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Habitat management to conserve fungi: a literature review

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Habitat management to conserve fungi: a literature review

1. Summary

Fungi are of fundamental ecological importance, especially in relation to decomposition and nutrient dynamics. Their biochemical properties have many potential benefits for man. There is ample justification for conserving fungi.

Woodland management to conserve decomposer fungi should aim to provide an abundance of elderly trees with rotting branches intact, fallen dead wood and leaf litter in a variety of situations but particularly in damp sheltered conditions. However, mycorrhizal fungi favour areas where there are not accumulations of leaf litter on the soil surface. Some lightly disturbed areas such as footpaths, unsurfaced tracks and lightly grazed woodland support particular types of rare fungi. Ancient woodland is likely to be more species-rich than secondary plantations. Heavy trampling and nutrient enrichment are damaging to fungi. Wood chips may benefit a few species at the expense of the majority.

The richest assemblages of grassland fungi are found where there is a long history of grazing, though in some circumstances mowing can be a viable alternative except for those fungi associated with herbivore dung. Neglect which causes a mat of dead grass to accumulate is best avoided. Poaching of the turf and nutrient enrichment, particularly the use of inorganic fertilisers, are also damaging.

Little is published about conservation of fungi in other habitats but the same principles of maintaining long-established management and avoiding nutrient enrichment apply to fens, dunes and heaths. The burning of vegetation, whether as a heathland management method or as a woodland bonfire, creates habitat for some rare fungi.

Over-zealous collecting of fungi, especially in woods and using indiscriminate collecting methods such as raking, can be damaging to fungi and to the invertebrates dependent on them.

Fungi are rarely threats to traditional broad-leaved forestry. Fungal epidemics in forests are usually caused by alien fungi to which the trees have no natural resistance, or by trees being grown in sub-optimal conditions which cause them stress and reduce their natural resistance.

Rheoli cynefinoedd er mwyn gwarchod ffyngoedd: adolygiad llenyddol

1. Crynodeb

Mae ffyngoedd o bwysigrwydd ecolegol sylfaenol, yn enwedig mewn perthynas â madredd a dynameg maetholion. Efallai y gall eu nodweddion biocemegol ddod â nifer o fuddion i ddyn. Ceir digon o gyfiawnhad dros gefnogi'r arfer o warchod ffyngoedd.

Dylai dulliau o reoli coetiroedd sy'n ceisio gwarchod ffyngoedd sy'n madru pethau anelu at gynnig digonedd o goed ysgaw gyda changhennau pydredig cyfan, pren marw wedi disgyn, gweddillion dail mewn mannau gwahanol, ond yn arbennig mewn mannau cysgodol, llaith. Fodd bynnag, mae ffyngoedd mycorhisol yn ffafrio mannau lle na cheir lawer o weddillion dail ar wyneb y pridd. Mae rhai mannau y terfir rhywfaint arnynt, fel llwybrau troed, llwybrau heb wyneb, a choetiroedd sy'n cael eu pori'n ysgafn, yn cynnal rhai mathau o ffyngoedd prin. Yn ôl pob tebyg, fe fydd coetiroedd sy'n cynnwys hen goed yn fwy toreithiog o rywogaethau na phlanhigfeydd eilaidd. Gall sathru llawer ar y ddaear a gormod o faetholion niweidio ffyngoedd. Gall sglodion coed fod o fudd i ychydig o rywogaethau ar draul y mwyafrif.

Ceir y casgliadau mwyaf toreithiog o ffyngoedd glaswelltir lle ceir traddodiad maith o bori, er y gall lladd gwair fod yn ddewis arall posibl mewn rhai amgylchiadau, heblaw ar gyfer y ffyngoedd hynny a gysylltir â thail llysysorion. Gwell osgoi esgeulustod sy'n peri i garped o laswellt marw ffurfio. Hefyd, mae gorsathru a gormod o faetholion, yn enwedig defnyddio gwrtaith anorganig, yn niweidiol.

Ychydig sydd wedi ei gyhoeddi ynglyn â gwarchod ffyngoedd mewn cynefinoedd eraill, ond mae'r un egwyddorion, sef cael dulliau rheoli sydd wedi hen sefydlu ac osgoi cyfoethogi'r tir â maetholion, yn berthnasol i ffeniau, twyni a gweunydd. Gall llosgi llystyfiant, boed hynny fel dull o reoli gweundir neu fel coelcerth mewn coetir, greu cynefinoedd i rai ffyngoedd prin.

Fe all casglu gormod o ffyngoedd, yn enwedig mewn coedwigoedd, neu gasglu ffyngoedd yn ddiwahân trwy eu cribinio, fod yn niweidiol i ffyngoedd ac i greaduriaid di-asgwrn-cefn sy'n ddibynnol arnynt.

Pur anaml y bydd ffyngoedd yn bygwth coedwigoedd collddail traddodiadol. Fel arfer, ffyngoedd estron na all y coed ymwrthod â nhw, neu goed a dyfir mewn amgylchiadau heb fod yn ddelfrydol sy'n lleihau eu hymwrthedd naturiol, sydd wrth wraidd y gormodedd o ffyngoedd a geir mewn fforestydd.

2. Why fungi are important

As time goes on, it becomes clearer how vital wild fungi are in the world. Not so many years ago, they were widely seen in Britain as slightly sinister plants that killed trees and were mostly poisonous. Now, they are no longer classified as part of the plant kingdom but as a kingdom of organisms in their own right (Whittaker 1969; Carlile, Watkinson & Gooday 2001); and it is realised that fungi can contribute to soil fertility (Isaac 1998b; Merryweather 2001) and weed control (Kluth, Kruess & Tscharntke 2003), are sources of drugs and other useful chemicals (Höller *et al*. 2000; Raghukumar 2000), may be luxury food items, and form a large proportion of the world's biodiversity. It is true a few species can kill a mature tree, but fungal decay is often beneficial (see section 5 below).

