

WOOD-INHABITING MACROFUNGAL ASSEMBLAGES IN 43-YEAR-OLD REGENERATING WET *EUCALYPTUS OBLIQUA* L'HÉR. FOREST

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(with six text-figures and five tables)

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This study focuses on the diversity and ecology of wood-inhabiting macrofungal species assemblages in a regenerating tall, wet, native *Eucalyptus obliqua* forest in southeast Tasmania, 43 years after natural and anthropogenic disturbances. Two plots subjected to “clearfell, burn and sow” silviculture were compared with two other nearby plots that had experienced wildfire. A total of 90 species was identified from 619 macrofungal records during six fortnightly visits between May and July 2010. The plots with abundant live *Pomaderris apetala* trees in the understorey (i.e., those at Edwards Rd) had markedly different macrofungal assemblages from those with no or with sparse *Pomaderris apetala* (i.e., at Hartz Rd). This study provided evidence that a 43-year-old regenerating forest maintains a core of common wood-inhabiting macrofungal species irrespective of type of disturbance. Furthermore, species most frequently observed in older forests in Tasmania can also occur in younger managed forests if biological legacies such as large diameter wood, well-decayed wood, large living trees and a diversity of tree species remain after silvicultural treatment.

Key Words: wood-inhabiting macrofungi, *Eucalyptus obliqua*, *Pomaderris apetala*, wildfire, managed forests, Tasmania.

INTRODUCTION

Maintaining wood-decay fungal diversity is an essential part of a productive forest ecosystem, and many studies have addressed the effect of anthropogenic disturbance on assemblages of wood-inhabiting macrofungal species in forests, especially in the Northern Hemisphere (e.g., Bader *et al.* 1995, Czederpiltz *et al.* 1999, Christensen *et al.* 2004, Heilmann-Clausen & Christensen 2005). Nevertheless, forest conservation programs of many countries still completely neglect fungi as an official conservation priority or even acknowledge their existence (Heilmann-Clausen & Vesterholt 2008).

The fruit bodies are the most obvious sign of the presence of a wood-inhabiting fungus. Macrofungal fruiting bodies on wood perform important habitat functions in their own right, providing food and shelter for a myriad of faunal species (Pavoir-Smith 1960, Pielou & Verma 1968, Schigel 2007, Robinson *et al.* 2008). Some polypore species are considered to be indicators of old-growth forest and important for the persistence of specialist insects (Komonen 2001). Macrofungal fruiting bodies can provide habitat and food for other fungal species inhabiting dead wood (Jonsson *et al.* 2005). Nutrients (Ca, Fe, K, Mn, N, P, Zn) can be exported via fruit bodies from the wood and returned to the forest floor by animals ingesting the fruit body, or by the senescence of the fruit body, which, for most fungal species takes only a few days to several weeks (Vogt *et al.* 1981, Harmon *et al.* 1994, Buchanan *et al.* 2001).

Esseen *et al.* (1997) and Penttilä *et al.* (2006) suggest that many of the negative effects of forest management activities on wood-inhabiting macrofungal species are a result of the simplification of the structure of these managed stands compared with natural unmanaged stands, as trees in managed regrowth forests are younger, smaller diameter, with smaller branches. Forest management also greatly alters the disturbance dynamics and results in a reduction and

fragmentation of mature and old forests. The decline in the amount of dead wood, fragmentation of remaining natural dead wood habitats, and a change in the composition of the dead wood in current habitats have had dramatic effects on wood-inhabiting fungal communities (Heilmann-Clausen & Vesterholt 2008). Developing effective management protocols to minimise losses of macrofungal species depends on knowledge of what is an acceptable habitat loss or population reduction. This implies knowledge of the biological function and, in particular, the ecology of the individual fungal species (Arnolds 2001, Watling 2005).

In Australia, studies specifically on the ecology and diversity of wood-inhabiting macrofungi are few (see Fryar *et al.* 1999, Hopkins *et al.* 2011, Gates *et al.* 2011c) although wood-inhabiting macrofungi are generally documented as part of general macrofungal surveys (e.g., Packham *et al.* 2002, Robinson & Tunsell 2007, Robinson *et al.* 2008) without any attempt to analyse the data further. McMullan-Fisher (2008) undertook substrate fidelity analysis in her cryptogam study and concluded that there were suites of fungi with preferences either for small wood (≤ 5 cm diam.) or for large wood (> 5 cm diam.).

The most widespread forest type in Tasmania is wet *Eucalyptus obliqua* L'Hér. forest (Public Land Use Commission 1996). At maturity, *E. obliqua* can frequently reach heights of over 70 m (Kirkpatrick & Backhouse 1981). Wet *E. obliqua* forests in Tasmania need disturbance to regenerate (Gilbert 1959). The most common type of natural disturbance is wildfire, the frequency and intensity of which are important in determining the nature of the future forest environment (Wells & Hickey 1999). A fire interval ranging from 20 to 100 years will result in the development of a wet sclerophyll forest community, whereas longer intervals of between 100 to 350 years result in mixed forest communities (Gilbert 1959, Wells & Hickey 1999). Fire intervals of greater than 400 years cause a maturation of rainforest understorey species to form a dominant canopy

which restricts eucalypt recruitment and after the senescence of the older eucalypts creates a characteristic temperate rainforest (Gilbert 1959, Jackson 1968).

The current silvicultural method in the wet eucalypt forests of southern Tasmania is “clearfell, burn and sow” (CBS) on rotations of 80–100 years (Hickey *et al.* 2001). The CBS method removes all living trees of value and a high intensity fire is then applied to the area which incinerates the logging slash waste and produces an ash bed which is highly favourable to eucalypt seed germination. This method was considered to mimic the effects of a natural wildfire disturbance which is essential in the regeneration of tall, wet eucalypt forests in Tasmania (Jackson 1968). This operation, however, leaves very few (if any) biological legacies such as stags, coppicing burnt trees or remnant patches of living forest (Lindenmayer & McCarthy 2002). It is suggested that CBS operations more likely mimic an extreme natural wildfire event or a succession of wildfires at short intervals, as described in Jackson (1968).

The macrofungal species that colonise after fire disturbance in Tasmania are very different from the group of species present in a pre-disturbed forest (Gates *et al.* 2005, 2009). The post-disturbance colonisation of substrates by macrofungal species is likely to occur more rapidly after a wildfire event in a wet *E. obliqua* forest than after a CBS operation due to the greater presence of biological legacies, i.e., organically produced patterns and structures (as mentioned above) that survive the disturbance.

