

Macrofungal diversity and community ecology in mature and regrowth wet eucalypt forest in Tasmania: A multivariate study

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Abstract The biodiversity of macrofungi in mature and young regrowth Tasmanian wet forests is described at the species level and at the community level. The macrofungal communities studied were much more species-rich than their vascular plant counterparts, with the total number of macrofungal taxa outnumbering vascular plants by four to one. This ratio applied in both mature and young regrowth forest sites. Some 242 taxa of macrofungi were recorded, of which 132 were identified to species level, the remainder to species groups or higher taxa. Distinct communities could be discerned from multivariate analysis (ordination and classification) of vascular plant and macrofungal data from the mature and regrowth sites. The two vascular plant communities had different fire histories, and this difference is also assumed to account for the separation of the macrofungal communities of the two forest types. There was generally a high level of congruence between the vascular plant and the macrofungal communities. However, one young regrowth site, which was relatively close to the mature sites in the ordination space for the analysis of vascular plants, was distant from the mature forest sites for the analysis of macrofungi. Another regrowth site, which had experienced wildfire rather than silvicultural regeneration, clustered with mature sites for some analyses of the macrofungal assemblage. Variation in the macrofungal communities was correlated with a different set of the measured environmental variables than was variation in the vascular plant communities. Mature and young regrowth forests were found to have distinctly different macrofungal floras, with approximately 40% of the taxa in each forest type being restricted to that type of site. Suitable indicator taxa (restricted or preferential to particular forest types) for use in further studies are suggested.

Key words: Australia, fire, fungi, mature forest, ordination, regrowth forest, synecology, wet forest.

INTRODUCTION

Tasmanian vascular plant species and the forest communities they form are well documented (Reid *et al.* 1999). Considerable progress has also been made in research on lichen and bryophyte species and communities (Kantvilas 1988, 1990; Brown *et al.* 1994; Jarman *et al.* 1994; Moscal & Kirkpatrick 1995; Kantvilas *et al.* 1996; Jarman & Kantvilas 1997; Moscal *et al.* 1997). In contrast, for Tasmanian macrofungi, there is a field guide to common species in rainforests (Fuhrer & Robinson 1992), but no comprehensive modern taxonomic treatments for any groups and few studies at the community level. Only one of the papers listed in a bibliography of Tasmanian vegetation (Duncan 1985) includes fungi. Other studies on the ecology of Tasmanian macrofungi mostly relate to hypogean fungi (Taylor 1992a, 1992b; Johnson 1994),

or concern post-fire succession in terms of broad mycorrhizal types (Warcup 1991).

Floristic information for the macrofungi of general habitat types in Australia is meagre. Available lists are from single visits (such as Field Naturalist's Club forays) or rarely from more detailed sampling, such as the inventories for Two People Bay, Western Australia (Syme 1992) and Wilsons Promontory, Victoria (May 1998). Plot-based sampling was used to study macrofungal succession in rehabilitation and original Jarrah (*Eucalyptus marginata*) forest in Western Australia (Gardner & Malajczuk 1988; Hilton *et al.* 1989). Burns and Conran (1997) also used plots, and provided a multivariate analysis of their data to show that the phenology of a suite of macrofungi differed between nearby sites, but these authors did not directly compare the community present at the two sites. Succession of discomycetes after fire in South Australia was studied by Warcup (1990), using a single large plot, visited over several years.

A knowledge of biodiversity at the community and species level is essential to monitor the effectiveness of,

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or the need for reservation, and also to follow the effects of natural or artificial disturbance. In Tasmania, analyses of vascular plant reservation status have been made for communities (Kirkpatrick & Brown 1994) and species (Kirkpatrick *et al.* 1991). The effects of fire and logging disturbance on floristics have been documented by a number of authors (e.g. Hickey 1994). This work has been mainly limited to the consideration of vascular species, which may be poor predictors of non-vascular species composition (Allen *et al.* 1995). The conservation of fungal diversity is at present wholly dependent upon reserves selected on criteria unrelated to fungi. The adequacy of this approach needs assessment (May 1997).

The neglect of Australian fungi in studies of biodiversity is despite the ecological importance of many species as partners in mutualistic relationships with vascular plants (mycorrhizas), as pathogens and as decomposers, especially in forest ecosystems (May & Simpson 1997). Fungi exist in soil or in other substrata in their vegetative stage (the mycelium), which is not amenable to characterization in the field. Identification of fungal mycelia isolated from soil or mycorrhizas is now possible (see for example Jonsson *et al.* 1999), but techniques have not yet been developed to the stage where surveys of total fungal biodiversity at or near the species level can be carried in a cost-effective manner. Macrofungi produce readily visible fruit bodies (mushrooms, puffballs, and coral and bracket fungi etc.). Because fruit bodies can be readily counted and collected, this group was selected for study.

Taxonomic knowledge of Australian macrofungi is meagre in comparison with that of vascular and other non-vascular plant groups, but it is quite clear that there are many species. There are regularly as many species of fungi as vascular plants at any site, and as many as 50% of the fungal species appear to be undescribed (T. W. May, unpubl. data). Identification of macrofungi in the field is much more difficult than for vascular plants. Microscopic features must usually be examined, although once identified as present some species can be routinely recognized in the field. For other plant and animal groups where there is incomplete taxonomic knowledge, readily identifiable indicator taxa have been suggested as useful in investigating the presence of particular communities and their ecological condition (Kirkpatrick & Brown 1991; Yen & Butcher 1992).

Apart from some perennial bracket fungi, fruit bodies of macrofungi are relatively short lived (approximately 1–20 days). Different species appear at different times of the year, although individual species may not appear at the same time each year, nor necessarily even appear every year. Single samples thus do not suffice to characterize the mycoflora of a plot. Sampling must be carried out at intervals throughout the year and over several years. The total number of species present at a site may not be found until after more than 5 years of sampling (Arnolds 1995). Studies on macrofungal

synecology in the Northern Hemisphere provide background information on experimental design and sampling techniques (Arnolds 1981, 1992, 1995). A recent Canadian study (Villeneuve *et al.* 1989, 1991a, 1991b) demonstrated that useful information could be gained after only 2 years of intensive sampling. Approaches that use plot-based sampling in combination with multivariate analyses to distinguish macrofungal communities are rarely utilized (Arnolds 1992), and are yet to be applied in Australia.

