northwestern United States (Forsman and others 1984). Wood rats *(Neotoma* spp.), important owl prey in xeric forests, also feed on truffles (Maser and others 1978, Parks 1991). Many other mammals, including bear, deer, and mice consume EMF, as do nematodes, mollusks, and arthropods such as mites and insects (Wheeler and Blackwell 1984). Mycophagy is not limited to the Pacific Northwest; recently the Tasmanian bettong *(Bettonga gaimardi)* and other Australian mammals have been shown to live almost exclusively on trufflelike fungi (Claridge and May 1994). Preservation of a threatened or endangered species requires information not only on owls or small mammals, but also on the diverse EMF, which form the base of the food web on which those organisms depend.

A growing number of recreational enthusiasts view and collect mushrooms, including the diverse and elegant reproductive structures of EMF. Thousands of amateur and professional mycologists collect fungi and marvel at their complex forms, learn their identification, study their ecology, or simply savor the edible species. Mushroom clubs and societies are scattered across many continents and organize collecting trips and meetings to discuss their findings and share in their mycological experiences. Just as we recognize the enthusiasm of bird watcher, native plant, and other "nature loving" societies, so too must we recognize society's interest in a diverse fungal flora, many of which are fruiting bodies of EMF.

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[1] Color plates are shown on pages 8 and 9.

Various EMF fruiting bodies also are gathered commercially in the wild. Several dozen species of wild fungi are sold in the United States, and most are ectomycorrhizal. The most important EMF commercial species are the chanterelle *(Cantharellus formosus),* matsutake *(Tricholoma magnivelare), and king bolete (Boletus edulis)* (Molina and others 1993) (color plate 2). In the last decade in the Pacific Northwestern United States, supplemental income from EMF mushroom harvesting has grown substantially for unemployed timber industry and other rural workers. In 1992, nearly 11,000 people on a part- or full-time basis contributed over $41.1 million to the region's economy (Schlosser and Blatner 1995). Prices paid to pickers generally range from $2 to $100 per pound (0.45 kg) depending on quality and supply. The volume of EMF fruiting bodies shipped in 1992 from the Pacific Northwestern United States is estimated at nearly 4 million pounds, and harvest is an annual, multimillion dollar industry (Molina and others 1993). Certain EMF fruiting bodies in Europe have commercial value that exceeds the North American EMF varieties. For example, two truffle species, the French black truffle *(Tuber melanosporum)* and Italian white truffle *(Tuber magnatum)* sold for about $400 and $600 per pound, respectively, in European markets in fall 1996 (color plate 3). European truffle production has fallen steadily in France and Italy. In 1892, France produced 1,000 tons compared to current production levels of 10 to 100 tons (Hall and Brown 1989). The collapse of the truffle industry in Europe has only heightened concern regarding harvest and management of EMF from the Pacific Northwest.

There is increasing commercial interest in EMF as medicinals. Fungi have been fundamental to the development of modern antibiotics and other Pharmaceuticals ever since Fleming's discovery of penicillin from *Penicillium chrysogenum.* Secondary metabolites of many macrofungi, including shiitake *Lentinus, Ganoderma lucidum* and *Usnea* spp. have been shown to have antitumor or antibiotic properties (Nisbet and Fox 1991). Pharmaceutical companies are actively screening EMF from the Pacific Northwestern United States for useful metabolites (FEMAT 1994). The thousands of metabolites produced by fungi have many uses besides medicinal ones, and are therefore essential to the emerging biotechnology industry. Fungal metabolites are used in the agrochemical, fine chemical, and pharmaceutical industries, and in industrial services ranging from oil recovery to effluent treatment to bioplastics and biocontrol (Nisbet and Fox 1991). Presently, over 11,500 fungal species are maintained in intentional culture collections, primarily for industrial uses (Nisbet and Fox 1991). Yet, this represents only 0.8 percent of the estimated total number of fungal species (Nisbet and Fox 1991). Clearly, the odds of finding useful products from EMF are extremely high.