It has been discovered that most plant roots can form links with fungi, to the benefit of both plant and fungus (Allen 1996). While toadstools are the parts of fungi most often seen, these are only analogous to the fungus fruit, and most of a fungus consists of a network of fine strands (hyphae) penetrating the topsoil, the whole network of hyphae being called the mycelium. The association between a fungus and a plant root is called a mycorrhiza. The fungal mycelium collects water and dissolved minerals more efficiently from a much wider area than the plant's roots could cover, some of these nutrients being transferred to the plant; and the fungus gains sugars produced by the plant's leaves. Plants that fail to establish a mycorrhiza usually grow weakly if they grow at all. As well as improving the plant's nutrition, mycorrhizae may protect the plant against diseases and toxic metals (Lonsdale & Gibbs 1996; Colpaert & Van Tichelen 1996). Most remarkable of all, mycorrhizae link different trees, even different species of tree, and they transfer nutrients between trees from those with an excess to those with a shortage. By these various mechanisms, mycorrhizae help maintain tree diversity in natural woodlands (Perry, Bell & Amaranthus 1992) and the species of tree present in natural woodland may be partly determined by the types of mycorrhizae in the soil (Allen *et al*. 1995). This partly explains why recent secondary woodland is so obviously different from ancient woodland (Merryweather 2001). There is evidence that mycorrhizae are equally influential in grasslands and can even determine the growth form of a plant (van der Heijden *et al*. 1998; Streitwolf-Engel *et al*. 1997). The influence of mycorrhizae can also show higher up the food-web: caterpillars of the common blue butterfly fail to mature when feeding on plants that have no mycorrhiza (Goverde *et al*. 2000).

Fungi also have a vital role in decomposition of waste. Along with bacteria, worms, woodlice and other invertebrates, fungi break down wood, leaves and dung and help to release the nutrients back into the soil. Again most of the fungus comprises a network of hyphae, unseen within the wood or other substrate. Few organisms other than fungi have the enzymes able to decompose such tough materials as lignin and keratin (Dix & Webster 1995).

Fungi provide food and living space for hundreds of species of animal. Many toadstools will be found that have been partly eaten by mammals and molluscs. These browsers may benefit the fungus by dispersing the fungal spores in their droppings. There are also many hundreds of insect species that are completely dependent on fungi, breeding in toadstools or bracket fungi. Some, especially beetles using bracket fungi, are restricted to a particular fungus species (Komonen 2001). Many of the invertebrates which are classed as decomposers, such as woodlice and freshwater shrimps, get their nourishment not directly from dead leaves but from the bacteria and fungi growing on the dead leaves (Moss 1980). The fungal hyphae must convert the indigestible leaf chemicals into more readily assimilated material before the invertebrates can use it.

The strange chemistry of fungi is not restricted to decomposition enzymes. Antibiotics are produced from fungi and there is huge scope for more discoveries of valuable pharmaceuticals produced by fungi (Höller *et al*. 2000). Any loss of fungal diversity diminishes these possibilities.

The British have traditionally been reluctant to collect wild fungi for food, other than the field mushroom. The rise of foreign restaurants and food programmes on TV is relaxing our attitude to eating fungi of other types. While this is a benefit fungi can offer, it cannot be unreservedly promoted in a text dealing with conservation - see section 9 below.

Finally, fungi appeal to the senses by their beauty and strangeness. They are often delicate and short-lived, sudden in appearance above ground. They can be colourful. A few are smelly too.

3. Limitations of the advice

The following notes on habitat management are intended as guidance to nature reserve wardens, country park rangers, conservation-minded landowners and others who have no specialist knowledge of fungi but who wish to ensure that fungal diversity is maintained on their land. Few fungi are mentioned by name because a name is only useful if the fungus can be recognised. Accurate naming of most fungi is a job for a specialist (which the author is not) and anyone who has enough knowledge to identify fungi correctly probably has no need of these notes.

Most species of fungi are microscopic. While the ecological importance of these microfungi is not in question, active conservation of these and other microbes has barely begun. Consequently this document is mostly concerned with what most people recognise as fungi: the toadstools, brackets, puffballs etc. that are known as macrofungi. Nevertheless, Cannon, Mibey & Siboe (2001) described an approach to conservation of microfungi that has largely been adopted in Britain inadvertently: to consider rare plants as likely hosts of rare, host-specific microfungi and to target conservation measures at the host, recognising the need for conservation of populations throughout the plant's range since not all host populations will support the full range of microfungi. Helfer (1993) discussed the conservation of rust fungi and suggested a possible dilemma of whether to conserve a rare fungus which could harm its rare host plant.

In this and in most writings on fungus conservation, a major assumption is made which is far from proven. It is taken for granted that production of abundant fruiting bodies indicates a healthy fungus growing in its preferred habitat. Whilst a complete absence of fruiting bodies over many years is a good indicator that a fungus has died out, it may be wrong to take abundance of fruiting bodies as an indicator if mycelium health. There are numerous examples in other groups of organism (e.g. duckweed, water fleas) where the resting or dispersal stage of the life cycle is stimulated by environmental stress and does not indicate the organism is in ideal conditions. Indeed, Hawker (1954) concluded that truffles, the fruit bodies of subterranean fungi mycorrhizal on trees, were produced in low numbers while the fungus was well-nourished but increased greatly the year after the tree was felled when the mycelium began to starve.

