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RESEARCH ARTICLE

Direct and indirect effects of fire on microbial communities in a pyrodiverse dry-sclerophyll forest

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Abstract

1. Fire is one of the predominant drivers of the structural and functional dynamics of forest ecosystems. In recent years, novel fire regimes have posed a major challenge to the management of pyrodiverse forests. While previous research efforts have focused on quantifying the impacts of fire on above-ground forest biodiversity, how microbial communities respond to fire is less understood, despite their functional significance.
2. Here, we describe the effects of time since fire, fire frequency and their interaction on soil and leaf litter fungal and bacterial communities from the pyrodiverse, *Eucalyptus pilularis* forests of south-eastern Australia. Using structural equation models, we also elucidate how fire can influence these communities both directly and indirectly through biotic–abiotic interactions.
3. Our results demonstrate that fire is a key driver of litter and soil bacterial and fungal communities, with effects most pronounced for soil fungal communities. Notably, recently burnt forest hosted lower abundances of symbiotic ectomycorrhizal fungi and Acidobacteria in the soil, and basidiomycetous fungi and Actinobacteriota in the litter. Compared with low fire frequencies, high fire frequency increased soil fungal plant pathogens, but reduced Actinobacteriota. The majority of fire effects on microbial communities were mediated by fire-induced changes in litter and soil abiotic properties. For instance, recent and more frequent fire was associated with reduced soil sulphur, which led to an increase in soil fungal plant pathogens and saprotrophic fungi in these sites. Pathogenic fungi also increased in recently burnt forests that had a low fire frequency, mediated by a decline in litter carbon and an increase in soil pH in these sites.
4. *Synthesis*. Our findings indicate that predicted increases in the frequency of fire may select for specific microbial communities directly and indirectly through ecological interactions, which may have functional implications for plants (increase in pathogens, decrease in symbionts), decomposition rates (declines in Actinobacteriota and Acidobacteriota) and carbon storage (decrease in

ectomycorrhizal fungi). In the face of predicted shifts in wildfire regimes, which may exacerbate fire-induced changes in microbial communities, adaptive fire management and monitoring is required to address the potential functional implications of fire-altered microbial communities.

KEYWORDS
bacteria, *Eucalyptus pilularis*, fire, fungi, pyrodiversity, SEM, soil

1 | INTRODUCTION

Fire is a predominant driver of ecological dynamics in many terrestrial ecosystems world-wide (Bond et al., 2005; Keeley et al., 2011), where it influences the structure and composition of all biological life (Bowman et al., 2009). The resilience of ecological communities to disturbances such as fire reflects component processes of persistence, recovery and reorganisation, which are often context dependent and species specific (Falk et al., 2019; Seidl et al., 2016). In the last decade, feedbacks between climatic changes (such as increasing warming and droughts) and vegetation have led to an increase in the frequency and intensity of fires across forest ecosystems in many parts of the world (Boer et al., 2020; Bradstock et al., 2009;Coogan et al., 2019; Goss et al., 2020). For instance, in the last 2 years (2018–2020) 'extreme' or 'noteworthy' fire events have characterised the disturbance patterns of forests in Australia (resulting in >18 million ha being burnt) (Boer et al., 2020), British Columbia (>1.2 million ha burnt), Greece, the United Kingdom, northern Europe and Asia and other parts of North America (Coogan et al., 2019; Goss et al., 2020). Greatly altered fire regimes can produce novel conditions that exceed the ability of ecological communities to persist and recover, leading to community reorganisation, and altered ecosystem structure and function (Buma et al., 2013; Falk et al., 2019; Johnstone et al., 2016; Seidl et al., 2016).

Altered fire regimes pose a major challenge to the management of 'pyrodiverse' ecosystems, where high spatiotemporal variability in fire regimes may promote biodiversity—the 'pyrodiversity begets biodiversity' hypothesis (Parr & Anderson, 2006). The management of these ecosystems requires careful consideration of both the 'visible' mosaic of the most recent fire and the 'invisible' mosaic of prior fires at the landscape level; both these mosaics produce legacy effects that influence the recovery of ecosystems after fire (Bače et al., 2015; Bowd, Blair, et al., 2021; Bradstock et al., 2005). Moreover, understanding taxon-specific responses to different fire regimes is critical in facilitating ecologically appropriate adaptive management (Lindenmayer et al., 2007; Taylor et al., 2012). Ecological research in pyrodiverse forests is typically focussed on the responses of above-ground flora and fauna (Foster et al., 2017; MacGregor et al., 2020), and the responses of above-ground (leaf litter) and below-ground micro-organisms have been considered in far fewer studies, despite the integral ecological functions they provide (Bahram et al., 2018; Egidi et al., 2016; Hartmann et al., 2012; Kurth et al., 2013; Pérez-Izquierdo et al., 2021; Whitman et al., 2019).

Micro-organisms are key drivers of multiple ecological functions including decomposition, nutrient cycling, carbon storage, plant productivity and seedling survival (Fierer et al., 2007; Selosse et al., 2006). Microbial communities can facilitate the recovery of all other life-forms after disturbance (Claridge et al., 2009; Selosse et al., 2006). The influence of fire on microbial communities can be direct; through the combustion of live biomass, or indirect; through influencing plant–soil–microbial interactions (Barnes et al., 2017; Ibáñez et al., 2021; van der Putten et al., 2013; Wardle et al., 2004), and these effects vary with fire intensity and frequency, and the interactions among them (Dooley & Treseder, 2012; Muñoz-Rojas et al., 2016; Pérez-Izquierdo et al., 2021; Shen et al., 2015). For instance, during a high-intensity fire, soil temperatures can exceed 500°C, which can rapidly volatilise nutrients and combust organic matter and its resident microflora, including leaf litter on the soil surface (Certini, 2005; Granged et al., 2011). Fire-induced changes in the abiotic properties of soils or in leaf litter can also select for specific microbial communities ('environmental filtering'), which may have important functional implications (Kraft et al., 2015). For instance, a prolific increase in early-successional saprotrophs after fire can trigger the rapid decomposition of remaining organic matter, and subsequent release of CO_2 via respiration (Averill & Hawkes, 2016; Pérez-Izquierdo et al., 2021). Shifts in plant communities following fire also may influence the structural and functional dynamics of microbial communities, especially those which associate with plant roots and exhibit host specificity (Tedersoo et al., 2008; Valencia et al., 2018).

Previous studies in boreal and temperate forests across the globe have found short-term to mid-term (<15 years) disturbance effects on microbial communities following single disturbances (Muñoz-Rojas et al., 2016; Mushinski et al., 2018; Pérez-Izquierdo et al., 2021; Shen et al., 2015; Varenius et al., 2016; Visser, 1995; Whitman et al., 2019). However, comparatively few studies have analysed the mechanisms through which individual components of fire regimes, including fire frequency and time since fire (and their interactions) can influence microbial communities both directly and indirectly through their interactions with plants and with litter and soil abiotic properties. Understanding these indirect mechanisms is critical in developing a comprehensive insight into how and why microbial communities respond to fire (Bowd, Banks, et al., 2021).

Here, we address these knowledge gaps in a pyrodiverse dry-sclerophyll forest of south-eastern Australia. This study landscape is characterised by a mosaic of different fire histories across spatiotemporal scales (Foster et al., 2017), and provides a unique opportunity to disentangle the direct and indirect effects of time since fire, fire frequency and their interaction on soil and leaf litter bacterial and fungal communities. Specifically, we used this ecosystem to answer three important and interrelated questions. (1) *How does time since fire, fire frequency and their interaction influence bacteria and fungi in soils and leaf litter directly?* (2) *How are fungi and bacteria associated with vegetation and abiotic properties in the soil and leaf litter?* And, (3) *How do interactions between plants, microbes and abiotic factors mediate indirect fire effects on fungal and bacterial communities in soils and leaf litter?* Based on these research questions, we constructed three hypotheses that are outlined below.