The value of a small spatial scale study is that it provides baseline knowledge of an area in sufficient detail that can then be extrapolated to a larger landscape level. The accumulated knowledge from multiple small spatial studies has a use in assessing effects of habitat fragmentation on biodiversity. Furthermore, heterogeneity at the small-scale level may also indicate heterogeneity at a landscape level. Data analysis programs exist (see Holland *et al.* 2004) that can extrapolate small scale data into larger landscape level results leading to reduced costs (time, labour and travel) associated with intensive large-scale studies. Additionally, small spatial scale studies can gauge the success of specific habitat refugia, such as nature reserves and wildlife connectivity corridors.

The objectives of this study were to investigate the diversity of wood-inhabiting fungi in a 43-year-old regenerating *E. obliqua* forest by documenting the species numbers and species assemblages present, and to compare the effects of clearfell, burn and sow silviculture with the effects of wildfire on the wood-inhabiting fungi present in four plots. This is done within the context of an experimental design where two paired plots (one subjected to CBS and one which experienced wildfire) were examined at each of two localities in Tasmania’s southern forests. The CBS regenerating stands are even-aged stands of 43 years, whereas the wildfire stands are of mixed age due to the erratic nature of wildfire in the tall, wet, *E. obliqua* forests of southern Tasmania (Alcorn *et al.* 2001, Turner *et al.* 2009). The opportunity also presented itself to investigate if a short-term study at this small spatial scale can provide data that can be incorporated into forestry management protocols. Specific questions relating to the above aims included whether there was a relationship between the macrofungal species diversity and the dead wood characteristics such as its species, decay class, diameter class, and whether the wood was fallen, suspended or upright. Also examined were whether the wood-inhabiting fungal assemblages depended upon vegetation type, soil pH, canopy and ground cover,

and whether the diversity of the macrofungal assemblages on wood differed between the two disturbance treatments. We speculate about whether the findings from this study might influence the current use of CBS or alternatively, aggregated retention (ARN), a silvicultural procedure, in which “islands” of unharvested trees are retained for one or two rotations, under consideration for use in sustainable forestry in Tasmania. We further speculate whether there are any implications from this study on impacts on diversity of wood-inhabiting macrofungal assemblages from the intended harvesting of dead wood in Tasmania as a biofuel for power generation. We ask whether this short-term, small spatial scale study could reflect any results from similar, more intensive studies in *E. obliqua* forests of southern Tasmania, such as the one by Gates (2009).

MATERIALS AND METHODS

Study area, plot location and establishment

Four plots in native, tall, wet *Eucalyptus obliqua* forest in southern Tasmania, west of Geeveston were examined (fig. 1). All four plots, two from wildfire and two from a CBS forestry regeneration procedure, were part of larger forest tracts that had experienced disturbance in the years 1966/67. Two of these plots were directly opposite each other on either side of Hartz Rd, with the northern plot having been subjected to CBS regeneration and the southern plot having experienced wildfire. At Edwards Rd, the two plots were side-by-side on the north side of the road, the most easterly plot having been disturbed by wildfire in 1966/67, with the westernmost plot being a CBS plot. The four plots were used previously, along with other plots, as part of a study by Browning *et al.* (2010) on cryptogamic succession (mosses, liverworts and ferns) in these same regenerating wet eucalypt forests.

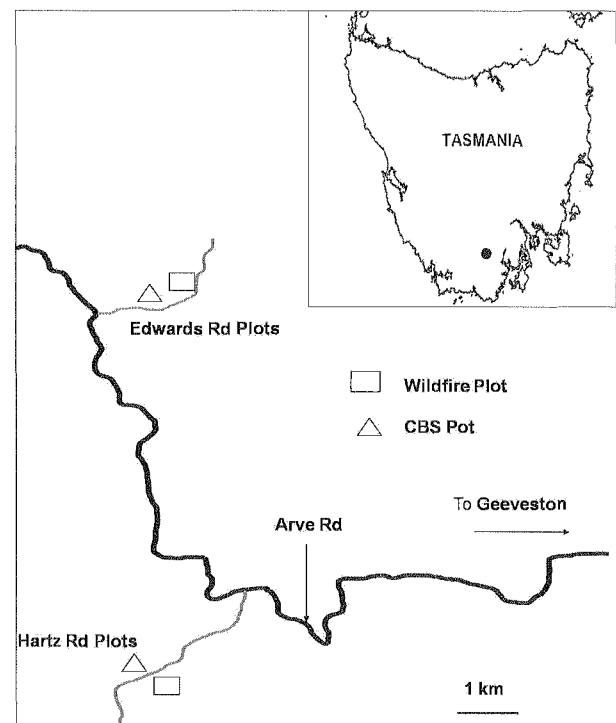


FIG. 1 — Map of site in southern Tasmania showing plot locations.

At each site (Hartz Rd and Edwards Rd), a 40 x 40 m plot was measured and marked out using twine, and each plot was divided into four 20 x 20 m quadrants.

Site characterisation

The slope, canopy cover, soil pH, ground cover and dominant vascular plants of each plot in the study were measured. The location of the chosen central point of each plot was determined with a handheld Garmin E-Trex[®]. The angle of slope was measured with a handheld Suunto[®] clinometer at three random positions within each quadrant. The 12 readings were then averaged to give an average slope for each site. The canopy covered by the dominant vegetation was measured at three random positions within each quadrant using a Forestry Suppliers Inc. Spherical Crown Densimeter[®]. At each position four observations (each facing north, south, east and west) were recorded. The averages of these readings were calculated to give a percentage canopy cover for each quadrant. Soil was sampled in three randomly generated locations within each quadrant. Samples were taken at a depth of 10–20 cm using a hand trowel, placed in a plastic bag and taken back to the laboratory for analysis using a Manutech[®] soil pH test kit to obtain an average soil pH for each quadrant. The percentage of ground covered by bare ground, litter, rock, bryophytes and dead wood separately was recorded at three random locations in each plot. For each component of ground cover, the percentage of cover was recorded as an absolute value and converted using a modified Braun-Blanquet cover class for analysing ground cover abundance data, as follows: 0=absent; 1=1–25%; 2=26–50%; 3=51–75%; 4=76–100%. The living stems of all vascular plants of height ≥ 1.5 m within each quadrant of each plot were identified to species using Eucflip (Wiltshire & Ports 2007) and Treeflip (Wiltshire & Jordan 2009). The diameter at breast height (DBH) of each stem was measured using a diameter tape measure. From these measurements, the basal area of each tree and the percentages of basal area at the plot level occupied by each tree species were subsequently calculated.