Tasmanian wet forests appear to have a rich macrofungal assemblage and also to provide more equitable conditions for the fruiting of macrofungi than many other Australian forests. Among Tasmanian wet forests, mixed forests generally result from regeneration after fire (Gilbert 1959) and are intermediate between wet sclerophyll and rainforest, having a canopy of relatively short-lived, fire-dependent eucalypts and an understorey of long-lived, fire-sensitive rainforest trees and shrubs (Reid *et al.* 1999).

The current study was carried out in Tasmanian wet forest with the objectives of: (i) documenting the macrofungal biodiversity at the species level (or as near as possible), and identifying possible indicator taxa; and (ii) applying plot-based replicated sampling to investigate the level of congruence between macrofungal communities and vascular plant communities, and their relationships to environmental variables.

METHODS

Site selection

Eight 50 m × 10 m sites were established in the Hermons Road–Esperance area near Geeveston in southern Tasmania. Sites were interspersed, with no two sites more than 5.5 km apart, and four sites were in each of mature mixed forest (sites M1–M4) and young regrowth forest (sites R6–R9). Site locations were: M1 (Australian Mapping Grid Zone 55, 5212962, 492334), M2 (5211133, 492483), M3 (5211022, 487698), M4 (5209818, 492715), R6 (5211565, 491760), R7 (5211835, 487771), R8 (5209693, 488745) and R9 (5209766, 487895). All sites had an overstorey dominated by *Eucalyptus obliqua* or *E. obliqua* and *Eucalyptus delegatensis*.

The mature forest was old growth forest with very limited past disturbance within it (selective logging), and/or close to it (tracking, roading, clearfelling). A 1984 aerial photograph revealed that both M1 and M3 had experienced relatively recent fires because M1 had regrowth eucalypts in the understorey and *Pteridium esculentum* (bracken) was noted in the immediate vicinity of M3. The young regrowth forest was 25–30 years old. Sites R7, R8 and R9 had been burned following logging. Aerial sowing was recorded

for R8 and R9, but natural seeding is assumed to have occurred on R7. Site R6 appeared to have been logged and naturally seeded following a wildfire.

Site layout

At each site, two parallel 50 m × 1 m transects were established, 8 m apart. Macrofungi were recorded within these transects, each of which was divided into five 10 m × 1 m subplots for the purposes of recording macrofungal abundance. To record vascular plants and a number of variables associated with microhabitat, each site was also divided into five contiguous 10 m × 10 m quadrats.

Identification of macrofungi and vascular plants

Macrofungi were those fungi with individual fruit bodies generally larger than 1 mm. Resupinate non-poroid macrofungi ('Thelephoraceae') were not recorded because of the difficulty of field identification, and hypogean macrofungi were also not sampled. Macrofungal fruit bodies were assigned to species (formally described or not) where practicable, and otherwise to species groups, or to higher level taxa (mainly genera). Individual species not formally described, or at least not readily keyed out in available literature, were referred to by a short descriptive phrase in quotes (e.g. *Cortinarius* sp. 'Bonang'). Species groups (such as *Cortinarius* spp. 'small brown') were used for taxonomically complex genera with many undescribed species. Categories used to identify material were almost always mutually exclusive, and can be considered as groupings of convenience to maximize the possibility of identification in the field, taking into account the many undescribed species and the lack of comprehensive handbooks. Some specimens not identifiable in the field were collected for later microscopic examination, but in general we regard the categories used as field taxa (henceforth abbreviated to 'taxa'). Voucher collections were made for most taxa and lodged at the National Herbarium of Victoria. Names of macrofungal species and higher taxa follow the *Catalogue and Bibliography of Australian Macrofungi* (May & Wood 1997; May *et al.* 2001). Names of vascular plants follow Buchanan (1995).

Sampling procedure

Macrofungi

On each sampling occasion, live fruit bodies were identified or collected from all of the subplots along each transect. A fruit body was defined as being live from the first visible appearance of the spore-bearing surface

until its disintegration. A gross abundance measure was noted for each taxon in each subplot. The following classes, based on the number of fruit bodies, were used: 0, 1, 2–10, 11–100, 101–1000 and 1001–10000; the midpoint of each class was used for summation. To prevent double-counting of long-lived fruit bodies on subsequent sampling occasions, brackets and hard fruit bodies were marked. Where marking was not practical, these taxa were not rerecorded on later visits unless comparison with previous surveys showed that there had been an obvious increase in fruit body abundance. Fruit bodies occurring on substrates more than 2 m above ground level were not recorded.

Between December 1994 and November 1995, the mature forest and young regrowth sites were sampled approximately every 6 weeks. If very few fruit bodies were present on the first transect of the first sites visited, the sample was not completed for other sites. This only happened on two occasions (April and August 1995). The eight complete samples were used in the final analysis.

Vascular plants

The vascular plant flora was recorded on each site in December 1994. Within each of the five 10 m × 10 m quadrats on each site, the cover abundance of each species was estimated using the following classes: 0–1%, 2–5%, 6–25%, 26–50%, 56–75%, 76–100%; the midpoint of each class was used for summation.

Environmental variables

Microhabitat

Ground cover and dead wood cover (assessed as percentage cover) were estimated on the sites during November 1995, using the same quadrats and cover classes as for the vascular plant assessment; the midpoint of each class was used for summation. Ground cover was assessed under the following categories: moss; rock (exposed); soil (exposed mineral soil); burnt stumps/logs; unburnt stumps/logs; ferns; cutting grass (*Gahnia grandis*). The dead wood and leaves standing or lying on the sites (to 2 m height) were described as dead wood cover. The following categories were used: leaves and twigs (< 0.5 cm diameter); sticks (0.6–5.0 cm diameter); branches (6–15 cm diameter); poles (16–30 cm diameter).