4. Recording fungi

It is hoped that the principles in these guidelines will be useful even on sites where the fungi have never been surveyed. Nevertheless, detailed records of fungi are useful to conservation and if a local mycology study group is willing to survey your site, please encourage them to do so. They may find fungus-rich features peculiar to your site which are not covered by this article. If they find rare species and can identify their ecological requirements, this will allow the site management to be fine-tuned. And it is only through the recording of fungi on a large number of sites covering all habitats that a national picture is gradually built up of which species are common or rare and which species are in decline and need targeted conservation effort. To find out if there is a fungus study group in your area, look on the Association of British Fungus Groups' website at http://www.abfg.org. But bear in mind that a single visit by mycologists will not produce a comprehensive species list for a site. A 21-year study of a patch of mixed forest in Switzerland recorded 408 species, of which 150 were found in only one year. Only eight species were found in all years. The number of new species added each year did not diminish over the course of the study, though the number of species found in a year varied from 18 in 1989 to 194 only three years later (Straatsma, Ayer & Egli 2001). A similar study in Abernethy Forest, Scotland, recorded

502 species over 21 years, again with no signs of the species list being close to complete (Tofts & Orton 1998). These studies demonstrate that only long-term surveys can approach a comprehensive inventory for a site; and that it is unwise to wait for a full inventory before deciding how to manage a site.

5. Trees and woodlands

As the decay of a piece of wood progresses, it supports a succession of fungi. Fenwick (1996) found 29 species of fungus (including microfungi) on beech logs in the first four years after the tree fell, even though the wood still showed little sign of rot. Speight (1989) estimated a completely dead tree takes 25 years to decompose, even longer in cold climates. In America, large conifer logs have been estimated to take as long as 500 years (Rayner & Boddy 1988). Heilmann-Clausen & Christensen (2003) studied the succession of fungi on beech logs in Denmark and found the sequence of fungi depended on which species initiated the decay (the primary decayer). There were three common primary decayers in their beech forest, but most rare fungi developed on logs where the primary decayer had not been one of these three common species. They also found forked logs were more species-rich than straight logs, probably because of their greater surface area. It is better to leave a few branches to go through the full decay process than to leave many branches temporarily then remove them for firewood. Heilmann-Clausen & Christensen (2003) found the most species-rich beech logs were well away from the forest edge and had extensive contact with the soil, both factors which helped to keep the logs moist. But they also found that logs in saturated or very dry conditions, though less species-rich, sometimes supported specialised fungi adapted to microclimatic stress. A "medium" amount of dead wood in a British woodland would be 20-40 cubic metres per hectare, with 10-50 standing dead trees per hectare (Kirby *et al*. 1998). Less than this would be typical of a tightly managed woodland where, for conservation purposes, less removal of wood would be desirable. Butler, Currie & Kirby (2002) suggested ways of judging how valuable a particular woodland is likely to be for species associated with dead wood (including insects, bats and birds, not just fungi). As well as definite records of these species, their criteria included the current amount of decaying wood, whether there has been continuity of this habitat, the presence of veteran trees, the size of the woodland, and the surrounding landscape.

The more wood which can be left to rot, the better, since each piece will differ. Every combination of sun, damp, diameter, species of tree and time of fall will offer opportunities for different species of fungus. Logs are best left scattered on the woodland floor rather than built into log piles where the upper layers may be too dry for much of the year. Whether the branch has already begun to decay whilst on the tree and whether it has been attacked by wood-boring beetles will also affect the fungi it supports. Heilmann-Clausen & Christensen (2003) stressed the importance of a continual supply of dead logs into the ecosystem, in order that the rapid turnover of species during the decay process does not lead to local extinctions. In Swedish spruce forests, Bader, Jansson & Jonsson (1995) found evidence of poor fungal dispersal and colonisation between spruce woods even though colonisation of logs within the same wood was efficient. Absences of certain fungi correlated with there having been felling up to 100 years previously. They suggested the dead logs present at the time of the survey may have been of too small size for some fungi, thus these species may return as the trees age and larger dead wood becomes available, but it appeared that local extinctions are not easily reversed.

The contrary findings of Nordén & Pallto (2001), that younger hazel stands supported more species of fungus and hazel stands with more dead wood had fewer species of fungus, need further investigation. The authors suggested competitive exclusion might reduce the number of fungi as stands age. Alternatively their results could be artefacts of inadequate sampling (eight woods in seven days in November 1996). Also the ages of the woods were inferred from the size of the largest hazel stool although in five sites these were of similar size, and all the hazel woods were thought to have developed on abandoned pasture, so it is likely none would have qualified as ancient woodland in the British sense.

Many fungi decompose only wood from certain tree species. Others are less particular. Different parts of the same tree can vary in their susceptibility to fungal decomposition. This variation is largely controlled by the types and levels of phenolic compounds within the wood, which inhibit fungal growth (Dix & Webster 1995).

Better than fallen branches, ancient living trees may be the most valuable fungus habitat in a wood. Ancient trees are valuable because they are the hardest to replace (a 70 year old tree can be replaced in a human lifetime, but a 300 year old tree cannot) and they may act as 'time capsules', carrying fungi that colonised in previous centuries and which in current conditions rarely find new habitat. Such trees are more typical of grazed parkland than of closed-canopy woodland.

Ancient trees are usually hollow and contain rotten heartwood within a "skin" of living wood. The fungi which cause heart-rot are more of a benefit to the tree than a threat. An aged tree which had not rotted at all would become too heavy to support itself and would be very vulnerable to wind throw. A hollow tree is much lighter and more flexible, and though its hollow branches are weaker, the reduction in weight more than compensates. New growth around a cavity tends to be of stronger than average wood and tree rings in this zone are thicker than normal which tends to compensate for the loss of strength caused by heart rot (Mattheck & Bethge 1998). In the famous October 1987 storm across southern England, very few ancient trees were blown over, but thousands of immature trees were. As well as lightening a tree, heart-rot also allows a tree to re-use the nutrients stored in its heartwood by growing aerial roots inside its hollow trunk which penetrate its own decaying centre (Read 2000).

