

# Fire impacts tropical communities of soil fungi through changes to plant community composition, litter and soil chemistry

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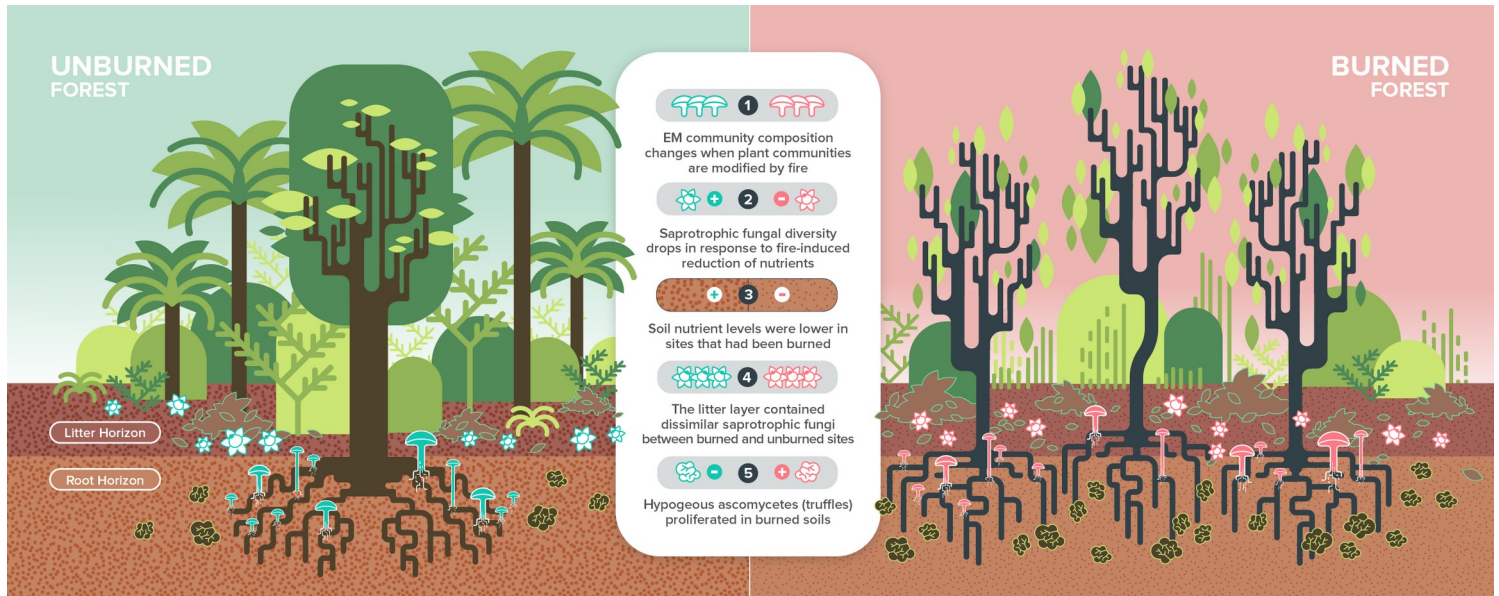
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## 7 **Abstract**

8 Fire has been predicted to be more severe and frequent in forests of the Australian Monsoon  
9 Tropics over the coming decades. The way in which groups of ecologically important soil fungi  
10 respond to disturbance caused by fire has not been studied in tropical forest ecosystems.  
11 Ectomycorrhizal (EM) fungi are important tree symbionts and saprotrophic fungi drive soil  
12 nutrient cycles. We analysed both publicly-available environmental DNA sequence data as well as  
13 soil chemistry data to test a hypothesis that fire events (1970 - 2017) in a contiguous tropical  
14 forest have altered the composition and diversity of EM and saprotrophic soil fungi. We tested this  
15 hypothesis by measuring community-level taxonomic composition, fungal diversity, species  
16 richness and evenness. We determined whether changes in fungal communities were associated  
17 with fire-altered soil chemical/physical properties, vegetation types, or the direct effect of fire.  
18 Soil fungi differed in abundance and community phylogenetic structure between forest sites that  
19 had experienced fire, and those sites dominated by unburned forest. Communities of EM fungi  
20 were structurally altered by fire at shallow soil horizons, as well as by vegetational changes  
21 between burned and unburned sites at deeper soil horizons. In contrast, fires influenced  
22 community composition of saprotrophic fungi by changing soil nutrient levels and altering litter  
23 composition. Pyrophilic, truffle-like EM fungi that rely on mycophagous mammals for dispersal  
24 were abundant at recently burned sites. We conclude that fire impacts EM fungi primarily by

25 changing plant communities, whereas fire impacts saprotrophic fungi by reducing soil nutrient  
26 levels and altering litter composition.

## 27 Graphical abstract



Credit: Sofia Houghton (2-column fitting image. Color to be used in print.)

## 28 Keywords

29 Soil, fungi, fire, ectomycorrhizal, saprotrophic, trophic, tropical, diversity, disturbance

## 30 1. Introduction

31 Soils contain some of the most complex and understudied ecosystems in terrestrial biomes,  
32 providing habitat for an estimated 25 % of described species (Decaëns et al., 2010). Most of the  
33 terrestrial carbon on Earth is in soils (Crowther et al., 2016), and they have been designated a  
34 ‘third biotic frontier’ after deep-sea benthic regions and tropical rainforest canopies (Hågvar,  
35 1998). Healthy soil ecosystems are undergirded by diverse communities of microorganisms  
36 dominated by fungi, bacteria, archaea and other eukaryotes, the taxonomy and function of which  
37 are largely unknown (Baldrian, 2019). Together, the microorganisms of this ‘living terrestrial skin’  
38 drive global biogeochemical cycles and power terrestrial ecosystems (Tecon and Or, 2017).

39 Fire is a major driver of disturbance in tropical forests (Silvério et al., 2019), including the  
40 Australian Monsoon Tropics (AMT), which is the most fire-prone region in Australia (Bowman et  
41 al., 2010). In the AMT, fire frequently intrudes from savanna into notophyll plant communities  
42 and initiates a process of post-fire seral development (Bowman, 2009; Cole et al., 2014). In this  
43 region, fire is a primary determinant of plant distribution, which in turn can influence the structure  
44 of microbial communities (Ettema and Wardle, 2002; Oudei et al., 2016; Sarmiento et al., 2017).  
45 An increase in fire frequency, severity and duration in the AMT is likely over the next decades  
46 due to anthropogenic climate change (Hubnerova et al., 2020).

47 Specific functional guilds of microorganisms respond differently to fire according to their  
48 trophic modes. The resilience of tropical ectomycorrhizal (EM) fungi after fire has been attributed  
49 to their ability to draw nutrients from plants (Alem et al., 2020). Fires impact soil microorganisms  
50 through changes in soil pH, water holding capacity, and availability of organic carbon, nitrogen  
51 and phosphorus (Pellegrini et al., 2019; Singh, 1994; Verma and Jayakumar, 2018). Soil enzyme  
52 activity, which reflects microbial metabolism in soil communities, also decreases immediately  
53 following fires, especially at shallow soil horizons (Certini et al., 2021). How different functional  
54 guilds of fungi respond to fire in a single tropical soil ecosystem has not been studied.