Macrofungal survey method

Each quadrant was visited fortnightly from 6 May–15 July 2010, a total of six visits. This was determined to be the ideal time for collection, covering the optimal fruiting season for the majority of Tasmanian macrofungi (Gates & Ratkowsky 2009), where a macrofungus is defined as a fungus that may be seen with the unaided eye. In the first five visits a 20 m transect was followed in each of the four quadrants in a

predetermined location and order. During the last visit (15 July 2010), each quadrant was surveyed randomly for 15 minutes. At each visit, the species binomial or ‘tag’ name of each macrofungus observed on fallen wood or a stag within 1 m on each side of the transect was recorded. Resupinate species, if not readily identifiable, were ignored due to time considerations and lack of taxonomic expertise. For each species, only its presence (not its abundance) was recorded, and its substrate was classified according to its diameter class, decay class and plant species. Voucher specimens of known species, to be deposited in the Tasmanian Herbarium (HO), were collected at the first encounter and dried in an air dryer for 24–48 hours in the laboratory. All species new to the authors were macro- and microscopically described. Valid names were obtained from the website Index Fungorum (<http://www.indexfungorum.org/names/names.asp>, viewed November 2010). For each macrofungal species, the diameter class, level of decay and species of substrate was also recorded. For wood size, three diameter classes (small, $D \leq 10$ cm; medium, $10 < D < 40$ cm; large, $D \geq 40$ cm) were used. The level of decay of each substrate was also classified into three classes— low, medium and high – based on appearance and structural stability using certain defined characteristics (table 1).

Statistical analysis

From the presence/absence data from the six fortnightly visits to each of the four quadrants of each of the four plots, species richness was calculated as the number of distinct macrofungal species observed. Randomised species accumulation curves were prepared to visualise the rate at which new species of wood-inhabiting macrofungi were observed over the study period, using the Mao-Tau estimator available in the package EstimateS (Colwell 2005). For species assemblages, non-metric multidimensional scaling (nMDS) and one of the routines (DISTLM) in the suite of programs for multivariate ecological data developed by M.J. Anderson and available as an add-on (PERMANOVA+) to PRIMER v6 (Clarke & Gorley 2006, Anderson *et al.* 2008) were used as inferential methods. DISTLM (and its associated plotting routine dbrDA) can be used on the macrofungal data recorded during the fortnightly visits because their use does not require any a priori distributional assumptions to be satisfied. Starting with the basic data tables of the presence or absence of each macrofungal species recorded on dead wood, similarity (resemblance) was defined using the Bray-Curtis measure (Bray & Curtis 1957). Significance levels were provided by permutation trials, using 9999 random permutations of the observed data set. The major question that was tested was

TABLE 1
Description of the characteristics assigned to each wood decay class

Decay Class	Characteristics
Low	Some to most of the bark is present; branches may retain twigs; wood is solid.
Medium	Bark is absent; log can be broken with some applied force, but is still structurally sound.
High	Log cannot support own weight; structure is soft and crumbly and can be broken or crushed easily by kicking; bryophytes, ferns and invading roots may be present.

whether there was an association between the macrofungal species lists obtained from each of the four quadrants of each plot and the living vascular plant species present in those quadrants. DISTLM uses two data matrices, one containing the Bray-Curtis resemblances among the macrofungal species lists in each of the 16 quadrants and the other containing the abundances of the vascular plant species present in those same quadrants. Conditional upon a significant P-value being obtained, DISTLM then establishes which of the vascular species best explained the differences among the macrofungal species assemblages at the quadrant level, and the graph available from dbRDA was used to visualise the differences.

RESULTS

Slope, canopy cover and soil pH

Table 2 summarises the mean slope, canopy cover and soil pH for the four plots. The slope of both plots at Edwards Rd was greater on average than at the Hartz Rd plots. The percentage canopy cover at all four plots was high with little difference between them, and the same was true of soil pH, the soils all being slightly acidic, with the difference in plot pH means being at most 0.5 of a pH unit.

TABLE 2
Site characteristics for each plot¹

Site	Slope (°)	% Canopy cover	Soil pH
Hartz Rd CBS	21 (19–22)	87 (81–90)	5 (4–6)
Hartz Rd Wildfire	20 (14–33)	93 (92–94)	5 (5–5)
Edwards Rd CBS	35 (27–50)	92 (91–94)	5.25 (5–6)
Edwards Rd Wildfire	30 (25–33)	93 (93–93)	4.75 (4–5)

¹ Entries are plot means, with the ranges from the four quadrants given in parentheses.

TABLE 3
Species of higher vascular plants with living stems of height ≥ 1.5 m, total number of stems and percentage basal area per plot (in parentheses), and total basal area of stems, in each of the four plots

Vascular plant species	Plot identification			
	HCBS	HWF	ECBS	EWf
<i>Acacia dealbata</i>	26(21.8)	23(11.1)	2(0.3)	5(2.6)
<i>Atherosperma moschatum</i>	6(0.3)	7(0.3)	2(0.0)	0(0.0)
<i>Eucalyptus obliqua</i>	41(66.7)	69(72.0)	50(53.2)	57(55.2)
<i>Eucryphia lucida</i>	0(0)	45(1.7)	1(0.7)	0(0.0)
<i>Nothofagus cunninghamii</i>	71(5.5)	638(14.6)	0(0.0)	0(0.0)
<i>Olearia argophylla</i>	23(3.9)	4(0.1)	154(5.7)	8(0.3)
<i>Phyllocladus aspleniifolius</i>	5(0.1)	3(0.0)	6(0.0)	0(0.0)
<i>Pittosporum bicolor</i>	1(0.1)	2(0.1)	0(0.0)	0(0.0)
<i>Pomaderris apetala</i>	22(1.6)	1(0.0)	809(40.1)	571(41.9)
Total stems (% BA)	195(100)	792(100)	1024(100)	641(100)
Stems total basal area (m ² /ha)	68.7	69.6	62.6	53.8

HCBS=Hartz Rd CBS; HWF=Hartz Rd Wildfire; ECBS=Edwards Rd CBS; EWf=Edwards Rd Wildfire.

Ground cover

There was little difference between the plots with regard to ground cover, with all plots having a large average cover of litter present (fig. 2). Both wildfire plots contained a slightly greater cover of dead wood on average than the CBS plots (fig. 2).

Vascular plant species composition

The total number of stems recorded over all plots was 2652 (table 3). The Edwards Rd CBS plot contained the most living stems of all plots with 1024 and the Hartz Rd CBS plot contained the least with 195 stems. The difference is mostly due to the large number of *Pomaderris apetala* Labill. at ECBS plus a smaller difference in *Olearia argophylla* (Labill.) F. Muell. ex Benth., which more than balanced the decreased numbers of *Nothofagus cunninghamii* (Hook.) Oerst. and of *Acacia dealbata* Link at that site. *Eucalyptus obliqua* was the dominant canopy species in all plots, with >50% basal area at each plot, although it was never the most numerous in terms of number of stems. Both Edwards Rd plots contained large numbers of *P. apetala*, which accounted for >40% of the basal area of those plots, to the detriment of rainforest species such as *N. cunninghamii*, *Atherosperma moschatum* Labill. and *Eucryphia lucida* (Labill.) Baill. This was in contrast to the Hartz Rd plots, which contained little or no *P. apetala*, but more rainforest species plus *A. dealbata*.