Ancient trees are often pollards. Pollarding promotes heart-rot, can reduce the strain on the trunk, and may rejuvenate the tree. However, repollarding ancient trees which have not been pollarded for many years has a much lower success rate than continuing an unbroken cycle of pollarding. Read (2000) gave detailed advice on how to decide if repollarding is for the best and how to go about it. Creating new pollards from young, vigorous standard trees is far less risky to the tree and is vital if the rare habitat of ancient trees is to be conserved in perpetuity. Once begun, pollards need repollarding at regular intervals (probably no more than 20 years) otherwise there will be a large crown of heavy solid branches on a hollow trunk, a combination very susceptible to collapse in high winds.

As described above, tree roots are host to mycorrhizal fungi, some of which are faithful to particular species of tree. Therefore, felling and replanting programmes should aim to preserve the species-composition of the wood. Natural regeneration is preferable to replanting, since soil brought in with saplings can introduce species of fungus which are not native to the wood (e.g. Watling 2001), and these could out-compete and eliminate the indigenous species. If timber extraction is unavoidable, selective logging is less disruptive to mycorrhizae than is clear-felling, and colonisation of young trees by mycorrhizae is likely to be easier if mature trees are close by to act as sources of hyphae (Keizer 1993). Such considerations of species continuity apply mainly to native ancient woodland, and are less important in recent secondary woodland where fungus communities are less likely to be rare and sensitive to disruption. Indeed, there is a natural succession of mycorrhizal fungi as plantations age (Shaw, Kibby & Mayes 2003) so disappearance of some species is inevitable in such situations.

Leaf litter is an important substrate for fungi which are decomposers, but leaf litter requires only tolerance and neglect, not positive management. Pine needles support a very different assemblage of fungi from those on the litter from broad-leaved trees (Hudson 1968). Eradication of invasive non-native trees and shrubs (e.g. rhododendron, laurel) may be necessary to prevent a build-up of tough, decomposition-resistant leaf litter. Fungal hyphae develop best in undisturbed soil and leaf litter, so severe churning of the soil, such as by timber extraction machinery, should be kept to a minimum.

Heavy grazing pressure in woods, if it causes severe poaching, is also very damaging. However, some scarce tooth-fungi are most commonly found on bare ground, either maintained by heavy grazing as in some deer-grazed Scottish pine woods, or along the edges of tracks or ditches. Thus long-established woodland tracks and rides need not be over-protected – the continued occurrence of the tooth-fungi may depend on the tracks continuing to be kept open by regular use – but the tracks should not be widened, resurfaced or misused to the point where erosion occurs (Marren & Dickson 2000; Marren 2000). Truffles are another group of fungi which are often most abundant along the edges of forest paths and in other patches of slightly disturbed forest soil, thus safeguarding their habitat requires a balance between maintaining enough disturbance to be beneficial while avoiding erosion. Accumulating leaf litter on the soil surface is thought to be detrimental to truffles and well-aerated soil may be what they require (Hawker 1954; Lawrynowicz 2001). Morels, a type of edible mushroom, are sometimes suddenly abundant in areas of woodland that have been disturbed, such as by clear-felling (Weber, Pilz & Carter, 1996) though such a phenomenon raises the question of whether a sudden abundance of fungal fruiting bodies after habitat disturbance is an indication of a healthy fungus or a do-or-die concentration on spore production by a fungus which finds its environment has become unsuitable.

Mycorrhizal fungi are often suppressed by leaf litter (Baar & Kuyper 1993) and its removal is recommended in some circumstances. Trees are most dependent on their mycorrhizae in nutrient-poor soils, and it is these areas where losses of mycorrhizal species are most severe when nitrogen pollution occurs. Jaenike (1991) suggested trees were dispensing with their energy-sapping fungal partners when nitrogen became plentiful. In pine plantations on former heathland in the Netherlands, air pollution has caused acidification and nitrogen-enrichment of the soil. There has been a build-up of pine needle litter that supports very few fungi, with mycorrhizal species almost extinct (De Vries *et al*. 1995). After the litter layer and humus were removed by the researchers, there was an increase in fungus species-richness within two years and the re-appearance of some species typical of the early years of a pine plantation. Very few species typical of aged pine plantations were found: the effect of litter removal was to return the fungus succession to an early stage rather than divert it to what would be expected in an old plantation if air pollution had not happened. Whilst the above research dealt only with pine plantations, Keizer (1993) noted the richness of mycorrhizal fungi on grassy road verges under oak and beech trees and considered the lack of leaf litter (it blows away) to be an important factor here too. Further trials are needed before stripping of leaf litter can be confidently recommended as a conservation measure. It may be as damaging to the decomposers as it is beneficial to the mycorrhizae.

Build-up of leaf litter and other sources of eutrophication (e.g. dogs, agricultural fertilisers) were highlighted by Marren (2000) as further threats to tooth fungi. Nitrogen enrichment can variously increase or decrease decay rates of woody and leaf litter, as it can stimulate cellulose-digesting enzymes but inhibit the production of lignin-degrading enzymes. This can cause major shifts in the fungal community and affect nutrient cycling within the soil (Lodge 2001).