55 Saprotrophic and EM fungi are two functional guilds of fungi in tropical forests that break  
56 down soil organic matter (SOM) (Fernandez and Kennedy, 2016). Gadgil and Gadgil (1975, 1971)  
57 proposed that competition and inhibition between saprotrophic and EM fungi suppress the  
58 decomposition of organic matter and increase the accumulation of organic carbon. Studies in  
59 northern-hemisphere coniferous ecosystems based solely on post-fire observations of macrofungal  
60 sporocarps are inconclusive, reporting lower EM diversity (Owen et al., 2019), higher saprotroph  
61 diversity and proliferation of rare pyrophilous species (Salo et al., 2019). Similar studies on the  
62 effect of fire on communities of saprotrophic and EM fungi in tropical forests have not been  
63 made.

64 We used data from culture-independent high-throughput sequencing of soils provided by  
65 the Biomes of Australian Soil Environments soil microbial diversity database to test the  
66 hypothesis that fire events (1970 - 2017) in a contiguous tropical forest have altered the  
67 composition and diversity of EM and saprotrophic soil fungi. BASE maps Australia's soil  
68 microbial diversity using culture-independent high-throughput DNA sequencing (Bissett et al.,  
69 2016). We measured community-level taxonomic composition, diversity, species richness and  
70 evenness. We determined whether observed changes were associated with the burn status  
71 (burned/unburned) of a site, the recency of a fire, and whether these changes were a result of  
72 altered soil chemical/physical properties or vegetation type due to fire. Understanding the  
73 response of soil microbe communities to fire in the AMT may provide management options for  
74 the protection of ecosystems under a changing climate.

## 75 **2. Materials and methods**

### 76 *2.1. Study site*

77 The Iron Range on Cape York Peninsula, Far North Queensland, is a mountainous coastal  
78 region of the Australian Monsoon Tropics (AMT) dominated by tropical rainforest and notophyll  
79 vine forest (Neldner and Clarkson, 1995; Webb, 1959). Sample sites for this study were selected  
80 to represent a spectrum of seral stages, from unburned to recently burned (*Table 1*).

### 81 *2.2. Sampling BASE data*

82 We downloaded 42 fungal amplicon community profiles from unburned and burned sites  
83 from the Biomes of Australian Soil Environments microbial diversity database (BASE), which  
84 were sampled and sequenced according to Bissett et al. (2016). The BASE project took soil  
85 samples of 1 kg from the litter (0–10 cm) and mineral soil (20–30) in February 2017. Soil  
86 chemical/physical properties including ammonium (NH<sub>4</sub>), nitrate (NO<sub>3</sub>), phosphorus (P),  
87 potassium (K), organic carbon (C), calcium (Ca) and pH were analysed and DNA was extracted

88 from samples as per protocols of the Earth Microbiome Project  
 89 (<http://www.earthmicrobiome.org/emp-standard-protocols/dna-extraction-protocol/>). The ITS1  
 90 region of fungal ribosomal DNA was amplified with the primers ITS1F and ITS4 (Gardes and  
 91 Bruns, 1993; White et al., 1990) and sequenced with 300 bp paired-end chemistry on an Illumina  
 92 MiSeq.

93 **Table 1** Study sites, fire history and floristic composition. (2-column fitting table.)

Site	Fires ceased	Vegetation type	Dominant trees	Dominant grasses
1	2017	Grassy woodland	<i>Corymbia intermedia</i> , <i>Lophostemon suaveolens</i> , <i>Acacia flavescens</i>	<i>Heteropogon contortus</i> , <i>Imperata cylindrica</i>
2	1995, one in 2014	Shrubland	<i>Dodonaea viscosa</i>	None
3	1970, one in 2006	Regenerating closed canopy forest	<i>Dillenia alata</i> , <i>Buchanania arborescens</i> , <i>Guioa acutifolia</i> , <i>Blepharocarya involucrigera</i>	<i>Cryptococcum oxyphyllum</i> , <i>Entolasia stricta</i>
4	1970	Regenerating closed canopy forest	<i>Atractocarpus sessilis</i> , <i>Buchanania arborescens</i> , <i>Acacia midgleyi</i>	None
5	1970	Regenerating closed canopy forest	<i>Phyllanthus praelongipes</i> , <i>Mallotus resinus</i> , <i>Mallotus polyadenos</i> , <i>Rinoria bangalensis</i>	None
6	Unburned	Regenerating closed canopy forest	<i>Nauclea orientalis</i> , <i>Buchanania arborescens</i> , <i>Vitex heligiton</i>	None
7	Unburned	Semi-deciduous mesophyll/notophyll forest	<i>Tetrameles nudiflora</i> , <i>Cordia dichotima</i> , <i>Canarium australicum</i> , <i>Lagerstroemia archeriana</i> , <i>Vitex heligiton</i>	None
8	Unburned	Semi-deciduous mesophyll/notophyll forest	<i>Cordia dichotima</i> , <i>Tetrameles nudiflora</i> , <i>Berrya javanica</i> , <i>Paraserianthes toona</i> , <i>Mimusops elengi</i>	None
9	Unburned	Semi-deciduous mesophyll/notophyll forest	<i>Tetrameles nudiflora</i> , <i>Blepharocarya involucrigera</i> , <i>Alstonia scholaris</i> , <i>Aleurites moluccana</i>	None
10	Unburned	Wet rainforest	<i>Terminalia complanata</i> , <i>Palaquium galactoxylum</i> , <i>Garcinia dulcis</i> , <i>Syzygium pseudofastigiatum</i>	None
11	Unburned	Wet rainforest	<i>Aleurites moluccana</i> , <i>Neonauclea glabra</i> , <i>Canarium australicum</i> var. <i>australicum</i> , <i>Archidendron hirsutum</i>	None

### 94 2.3. Processing of sequence data

95 ITS1 reads were identified and extracted with ITSx v1.1.3 (Bengtsson-Palme et al., 2013).  
 96 Quality filtering and construction of operational taxonomic unit (OTU) tables were performed in

97 QIIME2 v2020.11 (Bolyen et al., 2018) with the `dada2` `denoise-single`, `phylogeny align-`  
98 `to-tree-mafft-fasttree`, `diversity core-metrics-phylogenetic` and `feature-`  
99 `classifier classify-sklearn` functions. OTUs were generated from sequences with 97 %  
100 similarity, and taxonomy was assigned using the UNITE v8.2 fungal database (Abarenkov et al.,  
101 2010). Fungal community diversity was calculated from the ITS dataset rarefied to 5,000  
102 sequences per sample, based on rarefaction curves of Shannon's diversity index.

#### 103 2.4. *Statistical analyses*

104 Soil chemistry data for each site were analysed to establish whether nutrient content was  
105 correlated between samples exposed to fire at different time points and fungal community  
106 structure. A distance matrix of nutrient profiles for each site was constructed in R v3.6.3 (R Core  
107 Team, 2020) based on Bray-Curtis dissimilarities (Bray and Curtis, 1957) with the function  
108 `vegdist` in `Vegan` v2.5-6 (Oksanen et al., 2020) and visualized with non-metric multidimensional  
109 scaling (NMDS) (function `metaMDS`). Soil chemical/physical properties were analysed for  $\text{NH}_4$ ,  
110  $\text{NO}_3$ , P, K, C, Ca and pH. To establish whether fire history and other factors structured soil fungal  
111 communities, we constructed distance matrices from OTU tables based on unweighted UniFrac  
112 (Lozupone and Knight, 2005), which measures OTUs in terms of their phylogenetic relatedness  
113 and presence or absence between samples. We built PERMANOVA (`adonis`) forward models in R  
114 to assess variance between categorical variables related to soil chemical/physical properties and  
115 determine the significance and hierarchy of influence for sample depth, burn status  
116 (burned/unburned), vegetation type (shrubland, grassy woodland, regenerated closed canopy  
117 forest, semi-deciduous notophyll forest, wet rainforest), year of most recent fire and year of  
118 cessation of frequent fires. We visualized Bray-Curtis distances based on soil chemical/physical  
119 properties at each sample site with NMDS (`metaMDS`) in `Vegan` to assess differences between  
120 fungal communities in terms of soil chemical/physical properties.



