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Temporal dynamics of soil fungi in a pyrodiverse dry-sclerophyll forest

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Abstract

Fire is a major evolutionary and ecological driver that shapes biodiversity in forests. While above-ground community responses to fire have been well-documented, those below-ground are much less understood. However, below-ground communities, including fungi, play key roles in forests and facilitate the recovery of other organisms after fire. Here, we used internal transcribed spacer (ITS) meta-barcoding data from forests with three different times since fire [short (3 years), medium (13–19 years) and long (>26 years)] to characterize the temporal responses of soil fungal communities across functional groups, ectomycorrhizal exploration strategies and inter-guild associations. Our findings indicate that fire effects on fungal communities are strongest in the short to medium term, with clear distinctions between communities in forests with a short time (3 years) since fire, a medium time (13–19 years) and a long time (>26 years) since fire. Ectomycorrhizal fungi were disproportionately impacted by fire relative to saprotrophs, but the direction of the response varied depending on morphological structures and exploration strategies. For instance, short-distance ectomycorrhizal fungi increased with recent fire, while medium-distance (fringe) ectomycorrhizal fungi decreased. Further, we detected strong, negative inter-guild associations between ectomycorrhizal and saprotrophic fungi but only at medium and long times since fire. Given the functional significance of fungi, the temporal changes in fungal composition, inter-guild associations and functional groups after fire demonstrated in our study may have functional implications that require adaptive management to curtail.

KEYWORDS
Australia, dry-sclerophyll eucalypt forests, ectomycorrhizal, fire, fungi, time since fire

1 | INTRODUCTION

Fire is a major evolutionary and ecological driver that shapes the form and function of many forests globally. Fire can restore, modify or degrade the ecological values of forests depending on (a) the adaptive capacity of biodiversity (Clarke et al., 2009, 2013), (b) the legacy of prior disturbances and the presence of biological legacies (e.g. seeds, large old trees, resprouting plant organs; Bowd, Blair & Lindenmayer, 2021; Bradstock et al., 2005; Franklin et al., 2000) and (c) the characteristics of the most recent fire and the historical fire-regime (fire frequency, severity and return intervals) within a given ecosystem (Bowman et al., 2020; Keeley, 2009; Keeley et al., 2011). In recent decades, climatic changes have altered natural disturbance patterns and increased the risk and occurrence of frequent, large-scale, high-severity wildfires in many forests worldwide (Abatzoglou & Williams, 2016; van Oldenborgh et al., 2020; Williams et al., 2019). These include forests in Australia (Boer et al., 2020), North America (Goss et al., 2020), Canada (Goss et al., 2020), Asia (Shiogama et al., 2020) and Europe (Seidl et al., 2017; Sommerfeld et al., 2018) including ecosystems where fire has historically been rare or absent such as tropical rainforests and tundra (Barlow et al., 2020; Kelly et al., 2020). Under altered fire regimes, postfire recovery may be impeded, resulting in shifts in the composition, structure and function of forests (Buma et al., 2013; Stevens-Rumann & Morgan, 2016; Tepley et al., 2018). In the current period of widespread environmental change, understanding how biodiversity responds to and recovers from fire is critical to conservation and in facilitating ecologically appropriate adaptive management (Kelly et al., 2020; Lindenmayer et al., 2007).

Forest recovery after fire is characterized by temporal changes in above-ground biomass, vegetation structure and composition (Bowd, McBurney & Lindenmayer, 2021; Johnstone et al., 2016; Nolan et al., 2021; Tepley et al., 2018), and the presence of particular species assemblages that may characterize distinct successional stages (Donato et al., 2012; Pulsford et al., 2014; Swanson et al., 2011). However, the recovery of above-ground biodiversity in forests after fire is inherently tied to the recovery of below-ground biodiversity, particularly fungi. Fungal communities have critical functional roles in forest ecosystems (Anthony et al., 2022; Claridge et al., 2009; Pérez-Valera et al., 2020; Wagg et al., 2014). For instance, fungi can: (1) enhance plant growth and seedling survival by forming mycorrhizal (symbiotic) associations with most plant species, often increasing nutrient acquisition (van der Heijden et al., 2008, 2015), (2) provide valuable food sources (fungal fruiting bodies) for mycophagous mammals (Meyer et al., 2008; Trappe et al., 2005), (3) stabilize soils (Claridge et al., 2009; Filialuna & Cripps, 2021) and (4) decompose organic matter and plant-cellulose (Baldrian & Valášková, 2008), which in turn, (5) regulate carbon and nutrient cycles (Lindahl et al., 2002).

Fire can influence fungal communities directly by causing mortality through soil heating and the consumption of upper organic soil horizons (Certini, 2005; Peay et al., 2009) or indirectly by modifying soil properties and the composition of plant communities that may select for specific fungal species including those that are fire-tolerant or early-colonizers (Barnes et al., 2017; Dove et al., 2022; Ibáñez et al., 2022; van der Putten et al., 2013). Fungal species can also exhibit specific attributes that influence their capacity to survive fire or re-establish after fire, which are analogous to plant species with fire-resistant life history traits (Enright et al., 2022; Keeley et al., 2011; Whitman et al., 2019). These attributes include: morphological structures of extramatrical mycelium that optimize nutrient acquisition (Agerer, 2001; Weigt et al., 2012), specific functional associations (e.g. symbiosis, saprotrophism, parasitism) (Rodriguez-Ramos et al., 2021), the capacity to break down postfire resources (e.g. pyrogenic organic matter; Dove et al., 2022; Enright et al., 2022) and the presence of heat-resistant reproductive propagules (e.g. spores and sclerotia) that may germinate after fire (Glassman et al., 2016; Peay et al., 2009; Smith et al., 2015) or become air-borne to facilitate dispersal (Chen & Cairney, 2002; Fox et al., 2022; Kobziar et al., 2018). Differences in the availability of resources (e.g. sufficient habitat and abiotic conditions) and the timing of recovery and colonization (i.e. priority effects) may also influence fungal community composition after fire, as well as interspecific interactions that involve fungi such as predation, competition and facilitation (Boddy, 2000; Faust & Raes, 2012; Kennedy, 2010). For instance, fire-induced declines in ectomycorrhizal fungi may reduce their competition with fire-tolerant saprotrophs, resulting in early-successional dominance by saprotrophs and subsequent rapid decomposition (Averill & Hawkes., 2016). Conversely, as ectomycorrhizal fungi recover and resource availabilities change with increasing time since fire, inter-guild competition rates may increase, in turn increasing carbon storage and reducing decomposition rates (Boddy, 2000; Faust & Raes, 2012; Kennedy, 2010).

While some fungi are resilient to wildfire, others may be more sensitive, including ectomycorrhizal fungi; this has been demonstrated in both boreal forests (Holden & Treseder, 2013; Pérez-Izquierdo et al., 2021; Treseder et al., 2004; Visser, 1995) and temperate forests (Bowd et al., 2022a; Chen & Cairney, 2002; Yang et al., 2020). The recovery of ectomycorrhizal fungi may occur alongside vegetation recovery and the concomitant accumulation of organic matter (Duhamel et al., 2019; Hart et al., 2005; Treseder et al., 2004). The abundance and diversity of ectomycorrhizal fungi after fire may also vary across taxa with different morphological structures [sensu ‘exploration types’ (Agerer, 2001)], as characterized by variation in the number of emanating hyphae and the presence of rhizomes (Olchowik et al., 2021). These include ectomycorrhizal fungi with ‘contact’, ‘short-distance’ (coarse, delicate), ‘medium-distance’ (fringe, smooth, mat) and ‘long-distance’ extramatrical mycelium (Olchowik et al., 2021). While there have been relatively few studies on the influence of fire on ectomycorrhizal exploration types (but see Olchowik et al., 2021), variation in abiotic conditions postfire (Bowd et al., 2022a; Certini, 2005) may select for fungi with specific ectomycorrhizal exploration types that take up and transfer nutrients at different spatial scales (Agerer, 2001; Burgess et al., 1993; Cairney & Burke, 1996). For instance, short-distance ectomycorrhizal fungi, which preferentially take up inorganic nitrogen (Lilleskov et al., 2011) may be more abundant immediately after fire where inorganic nutrients temporarily increase (Wan et al., 2001). By contrast, longer-distance ectomycorrhizal fungi, which specialize in the uptake of organic N and have a high carbon demand (Lilleskov et al., 2011), may be more abundant in later-successional, less-disturbed environments as below-ground carbon allocation increases (Lilleskov et al., 2011; Tedersoo & Smith, 2013).