In modern forestry, brashings are likely to be fed into a chipper rather than left to rot where they fall. Prunings from urban landscaping schemes are also usually chipped. The resulting woody compost is a new man-made habitat with no close equivalent in nature, and has proved very suitable for certain species of fungus (Shaw & Kibby 2001). It has a large surface area : volume ratio, is easily penetrated by hyphae, below the surface it remains damp, and the centre of large piles can be much warmer than air temperature. Several species of toadstool have recently been found for the first time in Britain growing on woodchips used as a mulch in ornamental sites such as roundabouts and parks. These species new to Britain are mainly from abroad rather than being undiscovered native species, and as aliens they are of interest but not of great conservation importance. It is not known how they colonised the woodchips, but local authorities often store woodchip mountains at depots where chippings from many sources are mixed and composted, so fungi brought into the country with ornamental shrubs could spread throughout large volumes of chippings and then be widely distributed. In view of the risk of introducing alien species, it is recommended that any woodchips used in native woodland should not be imported from other sites. The use of woodchips made from on-site thinnings may benefit some native fungi so could be a positive conservation tool. However, even here there are drawbacks. If a few species of fungus become unusually abundant on the woodchips, it may be at the expense of the species-richness as a whole and many species could be eliminated from the area under woodchips; and a layer of woodchips tends to eradicate the green plants too - indeed, that is the main reason for using woodchips in gardens.

Woodchips on conservation sites should be used cautiously and restricted to very limited areas. The value of conserving alien species of fungus, particularly those species dependent on alien species of tree, is currently under discussion (Evans 2003). Whatever consensus emerges regarding conservation of those aliens already present, introducing more alien species involves a risk to our native fungi and should be avoided.

6. Grasslands

As in woodland, grassland fungi are a mix of decomposers and mycorrhizae though it is not always known which macrofungi are in which category and some species may be in both. Most mycorrhizal species in grassland are microfungi. Fungus-rich grasslands are not always rich in flowering plants (Rotheroe 2001), thus there is the risk that they will be overlooked and their value not recognised in habitat surveys. Bardgett (1996) reported that in upland grassland, live mycelium was most abundant in heavily grazed, free-draining, base-rich soil and that cessation of grazing led to a build up of dead mycelium and acidification of the soil.

There is a suite of grassland fungi, the waxcaps, earth-tongues and fairy clubs, which appear to be highly sensitive to inorganic fertilisers (Arnolds 1989; Marren 1998). They are currently receiving much attention from conservationists because the widespread 'agricultural improvement' of pasture (involving inorganic fertilisers, re-seeding with productive grass strains and eradication of broad-leaved weeds using herbicides) has left some of these species, and sites rich in these species, very rare in Britain. Waxcaps are most abundant and diverse in permanently grazed or frequently mown, free-draining, mesotrophic grassland, with a few species confined to more alkaline or acidic sites. Waxcaps and their allies tend to be sparse in waterlogged areas and in the driest free-draining grassland. However, Griffith, Easton & Jones (2002) reviewed waxcap ecology and found several of the best waxcap grasslands in Britain have had some agricultural improvement in the past and some were ploughed during or just after the Second World War. It appears that inorganic fertiliser causes the immediate cessation of fruit body production, but that waxcap mycelium is more tolerant and survives a degree of improvement, remaining undetected until fruiting restarts a few decades later. Liming may have a similar effect, as Griffith, Easton & Jones reported the near absence of waxcap fruiting bodies on plots treated annually with lime for the previous three years, whilst a different experiment produced an abundance of waxcaps 3-5 years after a single application of lime. Griffith, Easton & Jones also tried to study waxcap nutrition and their results of isotope analysis suggested waxcap mycelia may be breaking down the more difficult to digest fraction of humus deep in the soil horizon. This would account for the restriction of waxcaps to long-established swards. There is thus hope that with the correct management, consisting of permanent grazing and no further applications of inorganic fertiliser or lime, even species-poor pastures could become waxcap-rich grasslands within a few decades. Severe poaching of pasture is to be avoided as it fragments and destroys the fungal hyphae, but it is better to risk slight poaching than to relax grazing and allow a tall sward to develop. Sheep are recommended for grazing waxcap grasslands, with 12 of the top 15 Welsh sites being sheep-grazed (Rotheroe 2001; Evans & Holden 2003) but other livestock can give good results.

Opinions differ over whether the waxcap assemblage can be sustained by hay-meadow management. There are examples of waxcap-rich permanently grazed grasslands which lost their waxcaps within a few years when a switch to hay-making occurred (R.G. Woods pers. comm.), though it is not known whether the mycelium survives undetected. On the other hand, a major survey of Somerset waxcap grasslands (Thompson 2000) found that management for hay did not necessarily impoverish the waxcap assemblage. Two waxcap-rich fields were found that were managed only for hay with not even aftermath grazing. (Nauta & Jalink (2001) also discussed mowing and grazing, on dunes – see section 7 below).

Whilst the typical hay mowing regimes, one or two cuts per year, are not necessarily good for waxcaps, it is proven that more frequent mowing can maintain a waxcap assemblage. In old churchyards, waxcaps can be diverse in areas that are mown frequently and the clippings removed. These tend to be the parts of the churchyards currently in use for burials. Waxcaps don't thrive in the areas with older graves where mowing is often neglected (R.G. Woods pers. comm.). Removing the clippings to prevent a build-up of partly decayed leaf litter seems to be a very important aspect of managing for waxcaps by mowing.

Waxcaps, earth tongues and fairy clubs can be abundant and diverse in lawns. Long (2002) studied several such lawns in Leicestershire and suggested several contributory factors. All the rich lawns were old, from 70 years to 180 years in the best example. He considered they got richer in fungi as time passed, rather than being relics, on the grounds that one lawn had steadily increased in grassland fungal diversity over the last 19 years as it approached 100 years of age. The presence of nearby trees to act as hosts for mycorrhizal species probably also contributes to fungal richness. Also considered important was the lack of modern lawn management: no fertilisers, weedkillers or scarification to get rid of moss. Turf with waxcaps is often very mossy, and Arnolds (1989) found a sward which lost its waxcaps also lost its moss. This does not suggest mosses and waxcaps are interdependent, and mossy turf certainly does not indicate a site rich in waxcaps. However, it may be that on a good waxcap site, monitoring of moss abundance would be an indirect method of monitoring how management is suiting the waxcaps.

