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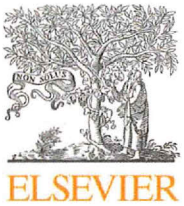

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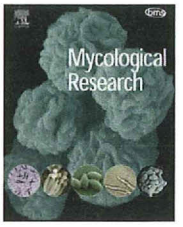

Diversity and habitat relationships of hypogeous fungi. III. Factors influencing the occurrence of fire-adapted species

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ABSTRACT

Among the huge array of hypogeous ectomycorrhizal fungi so far documented from Australia, six genera and more than 30 species occur within the family Mesophelliaceae, all of which show various adaptations for surviving in fire-prone landscapes. These mostly endemic fungi are critical to postfire reestablishment of regenerating vegetation, and their fruit-bodies provide essential food resources for diverse ground-dwelling fauna. We developed habitat models for five common representatives of the Mesophelliaceae based on repeat collections of their fruit-bodies from 136 study plots situated along a series of environmental gradients across the south-eastern mainland of Australia. At a meso- or landscape scale, temperature influenced the occurrence of Castoreum *radicatum,* Mesophellia *clelandii* and *Nothocastoreum cretaceum,* with the type of response varying. Below a threshold, C. *radicatum* preferred sites with cooler mean annual temperatures. In contrast, M. clelandii and N. *cretaceum* had optimal ranges of temperature, above and below which the probability of detecting them dropped. Also at a landscape scale, C. *radicatum* was more likely to be detected at sites with lower levels of precipitation during the driest quarter of the year. At a micro-site scale, M. clelandii and N. *cretaceum* were more likely to occur in stands with an intermediate number of host eucalypt stems, likely relating to successional age of the stand. Sites with a higher number of large fallen trees were more likely to have N. cretaceum, while sites with intermediate litter depths were more likely to have C. radicatum and M. c1elandii. *Mesophellia glauca* and M. trabalis showed no consistent patterns. They are apparently the most broadly adaptable in terms of the independent variables tested. Although fire has been previously suggested to be heavily implicated in the life cycle of several members of the Mesophelliaceae, we found no relationship between time since disturbance by fire and other factors and likelihood of occurrence. Instead, other habitat attributes appeared to be more important in explaining their distribution. The complex

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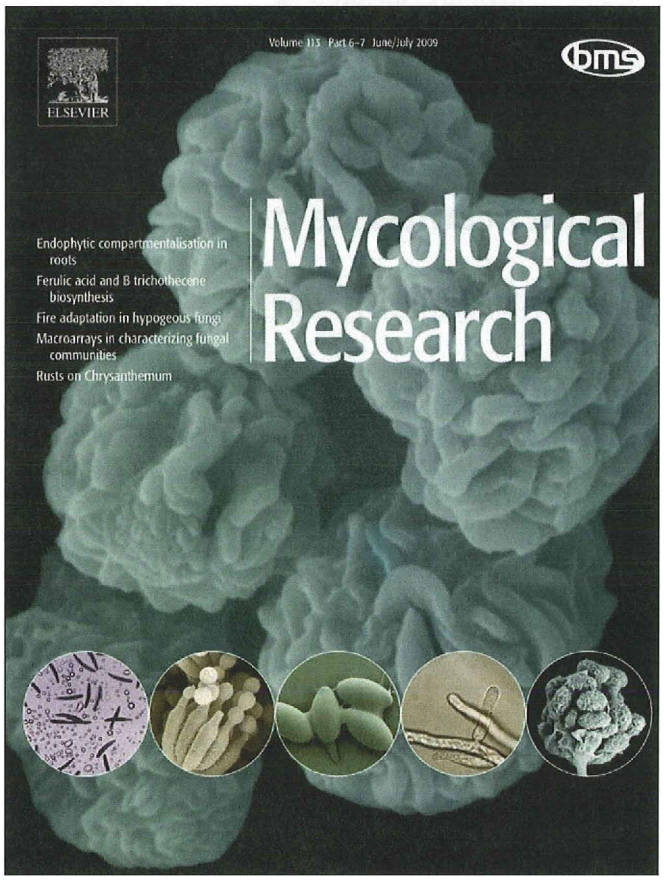

and differing responses of the species of Mesophelliaceaestudied here, to features of their environment, reinforce the need to manage multiple-use forest landscapes across the region for a diversity of attributes.

Introduction

In a recent commentary, Lilleskov & Parrent (2007)observed that knowledge about factors influencing the distribution and occurrence of mycorrhizal fungi across forested landscapes is still in its infancy. This is certainly true for Australia, where the diversity of mycorrhizal fungi in *Eucalyptus*-dominated forests, particularly that of hypogeous (underground-fruiting) species, is only just being recognised (Claridge 2002). The taxonomy of Australian hypogeous fungi has been notably advanced over the past few decades, thanks in considerable part to traditional morphological methods and more recently to the availability of molecular tools (Hosaka et *al.* 2006). Knowledge of the ecology of these species lags far behind that of taxonomy, however, an unfortunate circumstance in light of their apparent importance as ectomycorrhizal associates oftrees and shrubs and as majorfood resources for diverse animals, including several that are threatened or endangered (see Claridge & May 1994;Claridge 2002).