Several recent studies have focussed on documenting the responses of fungi to fire in forests of the Northern Hemisphere (Enright et al., 2022; Pulido-Chavez et al., 2021; Whitman et al., 2019). However, despite their critical role in driving aboveground recovery after fire, the temporal dynamics of fungal responses to fire are poorly documented at finer taxonomic scales (e.g. with regard to fungi that vary in ectomycorrhizal exploration strategies, trophic guilds, 'inter-guild' associations; Twieg et al., 2007; Visser, 1995). This knowledge is especially limited in some ecosystems such as Australian eucalypt forests (Ammitzboll et al., 2021; Bowd et al., 2022a; Taudière et al., 2017; for comparisons of logging versus burning). Despite this, fire-prone eucalypt forests occur over 100 million hectares in Australia (ABARES, 2018) and are dominated by vegetation with ectomycorrhizal associations (Brundrett & Tedersoo, 2018), which facilitate tree growth, resilience and survival across many nutrient-limited ecosystems (Policelli et al., 2020; Scott et al., 2013). Given their critical role in facilitating postfire recovery, understanding how fungal communities respond to fire over time in these and other ecosystems is important, not only for forest conservation but also for understanding about the maintenance of key ecological functions, and for future management and planning (McMullan-Fisher et al., 2002; Taudière et al., 2017; Visser, 1995).

In recent work, Bowd et al. (2022a), described the direct and indirect (soil and plant-mediated) mechanisms through which fire can alter litter and soil microbial communities. Here, we complement this previous work with the addition of new long unburnt sites, providing a comprehensive set of analyses to advance our understanding of the temporal responses of fungal communities to fire in the dry-sclerophyll *Eucalyptus* forests in eastern, coastal New South Wales, Australia. Specifically, we used ITS meta-barcoding to quantify fungal responses to fire in forest soils across three time periods since last fire: short (3 years), medium (13–19 years) and long (>26 years). We focussed on quantifying these responses with respect to community composition, individual fungal amplicon sequence variants, ectomycorrhizal exploration strategies (Agerer, 2001), fungal functional groups (saprotrophic, symbiotic and pathogenic; Rodriguez-Ramos et al., 2021) and inter-guild associations (Fernandez & Kennedy, 2016; Gadgil & Gadgil, 1971). This comprehensive approach allowed us to elucidate the influence of fire on fungal communities across multiple scales and ask: (1) How do fungal communities and (2) inter-guild fungal associations change with time since fire?

Based on our current understanding as outlined above, we made four key predictions on the potential outcomes of these two research questions. Specifically, we hypothesized that: (H1) Differences in the composition of fungal communities will be more pronounced between sites with a short (3 years) time since fire and those with longer times since fire, than between sites with medium and long times since fire. (H2) The composition and relative abundance of ectomycorrhizal fungi will be more sensitive to time since fire than would other functional groups of fungi. (H3) Different ectomycorrhizal exploration types will vary in their response to time since fire. For instance, we predicted that short-distance ectomycorrhizal fungi will increase with recent fire. And, (H4) Negative associations between saprotrophs and ectomycorrhizal fungi will increase with time since fire.

2 | METHODS

2.1 | Site description

We completed this study in the dry-sclerophyll eucalypt forests of Booderee National Park, located in the Jervis Bay Territory of south-eastern Australia, 200 km south of Sydney (Figure 1). These forests constitute >35% of the vegetation of the park and are dominated by fire-tolerant species including overstorey eucalypts: *Eucalyptus pilularis* and *Eucalyptus botryoides*; midstorey species: *Banksia serrata* and *Acacia longifolia*; and understorey species: *Pteridium esculentum* and *Lomandra longifolia* (Foster et al., 2017; Kubiak, 2009). The fire history of Booderee National Park has been well-documented since 1957 and includes a spatially diverse history of both prescribed fire and wildfire (Foster et al., 2017). Six (>5 ha) wildfires have occurred in the park: 1962, 1972 (two fires), 2002, 2003 and most recently in 2017 (Foster et al., 2017; Lindenmayer et al., 2014). The dry-sclerophyll vegetation makes these ecosystems particularly fire-prone, and they have the potential to experience regular major fires every 5–10 years, although intervals between fires may decline with climate change (Bradstock, 2010). The park has, on average, experienced 4.18 fires per year (median size of 7.02 ha) between 1957 and 2012 (Foster et al., 2017). See further site descriptions in Bowd et al. (2022a).

2.2 | Study design

We designed our study to encompass the temporal diversity of fire in the dry-sclerophyll forests of Booderee National Park. To do this, we used spatial GIS layers: a 1-m digital elevation model and fire perimeter maps to identify unique fire histories and topographical variation across the region. These data guided the selection of 42 sites (10 m × 10 m) located on slopes <20°, with an aspect of between >135° and <225°, and an elevation of between 7 and 111 m above sea level (ASL). Sites also were characterized by belonging to one of three different time since fire categories: (1) Short (3 years since last fire in 2017; $n = 18$ sites, 31–111 m ASL); (2) Medium (13–19 years since last fire in 2001, 2003 or 2007; $n = 18$ sites, 7–82 m ASL) and (3) Long (>26 years since last fire in 1994, 1983 or 1982; $n = 6$ sites, 31–59 m ASL; Figure 1). Sites with a short and medium time since fire had also experienced one of three different fire frequencies between 1957 and 2018: (1) high (>5 fires; $n = 12$ sites); (2) moderate (3–4 fires; $n = 12$ sites); (3) low (1–2 fires; $n = 12$ sites). Sites with a long time since fire experienced low fire frequency only (1–2 fires). Only six long time since fire sites could be included in the study due to the limited spatial extent of this time since fire in the study area.

2.3 | Data collection

In June 2020, in each of the 42 sites (10 m × 10 m), we undertook extensive soil analysis from the topsoil (Bowd et al., 2022b). Specifically, we collected nine 0–10 cm soil cores from the centre and along the