Some fungi will rapidly colonise new grassland but it is likely to be species-poor for many years, even with sympathetic management (Brand 2002). The more nutrient-enriched the soil is, the longer it is likely to take for a diverse assemblage of grassland fungi to appear.

Herbivore dung is a characteristic fungal habitat in pasture. The majority of these "coprophilous" fungi are microscopic but there are also numerous macrofungi dependent on dung (Richardson & Watling 1997). The species found will depend to some extent on the habitat in which the dung falls (Nyberg & Persson 2002) and on the type of grazing animal. Fungal spores may need to pass through an animal's gut in order to break dormancy (Isaac 1998a) and the chemical composition of the dung depends greatly on the digestive system of the grazer. Thus there are big differences in the fungal assemblage found on dung of horses compared to ruminants, while rabbit and grouse droppings also have characteristic fungi (Ing 1989; Richardson 1998, 2003). Ideally, therefore, pasture management should maintain grazing by the same type of livestock as has been used in the past. Richardson (2001) found there were more species of fungus (mostly microfungi) in dung samples collected from October to March than in samples collected between April and September, but very few species were found only in one period so time of grazing seems to be of little importance in conserving the dung fungi. Obviously, switching to a mowing regime would be disastrous for fungi dependent on dung.

It is probable that the use of veterinary drugs and food supplements eliminates some dung fungi. One of the rarest British species, the nail fungus *Poronia punctata*, used to be widespread in Britain in the era of horse-drawn transport but is now found mainly in the New Forest and Dorset heathlands with only occasional records from elsewhere. A suggested reason for its decline is that it requires dung produced by horses and ponies grazing solely on natural, coarse vegetation free from fertilisers (Dickson 1997). Most horses these days feed on improved pasture and are given food supplements, anti-helminthic drugs, antibiotics, etc., which make their droppings unsuitable for the nail fungus (Webster 1999).

7. Other major habitats

Compared to woodlands and grasslands, there seems to be little published about management of other major habitats for the benefit of fungi. Keizer (1993) commented on the lack of knowledge about the fungi of fens and suggested that the fungi of peat bogs, sand dunes and heaths need no special management as they are suited by the regimes used to conserve other aspects of their wildlife. This may be partly true, but it implies there are no conflicts between the management requirements of birds, reptiles, invertebrates and flowering plants. Perhaps if all these high-profile groups are being catered for, management will be so diverse that fungi will be bound to find their niche somewhere.

Keizer (1993) recommended sod-cutting and grazing of heathland, especially where remedial management is required on heath that has become dominated by purple moor-grass *Molinia*. There are also instances of rare fungi appearing on heathland after a fire (Yao, Spooner & Legon 1998; Allison 2001; Anderson 2001b). During the burning of heather, the temperature above ground can exceed 800°C for about a minute, but 2 cm below the surface 45°C was found to be the maximum and there was no detectable change below 4 cm (Webb 1986). Provided the fire passes quickly and does not remove the humus layer, fungal mycelium a few centimetres below the soil surface is thus well placed to survive and to take advantage of the flush of nutrients that fire releases. However, managing heath by burning can be very damaging to other forms of wildlife and can promote the spread of bracken so needs careful consideration. No more than a small proportion of a heath should be burned in any one year, and some refuge areas should be established which are never burned. Symes & Day (2003) discussed the use of fire for heathland management, though not in relation to fungi.

Rotheroe (1992, 1993, 1995) noted the importance of grazing or mowing to maintain a rich fungal assemblage on sand dunes. He also commented that dune slacks within plantations of trees produced fruiting bodies at times when none could be found in slacks outside the plantations, and suggested that shelter given by the plantation prevented desiccation by the wind and thus benefited dune fungi, not to be confused with an arguable enrichment of the fungus community by species associated with the trees (Rotheroe 1992). Nauta & Jalink (2001) also discussed the relative merits of mowing and grazing on dune grassland, concluding that each produced a valuable fungal habitat but with different suites of species. They found grazing permitted development of scrub and small woods, and so supported more mycorrhizal fungi, plus of course coprophilous species. Both grazing and mowing produced waxcap-rich grassland after about a decade, most species-rich in the mown area.

Fungi may be abundant in aquatic habitats and their assemblages can be species-rich, especially in fresh waters. They play as important a role in nutrient cycling as their terrestrial counterparts. However, the aquatic species are invariably microfungi and are too poorly known to be considered here. There is evidence that, not surprisingly, different substrates support different species, with the fungal assemblage on leaf litter differing from that on wood (Gulis 2001). Dix & Webster (1995) reviewed the fungi of freshwater and marine habitats.

8. Microhabitats

There are some niches occupied by fungi which could easily be lost from a site because their value is not realised. Areas completely lacking in green vegetation may support cup fungi whose hyphae are able to scavenge nutrients from such unpromising substrates as crushed slate or abandoned cement powder. They often appear in newly laid gravel car parks or on bare hard soil along paths. The value of such bare ground should be recognised and the temptation to try to revegetate such areas by seeding them or diverting the path should be avoided.