Conservation

Much concern about the conservation of EMF diversity has come from Europe where populations have declined over the last three decades (Arnolds 1988, Arnolds 1991). Many factors may be involved including decline in the vitality of forest trees, large-scale conversion of forests to other uses such as agriculture and urban development, and various other anthropogenic factors. In areas where forest have not been cleared, they often have been altered, and the EMF associated with scattered host plants in pastures, lawns, gardens, and suburban areas is not as rich as that of the original undisturbed forest. Reduction in EMF diversity is likely anywhere host vegetation is intensely used and composition simplified

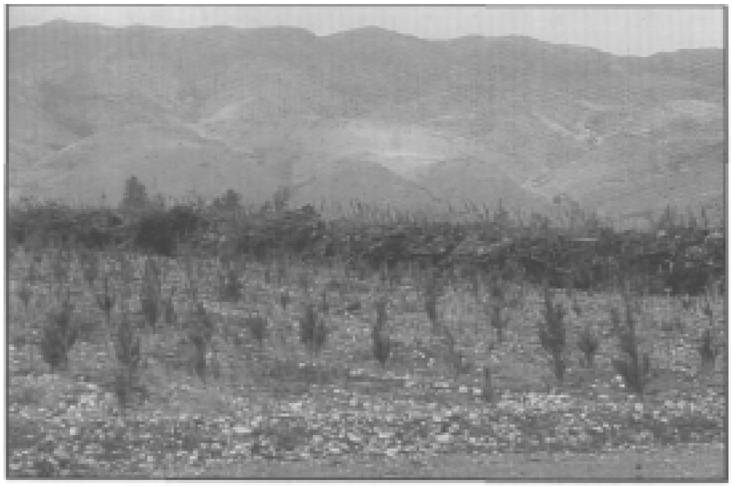


Figure 3—Two-year-old plantation of the introduced species *Pinus radiata* following clearing of native Nothofagus forests.

(Amaranthus and Perry 1987). For example, in New Zealand, clearing Nothofagus forests and planting introduced species *Pinus radiata* D. Don is common and reduces the diversity of indigenous EMF (fig. 3). In Europe, replacment of EMF-rich native deciduous and *Pinus* forests with relatively EMF-poor monocultures of exotic trees such as *Picea abies* L. Karst, and *Pseudotsuga menziesii* also reduces the quality of EMF habitat (Jansen and De Vries 1988). Intensification and industrialization of agriculture also has had several unintended effects on EMF. Of particular importance has been the application of organic dung and artificial fertilizers, which decrease fruiting of EMF (Kuyper 1988).

The most dramatic fungal declines in Europe have been associated with increases in various types of pollution (Arnolds 1988). During this century, most of the European continent has experienced large increases in atmospheric chemical emissions of NOx, NHx SO2, and O3. In addition, other forms of environmental contamination such as the Chernobyl nuclear accident have contaminated vast areas of Europe and parts of Asia for edible consumption of EMF (color plate 4) (Denegri and others 1987). Decline in *Cantharellus cibarius,* has been documented in the Netherlands and correlated to acid rain deposition patterns, but not to levels of mushroom harvesting (Jansen and van Dobben 1987). Acid precipitation, caused by burning high-sulfur coal for power generation not only harms trees directly, but also damages the soil and EMF associated with the trees (Kowalski 1987). Heavy industrial pollution and reductions in fungal diversity also have been documented in Germany and Czechoslovakia (Vosatka and others 1991). Decreases in sporocarp diversity have been correlated with a decrease in mycorrhizal root colonization (Jansen and DeVries 1989). The level of mycorrhizal colonization has decreased significantly in a survey of conservation sites in Great Britain (Woodin and Farmer 1993). Increasing evidence and concern over decline of EMF in Europe has alerted mycologists world-wide of the potential impact on fungal diversity by air pollution.