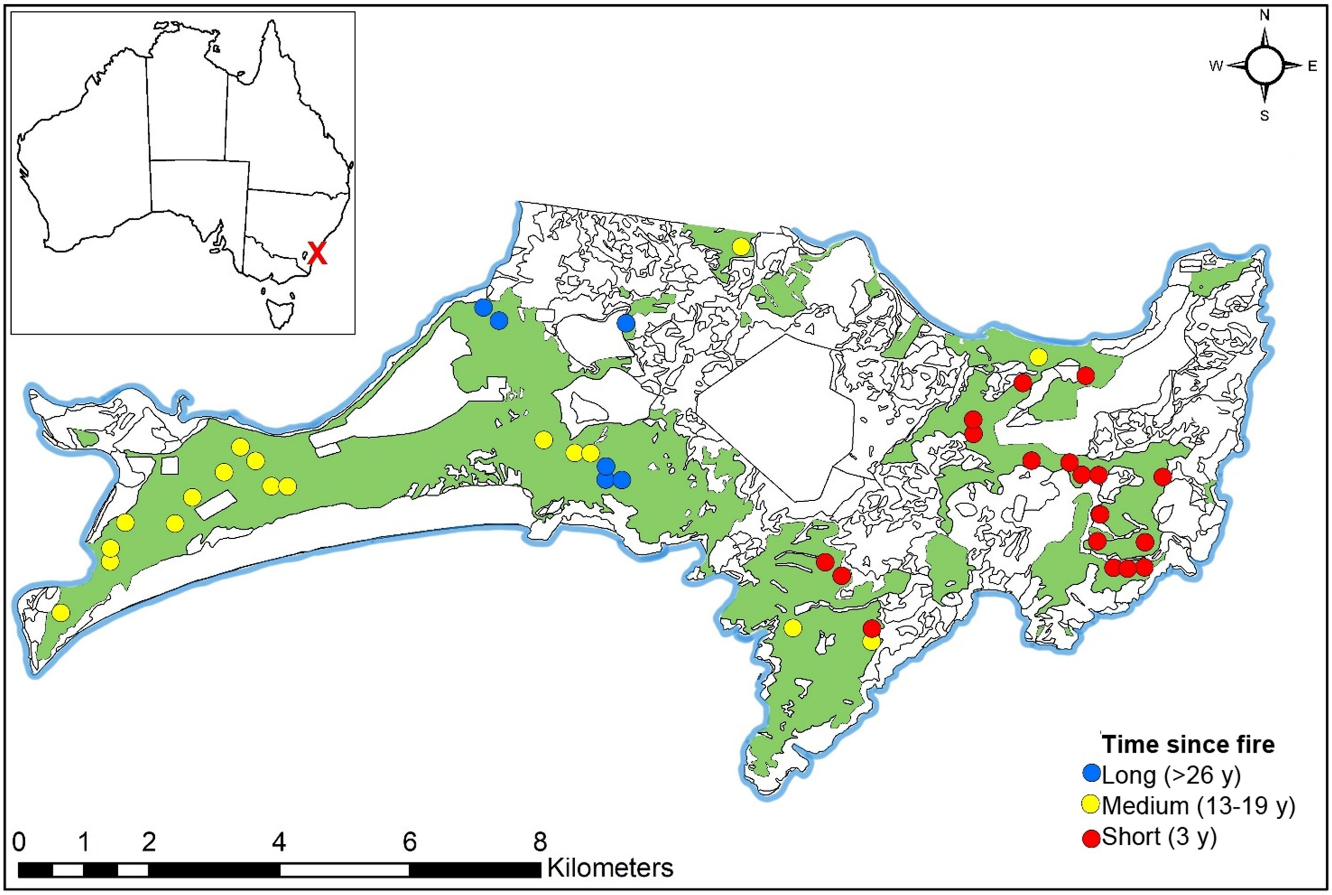

FIGURE 1 Map of all 42 field sites and their respective time since fire (Long: >26 years since fire, Medium: 13–19 years since fire and Short: 3 years since fire) in Booderee National Park. Light green indicates the distribution of dry-sclerophyll *Eucalyptus* forests in the Park. Blue border indicates where the peninsula meets the ocean.

perimeter of each site. We then pooled and mixed soil samples from each site to create a single composite sample and then took subsamples of this for DNA analysis (stored at −22°C). We also collected an additional soil subsample to determine soil moisture and used the remaining soil of each sample for analysis of abiotic soil properties.

2.3.1 | Soil analysis

Each soil sample was analysed to quantify measures of 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) as described in detail in Bowd et al. (2022a) (Figure S1).

2.3.2 | DNA isolation, amplification and raw data processing

DNA was extracted from the soil in each site using DNeasy PowerSoil Pro Kit (QIAGEN) following the manufacturer's instructions. From these extractions, PCR amplification and sequencing were performed by the Australian Genome Research Facility in Melbourne, Australia as described in detail in Bowd et al. (2022a). Briefly, PCR amplicons were generated for fungi (ITS2 region) using primers: FITS7 (GTGAR TCATCGAATCTTTG) (Ihrmark et al., 2012) and ITS4 (TCCTCCGC TTATTGATATGC) (White et al., 1990). PCR conditions for both amplicons were: 1 cycle at 98°C for 20 s, followed by 30 cycles of 98°C for 10 s, 60°C for 10 s, 72°C for 30 s and one final cycle at 72°C for 5 min. Thermocycling was completed with an Applied Biosystem 384 Veriti and using Platinum SuperFi II mastermix (Life Technologies) for primary PCR. The first-stage PCR was cleaned using magnetic beads, and samples were visualized on 2% Sybr Egel (Thermo-Fisher). A secondary PCR to index the amplicons was performed with Platinum SuperFi II mastermix (Thermo-Fisher). The resulting amplicons were cleaned again using magnetic beads, quantified by fluorometry (Promega Quantifluor) and normalized. The equimolar pool was cleaned a final time using magnetic beads to concentrate the pool and then measured using a High-Sensitivity D1000 Tape on an Agilent 2200 TapeStation. The pool was diluted to 5 nM and molarity was confirmed again using a Qubit High-Sensitivity dsDNA assay (ThermoFisher). Sequencing was then performed on an Illumina MiSeq with a V3, 600 cycle kit (2 × 300 base pairs paired-end) and a 25% PhiX spike-in to improve nucleotide diversity.

Fungal raw sequences were processed using QIIME2 software (qiime2-2020.2; Bolyen et al., 2019), and sequence quality control, denoising, chimera detection and clustering into Amplicon Sequence Variants (ASVs) were performed using 'DADA2' (Callahan et al., 2016) with parameters: –p-trunc-len-f 250 –p-trunc-len-r 250. ASVs with <10 reads across all samples were removed for downstream analysis. Taxonomy was assigned to fungal ASVs using classify-sklearn with the UNITE database (v.8) (Abarenkov et al., 2010), with confidence set to 0.7 (Bokulich et al., 2018). Nonfungal ASVs were excluded prior to any further analysis. Based on appropriate taxonomic matches, we used the fungal traits database 'FungalTraits' (Põlme et al., 2020) to assign functional groups ('primary lifestyles') to 67.57% of ASVs at the genera level only. These included: (1) saprotrophic fungi (wood, litter, soil, dung, pollen and unspecified saprotrophs), (2) ectomycorrhizal fungi, (3) pathogenic fungi (plant pathogens, animal parasites, mycoparasites, lichen parasites) and (4) epiphytic and endophytic fungi (root, foliar). We summed the rarefied abundance of all saprotrophs to create a composite measure of these fungi ('all saprotrophs'). We note the potential of some fungi to perform multiple functional roles under certain ecological conditions ('secondary lifestyles'); however, we did not consider these in our study. Using 'FungalTraits', we further categorized ectomycorrhizal fungi by their exploration types, which describe morphological differences in hyphae that influence nutrient acquisition strategies (Agerer, 2001). These exploration types were contact, long-distance, medium-distance (fringe, smooth, mat) and short-distance (coarse, delicate). We did not examine arbuscular-mycorrhizal fungi because of a paucity of Glomeromycetes (arbuscular-mycorrhizal fungi) in our dataset (5 unique ASVs).

2.4 | Statistical analyses

2.4.1 | Rarefaction

To account for uneven sequencing depths, we rarefied ASV sequences in each sample to the lowest number of total sequences in a given sample across the 42 sites (53,202 sequences) using the 'phyloseq' package in R (McMurdie & Holmes, 2013). This process resulted in the removal of 39 unique ASVs where the rarefied total number of combined sequences across all sites was equal to zero. Thereafter, all analyses were conducted using rarefied data of 4049 fungal amplicon sequence variants (ASVs) from 2,234,484 rarefied DNA sequences (Figure S2).

2.4.2 | Temporal patterns of fungal communities after fire

Fungal community composition: To test our first two hypotheses (H1 and H2), we first produced three separate NMDS plots to visualize differences in community composition across sites with different times since fire (as categorical variables) for all fungi, and separately for ectomycorrhizal fungi and saprotrophic fungi. We generated these plots from Bray–Curtis dissimilarity matrices based on the relative abundances of all fungal ASVs, ectomycorrhizal ASVs only and saprotrophic ASVs only. These data were square-root transformed to account for the potential influence of disproportionally high or low abundant taxa. We overlayed 95% confidence ellipses for each time since fire category onto each NMDS plot calculated using the *stat_ellipse* function of 'ggplot2' package (Wickham, 2016).