Recognising this deficiency, we designed a study to combine research on taxonomy and ecology of hypogeous fungi by sampling them from different forested sites in southeastern mainland Australia. Preliminary results were described in Claridge et *al.* (2000a,2000b). Relationships between the different fungal species collected and their ectomycorrhizal host trees, as revealed from our data, have also been reported (Jumpponen et *al.* 2004).Since our earlier studies, we have repeated samplings of hypogeous fungi from each study site over a longer time, collecting many more species and increasing the encounter rate of individual species to further examine patterns in the occurrence of more commonly collected taxa. In this paper we present results of our modelling of habitat relationships of selected fire-adapted species in the genera Castoreum, Mesophellia, and Nothocastoreum, family Mesophelliaceae.

The Mesophelliaceae is endemic to Australasia, with most species known only from Australia. Fruit-bodies of species within the family typically survive the wildfires commonplace in Eucalyptus-dominated forests across the continent. This is partly because of their anatomy and partly because many fruit deeply enough in the soil to avoid lethal heat (Johnson 1995; Claridge et *al.* 2001; Claridge 2002; Claridge & Trappe 2004; Vernes et *al.* 2004). Accordingly, they can be vital to postfire survival of small marsupials such as rat-kangaroos (bettongs and potoroos) and bandicoots, which feed on them preferentially when other food resources may be initially scarce in the postfire environment.

Molecular phylogenetic analyses have established that the Mesophelliaceae belong in the order Hysterangiales (Hosaka et *al.* 2006).The family includes Mesophellia (including *Malajczukia*), the type genus; plus *Andebbia, Castoreum, Gummiglobus, Gummivena,* and *Nothocastoreum.* The genus *Malajczukia,* segregated from *Mesophellia* on morphological grounds (Trappe et *al.* 1992), has since been found by molecular analysis to be congeneric with *Mesophellia* (Hosaka et *al.* 2006; W. Colgan and J.M. Trappe, unpublished data).

Members of the Mesophelliaceae all produce a powdery spore mass but have various unique morphological characters so far without parallel in the Kingdom Fungi. *Mesophellia* (Fig 1) and *Andebbia* are constructed with a thin, brittle outer peridium. Underlying that surface layer is a thick, soft layer permeated with ectomycorrhizae of associated *Eucalyptus* ectomycorrhizae. Within that layer is a relatively thin endoperidium. The centre of the basidiomata is occupied by a rubbery core attached to the endoperidium by trabeculae, i.e. minute to robust columns. The spores are born in the space between the endoperidium and core amongst the connecting columns (Dell et *al.* 1990;

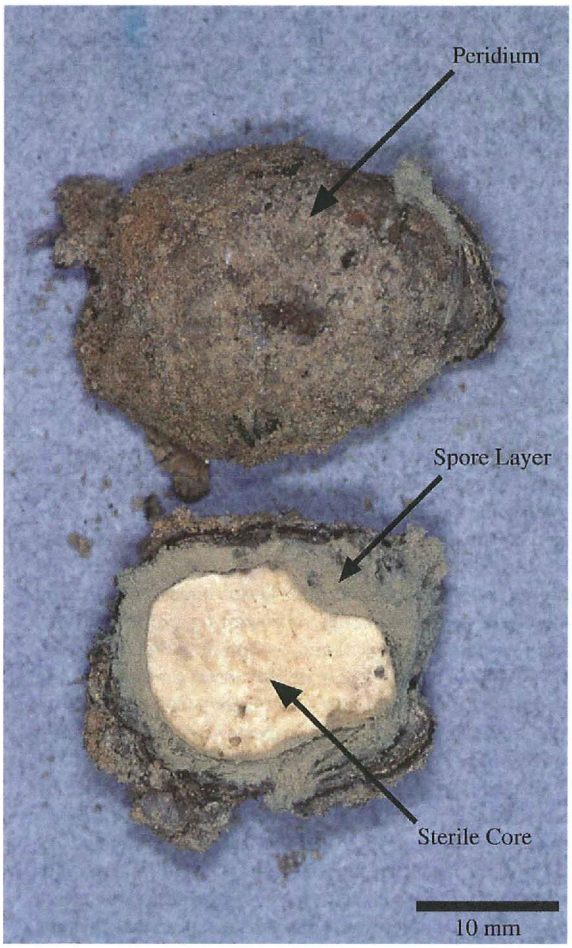

Fig 1 – Cross-section through the fruit-body of *Mesophellia clelandii*, highlighting major morphological features common to the genus.

Trappe et al. 1992, 1996). The manner in which these structures enable spore dispersal by animal mycophagy has been described by Claridge et al. (2001) and Claridge & Trappe (2004). *Castoreum*, Gummiglobus and *Gummivena* lack the unique central core of the two aforementioned genera but characteristically have gummy, elastic tissue in the peridium (Dell et al. 1990; Trappe & Castellano 1996; Trappe & Bougher 2002). This tissue, composed of gelatinised hyphae that can be stretched from diameters of 5+ um to <1 um before breaking, is novel to these genera so far as we know. Its function is unknown but may relate to protecting the basidiomata from attack by arthropods. *Nothocastoreum* lacks the central core of Mesophellia and the gummy hyphae of the other three genera (Beaton & Weste 1984). instead, it fruits near the soil surface and its peridium becomes thin and brittle at maturity. When raked out by a mycologist or scraped out by an animal, the top of the peridium breaks away and spores are released into the air.