121 Sequences that represented ectomycorrhizal and saprotrophic fungi were identified with  
122 the FUNGuild v1.1 (Nguyen et al., 2016) Python script on an ITS OTU table rarefied to 5,000  
123 sequences and with singletons removed. Only ‘probable’ and ‘highly probable’ assignments were  
124 retained. To detect linear correlations between sample alpha diversity and soil chemical/physical  
125 properties, we generated Shannon’s diversity (entropy) values (Shannon, 1948) for all samples in  
126 QIIME2 (`qiime diversity alpha`) and Pearson’s correlation coefficient, which measures the  
127 strength of a linear relationship between two variables, with `rcorr` in the R package `Hmiscv4.4-2`  
128 (Harrell, 2021). We used redundancy analysis (RDA) in R with the package `GGORD` (Beck,  
129 2017) to extract and summarise the variation in response variables (sample fungal community  
130 composition, individual taxa) and explanatory variables (burn status, soil chemical/physical  
131 properties) based on Hellinger-transformed OTU tables to give lower weights to rare taxa. `Krona`  
132 v2.7.1 (Ondov et al., 2011) was used to visualise the proportional taxonomic composition of  
133 fungal communities.

### 134 **3. Results**

#### 135 *3.1. Sequence data*

136 After DADA2 quality filtering in QIIME2, we retained 722,732 ITS sequences from 42  
137 samples, which clustered into a total of 6960 fungal OTUs, from which we identified 165 EM and  
138 654 saprotrophic taxa.

#### 139 *3.2. Soil chemistry*

140 PERMANOVA indicated that sample depth ( $P=0.001$ ) and burn status, i.e. whether or not  
141 a site had been burned ( $P = 0.012$ ) had the most influence on fungal communities (*Table 2*).  
142 Interactions between variables were associated with differences in soil chemistry. Depth interacted  
143 with burn status ( $P = 0.001$ ), vegetation type ( $P = 0.001$ ), year of cessation of frequent fires ( $P =$   
144  $0.010$ ) and year of last fire ( $P = 0.010$ ). NMDS showed that samples clustered primarily with

145 sample depth and burn status (*Figure 1*). The greatest variability in soil chemistry was in outlier  
146 samples from unburned mesophyll/notophyll rainforest.

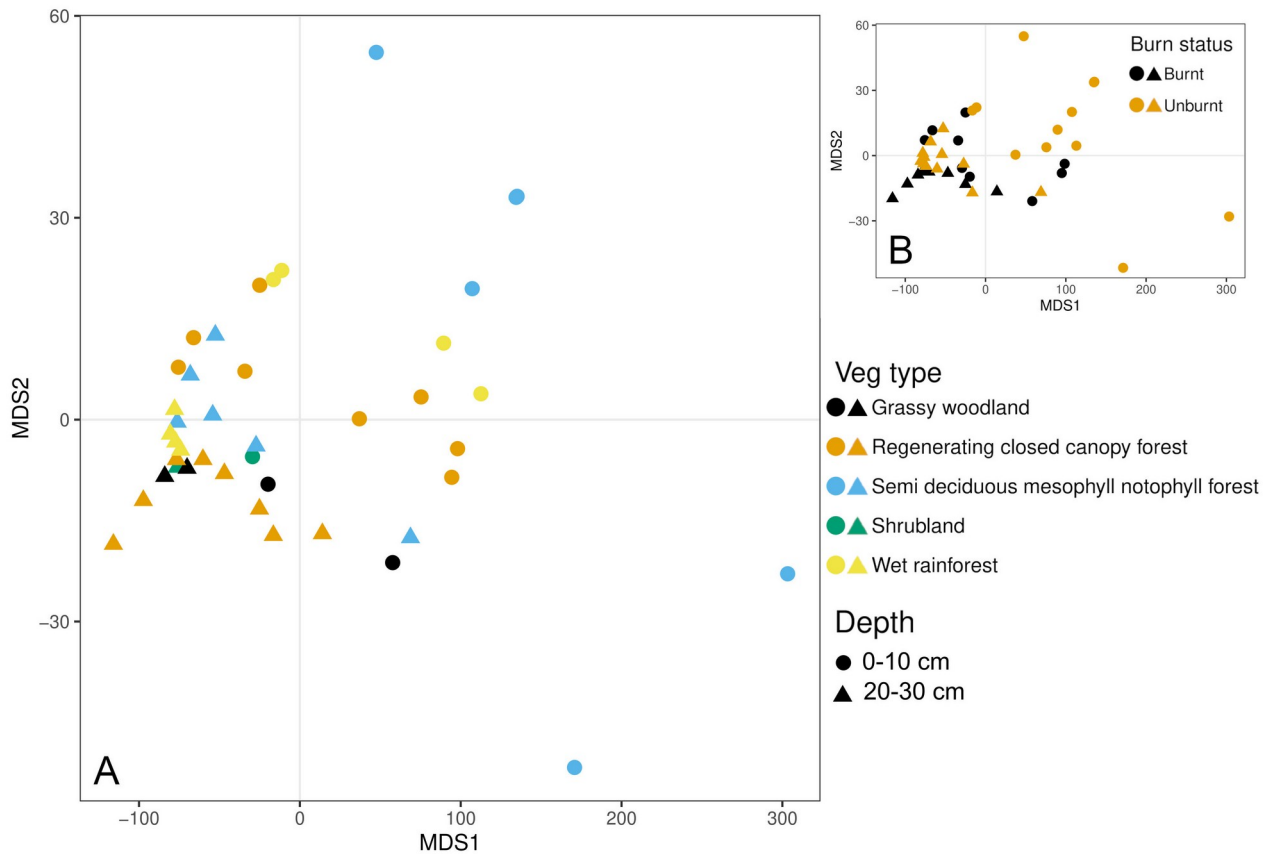
**Table 2** PERMANOVA of relative influence on soil chemical/physical properties of sampling depth, burn status (burned/unburned), vegetation type (shrubland, grassy woodland, regenerating closed canopy forest, semi-deciduous notophyll forest, wet rainforest), year of most recent fire and year of cessation of frequent fires. Sampling depth and burn status were important factors associated with differences in soil chemistry between sites. (*Single-column fitting table.*)

	<i>Df</i>	<i>F model</i>	<i>R</i> <sup>2</sup>	<i>P</i>
<b>Depth</b>	1	26.5986	0.352	<b>0.001</b>
<b>Burn status (burned/unburned)</b>	1	6.5186	0.086	<b>0.012</b>
<b>Vegetation type</b>	4	1.0067	0.053	0.410
<b>Year of most recent fire</b>	2	0.0288	0.001	0.979
<b>Year of cessation of frequent fires</b>	2	0.0288	0.001	0.980