It is well known that bonfire sites develop a succession of mosses over the years. There is also a suite of specialist fungi found on the ash, scorched soil or charred wood (Ramsbottom 1953). For some of these species, the attraction of a bonfire site is the heat-sterilised soil in which there are no competitors (Dix & Webster 1995). For others, the high nutrient level provided by the ash is the critical factor. To conserve these interesting species, it is important that the same bonfire site is not used too regularly. Petersen (1970), studying fungus fruiting bodies on Danish bonfire sites in woodland, found some species appeared about 6 weeks after a bonfire while others took over 2 years to make an appearance and continued to fruit until at least 4 years after the fire, by which time the bonfire site was almost indistinguishable from the surrounding vegetation. Bonfire sites in conifer woodland developed different fungi to bonfire sites in broad-leaved woodland. To conserve bonfire fungi, therefore, a gap of 3 years between fires on the same site should be enough to allow the characteristic fungi to develop and disperse their spores, though a longer gap would be better still. A balance is needed between having too much woodland floor burned and not providing continuity of the bonfire habitat. If at least five bonfire sites are established in a wood and one is used each year in rotation, there will always be a freshly burnt site suitable for colonisation. Petersen (1970) considered some bonfire fungi were associated more with the mosses that colonise the burnt patch than with the burning, as these fungi could also be found with the same mosses in unburnt places.

The small grey spherical fungus *Glischroderma cinctum* is only known in Britain from charcoal heaps in the Wyre Forest (Shropshire and Worcestershire) (Rea 1912). It may not have been found for many years but could still survive on charred wood or as spores. There has been a recent revival in the British charcoal industry and it would be worthwhile leaving some charcoal piles in British woods in case *G. cinctum* can also be revived.

There is a genus of fungi, *Onygena* (four British species), which grows on such long-lived animal wastes as horns, hooves, beaks and feathers (Keizer 1997). Therefore such items should be tolerated rather than removed for the sake of tidiness or as souvenirs. Owl pellets are a frequent micro-habitat for *O. corvina*, worth consideration on those nature reserves where owl pellets are routinely removed for scientific study.

9. Picking fungi for food

Opinions differ, even among conservationists, on whether collecting fungi for food is a threat to the fungi (Rotheroe 1998). Some argue that because the toadstool is equivalent to a fungus fruit, picking it does no more harm than does picking blackberries. Others take the view that anything which reduces the number of fungus spores released must be a long-term threat to the fungus. A third position is that we don't know whether collecting is a threat, so the precautionary principle decrees collecting wild fungi should be restricted until there is evidence to settle the matter.

It is indisputable that mushroom picking has a long history in Britain, and to some people this alone justifies its continuation. However, some important factors have changed in recent decades. The traditional quarry, the field mushroom, is found in permanent pasture that has not had artificial fertilisers. Such habitat has diminished by over 90% since the demise of the cart horse as the agricultural power source, with much pasture converted to arable and the almost universal 'improvement' of the remainder. Secondly, modern mushroom hunters concentrate on woodland species rather than the field mushroom, so the focus of collecting has shifted to a completely different habitat. Thirdly, the demand for mushrooms is such that a living can be made from collecting, and professional fungus collectors do not always pick just the edible ones. The more unscrupulous use a rake to collect all fungi from areas of woodland floor and sort the catch afterwards. This means that inedible species and mushrooms of edible species which are too old to eat are needlessly destroyed. Perhaps more serious is the disturbance to the litter layer and topsoil. The use of rakes for collecting mushrooms has been banned on some US Forest Service land because it is too damaging (Rowe 1997). Leaf blowers are used by some collectors to remove the leaf litter and reveal mushrooms that are just emerging from the litter layer. This too is very disruptive to the woodland floor. Most commercially collected woodland fungi are mycorrhizal, and studies in America and Switzerland have shown careful picking of such mushrooms does not affect the yield in future years, but trampling certainly can reduce future yields (Amaranthus & Pilz 1996).

The British Mycological Society advocates the precautionary principle (Leonard & Evans 1997), and there is certainly much more information needed before commercial mushroom harvesting can be declared sustainable. We need to know more about the long-term effects on the fungal hyphae. We know very little about the factors controlling the establishment of new fungi from germinating spores - if conditions suitable for germination can be made more prevalent, a smaller number of spores may be needed to establish new colonies of fungi, thus intensive collecting of fungi would be less damaging. Finally we know very little about the effects of commercial collecting on the hundreds of invertebrates that breed in fungi. Among palaearctic beetles, 349 species in 57 families are known to be dependent on fungi (Anderson 2001a, citing Benick 1952). One family of flies alone, the fungus gnats or Mycetophilidae, contains 451 British species (Chandler 1998), all dependent on fungi for breeding sites. Each invertebrate requires a different ecological niche. Some invertebrates breed in many species of fungus but others are more restricted and some require a particular species of mushroom (Hackman & Meinander 1979). But for many fungus-dependent invertebrates such basic knowledge has yet to be collected, not to mention other ecological details such as temperature preferences, pupation sites, geographical range, dispersal potential, and capacity to remain dormant when fungi are not fruiting. Thus even if commercial collecting of fungi proves to be harmless to the fungi, the vulnerability of the hundreds of dependent invertebrates will need to be taken into account.

A sensible precaution, therefore, would be to limit in some way the collecting of mushrooms for food to prevent the majority of a species' annual production being removed. This could be by land-owners designating no-go areas within a wood (though one needs to be sure all the collectable species occur in these areas), limiting the days on which collecting is permitted, or limiting the number of collectors by a permit system issued only to those who can recognise the edible species, and not allowing leaf blowers and indiscriminate collecting methods such as raking. *The Wild Mushroom Pickers Code of Conduct* (English Nature 1998) suggests that per visit no more than 1.5 kg of fungi should be collected; not more than half the fruiting bodies of any one species should be collected; only fully expanded mushrooms, not "buttons", should be taken in order to permit some shedding of spores; and rare species should not be collected except the minimum amount for scientific purposes, such as to confirm the identification. Collection of over-ripe fruiting bodies should also be avoided, as they will not be fit for consumption and are most likely to contain fungus-eating insect larvae and pupae.