Hypothesis 1 *Fire will influence microbial communities both directly and indirectly through interactions with plants, microbes and abiotic properties. This is because while microbial communities may be sensitive to direct fire effects (via fire-induced mortality) (Bååth et al., 1995; Glassman et al., 2016), they also have well-known associations with abiotic and biotic properties (Bowd et al., 2022; Tedersoo et al., 2014; Wardle & Jonsson, 2014) that can also be altered by fire (Bowd, Banks, et al., 2021; Butler et al., 2019; Foster et al., 2017; Pellegrini et al., 2018).*

Hypothesis 2 *Direct and indirect fire effects will vary within and between microbial communities and groups, likely reflecting species-specific physiological and ecological differences, disturbance tolerances and specific functional roles (Bååth et al., 1995; Sun et al., 2015; Voriskova & Baldrian, 2013; Wardle & Jonsson, 2014; Waring et al., 2013). For instance, we predict that symbiotrophs and endophytic fungi will be strongly influenced by vegetation properties, whereas microbes associated with decomposition (including saprotrophs and Actinobacteriota) would be more regulated by abiotic properties that may be related to the availability of organic matter.*

Hypothesis 3 *(a) Litter microbial communities will be influenced by time since fire more than by fire frequency. This is based on the notion that fire consumes leaf litter layers, which may 'reset' the litter microbiome with each successive disturbance (Cornelissen et al., 2017). In contrast, we also hypothesised that: (b) the long-lived legacy of prior disturbances on soil environments will result in effects of both fire frequency and time since fire on soil microbial communities, but to a lesser extent than effects on litter microbes (Bowd et al., 2019; Muqaddas et al., 2015; Pellegrini et al., 2018).*

2 | MATERIALS AND METHODS

2.1 | Study description

We conducted our study in the dry-sclerophyll forests of Booderee National Park, located in the Jervis Bay Territory of south-eastern Australia, 200 km south of Sydney, New South Wales (Figure 1). This region is characterised by a temperate climate, with an average annual rainfall of 1240 mm and maximum temperature of 24°C in summer (February) and 15°C in winter (July) (Lindenmayer et al., 2014). Rainfall is typically highest during colder months (April–July; mean > 100 mm per month) and lowest in warmer months (October and December; mean ≤ 62 mm per month) (Bureau of Meteorology, 2021). The underlying geology is dominated by Permian (~260 million years old) sandstone covered by Pleiostocene (1.6 million years old) sand dune systems (Lindenmayer et al., 2014). Drysclerophyll forests constitute >35% of Booderee National Park and are dominated by species capable of resprouting after fire (Foster et al., 2017). These include overstorey species: *Eucalyptus pilularis* and *Eucalyptus botryoides*, midstorey species: *Banksia serrata*, *Acacia longifolia* and understorey species: *Pteridium esculentum* and *Lomandra longifolia* (Foster et al., 2017; Kubiak, 2009). The remaining area of the park is occupied by other vegetation types including shrubland, woodland and heath (Taws, 1997).

Booderee National Park has a diverse history of wildfire and prescribed burning that has been well-documented since 1957 (Foster et al., 2017; Lindenmayer et al., 2014). The region experienced 230 fires between 1957 and 2012 (average of 4.18 fires/year; median size per fire of 7.02 ha), with most areas burnt between one and four times in that 55 years period (Foster et al., 2017). The majority of these fires were small and low intensity, however, six large wildfires (>5 ha) have occurred in the years 1962, 1972 (two fires), 2002, 2003 and 2017 (Foster et al., 2017, Lindenmayer et al., 2014). The recent fire history of the park is spatially highly variable due to the combination of fire management (prescribed burning and containment of wildfires) and the peninsula location of the park, where western water bodies reduce the likelihood of fire in adjacent forest during periods of high-fire risk weather (Figure 1). Because of their vegetation characteristics and climatic conditions, the dry-sclerophyll forests of Booderee National Park have the potential to experience regular major fires (5–10 year intervals) (Bradstock, 2010), which may increase in frequency in the next few decades through climate warming (Bradstock et al., 2009).

2.2 | Experimental design

We designed our study to encompass the diverse mosaic of fire histories that characterise Booderee National Park. To guide site selection, we used spatial GIS layers of vegetation types (Taws, 1997), a 1 m digital elevation model, and fire perimeter maps (provided by Booderee National Park) to classify all areas of the park by vegetation type, time since fire and fire frequency (number of fires since 1957). We then superimposed a 200 × 200 m grid of points across all dry-sclerophyll forest areas in the park and extracted fire variables, slope and aspect for each grid cell to generate a list of potential sample sites. To control for other sources of potential variation, we excluded areas within 50 m of roads or other disturbances and sites with slopes >20° or south-facing aspects (aspect >135° and <225°). We then randomly selected six sites from each of six factorial

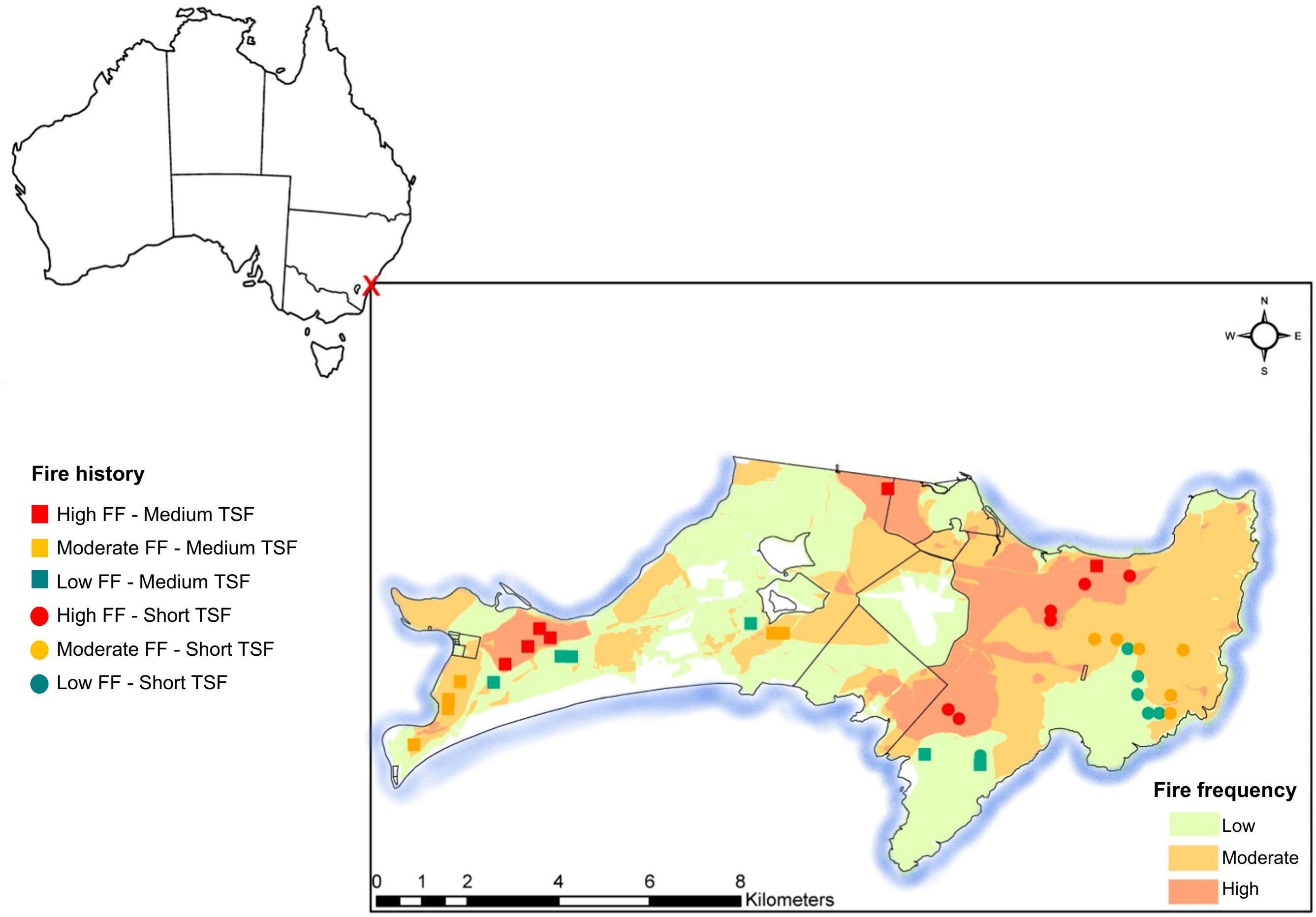


FIGURE 1 Location of 36 study sites in Booderee National Park, south-east Australia, across different fire histories. Sites were categorised based on fire frequency (FF) (low, moderate, high) and time since fire (TSF) (short, 2–3 years; medium, 10–20 years). Blue shading indicates the coastline of the peninsula

combinations of time since fire and fire frequency. Specifically, we considered two levels of time since fire: (1) short (2–3 years: last fire in 2017) and (2) medium (10–20 years: last fire in 2001, 2002, 2003 or 2007), and three levels of fire frequency: (1) high (>5 fires in the 61 years between 1957 and 2018), (2) moderate (3–4 fires) and (3) low (1–2 fires). This gave a total of 36 sites (Figure 1). This factorial design allowed us to test the influence of time since fire and fire frequency, and their interaction, on microbial communities. We constructed a 10 × 10 m plot for sampling at each site.