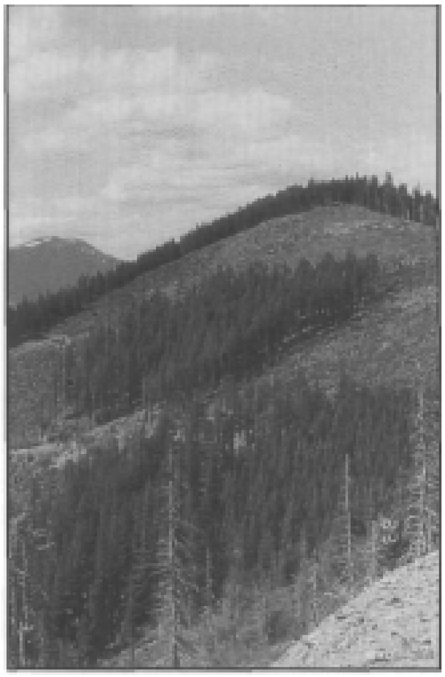


Figure 4—Mature forest fragments in southwest Oregon USA retain high levels of EMF when compared to surrounding young even-aged plantations.

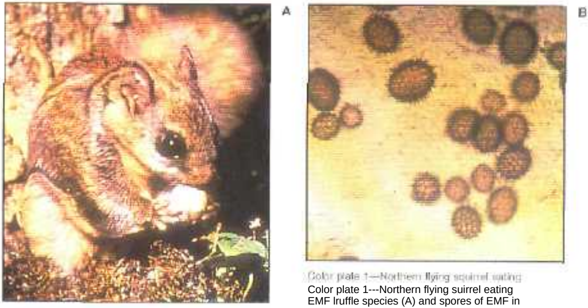
Conservation efforts in the Pacific Northwestern United States require understanding EMF diversity in terms of ecology and distribution. Studies of fungal diversity usually have focused on differences among stand types or ages (e.g., Bills and others 1986, Luoma 1988, Villeneuve and others 1989). Miller (1983) reported EMF diversity in stands of different ages of western white pine *(Pinus monticola* Dougl. ex D. Don), and diversity was substantially higher in 175-year-old stands than in younger ones. Similarly, young plantations had significantly less EMF truffle diversity compared to surrounding mature forest fragments (Amaranthus and others 1994) (fig. 4). Prompt reforestation replaces the hosts, but many years to decades may be needed for the regeneration to again produce diverse EMF fruiting bodies, and it is unknown what percentage of EMF species may eventually recolonize the affected area. More than four times more EMF truffle species were found in mature forest fragments (180 years old) than only in plantations (4 to 27 years old). Truffle diversity tends to be low in young stands until canopy closure, after which diversity increases over time.

In the Pacific Northwestern United States, current levels of EMF diversity are great. Luoma (1988) investigated hypogeous fungal communities along gradients of wet to dry and young to old Douglas-fir stands and reported maximum diversity in the mesic mature (about 175-year-old) stands. Although some species of hypogeous fungi were restricted to the oldest stands, more were restricted to wet or dry habitats. This could be because the moisture gradient was sampled more intensively than the age gradient. In another study, (Luoma and others 1996) 15 Douglas-fir stands of 7 hectares each were sampled for 3 years during spring and fall peak fruiting seasons across the Pistol River basin of southwestern Oregon. Collections include 43 species of ectomycorrhizal truffles from plots totaling 0.75 hectare, and 100 species of ectomycorrhizal mushrooms from plots totaling 4.5 hectares. Over 190 ectomycorrhizal morphotypes were discerned from 189 soil cores totaling a soil surface area of only 0.45 square meter (Eberhardt and others 1996, Luoma and others 1996). These Douglas-fir forests contain among the highest level of ectomycorrhizal diversity ever studied. Over the long term, the high level of ectomycorrhizal diversity observed may equip Douglas-fir to functionally adapt to changing conditions and grow well for decades and centuries.

Fungal propagules including spores and hyphae do not remain viable for long periods. Ectomycorrhizal fungi spores, for example, are lost to predation, germination under unsuitable conditions, and weathering (Miller and others 1994). To maintain EMF diversity over the long term, plants and their fungal symbionts need to migrate in close temporal proximity (Perry and others 1990). For example, moraines are colonized by gymnosperms only after airborne EMF are deposited or after mycophagous mammals defecate viable fungal spores on the new soil (Cazares and Trappe 1994). Pocket gophers burrowing in the ash of Mount St. Helens similarly aided plant colonization (Allen and others 1992).