Mesophellia, including Malajczukia, was mono graphed with 22 species by Trappe et al. (1992, 1996); we have since discovered a few new, as yet unpublished species. In our study area we encountered M. clelandii, M. glauca, and M. trabalis, each on enough plots to be included in our habitat modelling. The genus *Castoreum* has not been monographed in total; our draft manuscript on this genus contains seven species (J.M. Trappe & A.W. Claridge, unpublished data); only C. *radicatum* occurred with enough frequency for habitat analysis. One species of Nothocastoreum, N. *cretaceum* (Beaton & Weste 1984), has been described. It occurred on enough plots for habitat analysis. Gummiglobus agglutinosporus and Andebbia *pachythrix* occurred on our plots but at too low a frequency for analysis. *Gummivena* is known only from Western Australia so was not found in the study.

Materials and methods

Study *area and* site selection strategy

The study area within the eastern part of Victoria (East Gippsland) and adjacent New South Wales in southeastern mainland Australia comprises a rectangle of forested land bounded by the longitudes 147°30'E and 150°0'E and latitudes 36°30'S and 38°0'S (Claridge et al. 2000a, 2000b). Within this geographic area we selected a series of sites for sampling fruit-bodies of hypogeous fungi, representing a stratified sample of the climatic, geological and topographic features of the region. We linked a 250 x 250 m digital elevation model to the climate prediction system BIOCLIM (Busby 1986; Nix 1986) to derive spatial estimates of nine important climatic parameters. Values for these estimates for each grid cell within the study area were then run through an ordination process by the pattern analysis software PATN (Belbin 1989) to derive 20 higher order 'climate groups'. Output from the climate stratification scheme was then overlayed on to a geological map for the entire study area, and from this overlay a series of climate group-geological classes were derived. For practical reasons we sampled a reduced set of these: the 24 combinations chosen were typically more broadly distributed across the landscape and readily accessible all-year-round by public road. As a final level of stratification, sites were chosen within four major topographic strata (ridge/upper slope, sheltered slope, exposed slope and gully/lower slope). A final set of 136 sites, each measuring 50 x 20 m in dimension, were identified for sampling. Further details about site selection, including information on the source of primary data used in the stratification process, are described in Claridge et al. (2000a, 2000b).

Detection *and processing of fungi*

We used the presence of fruit-bodies on each study plot as a means of assessing the occurrence of different hypogeous fungi. In brief, on each sampling event, we collected the fruit-bodies of such fungi within each 50 x 20 m plot by a time constraint method. Four people raked the soil-litter surface within each plot for a total of 100 person-minutes each time, using four-tined garden cultivators. The time taken to sample fruit-bodies was previously determined to allow the number of species within each plot to be sampled with high precision (Claridge et al. 2000a). All fruit-bodies excavated during raking were collected in wax-paper bags, labelled for date, site and collector. Characteristics of fresh fungal fruit-bodies were noted at the end of each field day, particularly size range, shape, surface texture and colour, colour changes with bruising, and odour. For each collection of members of the Mesophelliaceae, sub-samples of fruit-bodies were cut in vertical slices with a sharp razor-blade and notes recorded on the thickness and layering of the peridium (outer skin), the glebal (spore mass) colour and general structure. Based on these features, each collection was ascribed tentatively to genus. Collections were then dried in a food dehydrator (45°C for 8-10 h), weighed and then placed in labelled paper envelopes. In the laboratory, these were identified to species by one of us (J.M. Trappe), using existing published and unpublished taxonomic literature (i.e. Beaton & Weste 1984; Trappe et al. 1996).

Time constraint searches for fruit-bodies of hypogeous fungi were conducted on each of the 136 plots on five separate occasions: autumn (May-June) and spring (November) 1996, autumn 1999, autumn 2001, and autumn 2003. Autumn sampling was emphasised because earlier research had identified it as the time in south-eastern mainland Australia when the greatest diversity of hypogeous fungi produce fruit-bodies (Claridge et al. 1993), a conclusion reinforced by our results in our spring sampling in 1996 (Claridge et al. 2000a).

Measurement of environmental attributes

A series of meso- and microscale environmental attributes were measured for each site (Claridge et *al.* 2000a, 2000b). Initially, raw values for the nine climatic parameters used in the survey stratification process were estimated for each study site using BIOCLIM (Claridge et al. 2000a). These values, together with data on geology, comprised the meso-scale or 'upper level' variables used in subsequent statistical modelling. On-site, we also measured a series of habitat attributes, including features of topography, disturbance history, vegetation floristics and structure, structure of nonliving components of habitat and substrate. Collectively, these represented the microscale or 'lower level' variables. The rationale for, and measurement of,

each of these attributes is described briefly below. Claridge et *al.* (2000a, 2000b) provide detail about these variables.

Slope and aspect influence the occurrence and relative abundance of different hypogeous fungi in some forest habitats (Claridge et *al.* 1993). Aspect particularly influences the level of solar radiation a site receives and in turn helps regulate soil moisture. Dry and exposed aspects may produce fewer fruit-bodies than sheltered protected aspects or favour the occurrence of species that produce desiccation resistant fruit-bodies (Claridge et *al.* 1993). In our study, slope was measured in degrees by clinometer from a point in the centre of each 50 m x 20 m site, while azimuth (aspect) was measured in degrees using a compass from the same point. For later statistical analyses, aspects were grouped into four major classes: N (45-315°), E (45-135°), S (135-225°), and W (225-315°). Where possible, sites were selected for no signs of recent logging or fire, but most had experienced some form of past disturbance. Within the 50 x 20 m boundaries of each site the number of cut stumps was counted. Presence of fire scars on trees was also recorded at each site, linking these with available fire history information to establish both the time since last fire and the type of last fire (prescribed vs. wildfire). Fire histories provided by regional land management offices were in a combination of hard-copy and digital form. For later statistical analysis, fires were either classed as prescribed (category 1) or wild (category 2). This separation was deemed necessary because prescribed fire is likely to influence understorey vegetation composition and structure more greatly than wildfire, particularly when applied frequently (Catling 1991). Times since last fire were grouped into four categories: 1 = 0-10 y, 2 = 10-20 y, 3 = 20-30 y, and 4 = >30 y.