We tested for spatial autocorrelation across our multivariate datasets (i.e. all fungi, ectomycorrhizal fungi and saprotrophic fungi). To do this, we first performed a Mantel test (based on Spearman's correlation coefficients) on the Bray–Curtis dissimilarity matrices of all (square-root transformed) fungi, ectomycorrhizal and saprotrophic fungal relative abundances and spatial (site longitude and latitude) distances between sites (haversine distance matrix) using the 'geosphere' (Hijmans, 2021) and 'vegan' packages in R (Oksanen et al., 2013). We further investigated the potential of spatial autocorrelation to influence the community composition of all fungi, and ectomycorrhizal and saprotrophic fungi, by constructing dbMEM (distance-based Moran's Eigenvector Maps) eigenvectors to use as spatial explanatory variables in multivariate analyses using the 'adespatial' package in R (Borcard et al., 2018; Dray et al., 2017). To select influential dbMEM eigenvectors, we performed Redundancy Analysis (RDA) on detrended, Hellinger-transformed abundance data for each multivariate dataset (Borcard et al., 2018). We then applied a forward selection process on dbMEM eigenvectors with positive spatial correlation using a double-stopping criterion (Blanchet et al., 2008; Borcard et al., 2018). This process revealed no significant associations between all fungal and ectomycorrhizal fungal community composition, respectively, and dbMEM eigenvectors ($p > .05$). However, we found a minor but significant association ($p = .03$, $R^2 = 0.03$) between one dbMEM eigenvector and saprotrophic fungal community composition. Thereafter, we used this dbMEM eigenvector as a spatial explanatory predictor variable in subsequent multivariate analysis for saprotrophic fungi only.

To quantify the influence of time since fire on the composition of fungal communities (all fungi, ectomycorrhizal fungi and saprotrophic fungi) (H1 and H2), we conducted a PERMANOVA from the same Bray–Curtis similarity matrices using the *adonis* function in the 'vegan' package in R (Oksanen et al., 2013). We included elevation and a dbMEM eigenvector (spatial-proxy variable for saprotrophs only) as covariates in the PERMANOVA to account for their potential influence on both time since fire and fungal communities. To complement this analysis, we conducted post-hoc pairwise testing across levels of time since fire [long (>26 years), medium (13–19 years), short (3 years)] to compare their individual effects on fungal community composition using the 'pairwise. adonis' package (Martinez Arbizu, 2020) in R.

We identified correlations between the community composition of fungal communities (all fungi, ectomycorrhizal fungi and saprotrophic fungi) and environmental variables including soil properties (soil moisture, NH_4^+, NO_3^-, P, K, S, C, electrical conductivity, pH), fire frequency, dbMEM (spatial-proxy variable for saprotrophs only) and elevation using the *envfit* function in the 'vegan' R package on the same NMDS plot. This allowed us to identify potential drivers of compositional changes with time since fire. We overlayed significantly correlated ($p < .05$) variables on the NMDS plot as bi-plots proportional to the strength of the correlation. Prior to running this analysis, we also checked for correlations between abiotic soil properties and removed any variables that had a Pearson's correlation coefficient > 0.75 with other variables. Through this process, we removed sulphur, which was highly correlated with conductivity.

Fungal ASV differential abundance: To further describe successional changes in fungal communities after fire at a finer taxonomic scale (H1 and H2), we performed a differential abundance analysis on individual fungal ASVs using the *DESeq* function in the 'DESeq2' (Love et al., 2014) package in R using negative-binomial generalized linear models. This function estimated the logarithmic fold changes in the relative abundance of individual fungal ASVs between contrasts of time since fire (Short vs Long, Short vs Medium, Medium vs Long). This identified species that responded positively (and increased in abundance) or negatively (and decreased in abundance) to a given time since fire, relative to another. We report fungal ASVs with significantly different abundances between contrasts of time since fire as those with adjusted p values of <.01 (Benjamini–Hochberg correction).

Fungal richness, evenness, functional groups and ectomycorrhizal exploration strategies: To test our third hypothesis, we constructed generalized linear models and negative-binomial hurdle models to investigate how successional changes after fire influenced the richness, evenness and relative abundance of fungal ASVs with different functional groups. Specifically, we constructed models for: (a) the abundance of saprotrophic (litter, wood and soil inhabiting) fungi and ectomycorrhizal fungi, and the abundance of ectomycorrhizal fungi with different exploration strategies [contact, short-distance (delicate and coarse) and medium-distance (coarse, mat and smooth)], (b) total fungal, ectomycorrhizal and saprotrophic richness (number of unique amplicon sequence variants) and (c) total fungal evenness (Pielou's evenness metric based on Shannon's diversity index). Each generalized linear model included time since fire (categorical variable), fire frequency (continuous variable) and soil properties and elevation to control for their potential influence. The soil properties that we used were soil moisture, ammonium, nitrate, phosphorus, potassium, organic carbon, conductivity and pH.

We performed model selection on each full model using the *dredge* function in the 'MuMIn' package in R and selected the model with the lowest Akaike information criterion (AIC) (Barton, 2020). We checked for spatial autocorrelation in model residuals using variograms employed by the 'geoR' package, in combination with the 'sp' (Bivand et al., 2013) and 'rgdal' (Bivand et al., 2021) packages in R and found no evidence of spatial dependence (Ribeiro & Diggle, 2001). We also checked all models for multicollinearity using variance inflation factors (VIFs) in the 'car' package in R (Fox & Weisberg, 2019). VIFs of all models were < 6, validating the independence assumption of our models. From each model, we generated predictions (estimated marginal means) for the diversity and relative abundance of each fungal functional group in relation to time since fire (where significant) holding nonfocal variables constant using the *ggpredict* function in the 'ggeffects' package in R (Lüdecke, 2018). We generated plots to visualize these predictions using 'ggplot2' (Wickham, 2016).

Specifically, we used Gaussian generalized linear models for normally-distributed measures of fungal abundance, evenness and for fungal richness where high counts approximated a normal distribution. For zero-inflated measures of abundance, we used negative-binomial hurdle models to model separately the probability of a zero outcome across all observations (ziformula = ~1) and associations conditional on the presence of a given fungal group within a site. We conducted hurdle models using 'glmmTMB' package in R and used the 'DHARMa' (Hartig, 2022) and 'performance' (Lüdecke et al., 2020) packages to check model fits. Further, to meet the assumptions of generalized linear models on fungal abundance, we log or square-root transformed response variables. We removed two influential outliers in the short-distance EcM (delicate) model identified through examination of residual plots where DHARMa analysis of model diagnostics revealed significant quantile deviations based on simulated residuals (Hartig, 2022). Outliers that did not influence the model outcome when omitted were retained in the final model.

2.4.3 | Fungal inter-guild associations

To test our fourth hypothesis focussed on inter-guild interactions after fire, we calculated Pearson's correlations between the total abundance of ectomycorrhizal and saprotrophic fungi for each time since fire category (after confirming assumptions of this analysis) and used the 'rstatix' R package to test their significance (Kassambara, 2021). We then tested for temporal differences in these inter-guild associations by checking for interactive effects between the abundance of saprotrophic fungi and time since fire on the abundance of ectomycorrhizal fungi using generalized linear models.

2.4.4 | Time since fire and soil properties

To elucidate how soil properties are influenced by time since fire we performed the univariate analysis of variance (ANOVA) for each soil property, as well as corresponding post-hoc Tukey tests at a significance level of 0.05.

3 | RESULTS

3.1 | Temporal patterns of fungal communities after fire

3.1.1 | Community composition

As indicated by PERMANOVA, time since fire had a small but significant effect on the composition of all fungi and ectomycorrhizal and saprotrophic communities (R^2 values <0.102, $p<.004$; Table S1). The corresponding NMDS plots (Figure 2) and post-hoc pairwise comparisons (Table S2) show overlapping but significant ($p<.05$) distinctions between the composition of fungal communities with times since fire (Table S2). However, there were no significant differences between medium vs long times since fire for either ectomycorrhizal or saprotroph communities (Table S2).