Macrofungal species richness

The six fortnightly visits yielded 90 species from 619 records on dead wood in the four plots surveyed. Of these, the 77 species believed to prefer wood as its substrate are listed in table 4 and were used in the subsequent statistical analyses. Table 4 also gives the number of records of each species, their wood decay class and diameter class, the plot in which they were recorded, the wood substrate species, and whether the wood was fallen, suspended, or a stag.

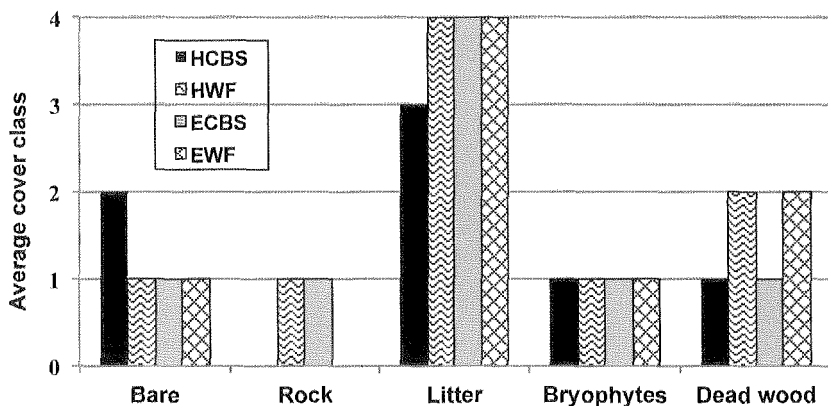


FIG. 2 — Average cover classes (modified Braun-Blanquet scores) for observed ground cover on each plot (HCBS=Hartz Rd CBS; HWF=Hartz Rd Wildfire; ECBS=Edwards Rd CBS; EWF=Edwards Rd Wildfire).

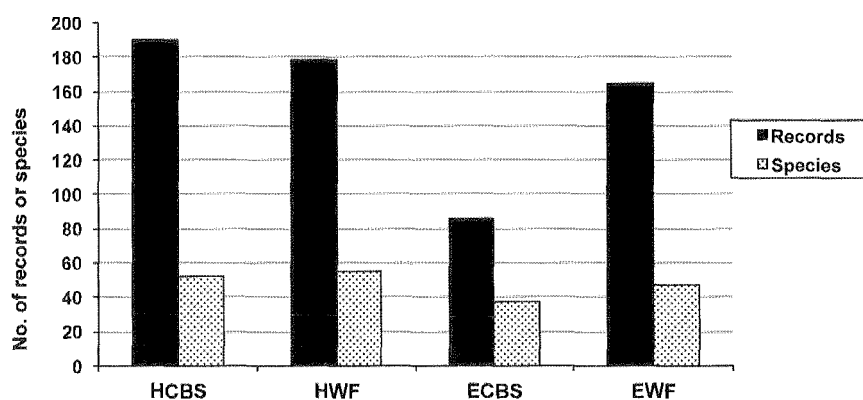


FIG. 3 — Number of records and number of species of macrofungi in each plot from six visits (HCBS=Hartz Rd CBS; HWF=Hartz Rd Wildfire; ECBS=Edwards Rd CBS; EWF=Edwards Rd Wildfire).

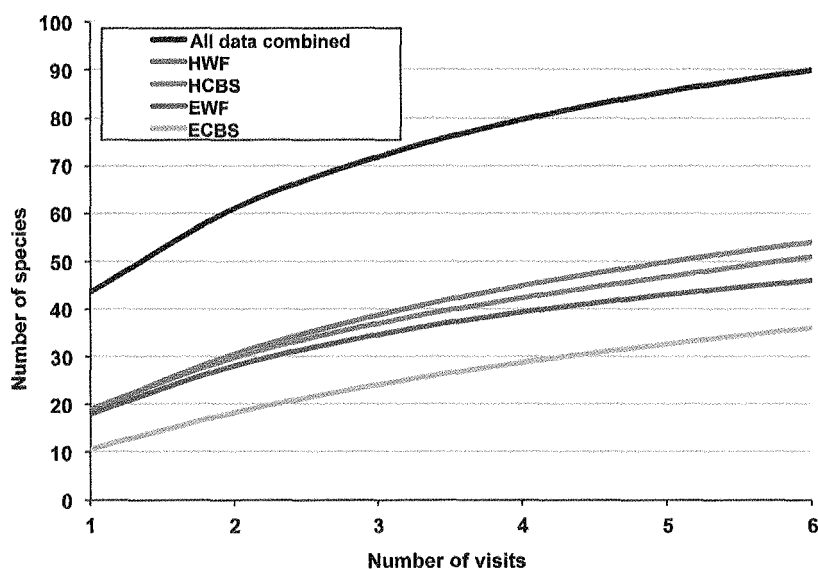


FIG. 4 — Randomised macrofungal species accumulation curves for each plot and for all plots combined (HWF=Hartz Rd Wildfire; HCBS=Hartz Rd CBS; EWF=Edwards Rd Wildfire; ECBS=Edwards Rd CBS).

TABLE 4
 Compilation of the 77 wood-preferring macrofungal species collected during the survey. The records are classified by their wood decay class and diameter class, the plot in which they were recorded, the wood substrate, and whether the substrate was suspended, not suspended, or a stag