The diversity of potential ectomycorrhizal host plant species was counted at each study site. Existing literature indicated that while the host-specificity of nearly all Australian hypogeous fungi is unclear, a broad range of tree and shrub species might be involved (Warcup 1980; Warcup & McGee 1983; Beaton et *al.* 1985; McGee 1986; Brundrett & Abbott 1991; Reddell & Milnes 1992; Iumpponen et *al.* 2004). Accordingly, potential eucalypt and noneucalypt ectomycorrhizal host species were recorded. The presence of nonhost plant species that contributed significantly to ground cover was also documented, including various ground ferns, tree ferns and sedges. Various structural attributes of the vegetation at each site were measured. Attributes of the eucalypts (basal area, number of stems and upper canopy cover) provided measures of the potential availability of hosts and indirectly indicated the availability of carbohydrates for the fungi: this is important because fruiting of hypogeous fungi undoubtedly relates to supply of carbohydrates from hosts to fungi (Maser et *al.* 1978). For ease of recording, these were measured from a 20 x 20 m subplot within the 50 x 20 m boundaries of each site (the centre of the 20 x 20 m subplot corresponding to that of the 50 x 20 m site). Basal area of eucalypts per hectare and number of eucalypt stems per hectare were calculated from the DBH of all live trees within the subplot. Canopy cover was measured for non eucalypt host plant species at each site. These included various indices of cover for each of three height strata: small-sized (0.5-2.0m) shrubs, medium-sized (2.0-5.0m) shrubs and large-sized (>5.0 m) shrubs. The same indices of cover were used to record the relative abundance of tree ferns, ground ferns and grasses and sedges. Although these latter groups of plants are not hosts for hypogeous fungi, except for sporocarpic arbuscular fungi in the genus Glomus, they might provide important microhabitat for the ectomycorrhizal species.

Hypogeous fungi are influenced by nonliving structural features of microhabitat. Accordingly, attributes such as the number of stags (dead standing trees) and fallen trees within each site were measured. Studies from the Northern Hemisphere have shown that the abundance of fallen trees particularly influences the occurrence and abundance of fruit-bodies of various hypogeous fungi. Well decayed fallen trees provide more or less continuously moist microhabitat that prolongs production of fruit-bodies (Amaranthus et *al.* 1994). Orientation of these trees on the slope has further influences: fallen trees lying along the contour accumulate other fallen nutrient-containing debris and litter on the uphill side (Maser & Trappe 1984). Accumulations of litter provide suitable habitat for some hypogeous fungi (Beaton et *al.* 1985; Claridge et *al.* 1993; Johnson 1994). Detailed measures of the litter were not recorded because of the relatively large scale (50m x 20 m) of sites. Instead, the litter depth (cm) and litter range (cm) were measured at 13 random points within the same 20 m x 20 m subplot used to measure the abundance and basal area of eucalypts. Percentage cover of litter was also visually estimated for the same subplot.

In addition to the measures of microhabitat described above, on-site soil characteristics were evaluated. Factors such as soil texture and nutrient status influence the occurrence and relative abundance of hypogeous mycorrhizal fungi (Perry et *al.* 1987; Claridge et *al.* 1993; Johnson 1994). At each site approximately 100 g of raked soil were collected at two locations and sealed in separately labelled zip-lock bags. From the same samples, soil texture was characterised by the techniques described by Northcote (1979). For statistical analysis four categories of soil texture were recognised: (i) clay, (ii) loam, (iii) clay-loam, and (iv) sand. Soil remaining from the samples was then air-dried and sieved through a 2 x 2 mm mesh. From these sieved samples, total nitrogen (N) and total phosphorus (P) concentrations were determined with a bench-top auto-analyser at the (then) Department of Forestry, the Australian National University. Values used in subsequent statistical analyses for soil moisture content, texture, and N and P content were the means of each duplicate set of samples.

Statistical modelling *procedures*

Relationships between occurrence of each hypogeous fungus within the Mesophelliaceae and environmental (climatic, landscape, and site-based) variables were modelled by use of binomial generalised additive models (GAMs) with spline smoothing functions applied to each predictor variable (Hastie & Tibshirani 1990; Yee & Mitchell 1991; Leathwick 1995). This form of analysis was chosen due to the ability of GAMs to deal with possible nonlinear relationships between the binomial response variable (presence or absence of a given fungal species) and the predictor variables.

Models were fitted for each of the five qualifying species of Mesophelliaceae by first adding climate covariates

separately and testing for significance. For pairs of covariates that were correlated, only one was fitted. All habitat/site covariates were then added and the final model determined by backwards stepwise elimination (see Claridge et al. 2000b for further details). A binomial error distribution was used and a drop-in-deviance test with $p = 0.05$ level of significance used for inclusion of variables in the model. The process of elimination of variables stopped when no remaining variables could be removed from the model without causing a significant increase in residual deviance. All significant and nonsignificant terms were then retested against the final model as a last check. All models were fitted using the GAM procedure in S-PLUS 2000 (Mathsoft Inc.).