Abiotic factors

The altitude and location of each site was obtained from global positioning system (GPS) readings using a Trimble GeoExplorer. The level of insolation at each site was obtained using aspect, slope and diffuse light as surrogates. Site aspect was recorded and coded as

follows: 1, facing 90–179°; 2, facing 0–89° or 180–269°; 3, facing 270–359°. The slope (in degrees) at each site was estimated. The diffuse light factor was assessed by hemispherical photography of the canopy, using a Tokina 17 mm, 1:3.5 fisheye lens and the method described by Anderson (1964, 1970). Canopy photographs were taken at approximately 1.2 m above ground level, at the centre and at both ends of each site, and with any immediately overhanging vegetation removed. For each site the mean value was calculated from the available photographs. The most recent geological survey (Forsyth *et al.* 1995) was used to determine the underlying geology at each site. This was coded as follows: 1, Jurassic dolerite and related igneous rocks; 2, Triassic fluviolacustrine sequences of sandstone, siltstone and mudstone. Inundation of sites was recorded in October 1995. Sites were classed as inundated if any part of them showed evidence of having been under water.

Analysis

For each of the sites, abundance estimates for macrofungi were obtained by summation across the 10 sub-plots and eight complete sampling occasions. Cover abundance estimates for vascular plants were obtained by summation and averaging of data from the five quadrats (assigning the results to the same classes as before). Presence/absence data were then derived. For the comparison of mature and young regrowth sites, four data sets were generated: (i) macrofungi, presence/absence; (ii) macrofungi, abundance; (iii) vascular plants, presence/absence; (iv) vascular plants, cover abundance. Values for ground cover and dead wood cover were obtained by summation and averaging of quadrat data (assigning the results to the original classes). Data were entered into a customised version of the ecological database DECODA (Minchin 1991).

Ordination, classification and vector analysis

Dissimilarity matrices were constructed by using the Bray–Curtis dissimilarity coefficient (Minchin 1991) for each of the four data sets. Standardization was applied to macrofungal abundance and vascular plant cover abundance data (taxa being standardized to unit maxima and then sites to unit totals). Ordination of each of the four data sets was achieved using MDS, a program for multidimensional scaling (Minchin 1991). The MDS program was initially run using global non-metric multidimensional scaling (Kruskal 1964) in four dimensions. The two dimensional solutions were saved and used as the starting points for the final MDS runs, using global hybrid multidimensional scaling (Faith *et al.* 1987) in four dimensions. Plots of stress ('badness

of fit' of the ordination regression) versus the number of dimensions indicated that in all cases 2-D solutions would give adequate representations of the data, with stress ranging from 0.05 to 0.13 for the four analyses. Two-dimensional solutions from the final MDS runs were plotted for each of the four data sets. Classification of each of the four data sets was carried out with TWINSpan, a program for two-way indicator species analysis (Hill *et al.* 1975), and with the PATN pattern analysis package (Belbin 1987), using UPGMA cluster analysis of the dissimilarity matrices. A minimum spanning tree was also produced by PATN to assist in interpretation of the ordinations. Vector analyses (Dargie 1984) were used to indicate the direction of micro-habitat and abiotic factors in relation to the ordination axes generated by MDS. Monte-Carlo simulation was used to test the significance ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$) of the maximized correlations (Minchin 1991).

RESULTS

Environmental variables

Young regrowth sites had slopes of 0–10°, whereas mature sites had slopes of 10–30° because of the paucity of accessible unlogged forest on flatter terrain. Insolation (as measured by diffuse light) varied considerably on both sites types, from 8.7 to 26.5% on mature sites, and from 6.1 to 37.8% on young regrowth sites. The underlying geology of the two sites (R8 and R9) was Triassic, with the remainder being Jurassic. Four sites (M3, M4, R6 and R9) showed evidence of inundation. The altitude of R6 was 539 m a.s.l., with the other sites in the range 307 to 465 m a.s.l. Young regrowth sites had higher cover of cutting grass (up to 38%), burnt stumps/logs (to 15.5%) and dead wood/sticks (to 3.5%), whereas cover for these three variables did not exceed 0.5% on mature sites. The cover of dead leaves and twigs was generally higher on young regrowth sites (38–63%) than mature sites (38% on M3 and 15.5% for the remaining three sites). Cover of unburnt logs/stumps was 15.5% on all mature sites, 15.5% on R7, 3.5% on R6, and 0% on R8 and R9. Combined cover of burnt and unburnt stumps/logs was similar across all sites. Moss cover was higher on mature sites (15.5–63%) than on young regrowth sites (3.5–15.5%), as was cover of ferns, which was no more than 0.5% on young regrowth sites, but 3.5% on M3 and M4, and 38% on M1 and M2. Values for cover of dead wood/poles, and dead wood/branches were similar for both site types (to a maximum of 3.5%). Soil cover and rock cover was 0.5% on most sites, with rock cover of 0% on R6 and 3.5% on R8, and soil cover of 3.5% on R7 and R8.

Taxon richness

Vascular plants

Sixty-two vascular plant species (all formally described) were found on the eight mature and young regrowth sites (Table 1), with 49 species recorded from the young regrowth sites, 42 species recorded from the mature sites and 29 species being in common. *Eucalyptus obliqua* was present on all eight and was the predominant eucalypt except on R6, where *E. delegatensis* was of equal cover, and on R7, where the latter species predominated. *Eucalyptus delegatensis* occurred on all young regrowth sites and two of the mature sites (M2 and M3). There was also some *E. regnans* on R9. *Nothofagus cunninghamii* was present on all mature sites, and also on R8. Other vascular plants present on seven or eight of the sites were *Anodopetalum biglandulosum*, *Monotoca glauca*, *Blechnum watsii*, *Cyathodes glauca*, *Gahnia grandis*, *Phyllocladus asplenifolius*, *Tasmannia lanceolata* and *Trochocarpa cunninghamii*, and a further 17 species occurred on at least some sites of both forest types. The proportion of species occurring on seven or eight sites was 15%. Thirteen species were restricted to mature sites, seven of these occurred on a single site, and six were found on three (*Grammitis billardieri* and *Prionotes cerinthoides*) or two sites (three species of *Hymenophyllum*). The epiphytic ferns (*Grammitis* and four species of *Hymenophyllum*) were present on M2 (one species), M3 (four species) and M4 (five species), but absent from M1 and young regrowth sites. Twenty species were restricted to young regrowth sites, 15 of these occurred on a single site, and five were found on four (*Pteridium esculentum*), three (*Acacia riceana* and *Leptospermum scoparium*) or two sites. The number of species restricted to one site across both site types was 22 (35%). *Pteridium esculentum* (on young regrowth sites) was the only species restricted to all sites of a particular forest type.