Fire frequency, elevation, soil pH, soil moisture, organic carbon, potassium and conductivity were all significantly associated with the composition of all fungal communities, and the composition of saprotrophic fungi was associated with fire frequency, soil moisture, potassium, organic carbon, dbMEM (spatial-proxy variable) and soil pH (Table S3 and Figure 2). Specifically, fungal communities in sites with a short time since fire (3 years) were associated with higher values of pH, and lower values of soil moisture, potassium and organic carbon, relative to medium and long time since fire sites (Figures 2, S1 and Tables S3, S7). By contrast, the composition of ectomycorrhizal fungi was associated with elevation only.

Using a Mantel test, we observed minor, but statistically significant, positive correlations between the distances between sites and the dissimilarities among sites for the ASVs for all fungi, ectomycorrhizal fungi and saprotrophic fungi (Mantel statistics: $r=0.24$, 0.16 and 0.23, respectively; p for all <.001). That is, all fungal, ectomycorrhizal and saprotrophic communities became slightly more

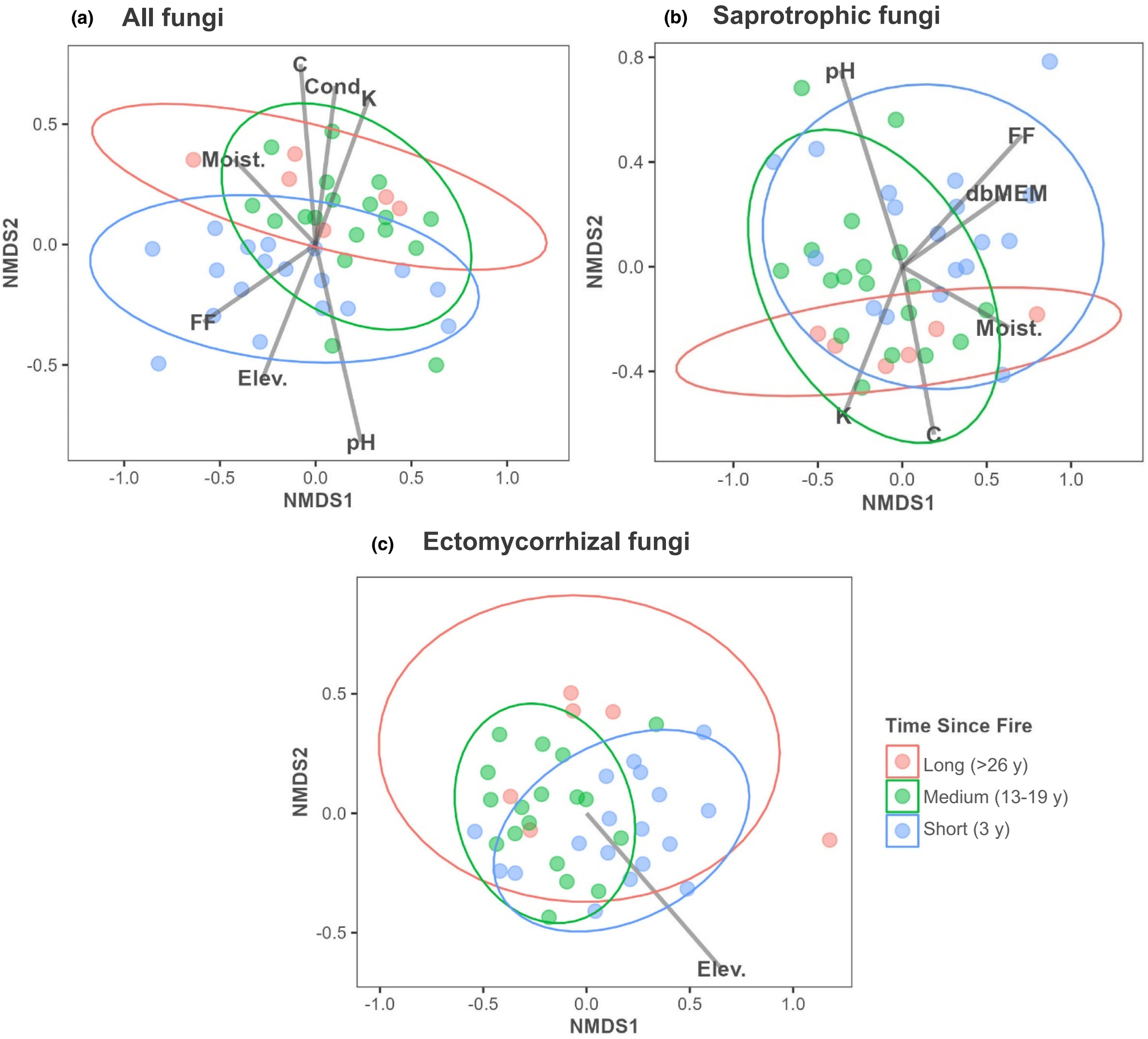

FIGURE 2 NMDS plots indicating groupings in the community composition of all fungal, ectomycorrhizal and saprotrophic fungal amplicon sequence variants in relation to time since fire. Significantly correlated environmental variables are overlaid as bi-plots derived from *envfit* with the length of the line indicative of the strength of the correlation. C, organic carbon; Cond., conductivity; Elev., elevation; FF, fire frequency; K, potassium; Moist, soil moisture. NMDS stress values: (a) 0.18, (b) 0.23, (c) 0.18. Ellipses represent 95% confidence intervals. dbMEM, Moran's eigenvector map (proxy for spatial variable).

dissimilar among sites as the sites became more physically separated (Figure S3). RDA revealed that only a single dbMEM eigenvector was associated with the composition of saprotrophic fungi ($p < .05$). This spatial-proxy variable was correlated with saprotrophic NMDS axes ($R^2 = 0.167$; $p = .027$), indicating that spatial variation had a minor influence on the composition of saprotrophic communities (Table S3).

3.1.2 | Differential abundance of fungal ASVs

Fungal ASVs in sites with a medium (13–19 years) or long (>26 years) time since fire predominantly belonged to the Ascomycota phylum (60.7% and 65.1% of total sequences, respectively) and to a lesser extent Basidiomycota (38.3% and 34.54% of total sequences, respectively). Fungal ASVs in sites with a short (3 years) time since fire had a similar total abundance of sequences that belonged to both Ascomycota and Basidiomycota (49.04% and 49.63% of total sequences, respectively). Fungal ASVs belonged to 157 families, and of these, Myxotrichaeceae and Cortinariaceae were the most abundant and both of these increased with time since fire (Figures S4, S5).

Soil saprotrophs had the highest relative abundance across sites with long (>26 years), medium (13–19 years) and short (3 years) times since fire (43.9%, 38.6%, 28.9% of total sequences in each category, respectively). Ectomycorrhizal fungi had the next highest relative abundance across sites with long, medium and short times since fire (28.4%, 27.9%, 20.4% of total sequences in each category, respectively). We identified seven ectomycorrhizal exploration types, including 'medium-distance (fringe)' (60.5%, 59.1% and 18.4% of total EcM sequences), 'contact' (32.6%, 18.9% and 6.2% of total EcM sequences) and 'short-distance (delicate)' (2.9%, 10.6% and 17.5% of total EcM sequences) in sites with long, medium and short times since fire, respectively (Figure 3).

Using a differential abundance analysis, we identified several fungal ASVs that were significantly ($p < .01$) influenced by time since fire. Specifically, with short (3 years) time since fire, 24 ASVs increased and 14 ASVs decreased relative to long (>26 years) time since fire, and 16 ASVs decreased and 5 ASVs increased relative to medium (13–19 years) time since fire. Ectomycorrhizal *Cortinarius* and *Russula* species declined in short time since fire, relative to both long and medium times since fire (Figures 3, 4). However, other ectomycorrhizal fungi increased with short time since fire relative to long time since fire, including *Inocybe*, *Sebacina*, *Elaphomyces* (all short-distance EcM), *Hysterangium* (medium-distance mat EcM) and *Lactifluus* (medium-distance smooth EcM) species. Short (3 years) time since fire also resulted in an increase in saprotrophic *Talaromyces* and *Trechispora*, and plant pathotrophic *Rickenella* species relative to sites with a long time since fire. Contrasts between long (>26 years) and medium (13–19 years) times since fire also revealed significant differences in the abundance of 32 fungal ASVs, of which 24 increased and 8 decreased. For instance, relative to long time since fire, medium time since fire resulted in a decline in the abundance of some ectomycorrhizal *Cortinarius* and *Russula* species, and an increase in ectomycorrhizal *Sebacina*, *Lactifluus*, *Hysterangium*, *Inocybe* and *Elaphomyces* species, and saprotrophic *Talaromyces and Trechispora* species (Figures 3, 4 and Table S4).