### 147 3.3. *Fungal community diversity and effects of soil nutrient levels*

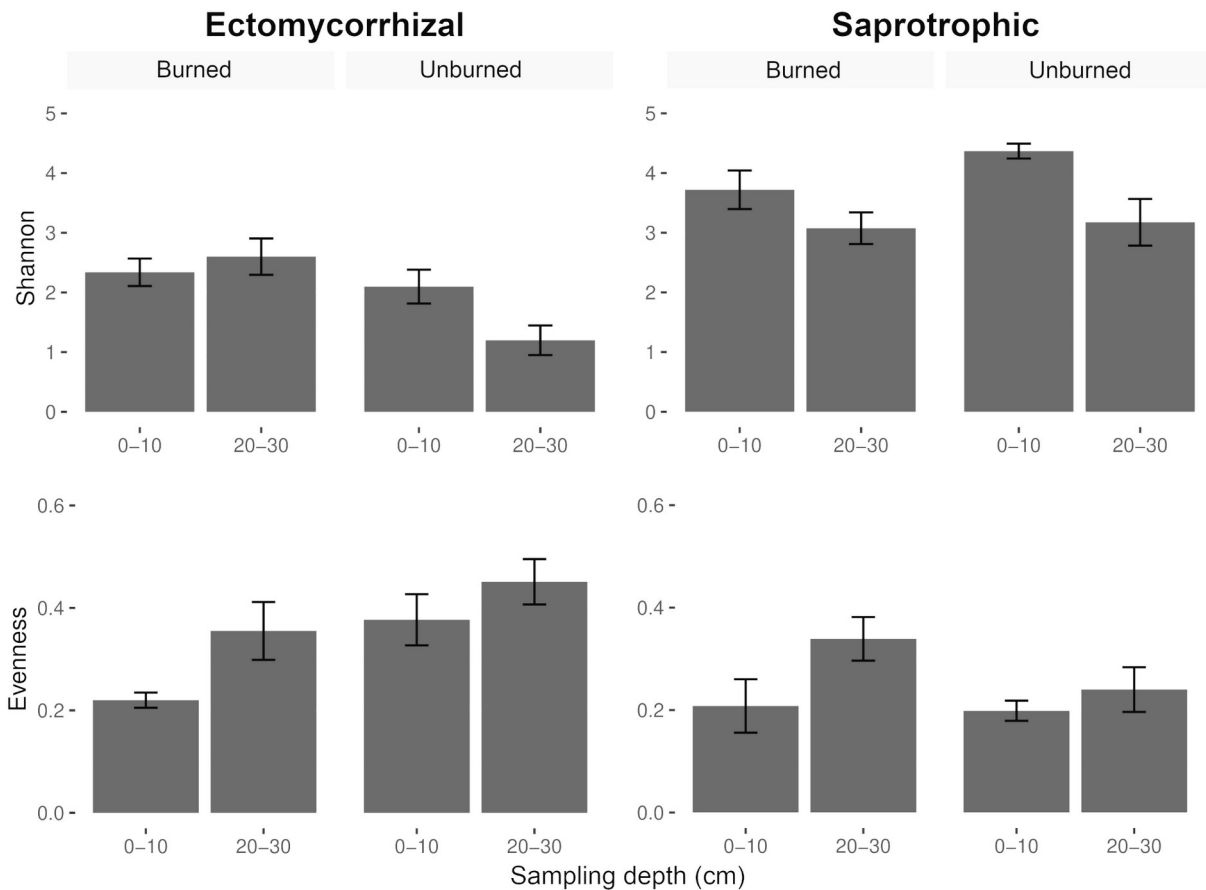
148 Shannon's diversity index (entropy) was higher for saprotrophic fungi than EM fungi  
149 (*Figure 2*), particularly in the litter layer (0–10 cm) at unburned forest sites. Shannon's diversity  
150 index of saprotrophic fungi correlated linearly with all measurements of soil physical/chemical  
151 properties. Diversity of EM communities correlated only with NH<sub>4</sub> (*Table 3*). In general, NO<sub>3</sub>, P,  
152 Ca and pH were higher in unburned than in burned sites. Increased diversity of saprotrophic fungi  
153 correlated with levels of soil NH<sub>4</sub>, NO<sub>3</sub>, P, K and Ca, and there was a marginally significant  
154 correlation with pH. Lower diversity of EM communities at several unburned sites was associated  
155 with elevated soil nutrient levels relative to burned sites, although this trend was less evident for  
156 K levels (*Figure 3*). At unburned sites, saprotrophs were more diverse at 0–10 cm depth if levels  
157 of NO<sub>3</sub>, P, K and Ca were elevated. Saprotrophic diversity was more variable at 20–30 cm depth,  
158 where nutrient levels were lower.





**Table 3** Pearson's correlation coefficient testing linear relationships between Shannon's diversity (entropy) of soil fungal communities and soil chemical/physical properties. P values <0.05 indicated by bold type. Diversity values for EM fungi correlated linearly with levels of soil NH<sub>4</sub>, but a relationship with soil chemistry was reflected more strongly in saprotroph diversity, which was highly correlated with levels of NH<sub>4</sub> as well as with NO<sub>3</sub>, P, K, Ca and pH. (Single-column fitting table.)

	Ectomycorrhizal		Saprotrophic	
	Pearson's correlation	P	Pearson's correlation	P
Ammonium	0.330	<b>0.035</b>	0.326	<b>0.035</b>
Nitrate	-0.018	0.913	0.464	<b>0.002</b>
Phosphorus	0.041	0.799	0.422	<b>0.005</b>
Potassium	0.186	0.243	0.511	<b>0.001</b>
pH level	-0.236	0.138	0.299	0.055
Calcium	-0.137	0.393	0.388	<b>0.011</b>