Results

Model for the occurrence of Castoreum radicatum

Fruit-bodies of C. *radicatum* were collected from 35 of the 136 study sites (26%). Three significant variables were included in the final explanatory model for the species: mean annual temperature (°C) ($p < 0.01$), precipitation of the wettest quarter of the year (mm) ($p = 0.05$), and average litter depth (cm) ($p < 0.05$). The probability of occurrence of C. *radicatum* decreased from a maximum of approximately 97% at 6.3° C to 20% at 10°C, or around 20% with each increasing 1°C temperature change. Above that threshold the probability of occurrence of the species remained similarly low. In relation to precipitation of the wettest quarter of the year the probability of occurrence of C. radicatum peaked at approximately 27% at 270 mm, declining to around only 3% at 500 mm. Finally, in relation to average litter depth, the occurrence of the species remained around 25-30% in the range 2-4 cm. Above and below this range the occurrence of the species declined to 8% when litter was near absent and 0% when litter depth was 6 cm or more. The general response of C. radicatum to each of the three significant explanatory variables is indicated in Fig 2.

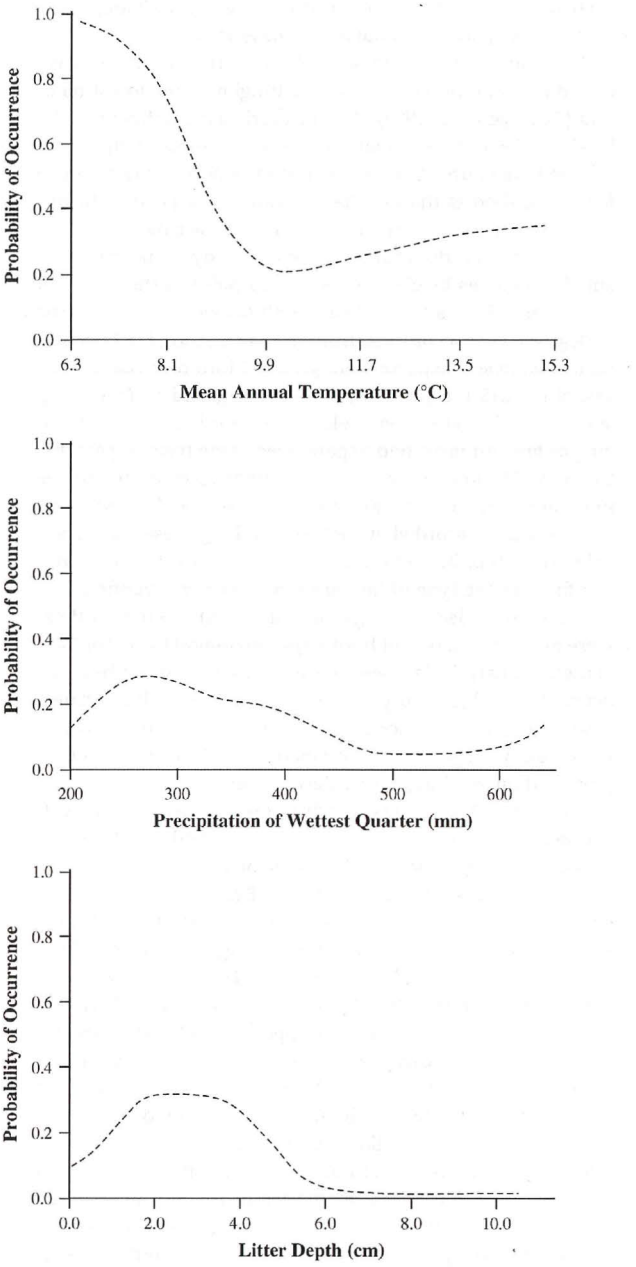

Fig 2 – GAM model developed for probability of occurrence of fruit-bodies of *Castoreum radicatum*, showing nature of effect of significant variables.

Model for the occurrence of Mesophellia clelandii

Fruit-bodies of M. *clelandii* were collected from 17 of the 136 study sites (13%). Three significant variables were included in the final explanatory model for the species: minimum temperature of the coldest month of the year (°C) ($p = 0.05$), the number of eucalypt stems present on a plot ($p < 0.01$), and the average litter depth (mm) ($p = 0.03$). Between the range in minimum temperature of the coldest month of -3.2-0.8°C, the probability of occurrence of M. clelandii increased approximately linearly from 0 to 30%. Above this temperature threshold the probability of occurrence of the species decreased to around 10% at 3.2°C. In relation to number of eucalypt stems on a plot, the probability of occurrence of M. *clelandii* increased from approximately 20% at 10 stems ha^{-1} to over 90% at 25 stems ha^{-1}. Above this threshold, the occurrence of the species declined, to approximately 20% once the density of eucalypt stems reached 40 stems ha^{-1}. Finally, the probability of occurrence of M. clelandii reached a maximum of approximately 45% when average litter depth was 4 cm. Either side of this threshold, the occurrence of the species declined to less than 10% at depths of around 0.6 cm and 3% at depths of 8 cm. The general response of M. clelandii to each of the three significant explanatory variables is indicated in Fig 3.