2.3 | Sample collection

2.3.1 | Plants

In 2019, we conducted vegetation surveys across all sites, stratified by stratum (understorey <2 m high, midstorey >2 m high, overstorey >10 m high). Specifically, in each 10 × 10 m plot, we visually estimated the projective foliage cover of all midstorey species. For the understorey, we estimated the abundance of plant species using a grid-based point-intercept method, where species were recorded when intersecting with an 18 mm diameter dowel rod at 100 points in each plot. We also recorded the presence and diameter at breast height (DBH, measured at 1.3 m above-ground height) of all overstorey trees from a 10 m radius circle, measured from the centre of each plot. Using these measures, we determined tree basal area at the site level using the sum of the cross-sectional area of all trees per unit land area. At the site level, we also pooled measures of overstorey and midstorey species richness to calculate midstorey–overstorey species richness (Appendix S1: Table S1). Where possible, we identified mycorrhizal associations for individual plant species (at the genus level) using an extensive literature search guided by Brundrett (2008) (Appendix S1: Table S2). These were: (1) Ectomycorrhizal, (2) Arbuscular mycorrhizal, (3) Ericoid-mycorrhizal and (4) Non-mycorrhizal. We were unable to determine the status of mycorrhizal associations for 11 of 70 plant species.

2.3.2 | Soils

In June 2020, we collected nine 0–10 cm soil cores from the centre and perimeter of each of our 36, 10 × 10 m plots. We pooled and mixed soil samples for each site to create a single composite sample. From each composite sample, we filled a 50 ml falcon tube with soil for microbial analyses, which was stored at −22°C prior to DNA extraction. We also collected and weighed an additional soil sample to determine soil moisture and used the remaining soil in each site for soil chemical analysis described in Appendix S2. These were: organic carbon (C) (%), soil pH ($CaCl_2$), available phosphorus (P) (mg/kg) and potassium (K) (mg/kg), electrical conductivity (dS/m), sulphur (S) (mg/kg), nitrate nitrogen (NO_3^-) (mg/kg) and ammonium nitrogen (NH_4^+) (mg/kg).

2.3.3 | Litter

In June 2020, we collected leaf litter samples from a single 2.5 m transect in the centre of each 10 × 10 m plot. Specifically, we collected approximately six handfuls of senesced leaf litter from the soil surface along the central line and either side of the transect at 30–40 cm intervals. We pooled all leaf litter samples from each plot to gain a composite sample for that plot (>30 g of leaf litter per plot). From each composite sample, we filled a 50 ml falcon tube with leaf litter for microbial analyses and stored it at −22°C prior to DNA extraction. We also collected and weighed an additional leaf litter sample from each site to determine leaf litter moisture. We air-dried remaining leaf litter for chemical analyses (total carbon, nitrogen (N), phosphorus, potassium and sulphur (%), litter pH and electrical conductivity (dS/m)) and to determine leaf litter moisture. See Appendix S2 for further details.

2.4 | DNA amplicon preparation and sequence analyses

DNA was extracted from soil and litter from each site using a DNeasy PowerSoil Pro Kit (QIAGEN) following the manufacturer's instruction. From these extractions, PCR amplification and sequencing was performed by the Australian Genome Research Facility. Specifically, PCR amplicons were generated for fungi (ITS2 region) using primers: FITS7 (GTGARTCATCGAATCTTTG) (Ihrmark et al., 2012) and ITS4 (TCCTCCGCTTATTGATATGC) (White et al., 1990); and for bacteria (16S gene: V3-V4 region) using primers: 341F (CCTACGGGNGGCWGCAG) and 805R (GACTACHVGGGTATCTAATCC) (Herlemann et al., 2011). See Appendix S2 for further details.

2.4.1 | Bioinformatics

The bacterial and fungal raw sequences were processed using QIIME2 software (qiime2-2020.2 (Bolyen et al., 2019). Paired-end, demultiplexed sequence reads were imported into QIIME2 using a fastq manifest format, and sequence quality control, denoising, chimera detection and clustering into amplicon sequence variants (ASVs) was performed using the DADA2 plugin in QIIME2 (Callahan et al., 2016) with the following parameters: –p-trunc-len-f 250 and –p-trunc-len-r 250 for both gene markers. ASVs with <10 reads across all samples were removed for downstream analysis. The closest taxonomic match of each sequence variant was then identified using the classify-sklearn function against the SILVA (v.138) (Quast et al., 2013) and UNITE fungal ITS databases (v.8) (Abarenkov et al., 2010) for bacteria and fungi respectively. The QIIME 2-feature-classifier for each gene dataset from the respective sequence and taxonomy files was trained before performing the taxonomic assignments.

Based on appropriate taxonomic matches, we assigned 71% (from soil samples) and 37% (from litter samples) of fungal ITS2 sequences to functional guilds and trophic groups using the 'FUNGUILD' database, where confidence was 'probable' and 'highly probable' using 'FUNGuildR' in R (Nguyen et al., 2016). Specifically, from the FUNGUILD database, we identified ASVs belonging to one of three trophic groups: 'Symbiotroph', 'Saprotroph' and 'Pathotroph' (including plant, fungal and animal pathogens), and two functional guilds: 'Ectomycorrhizal' and 'Plant pathogen'. Symbiotrophic fungi provide hosts with nutrients in exchange for carbon; saprotrophic fungi break down and metabolise dead plant parts; and pathotrophic fungi harm hosts by taking their carbon and/or nutrients (Nguyen and others 2016). In soil-derived samples, we examined only ectomycorrhizal symbiotrophs, and not arbuscular mycorrhizal fungi because our primer set largely excludes Glomeromycetes (arbuscular mycorrhizal fungi) which require taxa-specific primers (George et al., 2019). Moreover, we did not include ASVs that were assigned to multiple trophic groups or guilds in our analysis.

2.5 | Statistical analyses

Using the 'PHYLOSEQ' package in R, we rarefied bacterial and fungal datasets in soil and litter samples by the lowest number of sequences across sites and generated respective rarefaction curves (Appendix S1: Figure S1) (soil bacteria: 27,746 sequences; litter bacteria: 23,419 sequences; soil fungi: 53,202; litter fungi: 60,229) (McMurdie & Holmes, 2013). Thereafter, we used these rarefied numbers of sequences for each ASV as proxies for 'abundance' in all subsequent analyses.

2.5.1 | Derived vegetation variables

We standardised abundance measures of plant species across each vegetation strata using *z*-score transformations to account for different measurements among strata (mean = 0, standard deviation = 1). We then pooled these measures (z scores) for each plant species at each site to create a composite plant abundance × site matrix for use in multivariate analyses. Using these data, we generated a Euclidean distance matrix to perform a principal component analysis (PCA)

(Appendix S1: Figure S2). Thereafter, we used PCA1 scores (which explained 40% of the variation in plant community composition) as proxies for 'plant community composition' in structural equation models. From the same plant abundance × site matrix, we pooled measures (*z*-scores) of tree and shrub species that were known to host ectomycorrhizal fungi at the site level (including those associated with both ectomycorrhizal and arbuscular mycorrhizal fungi) (Appendix S1: Table S2). This served as a proxy for 'ectomycorrhizal plant abundance' and was also used as a covariate for ectomycorrhizal fungi only.

2.5.2 | Relationships between fire, microbes, abiotic properties and vegetation

To address our first two research questions, we employed a combination of multivariate analyses and structural equation modelling (SEM) to quantify relationships between the composition and abundance of microbial communities, abiotic and vegetation properties and fire. We then used SEMs to address our third research question by elucidating the direct and indirect effects of fire on microbial communities.

Multivariate analyses

We generated NMDS plots to visualise, and permutational multivariate analysis of variance (PERMANOVA) to test, the influence of time since fire and fire frequency on the composition of fungal and bacterial communities in litter and soil samples (Question #1). These analyses were based on Bray–Curtis dissimilarity matrices using the abundance of ASVs (square-root transformed) using the 'adonis' function in the 'VEGAN' package in R (Oksanen et al., 2013). We used the 'PAIRWISE. ADONIS' package (Martinez Arbizu, 2020) in R to conduct pairwise tests between the composition of individual microbial communities from both sample types in sites with moderate, high and low fire frequencies.