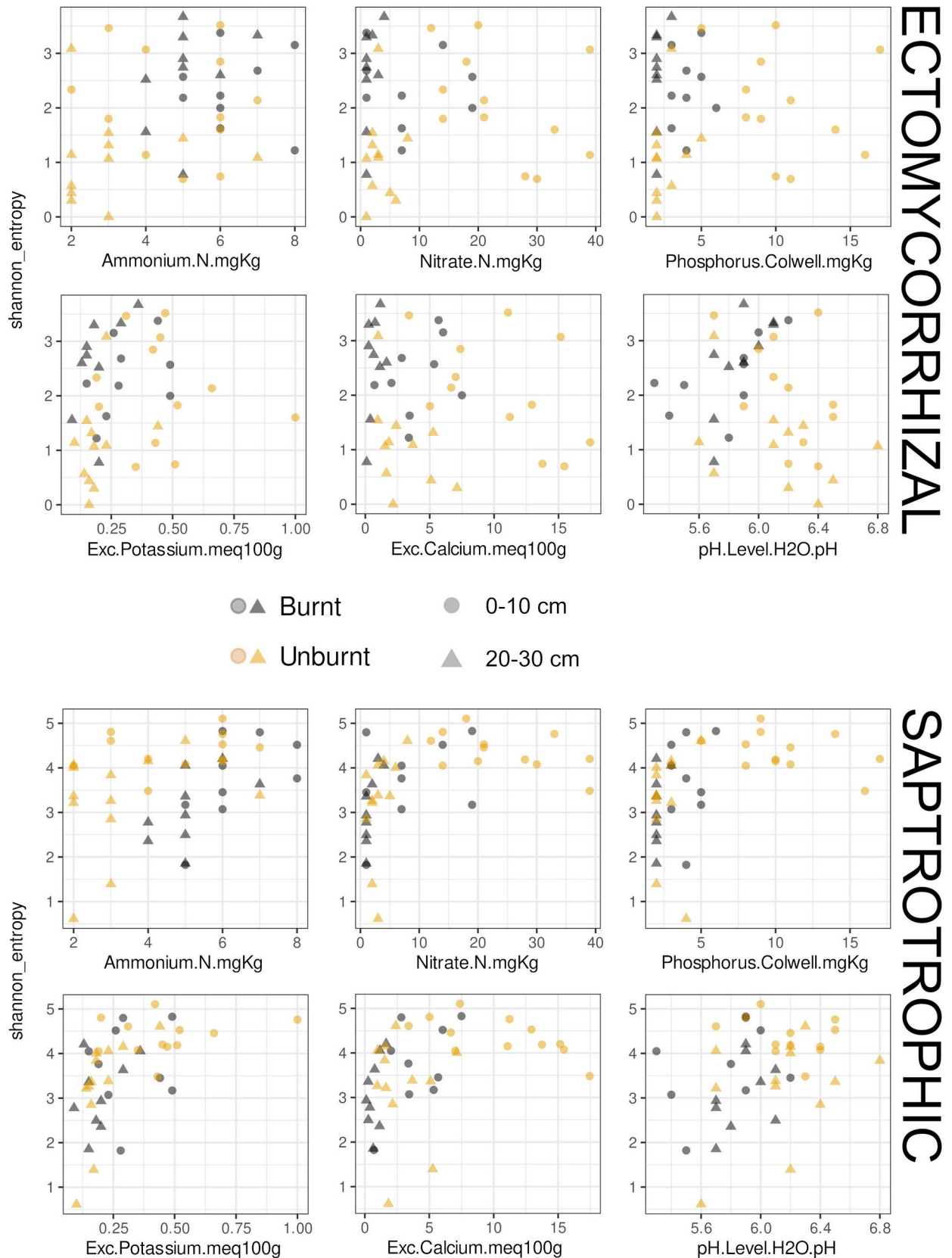
**Figure 2** Average Shannon's diversity values and Simpson's evenness (similarity of abundance between species) for EM and saprotrophic soil fungi at burned and unburned sites and at two sampling depths. Bars indicate standard error. In general, EM fungi were more diverse and less even at burned versus unburned sites, whereas saprotrophic communities were more diverse and less even at unburned sites. Average Shannon's diversity of EM fungi at unburned sites was lowest at deeper soil horizons, and EM communities at these sites had the highest average evenness values of all site types, indicating a late-successional community structure. (*Single-column fitting image.*)

### 159 3.4. Fungal diversity and community structure and effects of historical burning

160 Whether or not a site had been burned most influenced the community structure of  
 161 saprotrophic fungi at both sampling depths, and of EM fungi at 20–30 cm below the soil surface  
 162 (*Table 4*). The number of years that had elapsed since the most recent fire had most influence on  
 163 EM community structure 0–10 cm below the surface ( $P=0.005$ ). Vegetation type was the second  
 164 most important factor for EM fungi at 20–30 cm ( $P=0.011$ ). Saprotrophic soil fungi at 0–10 cm  
 165 depth were secondarily influenced by vegetation type ( $P=0.010$ ). The influence of years since the  
 166 most recent fire was marginally significant ( $P = 0.080$ ) at 20–30 cm depth. An interaction was

167 detected between vegetation type and the number of years since the most recent fire at 20–30 cm  
168 depth on the community structure of saprotrophic soil fungi ( $P=0.007$ ).

169 EM communities had higher average Shannon’s diversity indices and lower evenness at  
170 burned compared to unburned sites (*Figure 2*). Saprotrophic communities were more diverse and  
171 less even at unburned sites. Notably, the average Shannon’s diversity of EM fungi at unburned  
172 sites was lowest at deeper soil horizons (20-30 cm). EM communities at unburned sites had the  
173 highest average evenness values of all site types. NMDS of fungal community dissimilarity (Bray-  
174 Curtis) showed that samples clustered primarily according to burn status and depth (*Figure 4*).  
175 EM communities were more like each other at burned than at unburned sites. Soil saprotrophs  
176 were more similar at unburned sites than at burned sites.



**Figure 3** Shannon's diversity (entropy) for ectomycorrhizal and saprotrophic soil fungi plotted against soil physical/chemical properties (levels of  $\text{NO}_3$ ,  $\text{NH}_4$ , P, K, Ca & pH) at burned and unburned sites and at two sampling depths. Lower diversity of EM communities at several unburned sites was associated with elevated soil nutrient levels relative to burned sites, however this trend was less evident for K levels. At unburned sites, saprotrophs at 0-10 cm depth were more diverse if  $\text{NO}_3$ , P, K and Ca were present at elevated levels, whereas at a depth of 20-30 cm saprotrophic diversity was more variable and levels of those nutrients were lower. (2-column fitting image. Color to be used in print.)

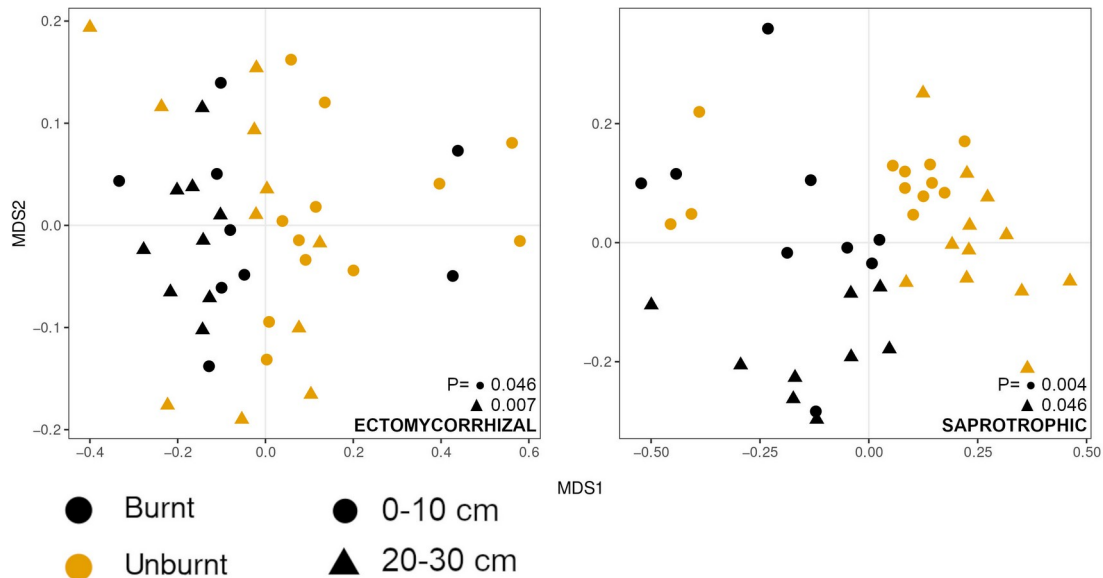
**Table 4** Results of PERMANOVA testing whether the burn status of a site (burned/unburned) and vegetation type (shrubland, grassy woodland, regenerating closed canopy forest, semi-deciduous notophyll forest, wet rainforest) were associated with changes in the community composition of ectomycorrhizal and saprotrophic soil fungi. Depth of sampling was a primary influence on community composition of EM (P=0.019) and saprotrophic (P=0.045) fungi, and datasets were split according to depth. All sites were included in the first analysis, as well as interactions between factors. Influence of years since most recent fire, years since cessation of frequent fires and interactions with vegetation type were subsequently analysed for burned sites only. P values <0.05 are shown in bold type. (2-column fitting table.)