Macrofungi

The number of taxa of macrofungi found on the eight mature and young regrowth sites over the eight visits was 242 (Table 1). Most were fleshy gilled fungi

(Agaricales and Russulales). Other macrofungi found on the sites were Boletales, Cantharellales, Tremellales, Dacrymycetales and polyporoid and clavarioid members of the Aphyllophorales (all Basidiomycota) and Helotiales, Pezizales and Xylariales (Ascomycota). Among the macrofungal taxa were 132 individual species, 33 of which are yet to be formally named. The other 110 taxa were species groups or higher taxa, used where material could not be assigned to individual species. A list of the taxa of macrofungi on the sites is available from the corresponding author.

On the young regrowth sites there were 168 macrofungal taxa, with 169 taxa on the mature sites (Table 1). There were 98 taxa that were preferential to mature forest (i.e. were found in at least twice as many mature sites as young regrowth sites). Among these, 74 were found only in mature forest, with 51 taxa found on one site, 22 taxa found on two or three sites, and only *Hygrocybe graminicolor* found on all four mature sites (Table 2). There were 84 taxa that were preferential to young regrowth forest. Of these, 73 were restricted to young regrowth forest, with 59 taxa found on only one site, 13 taxa found on two or three sites, and only *Discomycetes* sp. 'mustard erumpent' found on all four young regrowth sites (Table 2). The number of taxa found on only one site across both site types was 110 (45%). Sixty taxa were non-preferential. Twenty taxa (8%) were found on seven or eight sites, including *Bisporella citrina*, *Collybia butyracea*, *Collybia eucalyptorum*, *Cortinarius* sp. 'Bonang', *Discinella terrestris*, *Heterotextus miltinus*, *Mycena interrupta*, *M. epipterygia*, *M. sp. 'Acheron'*, *M. sp. 'pallid top'*, *M. sp. 'nitrous'*, *M. sp. 'Foley'* and a further eight taxa that were species groups or identified only to higher taxa. Ninety-five macrofungal taxa were found on both types of sites. Preferential taxa found on four sites of one forest type and only one of the other were, for mature sites, *Entoloma* spp. 'brown', *Mycena austrofilopes* and *Psilocybe* sp. 'papillate'; and for young regrowth sites, *Mycena erythromyces*. Preferential taxa found on three sites of one forest type and only one of the other were, for mature sites, *Chlorociboria* spp., *Inocybe australiensis*, *Leotia lubrica* and *Psathyrella echinata* (which were all on R6), and *Fomitopsis hemitephrum* and *Stereum illudens*; and for young regrowth sites, *Cortinarius* spp.

Table 1. Number of macrofungal taxa and vascular plant species found in mature forest and young regrowth sites

	M1	M2	M3	M4	Mature total	R6	R7	R8	R9	Regrowth total	Grand total
Macrofungi											
All taxa	73	61	78	113	169	102	86	60	47	168	242
Preferential taxa					98					84	
Restricted taxa					74					73	
Single occurrences	5	9	10	27	51	22	24	7	6	59	
Vascular plants											
All species	18	20	28	30	42	28	22	27	30	49	62

'large brown', *Cortinarius* spp. 'medium olive', *Gymnopilus* sp. 'wet forest', *Mycena sanguinolenta* and *Mycena* sp. 'grey cap, decurrent gills'. The only macrofungal taxa restricted to all sites of a particular forest type were *Hygrocybe graminicolor* (on mature sites) and *Discomycetes* sp. 'mustard erumpent' (on young regrowth sites). Occurrence of taxa across the sites is further considered in the next section (see also Table 2).

Ordination, classification and vector analysis

Vascular plants

Ordination of vascular plant data on both presence/absence and cover abundance gave a distinct separation

along the first axis between the mature mixed forest sites and the young regrowth sites (Figs 1,2). The cluster of young regrowth sites was closer in the ordination space to the cluster of mature sites for the ordination based on presence/absence than in that based on cover abundance. Classification of both presence/absence and abundance data using UPGMA also produced two distinct clusters, one containing the mature sites and one the young regrowth sites. On the dendrograms, there was a distinct gap between the level at which the clusters for each site type formed and the level at which the mature and young regrowth clusters joined. The minimum spanning tree for both data sets linked each of the sites within each forest type to another of the same type, with only a single link between any of the young regrowth sites and the mature sites

Table 2. Macrofungal taxa restricted to various combinations of mature and regrowth sites