We used the 'envfit' function in the 'VEGAN' R package, to determine correlations between topography (slope and elevation), abiotic properties and vegetation (soil and litter properties, tree basal area, understorey plant richness, mid-overstorey richness and the abundance of trees with ectomycorrhizal associations) and NMDS axes for bacteria and fungi in the litter and soil independently (litter bacteria, litter fungi, soil bacteria, soil fungi). In these analyses, for litter abiotic properties we used litter moisture, total C, P, K, N, pH and electrical conductivity, and for soil abiotic properties we used soil moisture, NH_4^+, NO_3^-, P, K, S, C and pH. For each NMDS ordination, we overlayed significantly correlated variables ($p < 0.05$) as biplots proportional to the strength of the correlation. Furthermore, we employed Mantel tests to test for correlations between each microbial Bray–Curtis dissimilarity matrix and (a) plant community dissimilarities (Euclidean distance matrix), and (b) the distances between sites (harvesine distance matrix) respectively. Mantel tests were based on Spearman's correlation and were conducted using the 'geosphere' (Hijmans, 2021) and 'VEGAN' packages in R (Oksanen et al., 2013).

Structural equation modelling

We constructed two, multi-level structural equation models (SEMs) (Lefcheck, 2016) to identify plant–abiotic–microbial associations, and to elucidate the direct and indirect effects of fire on bacteria and fungi in the soil (SEM #1) and litter (SEM #2) respectively. We designed these models based on hypothesised causal pathways (Figure 2) and performed them using the 'PIECEWISESEM' package in R (Lefcheck, 2016). Specifically, to construct each SEM pathway, we ran independent generalized linear models for each response variable and selected the best fitting model using the 'dredge' function in the MuMIn package in R (Barton, 2020). Microbial response variables were the abundance of: (a) fungal functional groups and dominant phyla: symbiotrophic fungi (ectomycorrhizal fungi in soils only), saprotrophic fungi, pathotrophic fungi, ascomycetous fungi, basidiomycetous fungi and fungal plant pathogens, and (b) bacterial phyla: Actinobacteriota, Acidobacteriota, Planctomycetota, Proteobacteria and Verrucomicrobiota in the litter and soil respectively. Full models for each microbial response variable included time since fire, fire frequency and their interaction, elevation, and the abiotic and vegetation properties (plant composition, mid-overstorey tree richness and tree basal area) described above (Figure 2). Abiotic soil properties were included in SEM #1 only, and those in the litter were included in SEM #2 only. Other investigated pathways in each SEM included the effects of fire on abiotic and vegetation properties (Figure 2). We performed log and square-root transformations on response variables where appropriate to meet the assumptions of normal error distribution for all pathways.

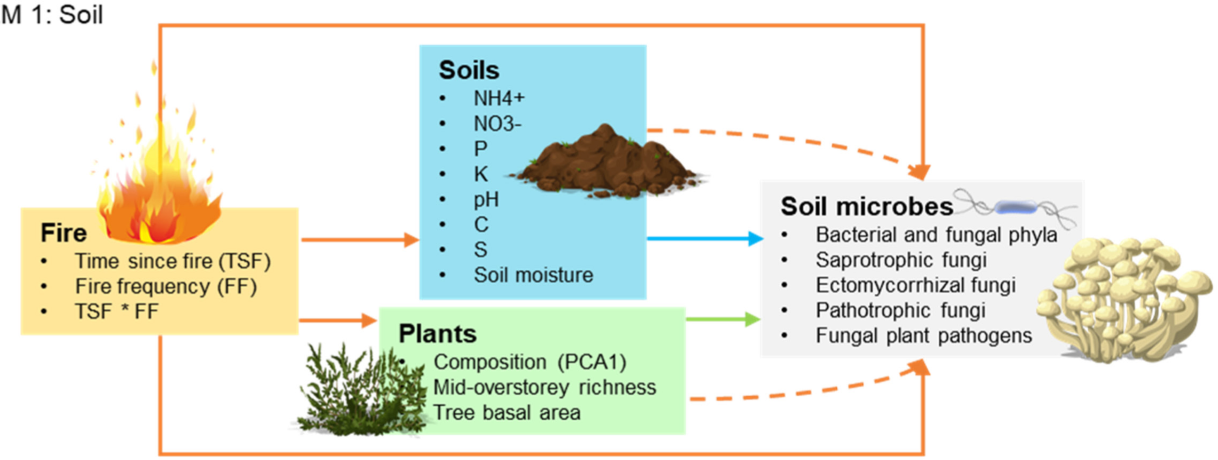
We used Shipley's tests of directed separation (d-sep) to test the conditional independence of variables not included in each respective path for each SEM (Shipley, 2013). If tests between variables voided this precondition, we included them in the respective path whenever ecologically appropriate, or excluded them from the base set of paths as non-casual interactions or likely bidirectional correlations (Lefcheck, 2016). For the final model, we standardised coefficients generated by each SEM by scaling them by standard deviations of the mean to compare relative effect sizes between response variables and to calculate the indirect effects of fire using multiplicative path tracing (by multiplying significant coefficients of interacting response variables) (Grace et al., 2015; Lefcheck, 2016).

3 | RESULTS

3.1 | Microbial community description

After rarefaction, we identified a total of 5631 unique fungal amplicon sequence variants (ASVs) across both sample types (3780 in soil and 3052 in litter samples) (Appendix S3). Soil fungal ASVs were assigned to one of eight phyla: Ascomycota, Basidiobolomycota, Basidiomycota, Chytridiomycota, Glomeromycota, Mortierellomycota, Mucoromycota and Rozellomycota. Of these, Ascomycota (55% of total sequences) and Basidiomycota (44% of total sequences) were dominant. In litter samples, fungal ASVs were assigned to one of four phyla: Ascomycota,

(a) SEM 1: Soil



(b) SEM 2: Litter

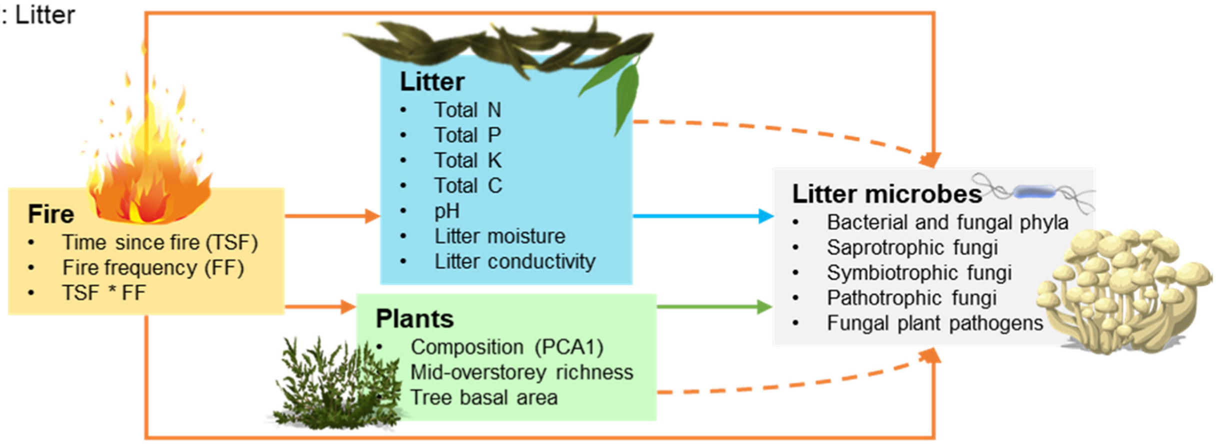


FIGURE 2 Complete paths investigated using piecewise SEM for (a) soil and (b) litter microbial communities respectively. Elevation was also included in each path prior to model selection for each response variable (not pictured). Dominant bacterial phyla were: Acidobacteriota, Actinobacteriota, Planctomycetota, Proteobacteria, Verrucomicrobiota and dominant fungal phyla were Ascomycota and Basidiomycota. Solid lines represent direct pathways and dashed lines indicate indirect pathways whereby fire can influence microbial communities indirectly via biotic–abiotic interactions

Basidiomycota, Mortierellomycota and Mucoromycota. Similar to the soil, litter fungi were predominantly ascomycetes (66% of total sequences) and basidiomycetes (32% of total sequences). ASVs unable to be classified to phylum level accounted for <1% of total sequences in soil samples, and 2% of total sequences in litter samples. In soil samples, saprotrophic–symbiotrophic (36%), symbiotrophic (22%) and ectomycorrhizal (21%) fungal ASVs were the most abundant. Meanwhile, saprotrophic fungi were most abundant in litter samples (21% of total sequences), of which, wood saprotrophs were dominant (15% of total sequences) (Appendix S1: Figure S3; Appendix S3).