	Depth (cm)	Factor	F model	R <sup>2</sup>	P
Ectomycorrhizal	0–10	<b>Years since most recent fire</b>	<b>1.93</b>	<b>0.22</b>	<b>0.005</b>
		<b>Burn status</b>	<b>1.32</b>	<b>0.07</b>	<b>0.046</b>
		Veg type	0.81	0.17	0.635
		Burn status:Veg type	0.73	0.20	0.797
		Years since cessation of frequent fires	1.19	0.15	0.177
		Years since most recent fire:Veg type	0.93	0.24	0.512
	20–30	<b>Burn status</b>	<b>1.37</b>	<b>0.07</b>	<b>0.007</b>
		<b>Veg type</b>	<b>4.26</b>	<b>0.52</b>	<b>0.011</b>
		<b>Burn status:Veg type</b>	<b>3.32</b>	<b>0.53</b>	<b>0.019</b>
		Years since most recent fire	1.01	0.13	0.552
Years since cessation of frequent fires		0.77	0.10	0.505	
<b>Years since cessation of frequent fires:Veg type</b>		<b>5.99</b>	<b>0.67</b>	<b>0.027</b>	
Saprotrophic	0–10	<b>Burn status</b>	<b>1.67</b>	<b>0.08</b>	<b>0.004</b>
		<b>Veg type</b>	<b>2.19</b>	<b>0.35</b>	<b>0.010</b>
		<b>Burn status:Veg type</b>	<b>1.80</b>	<b>0.37</b>	<b>0.031</b>
		Years since most recent fire	1.01	0.13	0.549
		Years since cessation of frequent fires	0.95	0.12	0.507
		Years since cessation of frequent fires:Veg type	2.06	0.41	0.086
	20–30	<b>Burn status</b>	<b>1.39</b>	<b>0.07</b>	<b>0.046</b>
		Veg type	1.22	0.23	0.164
		Burn status:Veg type	1.01	0.25	0.239
		Years since most recent fire	3.28	0.32	0.080
Years since cessation of frequent fires		1.10	0.14	0.299	
<b>Years since most recent fire:Veg type</b>		<b>5.22</b>	<b>0.63</b>	<b>0.007</b>	

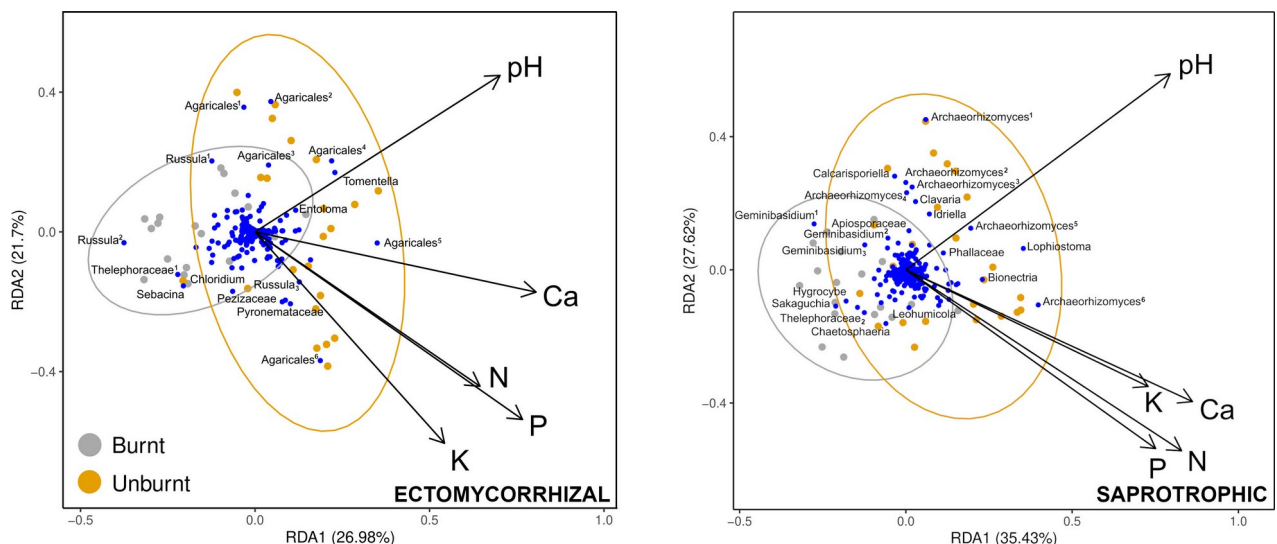
### 177 3.5. Abundance of specific fungal taxa at sites with contrasting nutrient profiles

178 Relationships were detected between the abundance of some EM OTUs and levels of soil  
179 nutrients (Figure 5). *Russula*<sup>3</sup>, Pezizaceae, Pyronemataceae and Agaricales<sup>5, 6</sup> were present in  
180 higher abundance in soil with elevated levels of N, P, K and Ca. *Entoloma* and *Tomentella* were  
181 associated with elevated pH, whereas *Sebacina*, *Chloridium* and Thelephoraceae 1 were  
182 associated with lower pH. Saprotrophic taxa associated with elevated N, P, K and Ca included  
183 *Bionectria*, *Leohumicola* and *Archaeorhizomyces* 6. Lower levels of these nutrients were

184 associated with *Geminibasidium* 1, 2 and 3 and Apiosporaceae. Increased pH was associated with  
 185 the saprotrophic taxa *Clavaria*, *Idriella* and Phallaceae, and lower pH with *Hygrocybe*,  
 186 *Sakaguchia*, *Chaetosphaeria* and Thelephoraceae 2.



**Figure 4** Non-metric multidimensional scaling showing differences in fungal community composition between burned and unburned sites at two sampling depths for ectomycorrhizal and saprotrophic fungi. Matrix based on Bray-Curtis distances. *P* values refer to PERMANOVA test for significance in differences in taxonomic community structure between burned and unburned sites at each sampling depth. Samples clustered primarily according to burn status and depth. EM communities were more similar to each other at burned over unburned sites. Soil saprotrophs were more similar at unburned sites than at burned sites. (Single-column fitting image. Color to be used in print.)



**Figure 5** Redundancy analysis (RDA) summarising variation in response variables (fungal community composition and individual taxa) and explanatory variables (soil chemical/physical properties) at burned and unburned sites. Blue dots represent individual fungal operational taxonomic units. Taxon and site dots appearing closer to arrow tips were associated with higher levels of that soil chemical/physical variable, whereas taxon and site dots appearing opposite to an arrow were associated with lower levels. An angle of 90 degrees indicates little or no correlation. Based on Hellinger-transformed OTU tables to give lower weights to rare taxa. (2-column fitting image. Color to be used in print.)