<i>n</i> = 4	<i>n</i> = 3	<i>n</i> = 2
Mature sites only (<i>n</i> = 4) <i>Hygrocybe graminicolor</i>	<i>Collybia</i> spp. 'greening' <i>Hypoxylon bovei</i> Polyporaceae spp. 'resupinate unknown'	<i>Agaricales</i> spp. 'gilled ear' <i>Cheilymenia coprinaria</i> <i>Collybia</i> spp. <i>Cortinarius</i> spp. 'dk brown galerinoid' <i>Cortinarius</i> sp. 'orange foot' <i>Cortinarius</i> spp. 'small olive' <i>Crepidotus</i> spp. <i>Entoloma</i> spp. <i>Galerina patagonica</i> <i>Galerina</i> sp. 'shaggy cap/ring' <i>Gymnopilus</i> spp. <i>Hypholoma brunneum</i> <i>Hypoxylon hians</i> <i>Lentinellus hepatotrichus</i> <i>Mycena</i> sp. 'Goonmirk' <i>Mycena</i> spp. 'liver pink' <i>Russula</i> sp. 'brown stainer' <i>Simocybe phlebophora</i> <i>Xylaria polymorpha</i> group
Mature sites + R6 only among regrowth sites (<i>n</i> = 5) <i>Chlorociboria</i> spp. <i>Inocybe australiensis</i> <i>Leotia lubrica</i> <i>Psathyrella echinata</i>	<i>Armillaria hinnulea</i> <i>Armillaria novaezelandiae</i> <i>Descolea</i> spp. <i>Hypoxylon rubiginosum</i> <i>Irpex zonatus</i> <i>Mycena</i> spp. 'white pleurotoid' <i>Stereum hirsutum</i>	<i>Calyptella</i> spp. <i>Cortinarius</i> spp. 'medium dark brown' <i>Discomycetes</i> sp. 'white on litter' <i>Flammulaster pulveraceus</i> <i>Hypholoma fasciculare</i> (yellow gills) <i>Inocybe</i> spp. 'smooth spores' <i>Inocybe</i> spp. <i>Steccherinum</i> spp.
Regrowth sites only (<i>n</i> = 4) <i>Discomycetes</i> sp. 'mustard erumpent'	<i>Cortinarius rotundisporus</i> * <i>Omphalina</i> spp. <i>Postia pelliculosa</i> <i>Tricholoma</i> sp. 'grey'	* <i>Bisporella</i> sp. 'yellow/green' <i>Clavulina cristata</i> <i>Clavulina</i> spp. 'grey' * <i>Dermocybe</i> sp. 'G3' <i>Discomycetes</i> spp. 'hairy' <i>Paxillus curtisii</i> * <i>Ramaria lorithamnus</i> <i>Rhodocybe</i> spp. <i>Russula</i> spp. 'purple/white'

Only taxa found on two or more sites are listed. *n*, number of sites; *not occurring on R6.

(R8 to M3). Using TWINSpan, presence/absence data gave a complete separation between mature and young regrowth sites in the primary division. *Pteridium esculentum* (bracken) was the indicator species, being found in all the young regrowth sites and in none of the mature sites.

Vector analyses associated with vascular plant data indicated that the environmental variables significantly correlated with the ordination axes were inundation,

cover of cutting grass, ferns and sticks. The last three of these factors appeared to differentiate between mature and young regrowth sites. Cover of cutting grass and sticks was higher in the young regrowth sites, whereas fern cover was higher in the mature forest sites. Although presence/absence and cover abundance data gave very similar results, the latter resulted in a higher significance value for cover of sticks (Figs 1,2).

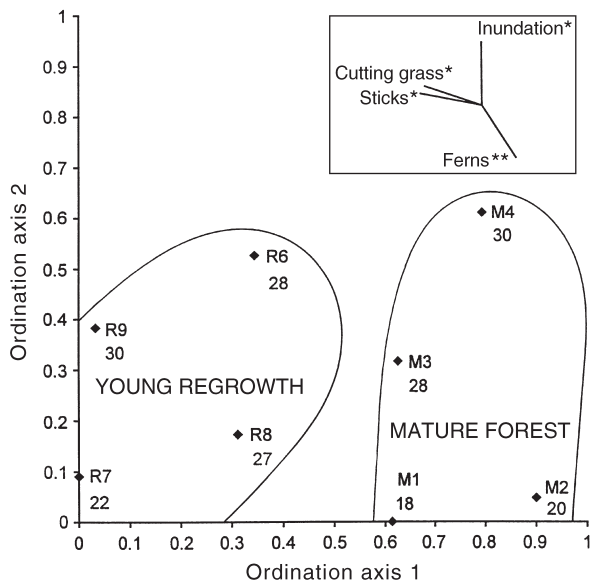


Fig. 1. Ordination of mature forest and young regrowth sites using vascular plant presence/absence data, showing taxon richness and vector analysis. * $P < 0.05$, ** $P < 0.01$.

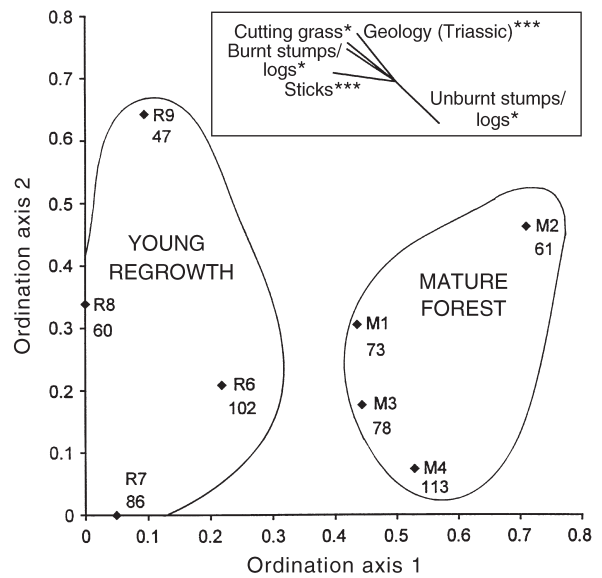


Fig. 3. Ordination of mature forest and young regrowth sites using macrofungal presence/absence data, showing taxon richness and vector analysis. * $P < 0.05$, *** $P < 0.001$.