After rarefaction, we identified 10,195 and 7705 bacterial ASVs from soil and litter samples respectively (2137 occurred in both sample types) (Appendix S3). Bacterial litter and soil ASVs were assigned to 18 and 31 phyla groups respectively. Actinobacteriota (34% and 36% of total litter and soil sequences respectively), Proteobacteria (26% and 19% of total litter and soil sequences respectively), Planctomycetota (22% of total litter and soil sequences), Acidobacteriota (8% and 12% of total litter and soil sequences respectively) and Verrucomicrobiota (7% and 6% of total litter and soil sequences respectively) were the dominant phyla. ASVs unclassified at the phylum level accounted for 0.02% of total soil sequences and litter sequences (Appendix S1: Figure S3).

3.2 | Microbial community composition

3.2.1 | Fungi

Time since fire, fire frequency and their interaction significantly influenced the composition of soil and litter fungal communities (Appendix S1: Tables S4 and S5). NMDS plots revealed clear distinctions in community composition between medium and short times since fire for both litter and soil samples (Figure 3). Elevation, pH and phosphorus also were associated with the composition of soil

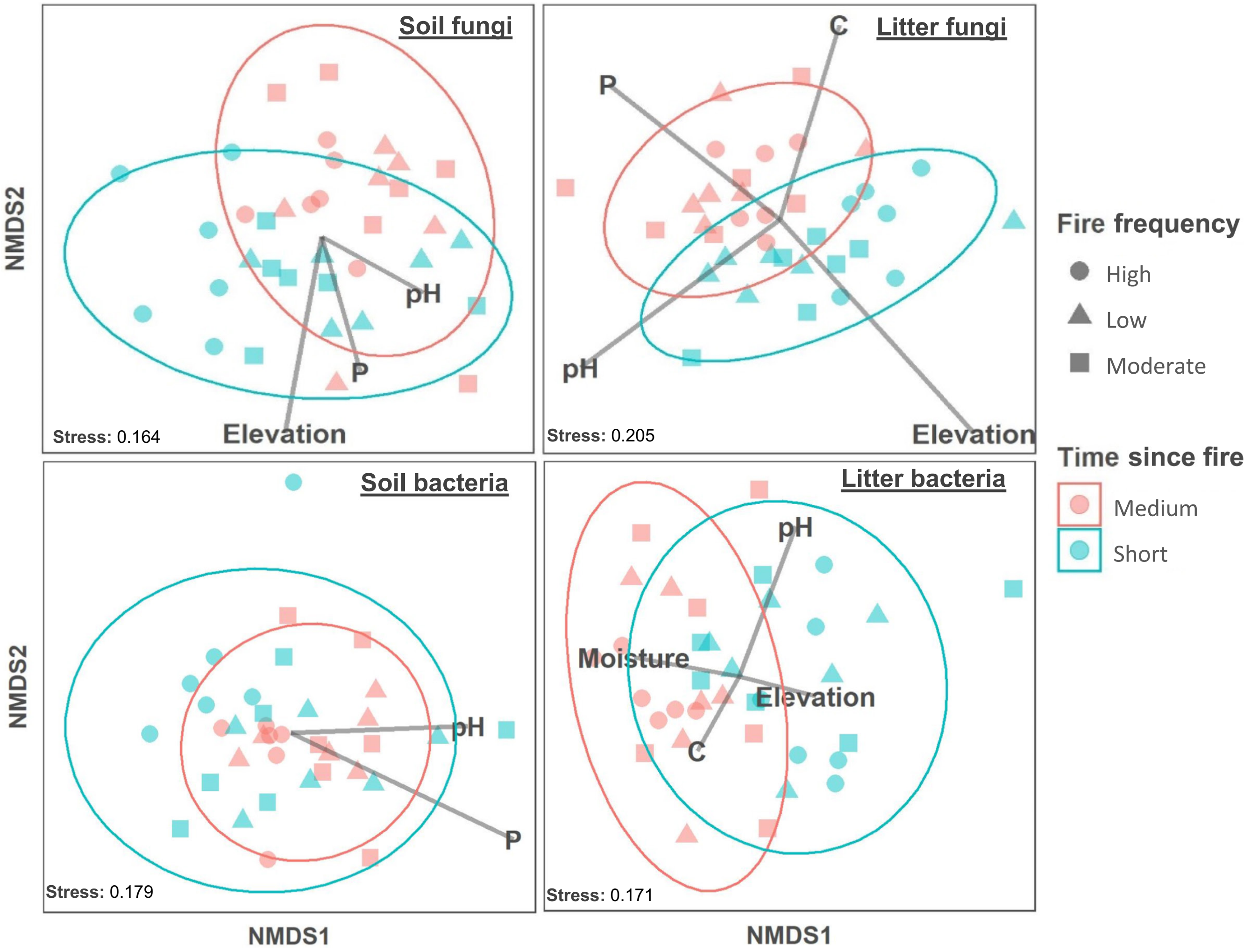


FIGURE 3 NMDS plots of the composition of soil and litter fungal and bacterial communities across all 36 sites, with significantly correlated environmental vectors overlayed (from envfit). Ninety-five per cent confidence ellipses are drawn for each time since fire (assuming a multivariate *t*-distribution)

and litter fungal communities, and litter carbon was associated with litter fungal communities (Appendix S1: Table S6; Figure 3). Mantel tests revealed weak positive correlations between the distances among sites and the composition dissimilarity of fungi in the litter (Mantel r statistic = 0.32; $p < 0.001$) and soil (Mantel *r* statistic = 0.24; $p < 0.001$) (Appendix S1: Figure S4). We also found weak positive correlations between the composition dissimilarity of plant communities and fungi both in the litter (Mantel *r* statistic = 0.21; p = 0.01) and in the soil (Mantel *r* statistic = 0.29; p = 0.001; Appendix S1: Figure S5).

3.2.2 | Bacteria

The composition of soil bacteria was influenced by time since fire and fire frequency, while the composition of litter bacteria was significantly influenced by time since fire only (Appendix S1: Table S4). We did not find any interactive effects of time since fire and fire frequency on soil or litter bacteria community composition (Appendix S1: Table S5). NMDS revealed some differences between the community composition of bacteria across different times since fire, however, distinctions were less obvious than those observed for fungal communities and were more evident in litter bacterial communities than those in the soil (Figure 3). Similar to fungal communities, the composition of soil bacterial communities was associated with phosphorus and pH, and litter bacterial communities were associated with elevation, litter carbon, pH and moisture (Appendix S1: Table S6; Figure 3). Mantel tests revealed very weak positive correlations between the distances between sites and the composition dissimilarity of bacteria in the litter (Mantel *r* statistic = 0.19; p = 0.001) and in the soil (Mantel *r* statistic = 0.11; p = 0.03) (Appendix S1: Figure S4). We also found weak positive correlations between the composition dissimilarity of plant communities and bacteria in the soil (Mantel *r* statistic = 0.28; p = 0.003), but no significant correlations in the litter (Mantel *r* statistic = 0.10; p = 0.14) (Appendix S1: Figure S5).

3.3 | Structural equation modelling

3.3.1 | Direct associations with soil microbes

Using structural equation modelling (SEM #1), we found evidence of direct associations between fire history, soil abiotic properties, plant properties, and soil bacterial and fungal communities (Fisher's $C = 280.344$, $p = 1$, df = 366). High fire frequency was associated with an increase in the abundance of pathogenic fungi and plant pathogenic fungi, but with a reduction in the abundance of Actinobacteriota. Moderate fire frequency was also associated with an increase in plant pathogenic fungi. Short time since fire was associated with a decline in ectomycorrhizal fungi and Acidobacteriota (Figure 4, Appendix S1: Table S7). Moreover, several abiotic soil and plant properties were significantly associated with the abundance of soil microbial communities including plant richness and composition, and soil moisture, carbon, sulphur, potassium and pH (Figure 4, Appendix S1: Table S7).

3.3.2 | Direct associations with litter microbes

Using a second structural equation model (SEM #2), we identified associations between fire history, litter abiotic properties and litter bacterial and fungal communities (Fisher's $C = 308.621$, $p = 1$, df = 410). In contrast to soil microbial communities, we found evidence of an association of only short time since fire with the abundance of litter microbial communities. Specifically, short time since fire was associated with a decline in Actinobacteria and basidiomycetous fungi, and an increase in ascomycetous fungi and Proteobacteria (Figure 4, Appendix S1: Table S7). Several litter abiotic and plant properties were significantly associated with the abundance of litter microbial communities including litter moisture, carbon, pH, potassium and nitrogen (Figure 4, Appendix S1: Table S7).