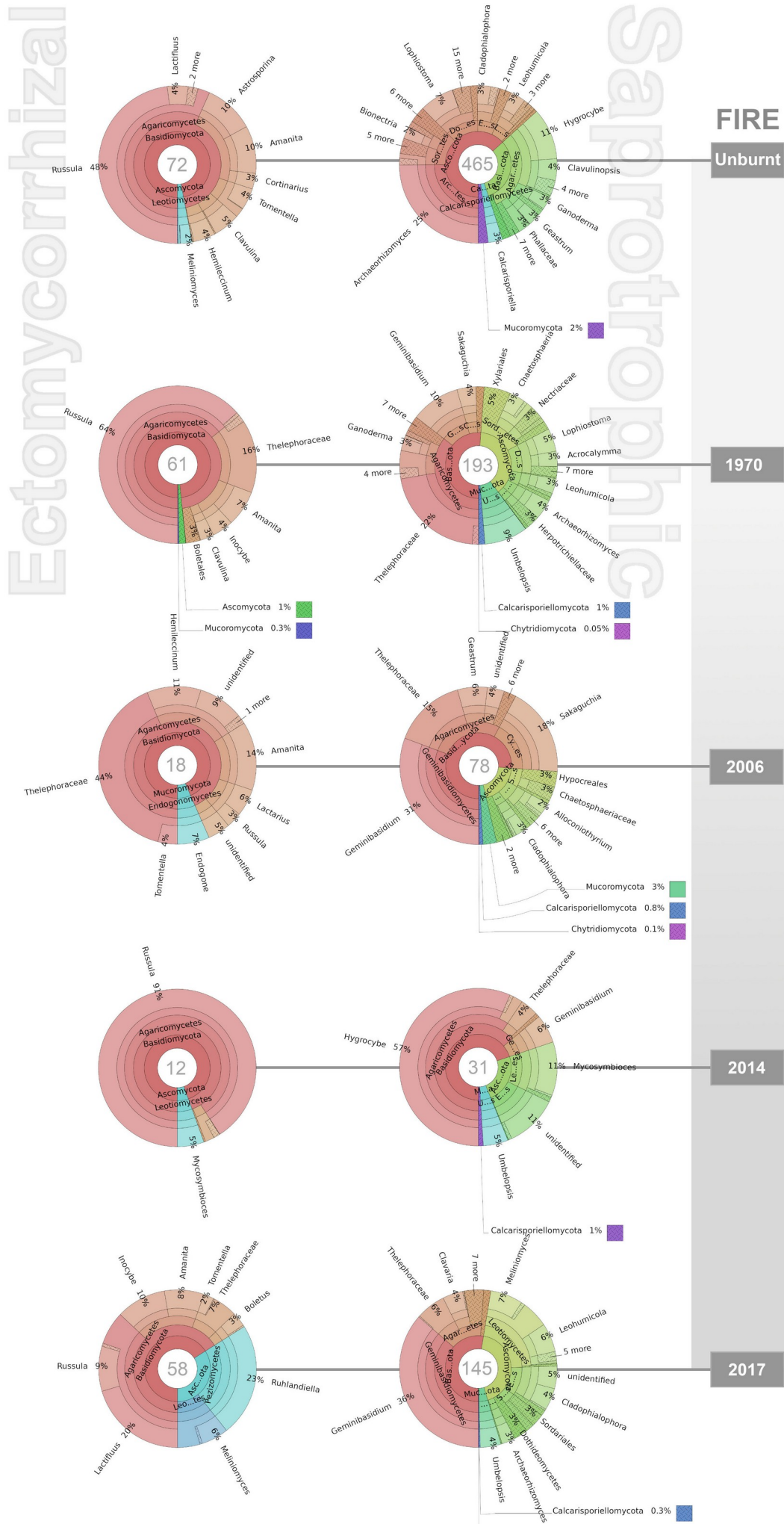


187 3.6. *Abundance of specific fungal taxa at sites with contrasting fire histories*

188 We assigned ecological guild and trophic mode for 165 EM and 654 saprotrophic soil taxa  
189 from 1,696 assigned OTUs with FUNGuild v1.1 (Nguyen et al., 2016). The basidiomycete taxa  
190 *Russula*, *Hemileccinium*, *Lactifluus*, *Amanita*, *Mycosymbiocytes* and Thelephoraceae were dominant  
191 at unburned sites and sites burned prior to 2015 (*Figure 6*). Ascomycota were present in increased  
192 abundance and taxonomic diversity, including *Meliniomyces* and the truffle taxon *Ruhlandiella*, at  
193 sites burned immediately prior to sampling in 2017. Species richness of EM fungi decreased  
194 linearly from the time of last fire, from 72 OTUs at unburned sites to 12 at sites burned in 2014.  
195 The exceptions to this trend were sites that were most recently burned, which had 58 EM OTUs.

196 Species richness was at least twofold higher for saprotrophs over EM at all sites, and up to  
197 6 times higher at unburned sites (*Figure 6*). Unburned sites were dominated by  
198 *Archaeorhizomyces* (Ascomycota) and *Hygrocybe* (Basidiomycota). Dominant saprotrophic taxa  
199 at burned sites included *Geminibasidium*, *Hygrocybe*, Thelephoraceae (Basidiomycota) and  
200 *Umbelopsis* and *Mycosymbiocytes* (Ascomycota). A similar trend of decreased species richness  
201 from the time of last fire was also evident for saprotrophs, from 465 OTUs at unburned sites to 31  
202 at sites burned in 2014, with 145 OTUs at sites that were most recently burned.

**Figure 6** (following page) Taxonomic composition and abundance of ectomycorrhizal (EM) and saprotrophic soil fungi at sites with different fire histories. Numbers inside circles in grey represent numbers of OTUs detected (species richness). Species richness of EM fungi decreased linearly from the time of last fire, from 72 OTUs at unburned sites to 12 at sites burned in 2014. (*2-column fitting image. Color to be used in print.*)



## 203 **4. Discussion**

204 Saprotrophic and EM fungi showed major community-level changes in response to fire,  
205 which interacted with and modified these functional guilds in different ways. Fire induced  
206 compositional changes in the dominant vegetation, which altered EM composition through the  
207 replacement of mycorrhizal hosts. The changes to EM composition were largely independent of  
208 alterations to soil chemistry. By contrast, the community composition, diversity and evenness of  
209 saprotrophic fungi changed after fire in response to reduced soil nutrient levels. We also detected  
210 fire-dependent shifts in the composition of saprotrophic fungi in litter at shallow soil horizons.

### 211 *4.1. Fire impacts ectomycorrhizal fungi by changing plant communities*

212 EM fungi are important tree symbionts in forest ecosystems. The taxonomic community  
213 composition and abundance of EM fungi differed between burned and unburned forest soils. EM  
214 fungi were strongly influenced by the dominant vegetation. In general, EM communities were less  
215 diverse and more even at unburned sites, which indicated a late-successional community structure  
216 dominated by a small number of taxa including *Russula* and *Amanita*. Successional shifts, in  
217 which EM community composition progresses from post-fire tree stand initiation to canopy  
218 closure, are well-documented (LeDuc et al., 2013; Longo et al., 2011).

219 The more recently a site had been burned, the lower the species richness of EM fungi,  
220 which was congruent with reports from temperate forests in the Northern Hemisphere (Kipfer et  
221 al., 2011; LeDuc et al., 2013; Rincón et al., 2014). An increase in EM species richness at sites  
222 burned immediately prior to sampling contrasts with other studies that showed immediate  
223 negative effects of fire on EM diversity. One explanation may be that ascomycete EM taxa were  
224 more diverse and abundant at burned sites relative to unburned sites. If fire had occurred the year  
225 prior to sampling, *Ruhlandiella* (hypogeous fungi, or truffles), which are dispersed primarily by  
226 mycophagous mammals (Claridge, 2002; Dundas et al., 2018), were the most abundant of this  
227 pyrophilic group. *Ruhlandiella* are known to fruit abundantly after bushfires (Kraisitudomsook et

228 al., 2019; Warcup, 1990). Reduction of undergrowth by fire also has the potential to increase  
229 mammalian access to the soil, which increases foraging and dispersal activity. Increased activity  
230 of pyrophilic taxa such as *Ruhlandiella* and those dispersed by mycophagous mammals may  
231 explain the short-term, post-fire increase in EM diversity.