Macrofungal species	Total records ¹	Wood decay class ²			Wood diameter class ³			Plot identification ⁴				Wood substrate ⁵					Wood suspended? ⁶			
		L	M	H	S	M	L	E _C	E _W	H _C	H _W	A	B	E	N	O	P	No	Stag	Yes
<i>Amauroderma rude</i> (Berk.) Torrend	1	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	0	1	0
<i>Armillaria novae-zelandiae</i> (G. Stev.) Herink	4	0	1	3	0	1	3	0	0	2	2	0	0	4	0	0	0	3	1	0
<i>Ascocoryne sarcoides</i> (Jacq.) J.W. Groves & D.E. Wilson	1	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1
Ascomycete "white brusing orange"	18	0	15	3	4	5	9	1	1	8	8	0	0	18	0	0	0	15	0	3
<i>Australoporus tasmanicus</i> (Berk.) P.K. Buchanan & Ryvardeen	3	0	2	1	0	1	2	0	0	1	2	1	0	2	0	0	0	3	0	0
<i>Biscogniauxia</i> sp.	1	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Bisporella</i> "green-yellow"	6	0	3	3	1	2	3	1	1	0	4	0	0	5	0	0	1	5	0	1
<i>Bisporella citrina</i> (Batsch) Korf & S.E. Carp.	5	1	4	0	2	2	1	2	0	0	3	0	0	5	0	0	0	5	0	0
<i>Byssomerulius corium</i> (Pers.) Parmasto	1	0	1	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0
<i>Callistosporium</i> "Maroon on wood"	3	0	2	1	0	0	3	1	0	1	1	0	0	3	0	0	0	2	0	1
<i>Calocera</i> "spathulate"	3	1	2	0	0	3	0	0	0	1	2	0	0	3	0	0	0	0	0	3
<i>Calocera guepinioides</i> Berk.	9	4	5	0	2	7	0	1	4	3	1	1	0	3	0	0	5	3	0	6
<i>Chlorociboria aeruginascens</i> (Nyl.) Kanouse	7	4	2	1	4	3	0	0	4	0	3	0	0	4	0	0	3	2	0	5
<i>Clavicornia piperata</i> (Kauffman) Leathers & A.H. Sm.	24	0	16	8	6	9	9	7	8	5	4	2	0	18	0	0	4	21	1	2
<i>Clitocybula</i> "Maria on wood"	1	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0
<i>Collybia eucalyptorum</i> Cleland	13	2	10	1	0	2	11	2	2	3	6	0	0	13	0	0	0	10	0	3
<i>Crepidotus</i> "orange"	2	0	2	0	0	1	1	1	0	1	0	0	0	1	0	0	1	0	1	1
<i>Crepidotus nephrodes</i> (Berk. & M.A. Curtis) Sacc.	6	0	2	4	3	3	0	0	2	3	1	1	1	3	0	0	1	3	0	3
<i>Daldinia grandis</i> Child	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0
<i>Exidia</i> sp.	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1
<i>Galerina patagonica</i> Singer	13	1	5	7	7	6	0	0	12	1	0	0	0	3	0	0	10	7	1	5
<i>Ganoderma australe</i> (Fr.) Pat.	2	0	1	1	0	0	2	1	0	0	1	0	0	2	0	0	0	1	1	0
<i>Gloeoporus taxicola</i> (Pers.) Gilb. & Ryvardeen	2	1	1	0	0	0	2	0	0	1	1	1	0	1	0	0	0	2	0	0
<i>Gymnopilus allantopus</i> (Berk.) Pegler	6	0	5	1	3	2	1	0	2	3	1	0	0	5	0	0	1	3	0	3
<i>Gymnopilus ferruginosus</i> B.J. Rees	9	0	6	3	1	2	6	2	0	2	5	0	0	9	0	0	0	7	0	2
<i>Gymnopilus tyallus</i> Grgur.	3	0	3	0	0	2	1	0	0	2	1	0	0	3	0	0	0	1	1	1
<i>Hericium coralloides</i> (Scop.) Pers.	1	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0
<i>Heterotextus peziziformis</i> (Berk.) Lloyd	18	11	7	0	13	5	0	2	6	7	3	0	0	16	0	0	2	10	0	8
<i>Hohenbuehelia</i> sp.	6	0	1	5	1	1	4	0	2	1	3	0	0	4	0	0	2	4	1	1
<i>Hypholoma brunneum</i> (Masse) D.A. Reid	2	0	1	1	0	2	0	0	0	0	2	0	0	2	0	0	0	1	0	1
<i>Hypholoma fasciculare</i> (Huds. : Fr.) P. Kumm.	24	1	17	6	6	12	6	5	1	10	8	0	0	24	0	0	0	17	0	7
<i>Hypocrea megalosulphurea</i> Yoshim. Doi	3	1	2	0	2	1	0	0	3	0	0	0	0	0	0	0	3	2	0	1
<i>Hypoxylon</i> aff. <i>placentiforme</i> Berk. & M.A. Curtis	16	7	7	2	6	9	1	3	13	0	0	0	0	1	0	0	15	8	0	8
<i>Hypoxylon crocopeplum</i> Berk. & M.A. Curtis	2	0	2	0	1	1	0	0	2	0	0	0	0	1	0	0	1	2	0	0
<i>Junghuhnia rhinocephala</i> (Berk.) Ryvardeen	10	2	7	1	6	4	0	3	7	0	0	0	0	0	0	0	10	6	0	4
<i>Lanzia lanaripes</i> (Dennis) Spooner	5	3	2	0	5	0	0	0	2	2	1	0	0	5	0	0	0	1	0	4
<i>Lentinellus pulvinulus</i> (Berk.) Pegler	11	1	6	4	3	8	0	0	7	2	2	3	0	1	0	0	7	9	0	2
<i>Marasmiellus affixus</i> (Berk.) Singer	60	26	32	2	33	27	0	4	19	16	21	0	0	55	0	0	5	14	1	45
<i>Melanotus hepatochrous</i> (Berk.) Singer	11	8	1	2	4	5	2	0	3	5	3	1	1	9	0	0	0	3	0	8
<i>Mollisia cinerea</i> (Batsch) P. Karst.	2	0	2	0	1	0	1	0	0	0	2	0	0	2	0	0	0	1	0	1