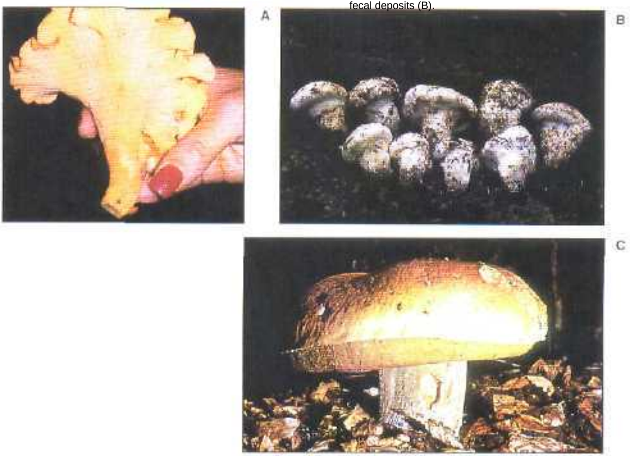
In the United States, the great numbers of EMF (many yet undescribed), wide distribution, and the relative lack of systematic mycologists has made it difficult to identify species that might be declining. Few areas have historical collections or census data to use as a baseline. No examples of EMF species decline have been documented in North America. Vast areas of North America, however, are unexplored mycologically, and accurate species distribution maps are generally unavailable. Until baseline surveys are undertaken across large areas, it will be difficult to know if fungi are endangered or increasing in specific localities.

Habitat conservation for EMF, in which areas of high EMF diversity are maintained according to a conservation or recovery plan, makes more sense than individual species conservation plans. In some cases, small areas may serve as refugia and dispersal of EMF. Amaranthus and others (1994) found 2.4-hectare mature forest fragments contained much higher levels of belowground fruiting EMF compared to surrounding plantations. Luoma (1988) found 47 species of hypogeous EMF in areas of mixed habitats in middle Cascade Range regions of the Pacific Northwestern United States (Andrews LTER), including two restricted to the oldest stands. Such high diversity of EMF in forests of the Pacific Northwest suggests that EMF diversity requires a mix of specific habitats and conditions. Some EMF may thrive in homogenized or intensively managed forests; however, most are likely inadvertently managed against. A diverse mosaic of host species, habitats, and structures promote EMF diversity at the landscape scale. Ectomycorrhizal fungi diversity will reflect the different major forest types, different successional stages within a given forest type, and distinctive communities and microhabitats that encompass a forest landscape. Stand-level silvicultural objectives can emphasize maintaining or developing conditions that favor diversity of EMF. For example, leaving a cover of large trees after regeneration harvests ("green-tree retention") maintains the energy source for certain EMF species and provides for more diverse age-class distribution.



Color plate 1---Northern flying squirrel eating

Color plate 1---Northern flying suirrel eating EMF lruffle species (A) and spores of EMF in fecal deposits (B).



Color Plate 2--*Canthrellus formosus* (A). *Tricholoma magnivelare* (B), *and Bolelus edulis* (C)

Color plate 3---Tuber magnatum (A) and Tuber melanosporum (B) in Italian truffle market.

Color plate 4---Package of Bolelus edulis, Albarelo, Italy, where Cesium 137 levels ranged between 10 and 100 radianuclei concentration per kilogram fresh weight 20 to 40 weeks after the Chemobyl accident. Elevated levels of Cesium reduced the consumption of Bolelus edulis from some parts of Europe for several years.