#### 232 4.2. *Saprotrophic fungi are impacted by fire-driven nutrient shifts*

233 This study showed that forest fire alters the structure of saprotrophic communities  
234 primarily by changing nutrient levels in the soil and by altering the composition of the litter layer  
235 through changes in plant community composition. Saprotrophic fungi were more diverse and less  
236 even at unburned sites, where levels of soil nutrients were higher. Unlike EM fungi, saprotroph  
237 diversity was influenced by levels of all soil nutrients measured, including a weak yet measurable  
238 influence of pH. Strong positive correlations between diversity of saprotrophic fungi and the soil  
239 quality indicators N, P and NH<sub>4</sub> have been reported (Chen et al., 2021), as well as increases in  
240 saprotrophic biomass and diversity in response to experimental addition of N to soils (Clocchiatti  
241 et al., 2020). In a global study, Ca was found to be the strongest predictor of soil fungal diversity  
242 (Tedersoo et al., 2014). In this study in the AMT, we found Ca, NO<sub>3</sub>, P and K were strongly  
243 correlated with saprotroph diversity.

244 Soil saprotrophs showed marked changes in species richness in response to fire. In  
245 recently-burned areas, the species richness of soil saprotrophs was almost double that measured at  
246 most other burned sites. Fungal saprotrophs were dominated by *Geminibasidium* (Basidiomycota)  
247 and *Meliniomyces* (Ascomycota) in recently burned areas. We found higher species richness and  
248 Shannon's diversity of saprotrophic over EM fungi regardless of a site's fire history. Salo et al.  
249 (2019) described an increase in saprotrophic fungal diversity immediately after fire, with  
250 saprotrophic succession in soil more rapid than in wood. In Australian Mountain Ash forests,  
251 distinctive communities of soil fungi appeared in the year after fire disturbance, followed by much  
252 longer seral phases dominated by non-pyrophilic species (McMullan-Fisher et al., 2002). As

253 outlined by Verma and Jayakumar (2012), low-intensity fires in 2017 may have increased the  
254 amount of organic material available, leading to a rise in saprotrophic diversity.

255 The dominant vegetation type shaped saprotrophic communities in the litter soil horizon,  
256 which indicated that certain types of organic litter may favour some fungal taxa over others. Wu et  
257 al. (2011) found that leaf type was one of the main drivers of fungal community biomass and  
258 composition. Lunghini et al. (2013) reported higher fungal diversity in mixed litter than in  
259 monospecific litter. We propose that fire-induced alterations to plant community composition lead  
260 to compositional changes in the litter layer, which in turn select for particular communities of  
261 saprotrophic fungi.

#### 262 4.3. *Soil chemistry was altered by fire*

263 Soil chemistry in the Iron Range has been altered by fire. Chemical/physical properties  
264 differed between burned and unburned sites and between the litter and mineral soil layers, with  
265 NO<sub>3</sub>, P, Ca and pH generally higher in unburned than at burned sites. This is congruent with  
266 current knowledge of fire-nutrient dynamics in tropical forests, where soil nutrients are depleted  
267 by recurrent fires (Bowman, 2009a). Conversely, occasional fires can cause a short-term increase  
268 in nutrient availability at shallow soil horizons via combustion of litter and soil organic matter.  
269 Low wind and high sub-canopy moisture generate fires of lower intensity in AMT forests than in  
270 savannas (Cochrane, 2003; Verma and Jayakumar, 2012). Vegetation changes can influence levels  
271 of soil nutrients, especially N (Evans et al., 2001; Zhou et al., 2018). We found a greater net effect  
272 of burning on soil chemical/physical properties, with no discernible patterns attributable to the  
273 different vegetation types studied. This suggests that alteration of nutrient profiles by fire has been  
274 direct, most likely through volatilization of litter and soil organic matter (Verma et al., 2019),  
275 rather than by indirect alterations to plant community composition.

276 We detected a strong correlation between levels of soil NH<sub>4</sub> and the diversity of EM fungi.  
277 There was no correlation between EM diversity and other soil chemical/physical properties

278 measured in this study. We propose that host availability and fire have a greater influence over  
279 rainforest EM community composition than levels of soil NO<sub>3</sub>, P, K, C, Ca and pH.

#### 280 4.4. *Different fungi at different depths*

281 Vertical partitioning of fungi as observed in this study applies broadly to EM-dominated  
282 soil ecosystems in tropical and boreal zones (McGuire et al., 2013). The type of vegetation  
283 structured EM communities in deep soil. The effect of vegetation type was weaker in the shallow  
284 litter layer, which is expected given the affiliation of EM fungi with tree roots. Primary notophyll  
285 rainforest in other areas of North Queensland has higher root biomass and root length compared to  
286 secondary forest (Hopkins et al., 1996). Deep soil horizons in unburned forests provide greater  
287 opportunity for EM colonisation of compatible hosts.

## 288 5. Conclusions

289 We support the hypothesis that tropical soil fungi are impacted by burning, which altered  
290 the abundance and phylogenetic structure of EM and saprotrophic communities in different  
291 ways. Communities of EM fungi were structurally altered by fire through vegetation changes at  
292 burned and unburned sites. Truffle-like taxa that are reliant on mycophagous mammals were more  
293 abundant at recently burned sites. In general, EM fungi at unburned sites had a late-successional  
294 community structure dominated by a small number of taxa. At burned sites EM diversity was  
295 higher and less even than at unburned sites. The diversity of saprotrophic fungi was impacted by  
296 reduced soil chemical/physical levels after fire. In the litter layer, the community composition of  
297 saprotrophs was influenced by changes in vegetation type.

298 Globally between 2007 and 2017, carbon sinks provided by terrestrial ecosystems  
299 removed an estimated 32 % of anthropogenic CO<sub>2</sub> emissions from the atmosphere (Le Quéré et  
300 al., 2018). Of these terrestrial sinks, tropical forests are some the largest due to their rapid growth  
301 (Keenan and Williams, 2018). Large savanna-dominated areas of Australia's tropical north could,



302 if protected from burning, support tropical forestry for carbon sequestration (K. Cook, pers.  
303 comm.), which may become a serious option for Australia as states begin to commit to net zero  
304 emissions (NSWDPIA, 2020). Any assessment of native tropical tree species for their utility in  
305 carbon forestry should consider their mycorrhizal symbionts and their tractability for the  
306 production of inoculum. Australia's tropical fungi have the potential to serve as a major biological  
307 resource over the approaching decades.

### 308 **CRedit authorship contribution statement**

309 **Jed Calvert:** Conceptualization, Methodology, Formal analysis, Investigation, Writing - Original  
310 Draft, Visualization, Project administration. **Alistair McTaggart:** Conceptualization,  
311 Methodology, Writing - Review & Editing, Supervision. **Lilia C. Carvalhais:** Methodology,  
312 Formal analysis, Writing - Review & Editing. **André Drenth:** Writing - Review & Editing,  
313 Supervision. **Roger Shivas:** Writing - Review & Editing, Supervision.

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318 the decision to submit the article for publication.

### 319 **Research data for this article**

320 The dataset and metadata supporting this article is available in the BioPlatforms Australia  
321 project's data portal under the sample accessions 42144–42185 ([https://ccgapps.com.au/bpa-](https://ccgapps.com.au/bpa-metadata/base)  
322 [metadata/base](https://ccgapps.com.au/bpa-metadata/base)), doi:10.4227/71/561c9bc670099.

## 323 **Declaration of competing interest**

324 The authors declare that they have no known competing financial interests or personal  
325 relationships that could have appeared to influence the work reported in this paper.

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