<i>Mucronella pendula</i> (Masse) R.H. Petersen	3	0	3	0	0	0	3	0	1	0	2	0	0	3	0	0	0	3	0	0
<i>Mycena</i> "gelatinous grey frilly"	2	1	1	0	2	0	0	0	2	0	0	0	0	0	0	0	2	1	0	1
<i>Mycena austrororida</i> Singer	3	1	1	1	0	3	0	2	0	0	1	0	0	3	0	0	0	1	0	2
<i>Mycena carmeliana</i> Grgur.	17	3	12	2	2	10	5	5	1	7	4	0	0	15	0	0	2	8	0	9
<i>Mycena interrupta</i> (Berk.) Sacc.	41	7	25	9	14	25	2	7	5	16	13	0	0	35	0	0	6	9	1	31
<i>Mycena kuurkacea</i> Grgur.	21	5	14	2	8	10	3	9	3	7	2	0	0	15	0	2	4	11	0	10
<i>Mycena maldea</i> Grgur.	7	0	6	1	0	4	3	0	0	1	6	1	0	6	0	0	0	4	0	3
<i>Mycena mulawaensis</i> Grgur.	23	3	14	6	4	16	3	0	2	12	9	2	0	19	0	0	2	16	0	7
<i>Mycena nargan</i> Grgur.	2	0	2	0	0	2	0	0	0	0	2	0	0	2	0	0	0	1	0	1
<i>Mycena subgalericulata</i> Cleland	19	1	17	1	2	3	14	3	5	6	5	0	0	19	0	0	0	16	0	3
<i>Panellus stipticus</i> (Bull.) P. Karst.	1	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1
<i>Pholiota multicingulata</i> E. Horak	12	2	7	3	4	7	1	1	8	3	0	1	0	5	0	0	6	7	1	4
<i>Pluteus atromarginatus</i> (Konrad) Kühner	1	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1
<i>Polyporus gayanus</i> Lév.	3	0	2	1	2	1	0	2	1	0	0	0	0	0	0	0	3	0	0	3
<i>Polyporus melanopus</i> (Sw. : Fr.) Fr.	4	2	2	0	0	4	0	0	4	0	0	0	0	0	0	0	4	2	0	2
<i>Postia dissecta</i> (Lév.) Rajchenb.	8	0	7	1	0	8	0	1	0	5	2	0	0	8	0	0	0	4	1	3
<i>Postia lactea</i> (Fr.) P. Karst.	1	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1
<i>Postia pelliculosa</i> (Berk.) Rajchenb.	6	0	5	1	2	1	3	1	2	0	3	1	0	5	0	0	0	4	1	1
<i>Postia punctata</i> Rajchenb. & P.K. Buchanan	10	0	8	2	0	1	9	3	3	0	4	0	0	10	0	0	0	8	2	0
<i>Postia subcaesia</i> (A. David) Jülich.	2	1	0	1	2	0	0	1	1	0	0	0	0	0	0	0	2	1	0	1
<i>Postia venata</i> (Rajchenb. & J.E. Wright) Rajchenb.	2	0	2	0	0	1	1	0	0	1	1	0	0	2	0	0	0	2	0	0
<i>Psathyrella</i> "pale brown gills"	1	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0
<i>Psathyrella echinata</i> (Cleland) Grgur.	2	0	2	0	0	2	0	1	0	0	1	0	0	2	0	0	0	1	0	1
<i>Psathyrella</i> sp.	3	1	1	1	1	2	0	1	1	0	1	0	0	2	1	0	0	2	0	1
<i>Pseudohydnum gelatinosum</i> (Scop.) P. Karst.	2	0	1	1	0	2	0	0	0	1	1	0	0	2	0	0	0	1	1	0
<i>Simocybe phlebophora</i> E. Horak	2	0	1	1	2	0	0	0	2	0	0	0	0	0	0	0	2	2	0	0
<i>Skeletocutis nivea</i> (Jungh.) Jean Keller	4	0	4	0	2	2	0	1	0	1	2	1	0	1	0	0	2	1	0	3
<i>Steccherinum ochraceum</i> (Pers.) Gray	3	1	2	0	2	1	0	0	3	0	0	0	0	0	0	0	3	3	0	0
<i>Stereum hirsutum</i> (Willd.) Pers.	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0
<i>Stereum illudens</i> Berk.	4	3	1	0	3	1	0	1	0	2	1	0	0	4	0	0	0	1	0	3
<i>Stereum ostrea</i> (Blume & T. Nees) Fr.	2	1	1	0	1	1	0	1	1	0	0	0	0	0	0	0	2	1	0	1
<i>Stereum rugosum</i> Pers.	25	17	8	0	13	12	0	0	8	8	9	0	0	24	0	0	1	13	0	12
<i>Tremella fimbriata</i> Pers.	1	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0
<i>Tricholomopsis rutilans</i> (Schaeff.) Singer	2	2	0	0	0	2	0	2	0	0	0	0	0	2	0	0	0	2	0	0
<i>Tubaria rufofulva</i> (Cleland) D.A. Reid & E. Horak	1	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1
<i>Vibrissea dura</i> G.W. Beaton & Weste	18	1	15	2	0	12	6	2	0	11	5	0	0	18	0	0	0	17	0	1
<i>Xylaria castorea</i> Berk.	1	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1
Totals ⁽⁷⁾	619	142	367	110	204	278	137	86	165	190	178	22	2	472	3	2	118	349	17	253

Notes: (1) Total no. of records; (2) Wood decay class, L=low, M=medium, H=high; (3) Wood diameter, S=small, D \leq 10 cm; M=medium, 10<D<40 cm; L=large, D \geq 40 cm; (4) Plot ID, E_c=Edwards Rd CBS=ECBS, E_w=Edwards Rd wildfire=EWF, H_c=Hartz Rd CBS plot=HCBS, H_w=Hartz Rd wildfire=HWF; (5) Wood substrate, A=*Acacia dealbata*, B=*Bedfordia salicina*, E=*Eucalyptus obliqua*, N=*Nothofagus cunninghamii*, O=*Olearia argophylla*, P=*Pomaderris apelata*; (6) Wood suspended? No=on ground, Stag=dead standing tree, Yes=suspended in air; (7) All totals at the foot of this table include the records for 13 species considered to prefer litter or soil rather than wood, but which were found in association with wood in this study.

The two Hartz Rd plots had a similar number of macrofungal records and species, with the CBS and wildfire plots having 54 and 51 species, respectively (fig. 3). At Edwards Rd the diversity was lower in both plots, especially the number of species in the CBS plot (36 compared to 46 in the wildfire plot). In the randomised species accumulation curves (fig. 4), the distances between the curve for the data from all plots combined and the curves for the individual plots suggest that the commonality among the species in the different plots is not high, each individual plot containing some unique macrofungal species, the identities of which may be determined from table 4.

Macrofungal species assemblages

The species assemblages in the four plots were different, as shown by the first two axes of a 3-d nMDS ordination (fig. 5, stress=0.09). The figure clearly separates the assemblages in the Hartz Rd plots from those in Edwards Rd, but within Hartz Rd there is a fair amount of overlap between the macrofungi in the CBS and wildfire plots. This overlap is not resolved on the third axis (not shown). The results of DISTLM regression modelling using the first two dbRDA axis (fig. 6), reinforces the message of the nMDS ordination, with the two plots at Hartz Rd clearly separated from the Edwards Rd plots and from each other, but with the two Edwards Rd plots overlapping and not separated on the third dbRDA axis (not shown). The important predictor variables are summarised in table 5, which shows that the number of live *P. apetala* stems was the main indicator of differences among the plots, with the number of live *O. argophylla* stems being the second most important. The physical properties of the plot quadrants, viz. the soil pH, slope, canopy cover and the components of the ground cover, did not contribute significantly to explaining differences in the macrofungi found in the experimental units.

DISCUSSION

Macrofungal species richness

The total of 77 wood-preferring species (table 4) is high compared to the diversity found at other locations in Australia (Hilton *et al.* 1989, 40 spp.; Burns & Conran 1997, 13 spp.; McMullan-Fisher *et al.* 2002, 35 spp.; Robinson *et al.* 2003, 63 spp.; Robinson & Tunsell 2007, 68 spp.). However, those studies were in Western Australia, South Australia or Victoria, in different forest types and where the macrofungal fruiting season is shorter in their warmer, drier climate compared

with Tasmania. Gates *et al.* (2011c), in a study conducted over a period of 14 months of fortnightly visits to a larger plot area (0.25 ha compared with 0.16 ha) not far from that of the present study, identified 308 species that can be classified as wood-preferring macrofungi. Of those 308 species, 69 were also found in this study. The remaining 239 species included many resupinate species, a group that due to time limitations could not be examined in great detail. In addition, Hopkins *et al.* (2011) found 91 putative operational taxonomic units (OTUs) from 18 living *E. obliqua* trees in an area close to the present study. However, that study was based on isolating fungi from the wood and identifying from cultures and from molecular techniques. Most of the OTUs could not be matched with a macrofungal fruit body and some may never form a fruit body during their life cycle. This further supports the notion that fungal diversity in *E. obliqua* forests is very high.