3.3.3 | Indirect fire effects on soil microbes

In addition to direct fire effects on soil microbial communities, we found evidence that fire can indirectly influence microbial

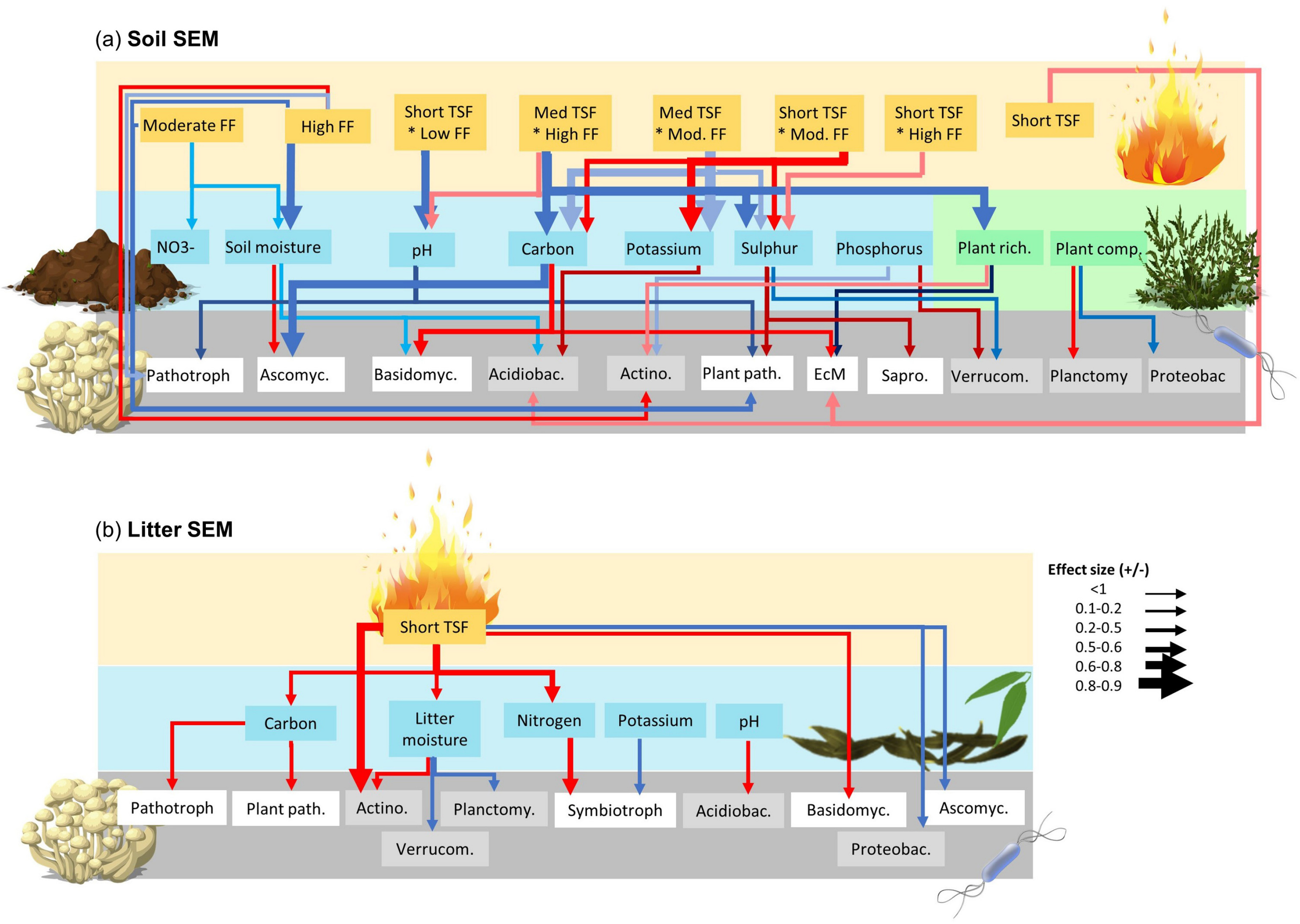


FIGURE 4 Direct and indirect pathways between fire frequency and time since fire, the abundance of microbial communities, and biotic and abiotic properties in the (a) soil and (b) litter identified using structural equation models (SEMs). Only significant ($p < 0.05$) pathways that intersected with a bacterial (grey) or fungal (white) response variables are displayed. Blue arrows indicate positive relationships and red arrows indicate negative relationships. Different shades of red and blue used to colour arrows are to increase readability only. The thickness of arrows represents standardised coefficients (effect size) derived from each SEM. See Appendix S1: Tables S7–S10 for full model details. FF, fire

communities through their interactions with soil abiotic properties and plant properties. These indirect fire effects accounted for most of the total fire effects on soil and litter microbial communities that we found, with effects most pronounced for soil fungal communities (Figure 5, Appendix S1: Tables S7–S9).

Soil pH, carbon and sulphur were identified as important mediators of fire effects on soil fungi, with soil moisture and potassium, and plant richness also mediating fire effects for some groups. Under low fire frequency, short time since fire increased soil pH (compared with medium time since fire), which had an indirect positive effect on pathogenic fungi and plant pathogenic fungi. Fungal plant pathogens and saprotrophic fungi also increased with high and moderate fire frequencies under a short time since fire, and this was mediated by a decline in soil sulphur. In contrast, fungal plant pathogens declined with an increase in soil sulphur with moderate and high fire frequencies under medium time since fire, and with a more acidic pH with high fire frequency under medium time since fire (Figure 5).

An increase in soil moisture with high and moderate fire frequencies mediated an indirect positive effect on Acidobacteriota and basidiomycetous fungi, and a negative indirect effect on ascomycetous