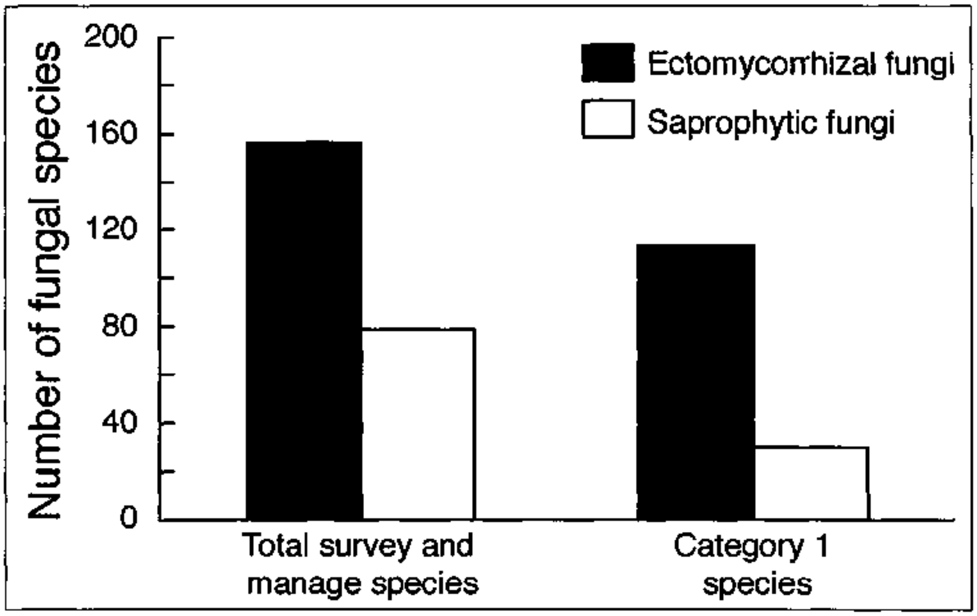


Figure 5—Number of ectomycorrhizal and saprophytic fungal species identified as survey and manage and category 1 survey and manage in the Northwest Forest Plan.

In spite of their importance, discussions of EMF conservation are not widespread. In at least two areas, however, forest planning has recognized the need to conserve fungal diversity. In the Pacific Northwestern United States, the Northwest Forest Plan (1994) provides directives on the incorporation of endangered species, including fungi, in future ecosystem management practices to comply with Federal laws. The Northwest Forest Plan standards and guidelines are focused on management of habitat for late-successional species and call for ecologists and botanists to create and maintain a database of known sites of endangered fungi, and to develop species or area management plans for them. Four components of survey and management were developed: (1) manage known sites, (2) survey before ground-disturbing activities, (3) develop extensive surveys, and (4) develop regional surveys. The highest priority is category 1 species where efforts have already been taken to acquire information on sites, make it available to project planners, and protect these areas from certain ground-disturbing activities. Ectomycorrhizal fungi consist of 70 percent of the fungal species in all four categories and 81 percent of the fungal species in the high-priority category 1 (fig. 5).

In 1985, 28 nations in Europe initiated the European Council for the Conservation of Fungi. The goals of the council included compiling and updating lists of threatened fungi, organizing databases and distribution maps, educating the public, and creating a unified system for documenting the occurrence of fungi on the continent (Hoiland 1994). To date, there are 16 species listed as group A, "...widespread losses, rapidly declining populations, many national extinctions and high-level concern." In the Netherlands, 944 fungal species have been listed in general decline. The most impacted functional group of macrofungi are EMF where nearly half (47 percent) of known species are in decline and 19 percent extinct or threatened with extinction (fig. 6)