The number of species present in each of the quadrants, used as a measure of species richness, did not lead to a significant difference due to treatment (CBS vs. wildfire) in this study, as the low species numbers in ECBS compared with EWF at Edwards Rd was not matched by the results at Hartz Rd (see fig. 3). Similarly, Browning *et al.* (2010) found that species richness of mosses, liverworts and ferns on coarse woody debris was not significantly different in CBS and post-wildfire 43-year-old plots in this same forest.

Macrofungal species richness – substrate species

A noteworthy result from the present survey is the fact that 95% of the 619 macrofungal records occurred on only two substrate species, viz. *Eucalyptus obliqua* (76%) and *Pomaderris apetala* (19%). Only three records (0.5%) occurred on *Nothofagus cunninghamii*, a sharp contrast to South America and New Zealand, where *Nothofagus* forests are the supporters of many native macrofungal species (for New Zealand, see McKenzie *et al.* 2000). In Tasmania, wood-inhabiting polypore species found on *Nothofagus* in South America (Rajchenberg 2006) prefer eucalypt wood rather than *Nothofagus* (Gates *et al.* 2011c). Evidence from previous surveys suggest that eucalypt-dominated forests are also rich in ectomycorrhizal macrofungal species in soil (Gates *et al.* 2011a) and in litter (Gates *et al.* 2011b). Further evidence comes from Western Australia (Robinson & Tunsell 2007), where there are no extant *Nothofagus* species, but which did occur in the past as a legacy from Gondwanaland (Bougher *et al.* 1994, Carpenter & Pole 1995). The modern Western Australian forests that are rich in macrofungi are dominated either by *Eucalyptus diversicolor* F.Muell. or *E. marginata* Sm., which is evidence that, in Australia, eucalypts may be the major vascular plant host of macrofungi. In the present study, *Pomaderris* was an important secondary host to *Eucalyptus*, with 35 species found on *P. apetala*, of which 13 were found only on this species (table 4). This reinforces the finding from Gates *et al.* (2011c), where fallen and suspended *P. apetala* occurred abundantly in two of the four plots surveyed and supported 85 macrofungal species of which 33 were only on that substrate. Fallen *P. apetala* produces a lot of small to medium diameter wood in the low or medium decay class, which can support what Rayner & Boddy (1988) refer to as “latent invader” fungi, an example of which is *Hypoxylon* aff. *placentiforme* Berk. & M.A. Curtis, found frequently in this study. Also, as *P. apetala* has a very smooth bark, it may

TABLE 5
DISTLM modelling using a stepwise procedure, showing the significant explanatory variables for the macrofungal assemblages

Explanatory variables entered	P-value	Cumulative R ² explained
<i>Pomaderris apetala</i>	0.0006	0.159
<i>Olearea argophylla</i>	0.0420	0.257
<i>Phyllocladus asplenifolius</i>	0.0219	0.357

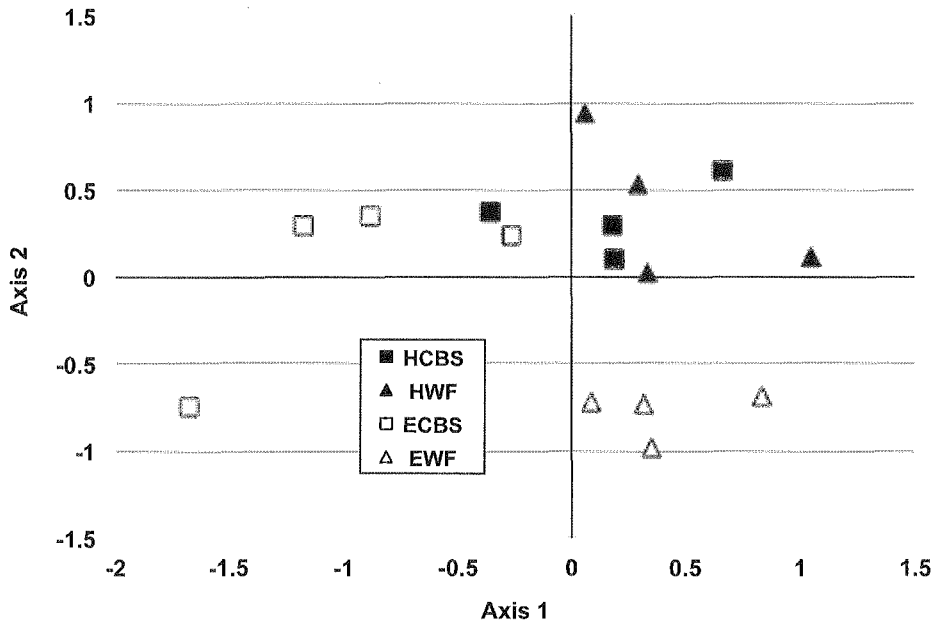


FIG. 5 — The first two axes of a three-dimensional non-metric multidimensional scaling ordination applied to the Bray-Curtis resemblance matrix obtained from the macrofungal species assemblages observed during the six visits (stress = 0.09) (HCBS=Hartz Rd CBS; HWF=Hartz Rd Wildfire; ECBS=Edwards Rd CBS; EWF=Edwards Rd Wildfire).