3.1.3 | Fungal functional and ectomycorrhizal exploration types

We identified associations between the relative abundance and richness of fungal functional groups and time since fire, controlling for the influence of soil properties and fire frequency (Figure 5). Short time (3 years) since fire was associated with a decline in total fungal richness ($p = .015$), relative to long time (>26 years) since fire. Short time since fire was also associated with a lower abundance of total ectomycorrhizal fungi ($p = .013$) and medium-distance (fringe) ectomycorrhizal fungi ($p = .003$), relative to long times since fire. By contrast, the abundance of short-distance (coarse) ectomycorrhizal fungi increased with medium ($p = .006$) time since fire and marginally with short time since fire ($p = .063$). The conditional abundance of medium-distance mat-forming ectomycorrhizal fungi also increased with medium (13–19 years; $p = .002$) and short ($p < .001$) times since fire, relative to long time since fire (Figure 5 and Table S5). We found no significant influence of time since fire or other covariates on total fungal evenness ($p > .05$; Table S5).

We found no direct associations between the relative abundance or richness of saprotrophic fungi with time since fire. However, we observed positive associations between organic carbon and total saprotrophic fungi ($p = .008$) and soil saprotrophs ($p = .001$). By contrast, several ectomycorrhizal fungal variables were negatively associated with organic carbon, including total ectomycorrhizal fungi ($p < .001$), long-distance fungi ($p = .001$) (conditional abundance), short-distance (delicate) fungi ($p = .002$), medium-distance (fringe) fungi ($p = .012$) and total ectomycorrhizal fungi richness ($p = .002$; Figure 5 and Table S5).

3.2 | Inter-guild fungal associations

At the functional-group level, we found strong negative Pearson's correlations between saprotrophic and ectomycorrhizal fungi at medium (13–19 years) ($r = -0.698$, $p = .001$) and long (>26 years) ($r = -0.832$, $p = .041$) times since fire (Figure 6). These correlations were absent from sites with a short (3 years) time since fire ($r = 0.061$, $p = .807$). Time since fire and the abundance of saprotrophs also had an interactive effect on the abundance of ectomycorrhizal fungi, indicating significant temporal differences in inter-guild associations (Figure 6 and Table S6).

3.3 | Abiotic associations with time since fire

ANOVA revealed time since fire was significantly associated with measures of soil potassium, organic carbon, conductivity and soil pH (Table S7). Corresponding Tukey tests indicated significantly lower measures of organic carbon, conductivity and potassium in

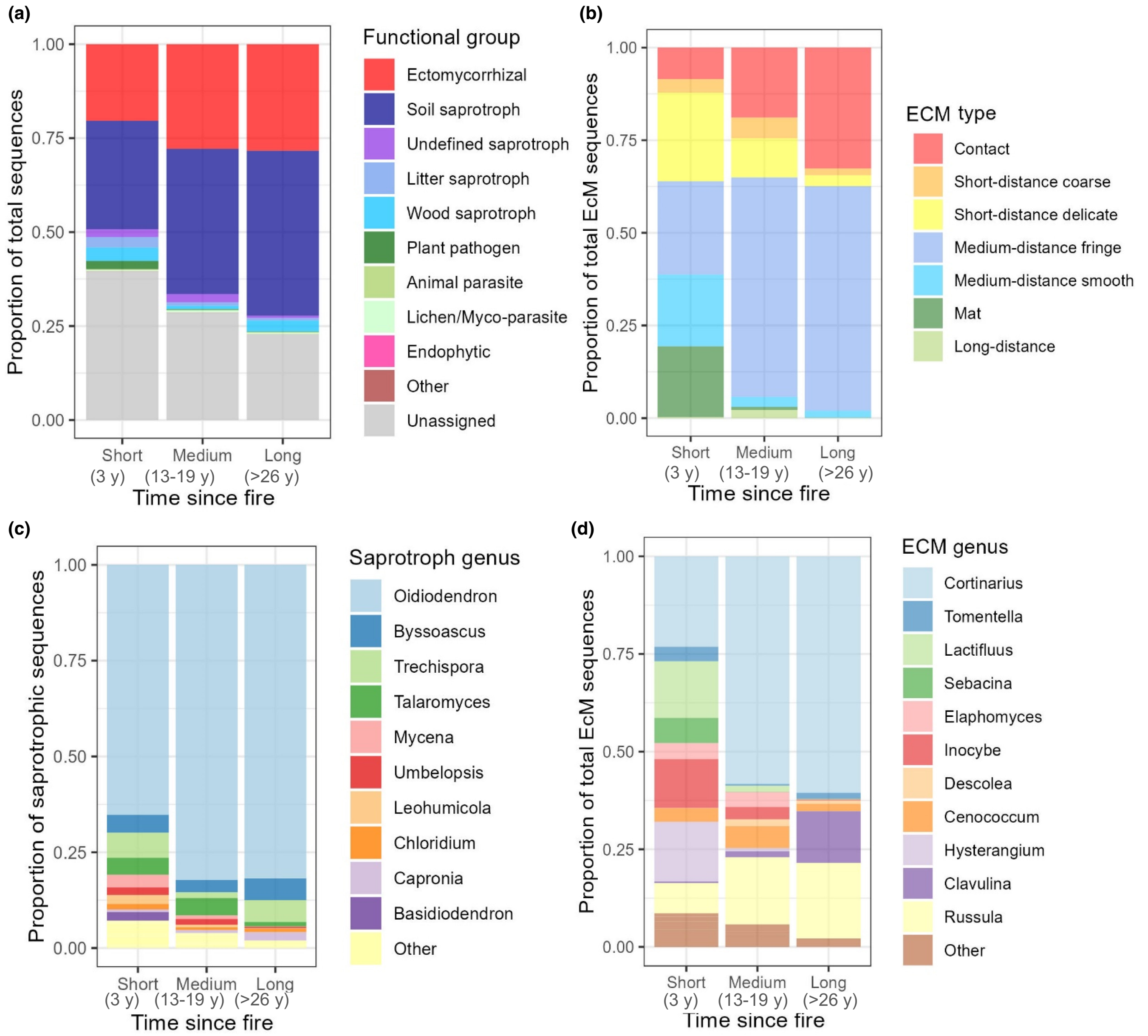

FIGURE 3 Proportion of total fungal sequences assigned to (a) functional groups, (b) ectomycorrhial (ECM) exploration types, (c) saprotrophic genera and (d) ectomycorrhizal (ECM) genera. Sequences are pooled across all sites within each time since fire category. 'Pathogenic' fungi include all plant pathogens, animal parasites, mycoparasites and lichen parasites.

sites with a short versus long time since fire. By contrast, soil pH increased in sites with a short time since fire, relative to both medium and long times since fire (Table S7 and Figure S1).