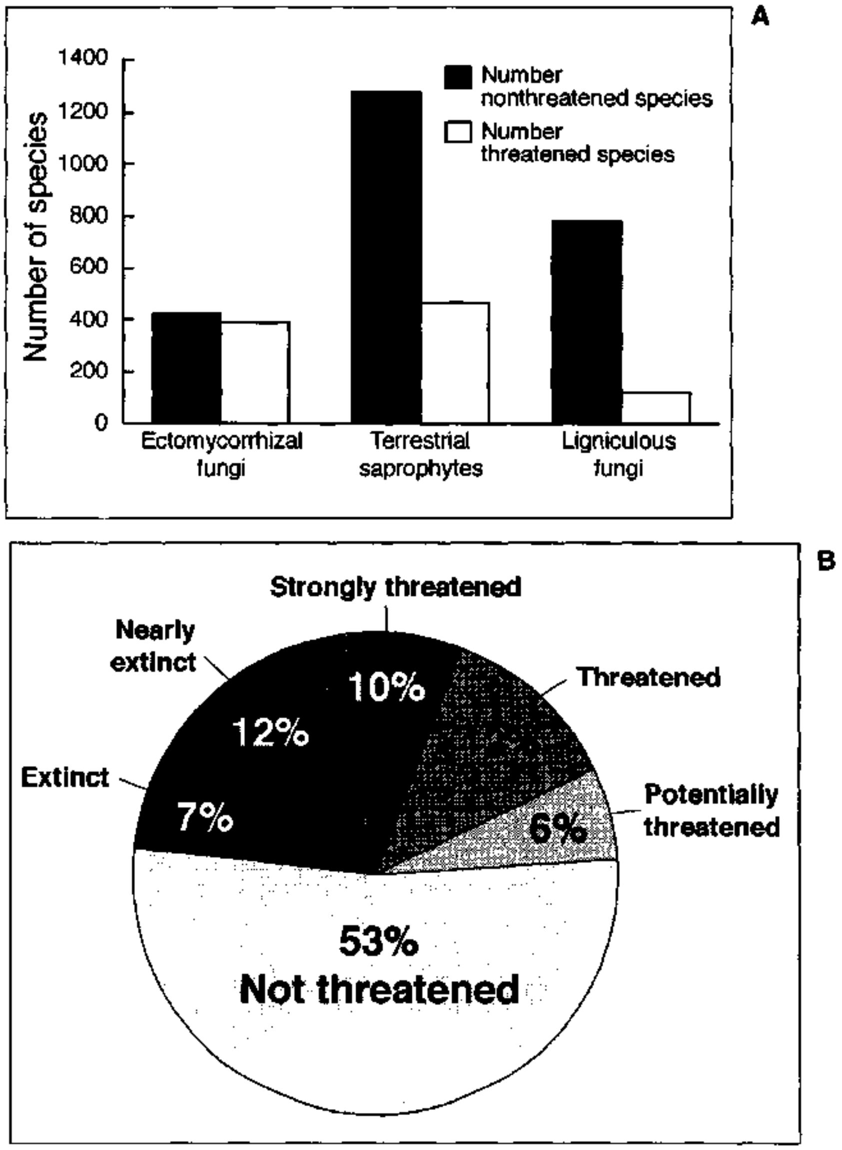


Figure 6—Number of nonthreatened and threatened species (A) of macrofungi in the Netherlands over main functional groups, and (B) percentage of ectomycorrhizal fungi in different categories of threat in the Netherlands (adapted from Arnolds 1989).

(Arnolds 1989). Many factors may be influencing the more prominent decline in EMF compared to saprophytic and ligniculous fungi. Direct damage to trees and loss of vitality with air pollution directly influences carbon allocation to EMF. Wide-spread alteration and loss of forest habitat selects against EMF which in many cases are highly specific to individual hosts and conditions. In addition, ectomycorrhizal fungi seem to have increased sensitivity to the acidification and nitrogen enrichment of soil compared to other macrofungi.

The European and FEMAT lists of threatened, endemic, and endangered fungi serve several goals: informing mycologists of the status and potential threat to EMF diversity, assisting conservation planners in evaluating management strategies or selection of nature reserves and ecosystems, and providing data for EMF species monitoring programs and other integrated monitoring programs. Such efforts are essential for conservation of EMF diversity for future generations. A broader appreciation for the conservation of EMF is needed, however. Ectomycorrhizal fungi are crucial to many ecosystem functions and have great ecological and economic value. Forest resilience, recovery, vigor, and composition are intricately tied to EMF diversity. In the future, EMF may play important roles as medicines and as bioindicators of sustainable ecosystems practices. Ultimately, conservation of EMF will depend on more extensive public perception of the important role of this highly diverse group of organisms.

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Ectomycorrhizal fungi (EMF) consist of about 5,000 species and profoundly affect forest ecosystems by mediating nutrient and water uptake, protecting roots from pathogens and environmental extremes, and maintaining soil structure and forest food webs. Diversity of EMF likely aids forest ecosystem resilience in the face of changing environmental factors such as pollution and global climate change. Concerns over decline of EMF have centered on pollution effects, habitat alteration, and effects of overharvest. Strategies for the conservation of EMF include decreasing levels of environmental pollutants and retaining diverse assemblages of native host species, habitats, and structures across a landscape.

Keywords: Conservation, diversity, ectomycorrhizal fungi, forest productivity, forest ecosystem, mushrooms, pollution, truffles.

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