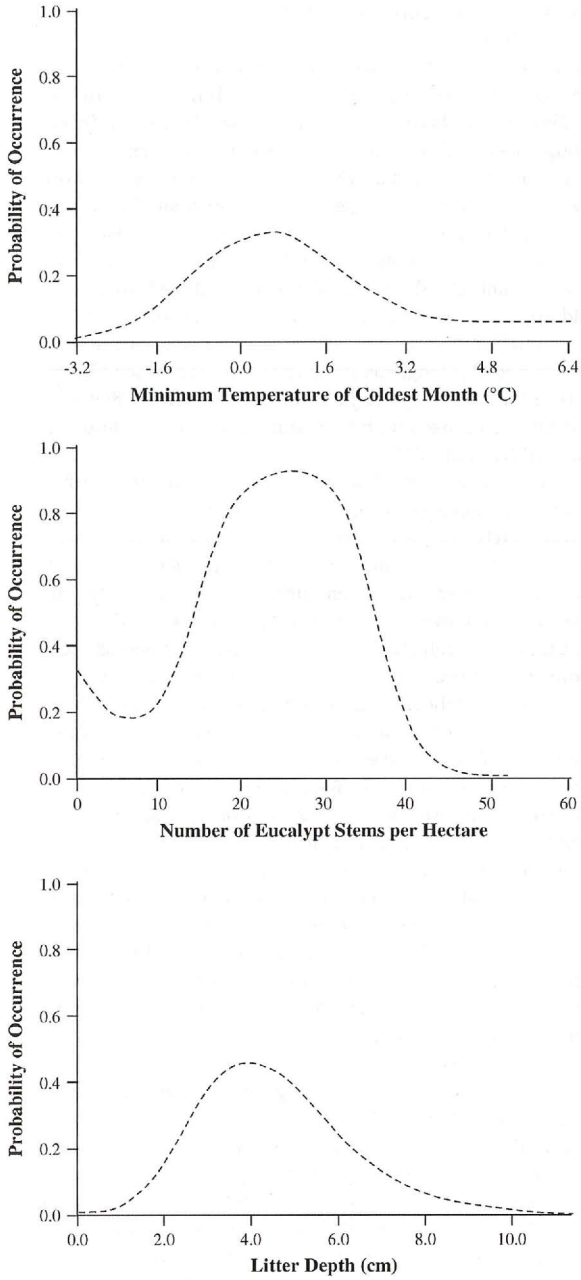

Fig 3 – GAM model developed for probability of occurrence of the *Mesophellia clelandii*, showing nature of effect of significant variables.

Model *for* the *occurrence of* the Nothocastoreum cretaceum

Fruit-bodies of N. *cretaceum* were collected from 14 of the 136 study sites (10%). Three significant variables were included in the final explanatory model for the species: the number of eucalypt stems (ha^{-1}) ($p = 0.05$), the number of fallen trees on a plot ($p = 0.05$) and mean annual temperature (^{o}C) ($p = 0.03$). The probability of occurrence of N. *cretaceum* peaked at around 45% when the number of eucalypt stems was approximately 25 trees ha^{-1}. Below this threshold it decreased to 0% when the number of trees was 5 ha^{-1} or less, while above it decreased to 0% when the number of trees exceeded 40 ha^{-1}. In relation to number of fallen trees, the occurrence of the species increased from around 7% when there were 5 trees on a plot to approximately 98% when there were 12 trees on a plot, or by 13% with each additional tree. Finally, the occurrence of N. *cretaceum* reached a peak of approximately 30% when mean annual temperature was 12.85°C, declining to 6.5% when temperature was around 10°C, and 0% at 15°C or above. The general response of N. *cretaceum* to each of the three explanatory significant variables is indicated in Fig 4.

Nonsignificance o*f variables for Mesophellia glauca and* M. trabalis

Fruit-bodies of M. *glauca* were collected from 37 of 136 sites (27%) and M. trabalis from 20 of the 136 sites (15%). No significant variables were detected for either species, so neither could be modelled.

Discussion

Meso- *and* microscale factors *influencing* the distribution *of fire-adapted* hypogeous *fungi*

Recent reviews have highlighted the paucity of information about factors influencing the occurrence of fungi (i.e. Lilleskov & Parrent 2007). Acknowledging this deficiency, we set out to describe features of the environment that might help explain the distribution of five members of the Mesophelliacae, a family of hypogeous fungi mostly endemic to Australia. To that end we determined that a range of measures of habitat, at both a meso- and microscale, were variously involved. At a meso- or landscapescale, climatic variables influenced the occurrence of all three species examined. Annual mean temperature was a significant variable in the models developed for Castoreum *radicatum* and *Nothocastoreum cretaceum.* The occurrence of *Mesophellia* clelandii fruit-bodies similarly altered in relation to average minimum temperature of the coldest month of the year. The varying responses of the three species to temperature-related parameters highlights that different taxa have differing landscape-scale habitat preferences. Within our study region, temperature regimes are influenced by altitude, with sites at higher elevations having cooler annual mean temperatures and cooler average minimum temperatures during the coldest parts of the year (Neave et *al.* 1996a, 1996b; Claridge et *al.* 2000b). For a species such as C. *radicatum,* for example, the higher detection rates at sites with colder minimum temperatures imply it is more likely to occur at higher elevations. In comparison, N. *cretaceum* was more likely to be detected in warmer sites at lower elevations. These preferences may well relate to different patterns in host-plant species distribution since many species of plants are also restricted in distribution (elevation) and/or growth by climatic factors such as temperature (i.e. Lindenmayer et *al.* 1997). In