4 | DISCUSSION

4.1 | Patterns of fungal community composition vary with time after fire

We found that the composition of all fungal communities (including ectomycorrhizal and saprotrophic communities) in the dry-sclerophyll forests of Booderee National Park varied substantially with time since fire. As hypothesized (H1), the composition of all fungal communities in recently burnt sites (3 years since fire) was the most different from that of both medium (13–19 years) and long (>26 years) times since fire, which had a similar community composition. Compositional differences in fungal communities between sites that differed in time since fire may reflect variation in species-specific physiological fire response traits, analogous to those observed in plant species in fire-prone environments, suggesting parallel evolutionary strategies (Clarke & Dorji, 2008; Enright et al., 2022; Fox et al., 2022; Whitman et al., 2019). These include the capacity to: (a) utilize postfire resources (Fischer et al., 2021; Raudabaugh et al., 2020), (b) tolerate heat and desiccation (e.g. via heat-tolerant spores or sclerotia) (Glassman et al., 2016) and (c)

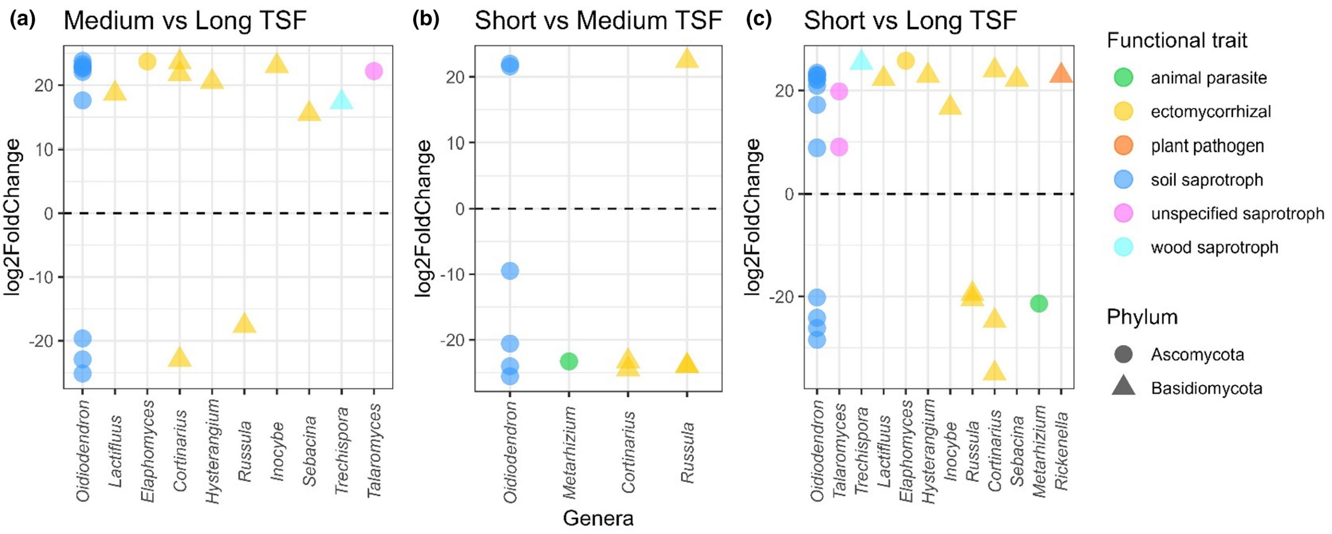

FIGURE 4 Significant ($p < .01$) differences in the relative abundance of amplicon sequence variants (ASVs) with different times since fire contrasts based on differential abundance analysis using DESeq2. Multiple points per genus represent different ASVs. Negative values indicate a negative response and positive values indicate a positive response to the time since fire contrast. Specifically, panels show changes in sites with a (a) medium (13–19 years) TSF, relative to long (>26 years) TSF; (b) short (3 years) TSF, relative to a medium TSF; and (c) short TSF, relative to a long TSF (Table S4). Only ASVs and their corresponding genera with significant differential abundance ($p < .01$) are displayed.

rapidly colonize environments after fire (Enright et al., 2022; Fox et al., 2022; Whitman et al., 2019). For instance, fire-induced declines in disturbance-sensitive *Cortinarius* and *Russula* species may be partially explained by substrate limitations in sites with a short (3 years) time since fire (Figure 3 and Table S7). This is because these species are typically associated with later-successional ecosystems rich in deposits of humus, litter and decayed wood, all of which may be consumed by fire (Hart et al., 2018; Pulido-Chavez et al., 2022; Twieg et al., 2007; Visser, 1995). By contrast, thermophilic and thermotolerant saprotrophs, such as *Talaromyces* species, increased in sites with a short time since fire (Houbraken et al., 2012), as did ectomycorrhizal species, which produce hypogeous fruiting bodies such as *Elaphormyces* and *Hysterangium* (Glassman et al., 2016; Peay et al., 2009; Smith et al., 2015). Indeed, *Hysterangium* species produce robust fruiting bodies with leathery-type skin, which may be resistant to desiccation, unlike the more fragile, fleshy fruiting body of many *Cortinarius* species, which may be sensitive to water loss (Claridge et al., 2000), and *Russula* species, which possess hydrophilic ectomycorrhizal structures (Agerer et al., 2000).

Previous studies have suggested that fungal communities may take more than a decade to recover after fire in other ecosystems (Dove et al., 2022; Holden & Treseder, 2013; Oliver et al., 2015; Pérez-Valera et al., 2018). Similarly, our research suggests fire can alter fungal community composition within the first two decades in our study area, with community recovery likely after this time. To better understand this critical phase of postfire succession, future studies would need to utilize chronosequences of sites where fires occurred between three and 13 years ago, as well as immediately postfire (0–3 years) where communities may be dominated by fire-tolerant fungal genera such as *Pyronema* species (Ammitzboll et al., 2021; Bruns et al., 2020; Fischer et al., 2021).

Fire can have substantial impacts on soil chemistry, such as by increasing pH and depleting nitrogen and organic matter (Table S7; Certini, 2005; Wan et al., 2001). Therefore, aside from the direct effects of fire, compositional differences in fungal communities may also be influenced by species-specific tolerances to fire-induced environmental changes (Bowd et al., 2022a; Yang et al., 2020). For instance, our findings suggest dissimilarities between the composition of total and saprotrophic fungal communities may relate to fire-induced declines in soil organic carbon and potassium, and increases in soil pH, with the most alkaline soils occurring 3 years postfire (short time since fire) (Figure S1 and Table S7). These findings are congruent with other studies that suggest soil properties, including soil organic carbon (or organic matter) and pH are prevailing drivers of fungal community composition (Brundrett & Tedersoo, 2018; Day et al., 2019; Glassman et al., 2017). In contrast to other groups, we found that the composition of ectomycorrhizal fungal communities was not associated with any environmental variables except time since fire and elevation. This suggests that the direct effects of fire (i.e. mortality caused by soil heating) or postfire changes in plant communities might be primary drivers of compositional change in ectomycorrhizal communities (Hewitt et al., 2013; Twieg et al., 2009).

4.2 | Functional groups of fungi change with time since fire

As hypothesized (H2), ectomycorrhizal fungi were disproportionally negatively impacted by fire (i.e. they significantly declined with decreasing time since fire), relative to saprotrophic organisms. Previous studies have demonstrated ectomycorrhizal fungi can recover in tandem with plant communities and with the