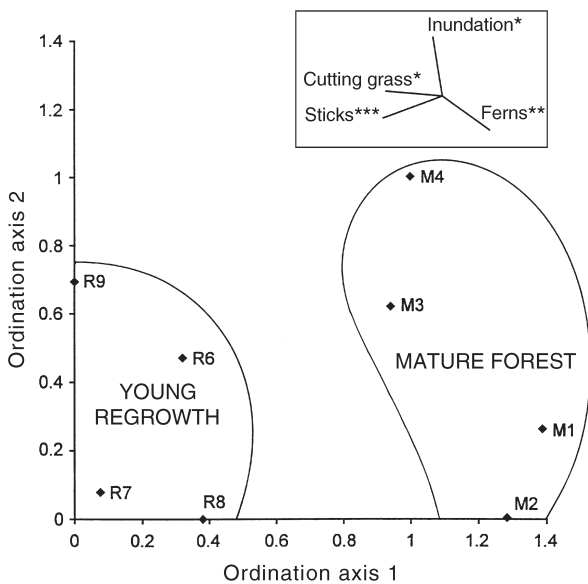


Fig. 2. Ordination of mature forest and young regrowth sites using vascular plant cover abundance data, showing vector analysis. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

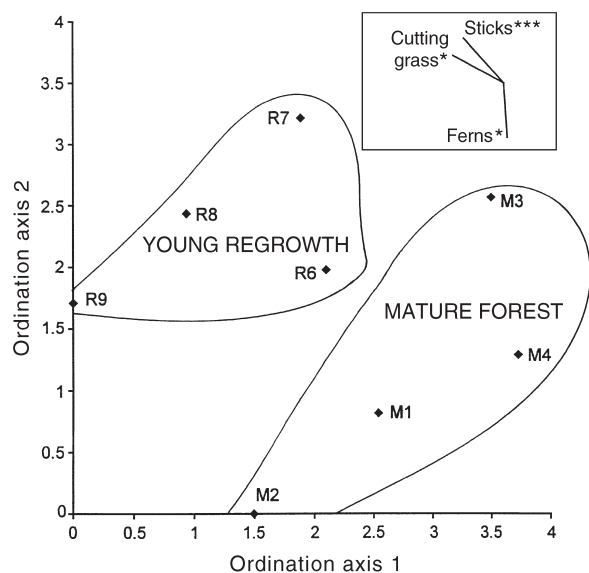


Fig. 4. Ordination of mature forest and young regrowth sites using macrofungal abundance data, showing vector analysis. * $P < 0.05$, *** $P < 0.001$.

Macrofungi

For macrofungal presence/absence data, the mature and young regrowth sites formed two well-separated clusters along the first axis, although R6 was close to equidistant in the ordination space between the nearest young regrowth (R7) and mature (M1 and M3) sites, and could be included with mature sites and still maintain two separate clusters (Fig. 3). The UPGMA classification produced two groups, one containing R7, R8 and R9, and with R6 clustering with the mature sites. In the minimum spanning tree, R6 linked to M3, but also to R7 and R8 (which links to R9), which does not support grouping R6 within a cluster along with the mature sites, but is consistent with a mature cluster and a young regrowth cluster. Using TWINSpan, macrofungal presence/absence data gave a complete separation between mature and young regrowth sites in the primary division.

For macrofungal abundance data, ordination did not produce a clear separation of mature and young regrowth sites along any single axis, although each group of sites could be enclosed by non-overlapping polygons. In the ordination space R6 was close to equidistant between the closest mature (M1) and young regrowth (R7) sites (Fig. 4). The UPGMA classification produced two clusters, one containing R7, R8 and R9, and the other with R6 again clustering with the mature sites. In this second cluster, R6 clustered first with M1, whereas M2 joined the other members of the cluster at the highest level of dissimilarity, and close to the level at which the two major clusters formed. The minimum spanning tree linked mature sites to each other, and young regrowth sites to each other, with a link from M1 to R6.

Because of the inconclusive position of R6 in relation to the other young regrowth sites and the mature sites, Table 2 lists not only macrofungal taxa restricted to two or more mature (23) or young regrowth (14) sites, but also taxa found on mature sites and only R6 among the regrowth sites, and also indicates those taxa restricted to regrowth sites that occurred on R6. On young regrowth sites, 10 of the 14 taxa restricted to this site type occurred on R6, whereas *Omphalina* spp. was absent from R6 but found on all three of the other sites. Support for grouping R6 with the mature sites is indicated by the 19 taxa that were found on mature sites and only R6 of the regrowth sites.

The vector analysis associated with the macrofungal abundance data gave somewhat similar results to the vascular plant data, with cover of cutting grass, ferns and sticks shown to be significant, although inundation was not significant. Again, cover of cutting grass and sticks was higher in the young regrowth sites, whereas fern cover was higher in the mature forest sites (Fig. 4). However, for macrofungal presence/

absence data, a different set of environmental variables was shown to be significant: cover of cutting grass, cover of sticks, burnt stumps/logs, geology and cover of unburnt stumps/logs. The first three variables were higher in young regrowth sites, whereas the cover of unburnt stumps/logs was higher in mature forest sites, although only the sticks vector was near parallel to the first axis, along which the sites were separated (Fig. 3). Geology was more likely to be Triassic on regrowth sites (only sites R8 and R9 being in this category).

Taxon richness

For ordinations of vascular plant and macrofungal presence/absence data (Figs 1,3) ordination axis 2 was aligned with taxon richness. When mature forest sites and young regrowth sites were considered separately, the individual sites within each grouping were found to be arranged according to taxon number along ordination axis 2. The only exception to this was site R6. Species richness of vascular plants was positively associated with inundation, but negatively associated with fern cover. There were no strong associations in the ordination space between taxon richness of macrofungi and the environmental variables.

Vascular plants and macrofungi

A plot of the scores from the first ordination axes of the vascular plant and macrofungi ordinations using

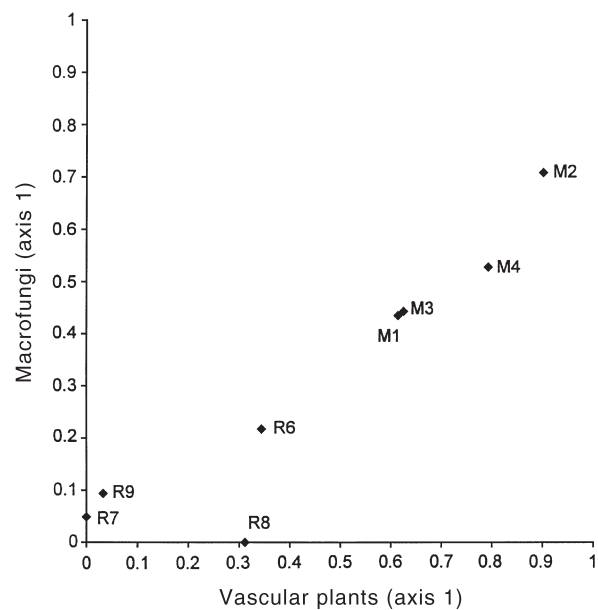


Fig. 5. Plot of scores from the first ordination axes of the vascular plant and macrofungi ordinations using presence/absence data.

presence/absence data (Fig. 5) shows a close correlation between the vascular plant and macrofungi ordination scores.