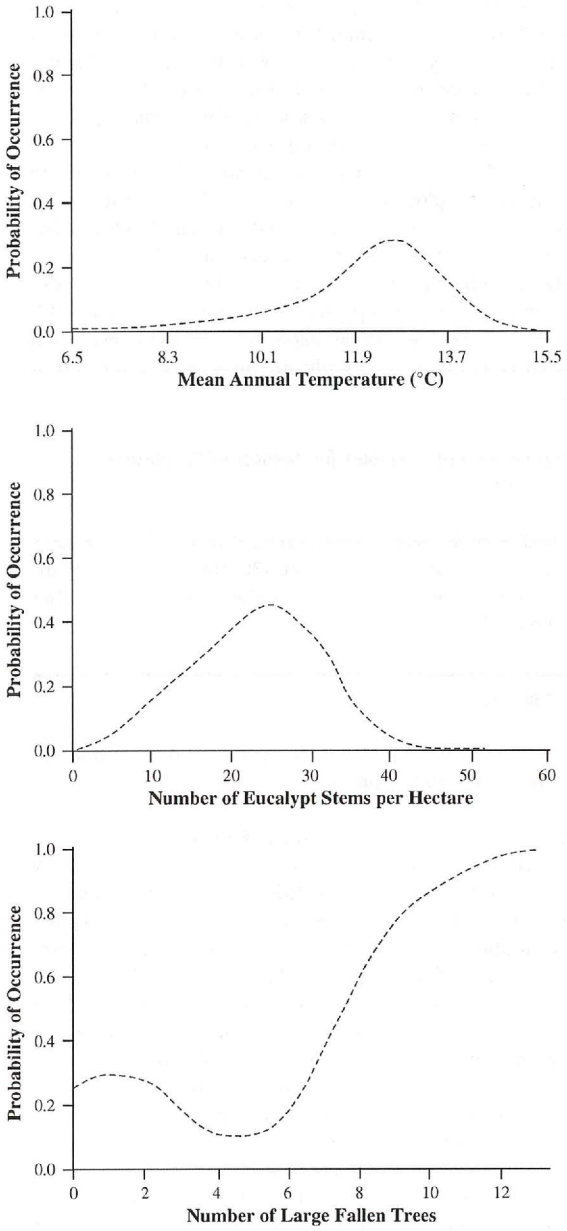

Fig 4 – GAM model developed for probability of occurrence of *Nothocastoreum cretaceum*, showing nature of effects of significant variables.

related work, jumpporien et *al.* (2004)identified that other hypogeous fungal species within OUT study area were more likely to be found in the presence of certain taxa of Eucalyptus and Acacia than others. These possible relationships need to be further explored among members of the Mesophelliaceae. The nonlinear response of M. c1elandiiand N. *cretaceum* to temperature parameters is also in keeping with studies of the landscape-scale distribution of plants within eastern mainland Australia, where species often occur at optima within a range in accordance with niche theory (ie. Austin & Heyligers 1989).

Precipitation of the wettest quarter of the year influenced the chances of detecting C. *radicatum,* with higher likelihood of finding its fruit-bodies at sites with lower levels of rainfall. Although observed at a landscape-scale, this pattern corroborates the results of Johnson (1995), who closely studied fruiting of hypogeous fungi at a single eucalypt forest site in Tasmania. There, the abundance of fruit-bodies of C. *tasmanicum,* a close relative of C. *radicatum,* only increased after periods of low rainfall. On the basis of these combined studies, it would appear that members of this genus are tolerant of reduced moisture levels. This response contrasts with that of other species of hypogeous fungi that rely on periods of high moisture for fruit-body production, or those whose distribution is limited to areas with high annual rainfall (see Johnson 1995; Claridge et al. 2000b).

On-site, the stocking density of host eucalypt trees influenced the probability of occurrence of fruit-bodies of C. *radicatum* and N. *cretaceum,* with both species being more likely to be detected at sites with an intermediate number of stems. Above and below stem densities of approximately 20-30 trees ha^{-1}, the likelihood of finding these species dropped, such that the overall shape of the response was bell-shaped. To some extent this type of response may well relate to successional stage of the individual sites. In eucalypt forests, sites with few stems per hectare are likely to be old-growth stands, while sites with many trees per hectare are more likely to be younger successional stands. Researchers elsewhere have determined that the species composition of hypogeous fungal communities may change with age of forest stand. For example, in the U.S.A. in north-eastern California, Waters et *al.* (1997) found that fruit-bodies of species such as *Hysterangium crassirhachis* and H. *coriaceum* were more numerous in old-growth fir (Abiessp.) stands than in 100-year-old fir stands. In contrast, other taxa such as *Gautieria* monticolaand *Thaxter*-ogaster *pingue* were more prevalent in the 100-year-old stands. On northwestern Washington State, North et *al.* (1997) determined that fruit-bodies of Elaphomyces *granulatus,* in particular, were far more prevalent in old-growth stands dominated by Sitka Spruce (Piceasitchensis)and Douglas-fir *(Pseudotsuga* menzeisii) than in managed young stands of these same tree species. Compositional changes in hypogeous fungal communities were also noted by Luoma et *al.* (1991) in different aged Douglas-fir stands in southern Oregon. In each of those studies, forest type was constrained, unlike our study that sampled fungi across many different vegetation types. Sampling for C. *radicatum* and N. *cretaceum* at sites with the same dominant eucalypt species but different regeneration histories may help clarify the relationship between stem density and chance of detection.