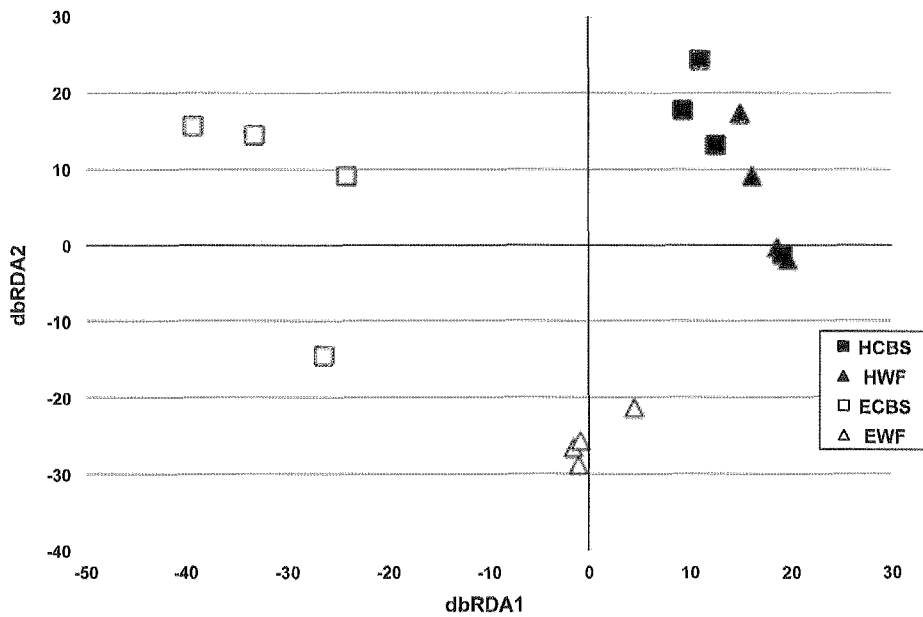


FIG. 6 — dbRDA graph of best DISTLM model, the points representing the macrofungal species assemblages pooled over six visits in four quadrants of each of the four plots (HCBS=Hartz Rd CBS; HWF=Hartz Rd Wildfire; ECBS=Edwards Rd CBS; EWF=Edwards Rd Wildfire).

present a more favourable surface for spore colonisation to some species of fungi (see Renvall 1995).

Macrofungal species assemblages – influence of site variables

The vascular plant community was shown to have a significant effect on the macrofungal assemblages found (table 5, figs 5 & 6). The important influence of the vascular plant communities was also shown for the southern wet *E. obliqua* forests of Tasmania by Packham *et al.* (2002), who found a distinct difference between the macrofungal assemblages in mature (generally long unburnt) and regrowth (recently burnt) forests.

Some further observations

Table 4 includes several species usually associated with old forests in Tasmania. These species occur either on large diameter wood, highly decayed wood, or are host specific. They are not confined to any one plot in this study but are found on biological legacies from a pre-disturbed stand irrespective of type of disturbance. For example, *Hericum coralloides* (see table 4 for naming authorities of the fungi) was found on a well-decayed stag of *N. cunninghamii* in the Hartz CBS plot, and *Australoporus tasmanicus* was found on a large diameter log in a high decay class in the Hartz wildfire plot. The common brown heart-rot fungus *Postia punctata* was present in all plots (mostly on large diameter wood in a medium decay class) except for Hartz CBS but even so it was noted on a very large *E. obliqua* log outside of the plot area but still within the CBS coupe. *Postia subcaesia* was the only heart-rot fungus found on small diameter wood. This fungus usually forms small fruit bodies, and a small fungus shouldn't require a large spatial domain, according to Rayner & Boddy (1988). Similarly, the small fruit bodies of *Skeletocutis nivea*, *Gloeoporus taxicola* and *Junghuhnia rhinocephala* were found only on small or medium diameter wood, with the last species being confined to *P. apetala*. In Tasmania, *J. rhinocephala* has not yet been found on any other wood species, although in the Melbourne Herbarium (MEL) there are collections of it occurring on *Acacia* species. Four *Stereum* species, viz. *S. ostrea*, *S. illudens*, *S. rugosum* and *S. hirsutum*, were absent from large diameter wood in a high decay class. This is consistent with their known existence as latent invaders of sapwood and as some of the first fungi to appear on freshly downed wood. *Galerina patagonica* was predominantly found on small and medium diameter wood in the medium and high decay classes (as in Gates 2009), with only a single record on wood in a low decay class in the current study. Generally, however, the agarics, in particular the majority of the *Mycena* species, were spread across all wood diameter sizes and decay stages as observed by McMullan-Fisher (2008) and Gates (2009). A notable exception is *M. subgalericulata* which commonly fruits on large diameter living *E. obliqua* trees (Grgurinovic 2003) and continues fruiting on the fallen large diameter wood. Species very commonly found in old *E. obliqua* forests, such as *Pluteus* spp., *Pleurotus purpureo-olivaceus*, *Plectania campylospora*, *Psilocybe brunneoalbescens*, *Hypoxylon bovei* var. *microsporum*, *Fomes hemitephrus* and *Tyromyces merulinus* were not observed. This could be related to the short duration of the study, the small area surveyed or, in the case of the CBS plots, the lack of biological legacies.

Implications for sustainable forestry management

The results of this study can assist in developing protocols for sustainable forestry management in Tasmania. The current silviculture process of CBS removes large living trees which would eventually end up being large dead wood in the natural cycle of a wet *E. obliqua* forest. Wildfire disturbance being non-stand replacing in these forests (Alcorn *et al.* 2001, Turner *et al.* 2009) and at intervals of ca. three fires per century leaves either large stags, which are the next input of large dead wood, or living trees which are not killed by the fire. Our results show that there is a number of species of macrofungi (e.g., *Australoporus tasmanicus* and *Ganoderma australe*) which are only found fruiting on large diameter wood. This suggests that biodiversity of a pre-disturbance stand (as measured using fruit bodies) can be maintained in a 43-year-old forest, irrespective of whether it is regenerating after CBS silviculture or as a result of wildfire, providing there is sufficient large dead wood remaining after disturbance and that conditions are conducive to fruit body formation. This study could also assist in assessing the impact of the currently trialled alternative silviculture treatment to CBS in southern Tasmania, i.e. ARN, where "islands" of pre-disturbance habitat are retained to maintain biodiversity. The removal of all dead wood for biofuel could affect wood-inhabiting fungi; however, it is not known how much dead wood is necessary to retain in each decay stages and size class. The important point from this study is that retaining dead wood of all sizes and decay stages is necessary to maintain wood-inhabiting macrofungal diversity irrespective of whether it is a wildfire or a silviculture disturbance and should be part of sustainable forestry management protocols for the wet *E. obliqua* forests of southern Tasmania.

CONCLUSIONS

We conclude that:

- Dead wood of different sizes and stages of decay is a substrate for a rich and diverse assemblage of macrofungal species, supporting the finding of Gates (2009).
- A short-term study in these forests, such as the current one, can provide informative data.
- The presence of *Pomaderris apetala*, which was very abundant at the Edwards Rd plots but very sparse at the Hartz Rd plots, significantly influenced the macrofungal species assemblages, supporting a suite of species not found on other substrates.
- The low number of macrofungal species fruiting on *Nothofagus* is surprising, in view of the importance of that genus in New Zealand and South America as a substrate for wood-inhabiting fungi.
- The results of this study on wood-inhabiting macrofungi complement those of Gates *et al.* (2005, 2011c), adding an age since wildfire (43 years) not considered in the earlier studies. It also had anthropogenic disturbance as a comparison.
- Further studies in forests at different ages of regeneration are needed before and after both natural and anthropogenic disturbance to obtain a better picture of the effects of disturbance on macrofungal diversity in these forests.

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