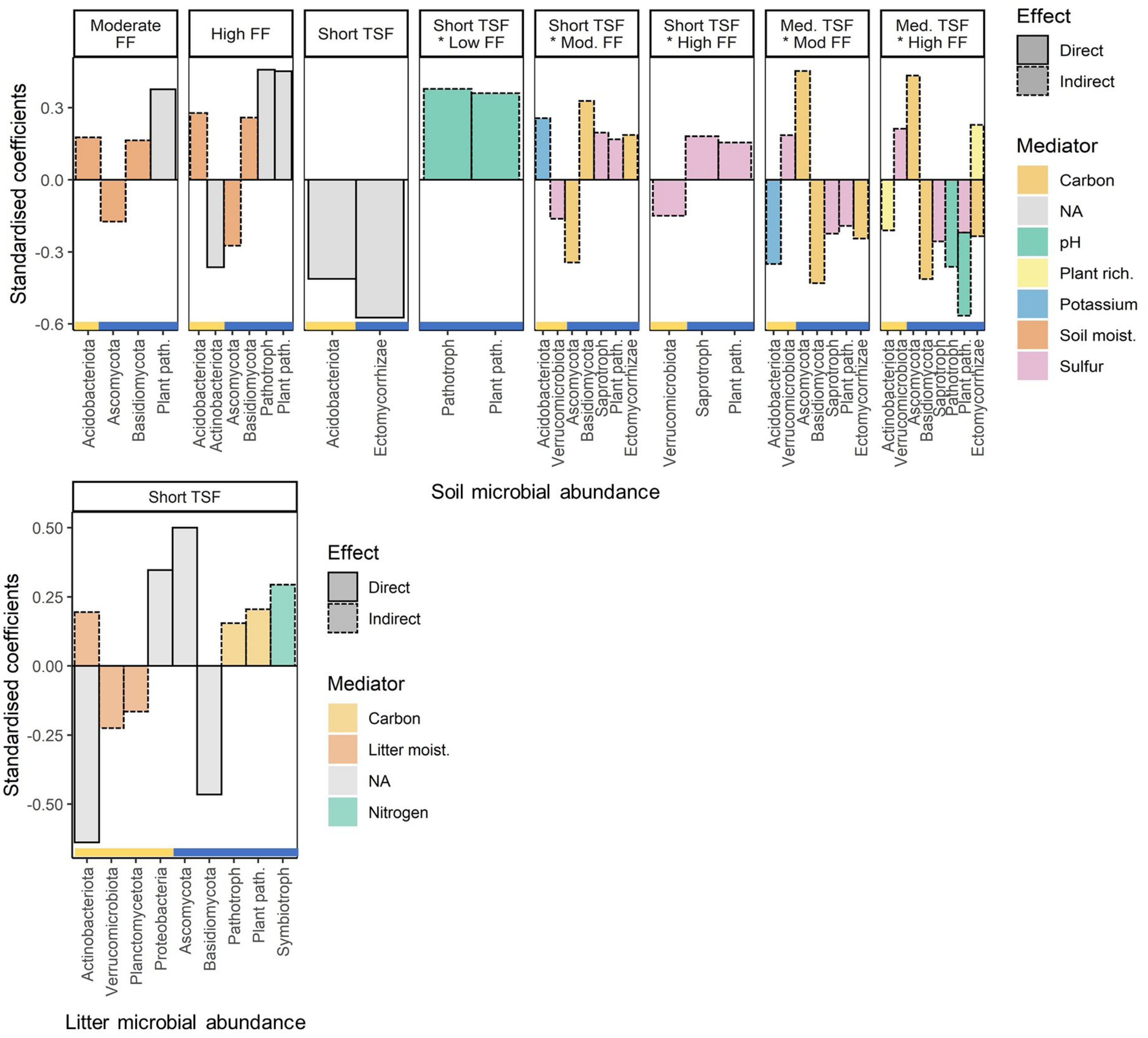


FIGURE 5 Indirect (dashed outline) and direct (solid outline) effects of time since fire (TSF) and fire frequency (FF) and their interactions (*) on the abundance of soil and litter microbial communities. Effects were calculated using multiplicative path tracing of standardised coefficients generated by each structural equation model. 'med.', medium TSF; 'mod.', moderate FF. Only significant effects are plotted ($p < 0.05$). Colouring on the *x*-axes highlight bacterial phyla (yellow) and fungal groups (blue). See Appendix S1: Tables S7–S10 for full model details

fungi. However, an increase in soil carbon with high and moderate fire frequencies under medium time since fire indirectly increased ascomycetous fungi but reduced basidiomycetous and ectomycorrhizal fungi. In contrast, declines in soil carbon with moderate fire frequency under short time since fire had the opposite effect on soil microbes.

Increases in plant species richness with high fire frequency under medium time since fire had an indirect positive influence on ectomycorrhizal fungi and a negative indirect influence on Actinobacteriota. Increases in potassium with moderate fire frequency under medium time since fire had a negative indirect effect on Acidobacteriota (Figure 5, Appendix S1: Tables S7–S9).

3.3.4 | Indirect fire effects on litter microbes

Time since fire indirectly influenced litter microbial communities by modifying abiotic litter properties. Specifically, short time since fire resulted in lower measures of litter nitrogen which indirectly increased the abundance of litter fungal symbiotrophs. It also reduced litter moisture, which had a positive influence on Actinobacteriota, but a negative influence on Planctomycetota and Verrucomicrobiota. Furthermore, short time since fire also reduced litter carbon, which indirectly increased the abundance of all fungal pathogens and fungal plant pathogens (Figures 4 and 5, Appendix S1: Tables S7–S9).

3.3.5 | Bi-directional or non-directional relationships

We also identified several bi-directional or non-directional associations between microbial community groups (phyla and functional groups) and between abiotic properties in the soil (SEM #1) and litter (SEM #2) respectively. For instance, in the soil, basidiomycetous and ectomycorrhizal fungi were negatively correlated with ascomycetous fungi, but positively correlated with each other, Proteobacteria and Acidobacteriota. Similarly, in the litter, we found negative correlations between litter basidiomycetous and ascomycetous fungi, Planctomycetota and Proteobacteria, and Verrucomicrobiota and ascomycetous fungi (Appendix S1: Table S10).

4 | DISCUSSION

4.1 | Temporal shifts in microbial communities with time since fire

We observed clear distinctions between the composition of fungal and bacterial communities between medium and short times since fire in the litter and soil (Figure 3). These compositional differences likely reflect simultaneous increases in fire-tolerant and early successional taxa including fungal pathogens, saprotrophs and Proteobacteria and declines in less-tolerant taxa including ectomycorrhizal fungi and Acidobacteriota with short time since fire. The influence of time since fire on microbial communities may be direct (via fire-induced mortality) or indirect, mediated through above- and below-ground abiotic (litter and soil) and biotic (plants) interactions (Adkins et al., 2020; Barnes et al., 2017; Bowd, Banks, et al., 2021; Wardle et al., 2004). In line with previous research, litter and soil pH was significantly correlated with the composition of all microbial groups (Day et al., 2019; Fierer & Jackson, 2006; Sun et al., 2015; Tedersoo et al., 2014), which may reflect fire-induced increases in pH caused by soil heating (Certini, 2005; Figure 3).

Consistent with previous research in other forest ecosystems, our findings suggest fire may influence microbial communities in the short–medium term (10–15 years) (Dooley & Treseder, 2012; Treseder et al., 2004). However, the recovery of some microbial communities post-fire can take multiple decades, which may influence their respective functional roles (Cairney & Bastias, 2007; Holden et al., 2013; Visser, 1995). Future research is required to gauge longer term responses of microbial communities to fire in forests which are poorly documented (Wardle & Jonsson, 2014).

4.2 | Indirect and direct fire effects on microbial communities

Associations between microbial communities and fire (Dooley & Treseder, 2012; Holden et al., 2013, 2016) and between microbial communities and biotic and abiotic properties (Bowd et al., 2022; Tedersoo et al., 2014; Wardle & Jonsson, 2014) have been well-documented, although their capacity to interact and influence these communities are seldom investigated (Bowd, Banks, et al., 2021). Despite this, it is widely recognised that fire is a key regulator of plant communities (Foster et al., 2018; Tepley et al., 2018) and nutrient cycles, and influences the input (e.g. mineralisation, N fixation), output (e.g. volatilization) and retention (e.g. immbolization) of key soil and litter nutrients, especially N and P (Certini, 2005; O'Connell, 1989). Consistent with our first hypothesis, we found evidence through structural equation modelling that fire can influence microbial communities both directly and indirectly, via biotic–abiotic interactions in the soil and leaf litter. Fire-induced changes in soil moisture, sulphur, carbon, pH, potassium and plant richness all mediated changes in soil microbial communities, and declines in litter nitrogen, moisture and carbon all mediated changes in litter microbial communities. Notably, most of the effects of fire on microbial communities were indirectly mediated, with effects most pronounced in the soil. This highlights the importance of investigating the indirect pathways through which fire can alter microbial communities that may otherwise go unrecognised within a given study, potentially underestimating total fire effects (Bowd, Banks, et al., 2021; Lefcheck, 2016). These new insights advance our understanding of the complexities of fire responses in forests that are inherently tied to their respective ecological interactions.

4.3 | Differences in fungal and bacterial fire responses

Consistent with our second hypothesis, fungi were more sensitive to fire than bacteria at the phylum and functional-group levels. Indeed, we observed direct and indirect fire effects on only three bacterial phyla in the soil: Acidiobacteriota, Actinobacteriota and Verrucomicrobiota, and four in the litter: Actinobacteriota, Proteobacteria, Verrucomicrobiota and Planctomycetota. Previous research has suggested that either fungal communities (Bååth et al., 1995) or bacterial communities (Bárcenas-Moreno et al., 2011; Wardle & Jonsson, 2014) are the most sensitive to fire, whereas others report similar effects on both communities (Holden & Treseder, 2013). In line with our findings, manipulative burning experiments in Mediterranean forests have demonstrated that some bacterial communities may be more resilient to, and recover faster from, increased soil temperatures (200°C) associated with fire, relative to fungal communities (Bárcenas-Moreno et al., 2011).

Differences in the responses of bacteria and fungi may reflect different thermal tolerances, competitive interactions (Bárcenas-Moreno et al., 2011), physiological and ecological attributes (Waring et al., 2013), and the influence of vegetation, abiotic properties and biogeography (Bååth et al., 1995; Wardle & Jonsson, 2014; Waring et al., 2013). Our findings are consistent with previous studies (Waring et al., 2013), demonstrating that at the phyla and functional group level, bacteria and fungi can be associated with different abiotic and biotic components. For instance, fire-induced changes in soil pH and soil carbon influenced the abundance of fungal communities only, and fire-induced changes in potassium influenced the abundance of bacteria only. However, we also observed similarities between the fire responses of some bacterial and fungal communities including Acidobacteriota, ectomycorrhizal and basidiomycetous fungi which were positively correlated with each other (Figure 5, Appendix S1: Table S10).