However, there is the risk that regulation would back-fire. Unscrupulous collectors will not be deterred unless a wardening scheme is in place, and the advertising of the regulations could attract more collectors to the site than would otherwise have visited. A permit system has been introduced in Epping Forest, Essex, limiting collectors to one visit per season (Morris, 2002). Some regulations fall into the category of token gesture: in the state of Umbria, Italy, collectors' baskets must have holes in, to allow the fungal spores to fall out while the collector is going about his business (Pacioni 1993).

Artificial cultivation of mushrooms is largely restricted to decomposer species, but recent advances in cultivating the more expensive mycorrhizal species, including truffles, may reduce the dependency of dealers on wild populations (Hall & Yun 2000).

10. Minimising fungal threats to trees

Fungi which can kill mature trees are relatively few in Britain. James (1990) listed only 27 species that attack timber, bark or roots, and most of these are not fatal to the tree but may kill branches or spoil the timber for certain uses. Many are only pests of non-native trees which are grown in commercial forests. Given the intimate co-evolution of trees and woodland fungi, it is not surprising that fungal epidemics are rare, and are usually caused by a non-native fungus being introduced inadvertently into a new ecosystem (e.g. Alder Die-back is a hybrid between two exotic species of *Phytophthora* (Brasier, Cooke & Duncan 1999); separate strains of Sudden Oak Death *Phytophthora ramorum*, both introduced, kill oaks in North America and other tree species in Europe (Brasier 2003); Dutch Elm Disease *Ophiostoma novo-ulmi* may have been introduced to Europe or have resulted from an evolutionary leap (Brasier 1990); Chestnut Blight *Cryphonectria parasitica* was introduced to North America and Europe on Japanese and Chinese chestnuts (Griffin 1986)). Climate change may cause fungal epidemics to become more common. Lonsdale & Gibbs (1996) show that the geographic ranges of pathogens are likely to expand if the climate warms, and the effects may be exacerbated by a drier climate increasing the frequency of drought stress in trees and altering the mycorrhizal community which can protect trees against root pathogens.

A few species may have been wrongly labelled as pathogens. It has never been proved whether moribund birch trees are in that state because they are colonised by the birch polypore, or whether birch polypore is only found on moribund birches (Rayner & Boddy 1988). Nevertheless, some people hold the view that fungi are a problem and should be discouraged in woods. Speight (1989) railed against obsessive “forest hygiene” in multiple-use woodland where intensive timber production is not the sole purpose, and called for re-education of the public and foresters in what a forest should look like. Oliver (1999) described English elms recovering from Dutch Elm Disease with the help of natural “virus-like pathogens” of the Dutch Elm Disease fungus (Sutherland & Brasier 1997), plus competition between virulent and sub-virulent forms of the fungus. Oliver pointed out how misguided was the “sanitation” policy of felling and burning diseased elms which was carried out in the 1970s. Current advice for controlling Alder *Phytophthora* is to simply coppice the affected trees. It is impossible to eliminate the fungus by felling and winching out trees showing the die-back symptoms, and trees can recover from the infection. Coppicing encourages recovered trees to regrow by providing space and light (Gibbs & Lonsdale 1998).

There are long-established ways of minimising the risk of serious fungal damage to timber crops without resorting to the chemical treatments, reviewed by Rayner & Boddy (1988). Larch canker is most serious when alpine genotypes are grown in mild lowland conditions, thus it is better to use lowland-sourced seed in Britain (Edlin 1948). Avoiding dense monocultures also helps: generous spacing of trees and a mix of species can prevent a pathogenic fungus from spreading from tree to tree (Edlin 1948).

The high water content of living wood is an inhibitor of fungal attack (Read 2000), thus trees are more likely to succumb when stressed by drought. It follows that damage to the roots, over-crowding and attempting to grow trees in drier places than they would naturally occur will make them more susceptible to drought-induced fungal attack. Water-logging too can make roots more susceptible to fungal infection.

None of these problems is likely to worry the manager of a semi-natural wood, where the occasional loss of a mature tree would just be accepted as part of the natural processes of the wood. A diverse fungus flora with its interspecific competition and parasitism is possibly the best insurance against any single fungus becoming a pest. Honey fungus, one of the more notorious tree killers, is not one species but several. *Armillaria mellea* is the worst pathogen, but the species usually found in woodland is the very similar *A. gallica*, which is far less likely to kill trees. The fungi which cause heart-rot are rarely pathogens: they just decay the dead central part of the limbs, reducing the timber’s value but not endangering the tree (Rayner 1993). An experienced forester will know at what age heart-rot will begin and will crop the timber before heart-rot affects it (Edlin 1948). Or he may take advantage of it – oak heartwood affected by beefsteak fungus can be ten times more valuable for veneer (Rayner & Body 1988).

How to treat pruning wounds was discussed by Rayner & Boddy (1988, p. 405). They pointed out that many fungicides used to treat cut surfaces of trees are also toxic to the tree and may promote colonisation by pathogens. Sealants may lessen decomposition, probably by reducing aeration of the wound. However, if sealants are applied imperfectly, they may promote fungal colonisation by producing a damp aerobic gap between the sealant and the wood. Biological control is suggested, by rubbing soil, cow manure or a mixed inoculum of fungi on the wound and relying on the resulting intense competition by a variety of species to limit the establishment of decay fungi and pathogens. Correct pruning technique also contributes to preventing fungal attack, particularly pruning during active growth so that callus formation is not delayed; and not cutting main branches so close to the base that the tree’s vascular sealing system is breached (Rayner & Boddy 1988).

11. In conclusion

Please remember the above are only broad-brush guidelines and cannot cover all the needs of the thousands of species of fungus found in Britain. Indeed, almost any form of mismanagement is likely to benefit a few species of maverick fungus so even unintentional damage to a habitat may have its consolations in the appearance of unexpected new species of toadstool. But if you are in charge of a site which is rich in fungi and the current management regime has been in place for many years, the best option is likely to be to carry on doing what you have always done.

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