DISCUSSION

Taxon richness

The macrofungal communities studied were much richer than their vascular plant counterparts, with approximately four times more macrofungal taxa than vascular plants. The ratio reflects that reported for fungi in general (Hawksworth 1991). It should be emphasized that the ratio for macrofungi on the Tasmanian sites will be an underestimate, as hypogean fungi were excluded and some of the field taxa employed could include multiple species. In addition, because only fruit bodies were identified, any macrofungi that fruited between sampling occasions or not at all during the study would have been missed, whereas it is unlikely that many vascular plants on the sites would have gone unrecorded. For each of macrofungi and vascular plants, the taxon richness was similar for combined young regrowth sites compared with combined mature forest sites. However, there was considerable variation among individual sites (Figs 1,3).

Forest types

The regrowth (recently burnt) and the mature mixed forest (generally long unburnt) sites were chosen in order to provide two distinct forest types across which to compare the assemblage of macrofungi, with the major difference being the age of dominant eucalypts resulting from fire history. Because of the difficulties of exactly matching sites within each site type, a variety of fire histories were in fact represented. Three of the regrowth sites were silvicultural burns, but the fourth (R6) had regenerated after wild-fire, whereas two of the four mature sites (M1 and M3) had also experienced relatively recent wildfires of unknown intensity. Nevertheless, as intended, the two forest types separated well along the first ordination axis. Cover of cutting grass and cover of sticks both appeared to be closely related to the fire history of the sites, with young regrowth sites having higher values than the mature forest sites. For presence/absence data, within the mature forest cluster, M1 and M3 were closest to the regrowth cluster, along the first ordination axis, suggesting an effect of their different fire history on vascular plant floristics. Site R6 was not markedly separated from other regrowth sites on its vascular plant assemblage.

Concordance between macrofungal and vascular plant communities

There was generally a good concordance between the pattern of the vascular plant ordinations (on both data sets) and that of the macrofungi ordination using presence/absence data (compare Figs 1–3). A close concordance between vascular plant and macrofungal presence/absence ordinations was confirmed when scores from the first ordination axes from the two data sets were plotted (Fig. 5). The two environmental factors significantly related to the first axis in the vascular plant ordinations (cutting grass and cover of sticks) were also significantly related to axis 1 for the macrofungal presence/absence ordination. It is also of interest that sites M1 and M3 (which had both experienced relatively recent fires) were closest on ordination axis 1 to regrowth sites for vascular plants, and were also so positioned in the macrofungi ordinations. All these results suggest that fire history is a strong determinant of the presence or absence of macrofungi.

The cover abundance of dead sticks was an indicator of the successional stage attained by the vascular plant community since the last fire. From observation, much of the fine dead wood was made up of species such as *Pomaderris apetala* (dogwood) that are early- to mid-successional wet sclerophyll shrubs. With regard to macrofungi, this dead wood may not only indicate the time since fire (the effects of which may occur through other variables such as soil fertility) but also have a direct link by providing colonization sites. Two taxa found on dead sticks were restricted to young regrowth sites: Discomycetes ‘mustard erumpent’ (all four sites) and Discomycetes ‘hairy’ (two sites).

Despite the generally high correlation between the vascular plant and macrofungi ordination scores (Fig. 5), site R8 was displaced toward the young regrowth sites in relation to macrofungi, and toward the mature forest sites in relation to vascular plants. At least two explanations are possible. First, this site had the lowest value for moss cover. This most probably reflects a difference in microclimate, particularly humidity, and would be consistent with the fact that site R8 was particularly open. Such a difference in microclimate may be more of a limiting factor for macrofungi than for vascular plants. Second, the current vascular plant composition of R8 included old growth rainforest components (*Nothofagus cunninghamii* and *Eucryphia lucida*), indicating that before logging it was a mixed forest site. In comparison, the current vascular plant composition of the other young regrowth sites would indicate that they had previously been wet sclerophyll forest with rainforest understorey elements. This composition would tend to displace site R8 towards the mature forest sites on the vascular plant ordinations. At least one putative obligate macrofungal associate of *Nothofagus* was recorded on R8 (*Cuphocybe*

sp. 'yellow brown'), but there was either a low number of other such associates, or they had not yet established on the site.

The other anomaly in comparing the vascular plant community with the macrofungal community was site R6. This clustered with the regrowth sites on its vascular plant assemblage, but with mature sites in some of the analyses of the macrofungal assemblages. Site R6 was also the only site not falling in sequence on ordination axis 2 with respect to vascular plant and macrofungal species richness. The position of a site with an unreplicated treatment must be considered with caution, and may well be due to another factor such as altitude (which was highest for R6). However, the fact that R6 had experienced a wildfire rather than a silvicultural regeneration burn is of interest because an effect has already been documented for epiphytic ferns, which have a lower frequency in silvicultural regeneration (Hickey 1994). A number of differences in the environmental effects of wildfire and regeneration burns have been documented (Resource Assessment Commission 1992; Hickey 1994), such as the creation of more microhabitats.

There was less concordance with vascular plant ordinations using the macrofungal abundance data (Fig. 4), although the vectors for sticks and cutting grass, as with all the other ordinations, related to the separation of the two forest sites. The different results for abundance may reflect both the rather arbitrary and non-continuous method used to assess fruit body abundance, and the unconfirmed value of this statistic as a measure of macrofungal 'volume' comparable to vascular plant cover abundance.