4.4 | Divergent fire responses within microbial communities

In support of our second hypothesis, we found evidence of contrasting responses to fire between phyla and functional groups within microbial communities (Figures 4 and 5). Notably, recently burned forests (2–3 years) had the largest negative associations with the abundance of ectomycorrhizal fungi and Acidobacteriota in the soil. Similar declines in ectomycorrhizal fungi with wildfire have been described elsewhere in boreal forests (Holden et al., 2013; Pérez-Izquierdo et al., 2021; Treseder et al., 2004) and temperate forests (Chen & Cairney, 2002; Yang et al., 2020). Aside from the direct effects of fire-induced mortality (Holden & Treseder, 2013), fire-induced changes in ectomycorrhizal fungi may reflect altered plant–soil–microbial interactions (Adkins et al., 2020; Bowd, Banks, et al., 2021; Treseder et al., 2004). For instance, we observed an increase in ectomycorrhizal fungi with an increase in overstorey and midstorey species richness in forests that had experienced high fire frequency under medium time since fire. These findings are consistent with other research which suggests that ectomycorrhizal fungi may recover in tandem with above-ground vegetation following fire (Duhamel et al., 2019; Hart et al., 2005). However, our findings suggest this is driven by increases in plant diversity rather than the basal area of mycorrhizal plants, which may reflect host specificity (Merges et al., 2018; Tedersoo et al., 2008).

Ectomycorrhizal fungi may also recover in conjunction with the accumulation of organic matter (Treseder et al., 2004). However, we report a negative association between organic carbon and ectomycorrhizal fungi, which mediated a slight increase in ectomycorrhizal fungi with moderate fire frequency, under short time since fire. In contrast, we found a positive association between ascomycetous fungi and organic carbon (which often dominate in early succession). These differences in associations may reflect competitive dynamics and potential niche separation between ectomycorrhizal fungi and ascomycetous fungi which were negatively correlated with each other. For instance, ectomycorrhizal fungi may be more tolerant of lower organic matter quality and therefore be better competitors under these conditions (Marañón-Jiménez et al., 2021). Negative associations between ectomycorrhizal fungi and organic carbon may also be explained by temporal differences in species-specific mycorrhizal dominance, which in turn, can influence carbon sequestration (Clemmensen et al., 2015).

In contrast to ectomycorrhizal fungi, we found that litter ascomycetous (predominantly saprotrophic) fungi increased with recent fire, and pathogenic fungi increased with moderate and high fire frequency. This may be explained by the combination of thermotolerance (Mushinski et al., 2018; Wilhelm et al., 2017) and reduced competition for resources including nitrogen because of declines in ectomycorrhizal fungi with recent time since fire (Averill et al., 2014; Fernandez & Kennedy, 2016; Gadgil & Gadgil, 1971; Sterkenburg et al., 2018). At the finer scale, our findings also demonstrate that fire-induced changes in abiotic properties can benefit both fungal pathotrophs and saprotrophs. These include a decline in soil sulphur in recently burnt forests with moderate and high fire frequencies (leading to an increase in both pathotrophs and saprotrophs), an increase in soil pH in recently burnt forests with low fire frequency, and a decline in litter carbon in recently burnt forests (leading to an increase in pathotrophs only). Moreover, fire-induced increases in pathogenic fungi may be explained by an increase in optimal ecological niches including fire-damaged trees and decomposing mycelium (Anthony et al., 2017; Brabcová et al., 2016; Parker et al., 2006; Shi et al., 2019), or may relate to the simultaneous decline in ectomycorrhizal fungi which can prevent the colonisation of pathogenic fungi on roots (Marx, 1972). Increases in pathogenic fungi after fire may also reflect an increase in dispersal rates, whereby aerosolised propagules can be transported by smoke (Kobziar et al., 2018).

4.5 | Substrate-specific fire effects on microbial communities

Consistent with the first component of our third hypothesis, fungal and bacterial communities in the leaf litter were more sensitive to time since fire than fire frequency, and less sensitive to fire frequency than their soil counterparts. These substrate-dependent effects are likely explained by the most recent wildfire 'resetting' leaf litter microbiomes, given fires combust most organic surface matter (Cornelissen et al., 2017). Where this occurs, the timing of species immigration during initial community assemblage may affect the diversity and distribution patterns of the litter microbiome—that is, the so called 'priority' effects that can influence its functional roles (Fanin et al., 2021; Veen et al., 2019). This may explain the higher abundance of ascomycetes (dominant in early-successional forests) and Proteobacteria, and lower abundance of basidiomycetes (dominant in older forests) and Actinobacteriota in the leaf litter of the most recently burnt forests (Sun et al., 2015; Voriskova & Baldrian, 2013).

Furthermore, in recently burnt forests, declines in litter carbon increased fungal pathotrophs, declines in litter nitrogen increased litter symbiotrophs and declines in litter moisture increased Actinobacteriota, but led to a decline in Planctomycetota and Verrucomicrobiota. High fire frequency can degrade litter quality and constrain decomposition rates (Butler et al., 2019). Our findings of fire-induced shifts in litter quality and subsequent changes in microbial communities may also influence decomposition rates, which should be the focus of future research efforts.

In contrast to the effects of fire on litter microbial communities and aligned with Hypothesis #3b, soil microbial communities were influenced by time since fire, fire frequency and their interaction. The diversity of fire effects on soil microbial communities is likely explained by the cumulative effect of recurrent fire on soils, which via successive volatilization and leaching of nutrients can exacerbate the depletion of nutrients including N and C long term (Figure 3) (Bowd et al., 2019; Muqaddas et al., 2015; Pellegrini et al., 2018).

4.6 | Ecosystem and management implications

Our findings indicate that microbial communities are strongly altered by recent fire in dry-sclerophyll forests, which may influence key ecological functions by selecting for specific taxa. For instance, fire-induced declines in microbial communities including Acidobacteriota and ectomycorrhizal fungi (Banerjee et al., 2018; Kalam et al., 2020) may impede plant-growth and seedling survival (Clemmensen et al., 2015; Simard, 2009), alter decomposition rates (via reducing competition with saprotrophs) (Sterkenburg et al., 2018), and reduce soil carbon stores (Averill & Hawkes, 2016). Declines in Actinobacteriota in the leaf litter may also alter decomposition rates (Eisenlord & Zak, 2010). Functional implications may be exacerbated by increases in fire frequency and an interaction between fire frequency and time since fire, resulting in increases in pathotrophic fungi, including plant pathogens with short time since fire which can degrade plant productivity and forest health (Maron et al., 2011; Yang et al., 2020). However, fungal pathogens may also regulate plant species diversity by suppressing the survival of plant seedlings at high densities ('Janzen–Connell hypothesis') (Bagchi et al., 2014; Connel, 1971; Janzen, 1970). Future studies are required to quantify the direct functional implications of the direct and indirect fire-induced shifts in microbial communities that we have reported.

Adaptive management may be required to mitigate some of the potential implications associated with direct and indirect fire-induced shifts in microbial communities. For instance, our findings highlight the importance of considering multiple components of the fire regime including the 'invisible' (past) and 'visible' (present) fire mosaic in land management, which can produce variable microbial responses. Therefore, land managers should consider the total-fire burden (of planned burns and wildfire), past and present, in land management and planning. Specifically, we suggest, prescribed burning should be avoided at short intervals. In dry-sclerophyll forests, this may allow specific microbial communities, including ectomycorrhizal fungi to recover from recent fire and subsequently deter the proliferation of pathotrophic fungi through competitive exclusion. However, further research is required to consider how fires of different severities may influence microbial communities in these forests to further refine the application of these recommendations. Complementary to adaptive management, the integration of microbial communities into ecological monitoring programs will assist in gauging taxon-specific long-term recovery rates and in identifying respective functional implications.

5 | CONCLUSIONS

Understanding the complex post-fire dynamics of microbial communities is pertinent in the current period of rapid environmental and climatic change, where forest ecosystems are experiencing considerable challenges. Increases in the frequency and intensity of wildfires have been predicted for many landscapes world-wide, and these include dry-sclerophyll Australian forests (Bradstock et al., 2009). Indeed, these predictions were realised in the recent 'Black Summer' extreme wildfires, which burnt >18 million ha of Australian landscapes in 2019–2020 (Boer et al., 2020; Collins et al., 2021; Nolan et al., 2020). Such increases in recurrent fires may exacerbate fire-induced changes in microbial communities directly, and through plant–litter–soil–microbial interactions, and amplify respective functional implications. In the face of these challenges, adaptive management may be required to mitigate some of the potential implications of fire-altered microbial communities.

AUTHORS' CONTRIBUTIONS

E.J.B. led the paper conception, writing and statistical analysis; C.F. established the experimental design of this project and conducted the vegetation surveys; E.E. conducted the bioinformatics analyses underpinning the microbial data and contributed to writing the

paper; D.B.L., D.A.W., P.K., G.J.C. and C.F. contributed to writing the paper.

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CONFLICT OF INTEREST

The authors declare no potential sources of conflict of interest.

PEER REVIEW

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SUPPORTING INFORMATION

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