In our study, the probability of occurrence of fruit-bodies of N. *cretaceum* increased with increasing numbers of large fallen trees (logs) on the forest floor. In eucalypt forests, such logs perform a range of ecosystem services including the recycling of nutrients, creating ground-layer heterogeneity and providing foraging and shelter sites for a range of biota, including fungi (Lindenmayer et *al.* 2002). When well decayed, fallen trees may provide a vital substrate for increased mycorrhizal activity as well as fruiting of fungi, including hypogeous

forms. For example, in southern Oregon Amaranthus et a1. (1994) found a strong positive association between production of fruit-bodies of a range of different hypogeous fungi and rotted coarse woody debris, relative to that in mineral soil. They noted that sites with high levels of rotted debris retained moisture better than sites without, extending fruit-body production during drier times of the year. North & Greenburg (1998) similarly noted a positive relationship between occurrence and density of fruit-bodies of E. *granulatus* and organic matter in the upper soil profile. In a field situation, we have often noted N. *cretaceum* fruit-bodies around other wood structures such as cut stumps or decaying sheets of bark (A.W. Claridge, unpublished data). It would appear that it is a favoured microhabitat for fruiting of this hypogeous fungus.

Organic matter levels in forest soils may also be regulated in part by the accumulation and decay of leaf litter. Average litter depth was an explanatory factor for describing the occurrence of C.*radicatum* and M.*clelandii.* C.*radicatum* fruit-bodies were more likely to be found at sites with intermediate litter depths: at either end of the spectrum (i.e. very shallow or very deep litter) the chance of detecting them decreased, such that a bell-shaped response curve was recorded. The response curve of M. *clelandii* fruit-bodies to litter depth was similarly bell-shaped, again being most likely to be detected at sites with intermediate litter depths. Within the same study sites, we had previously determined that the occurrence of two other hypogeous taxa, *Hysterangium infiatum* and Zelleromyces sp. nov., increased with increasing litter depth. In dry habitats or in drought conditions, hypogeous fungi have been found only under litter-covered soil, never in bare soil, in several studies in northern Victoria and southeastern New South Wales (J.M.Trappe, unpublished data). In contrast, fruit-bodies of *Chamonixia vittatispora* and Hymenogaster*levisporus* are more likely to occur at sites with minimal litter (Claridge et al. 2000b).These varying responses highlight that the patchiness of the leaf litter layer, in terms of depth, may help regulate the availability of preferred microsites for occurrence of different hypogeous species. In theory then, disturbances that result in homogenisation of the leaf litter layer, for example repeated fire events, would be expected to reduce the diversity ofhypogeous fungi. Similarly, long-term absence of disturbance, allowing uniform accumulation of deeper litter layers, may favour some species while reducing microhabitat for others. In the future it would be well worthwhile closely examining the influence of litter depths on these organisms in a series of manipulative experiments.

None of the independent variables in our study correlated with the occurrence of M.*glauca* or M.*trabalis.* This lack of response suggests a wide adaptability to environmental conditions within our study area, although it could also be that they respond to habitat variables that we did not measure.

Management of the *Mesophelliaceae in multiple-use* forests

In recent times, much has been made of the apparent association of members of the Mesophelliaceae with fire,with some authors suggesting a close relationship between time since fire and relative abundance of these organisms (i.e. Taylor 1991; Johnson 1995; Vernes et *al.* 2004; summarised in Claridge & Trappe 2004).At face value, the Mesophelliaceae are supremely adapted to surviving through fire, with fruit-bodies capable of withstanding heat and smoke. Postfire, these fruit-bodies are readily located by mycophagous mammals and their spores are dispersed back into the environment (Claridge 1992).This sets them apart from most other species of hypogeous fungi in Australia, particularly those whose fruit-bodies are eliminated when litter layers are temporarily removed in fires (Trappe et al. 2006).While it is tempting to focus on the fire phenomenon, across our study area we found no clear relationship between past fire history and the occurrence ofthe five species of Mesophelliaceae examined. Instead, other environmental parameters were found to be significant, or in the case of Mesophel1ia *glauca* and M. trabalis, none were significant. This suggests that it would be unwise to focus too much on the role of fire in promoting these fungi in isolation from other features of habitat that may play an equally important if not greater role in their occurrence. Fire may alter and even limit key attributes of habitat such as litter, fallen trees and stand density: our findings highlight that these structures are variously important for *Castoreum radicatum,* Mesophellia clelandii and Nothocastoreum *cretaceum.* Our data also suggest that fire does not alter habitats to favour M. *glauca* and M.*trabalis,* as indicated by lack of significance of time since last fire to their occurrence.

The complexity and varying responses of members of the Mesophelliaceae studied here to features of their environment, corroborates our earlier findings on a range of different and unrelated taxa (Claridge et *al.* 2000b). In combination, this reinforces the notion that multiple-use forests within our study region should be managed for a diversity of attributes to conserve fungal diversity: be that retaining large fallen trees, patchy litter layers of differing depth or changing tree stem densities across time and space. Management strategies that reduce such structural complexity, such as intensive logging regimes or broad acre fire regimes of too high frequency, may reduce microhabitat availability for different species of hypogeous fungi with varying environmental preferences.

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