In the study of Canadian macrofungal communities by Villeneuve *et al.* (1989, 1991a, 1991b), based on presence/absence data, analysis of different nutritional and substrata groupings of fungi gave different community structures. The diversity of some groups of fungi was highly related to vascular plant diversity, but in other cases was correlated with different factors such as tree cover. Separate analysis of trophic and substrate groupings based on more extensive sampling in Tasmanian forests would be worthwhile.

Environmental factors

When presence/absence data was considered, the macrofungal communities were sensitive to a different set of the measured environmental variables than the vascular plant communities. This was probably largely because of the selection of measured variables (stumps for example, are a known habitat for some macrofungi). The highly significant relationship of macrofungi (presence/absence data) with geology was somewhat surprising, particularly given the apparent lack of relationship of the vascular plant communities with this

factor. The lack of relationship for the latter is consistent with Jackson's (1965) model of Tasmanian vegetation, in which composition on more mesic sites was more uniform across geological substrates, specifically where the mean annual rainfall exceeded 1500 mm per year (as in the study area). On such sites the climatic climax was rainforest, with mixed forest occurring in areas of higher fire frequency. It is known that fungal communities can respond to changes in soil nutrient status. Hilton *et al.* (1989) found that fertilizer applications in jarrah forest led to an increase in fruit body numbers, primarily of some mycorrhizal and saprotrophic species. Fertilizer application also led to fruiting of some species not previously recorded. In the present study, fern cover was significantly related to the presence/absence of vascular plants and to both vascular plant and macrofungal abundance (Figs 1,2,4), possibly exerting its effect by providing/limiting colonization sites. It did not appear to affect macrofungal presence/absence (Fig. 3). Inundation, somewhat surprisingly, only appeared to be important in relation to the vascular plant communities (Figs 1,2), and was also related to vascular plant species richness, probably increasing the number of microhabitats sampled within a site.

Macrofungal habitat preferences/indicator taxa

Mature and young regrowth forests were found to have distinctly different macrofungal assemblages. Although more taxa were preferential to mature forest sites than to young regrowth sites, the numbers of macrofungal taxa restricted to type of site were very similar: approximately 40% of the taxa in each case. In some instances these apparently specialized habitat preferences may only reflect the scarcity of the taxa. The proportion of taxa found only on a single site was higher for fungi (45%) than for vascular plants (35%). Additional sampling may record some of these taxa from further sites. Because of the interval between samples, a short fruiting season (somewhat staggered between sites) could also give rise to isolated occurrences, thus inflating the proportion of restricted taxa. Nevertheless, some restricted and preferential taxa presumably do reflect a real preference for a given forest type.

There are few background data on the habitat and substrate preferences of Australian macrofungi against which to compare the results from the present study. Known ectomycorrhizal genera (*Cortinari*, *Dermocybe*, *Ramaria*, *Russula*) did not appear to be more common on either site type. *Nothofagus* was present on all mature sites and on R8. An association between ectomycorrhizal macrofungi and *Nothofagus* has been reported for some species of *Rozites* (Bougher *et al.* 1994). Although present in the general area, this genus was not sighted during our study, but a related

member of the Cortinariaceae, also presumably ectomycorrhizal, *Cuphocybe* sp. 'yellow brown' was observed only on M1 and R8, and the putatively ectomycorrhizal *Tricholoma* sp. 'hebeloma-like' occurred only on M4 and R8.

Only *Hypholoma brunneum* and the *Xylaria polymorpha* group were found in both M2 and M4 and were limited to these sites. Because these were the only sites not to have experienced a relatively recent fire, this may reflect something of the habitat preferences of these taxa. The suite of terrestrial discomycete species reported by Warcup (1990) as occurring in the first 3 years after fire at a South Australian sites was not recorded from the Tasmanian sites, which could be because of the small size of many of the species. However, Warcup (1990) did find that some fungi (such as *Anthracobia*) were found only in the first or in the second year immediately after fire, whereas the Tasmanian young regrowth forests were sampled at 25–30 years post-fire. Warcup (1990) found that other species that normally fruit on unburnt soil appeared in the second and third years after the fire. One such species, *Discinella terrestris*, was present on both young regrowth and mature sites.

Further studies should record the specific substrate and microhabitat of each fruit body so that detailed data on substrate and microhabitat specificity can be compiled and related to site type and environmental variables. Results from the present study are important in suggesting taxa that have different ecological preferences (Table 2). Given the high diversity of macrofungi, and the difficulties of identification, these taxa can form a useful set of target taxa to test for reliability as indicators in further studies of these and other forest types. In particular, some of the taxa for which ecological preferences are suggested are readily recognizable such as *Discomycetes* sp. 'mustard erumpent' and *Cortinarius rotundisporus* (for young regrowth) and *Hygrocybe graminicolor*, *Collybia* spp. 'greening' (with dark purple pileus and greening in KOH) and *Hypoxylon bovei* (for mature sites). If the wildfire-regenerated site R6 is considered along with the mature sites, then *Chlorociboria* spp., *Leotia lubrica* and *Psathyrella echinata* are highly distinctive taxa that appear to be specific to this habitat grouping.

Management implications and further research

The congruence between the vascular plant and macrofungal communities is encouraging from the point of view of conservation, because it is the vascular communities that currently serve as surrogates for the fungal community in the management of wet forests in Tasmania and elsewhere. However, the anomalies reported need to be further investigated through more extensive, replicated studies. There are also indications

of differential effects of silvicultural regeneration burns and wildfire on macrofungal flora. Further comparison is warranted of regrowth arising from silvicultural regeneration with that of a similar age arising from wildfire (Hickey & Wilkinson 1994; Hickey 1994). The comparison of macrofungal communities also needs to be extended across a wide range of forest communities (such as rainforest). The methods utilized in the present study need to be developed so as to allow more rapid surveys. Refinements should include development of meaningful and practical measures for recording abundance of macrofungi, and development of subsets of indicator taxa, for which the present study provides a starting point.

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