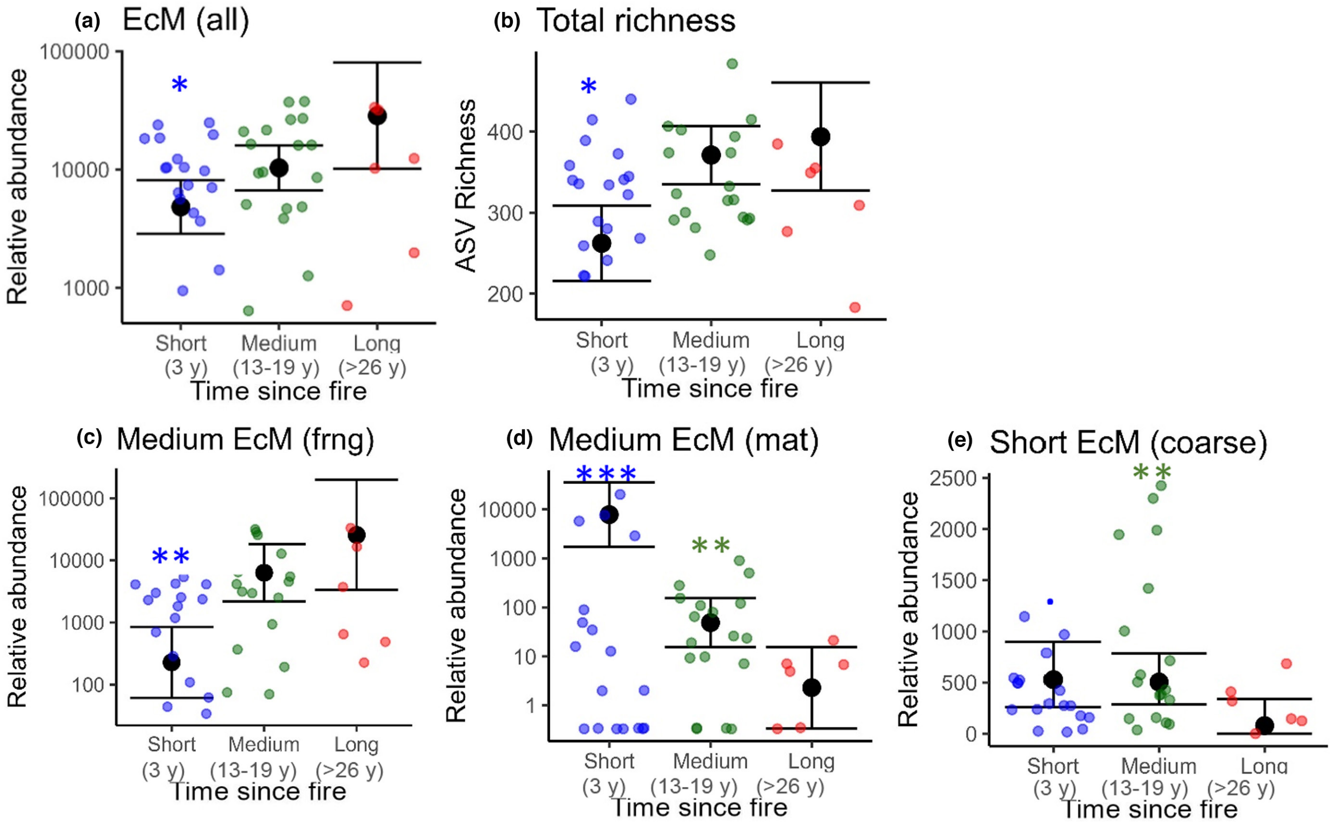

FIGURE 5 Predicted mean (large black dots with 95% confidence intervals) and raw (coloured dots) values of the relative abundance (total number of read counts) of: (a) all ectomycorrhizal fungi, (b) total fungal richness (total number of unique ASVs), and specific ectomycorrhizal exploration types: (c) medium-distance (fringe), (d) medium-distance (mat), (e) short-distance (coarse) with respect to time since fire. Predictions were generated from models where associations between time since fire and fungal response variables were significant and are adjusted for the mean of nonfocal variables in each model. Predictions for medium-distance (mat) ectomycorrhizal fungi are conditional on the presence of these fungi within a given site (generated from a negative-binomial hurdle model). The y-axis is on the log10 scale for plots (a, c, d) only to improve readability. $^{\cdot}p = .06$; $^{*}p < .05$; $^{**}p < .01$; $^{***}p < .001$ (relative to long time since fire). See Table S5 for further detail.

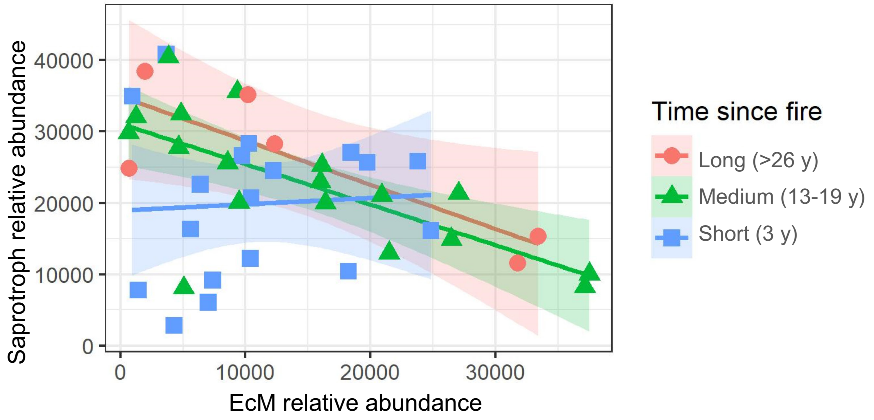

FIGURE 6 Relationship between the total relative abundance (total count of ASV reads) of saprotrophic and ectomycorrhizal fungi in sites with a long (>26 years) ($r = -0.832$, $p = .041$), medium (13–19 years) ($r = -0.698$, $p = .001$) and short (3 years) ($r = 0.061$, $p = .807$) time since fire. Shaded areas are 95% confidence intervals surrounding the linear trend line. Each point represents an individual site.

accumulation of organic matter (Bever et al., 2012), and may facilitate postdisturbance vegetation recovery (Cázares et al., 2005), especially when there is high host specificity (Agerer, 2001; Glassman et al., 2016; Tedersoo et al., 2008; Twieg et al., 2007). Low abundances of ectomycorrhizal fungi may negatively affect plant growth and seedling survival of ectomycorrhizal-dependent plant species after fire (van der Heijden et al., 2008, 2015). However, given the likely bidirectional relationships between the recovery of ectomycorrhizal fungi and host plant species post-fire, biological feedbacks may occur, which facilitate recovery or trigger deleterious trends in both components after fire (van der Heijden et al., 2008, 2015). Further investigations are required to elucidate the causal mechanisms underpinning temporal changes in the abundance of ectomycorrhizal fungi after fire, including in relation to plant community responses in our study system to complement our findings.

In contrast to ectomycorrhizal fungi, some saprotrophs may recover rapidly after fire due to having high heat tolerance (Carlsson et al., 2014), exposure to reduced competition, increased resources and the ability to grow and colonize rapidly independent of plant hosts (Pérez-Izquierdo et al., 2021; Sun et al., 2017; Yang et al., 2020). For instance, several saprotroph species increased in sites with a short time (3 years) and medium time (13–19 years) since fire, relative to sites with a long time since fire (unburnt for >26 years), such as *Talaromyces* and *Trechispora* species (Figure 3). By contrast, dominant ectomycorrhizal taxa had much lower relative abundances in sites with a short time since fire (e.g. *Cortinarius* and *Russula* species). Dry-sclerophyll eucalypt forests are typically resilient to frequent wildfires (i.e. around every 10 years), because dominant mature trees that associate with ectomycorrhizal fungi are not fire-killed but instead resprout after fire (Foster et al., 2017). Therefore, it is likely that the negative effects of fire on ectomycorrhizal may be even more pronounced and long-lasting in other forests where trees are fire-killed, resulting in substrate limitation (Pérez-Izquierdo et al., 2021), or in the case of complete stand replacement in clearcut logging operations (Ammitzboll et al., 2021; Bowd et al., 2022a). For instance, ectomycorrhizal fungi have been reported to decline markedly for more than a decade following stand-replacing disturbances in obligate-seeding eucalypt forests (Bowd et al., 2022a).

4.3 | Ectomycorrhizal exploration types differ in responses to time since fire

We found evidence of temporal differences in the abundance of some ectomycorrhizal fungi exploration types after fire (H3). Specifically, medium-distance, mat-forming ectomycorrhizal fungi, which have a limited range of exploration (Agerer, 2001), increased with recent fire. This could be related to the affinity of mat-forming fungi with plant seedlings, given these fungi can support plant seedling germination and establishment in postdisturbance environments (Griffiths et al., 1991). The abundance of short-distance (coarse) ectomycorrhizal fungi was also higher with medium (13–19 years) time since fire, and marginally higher 3 years postfire ($p = .06$). Increases in short-distance fungi in the short-medium (3–19 years) term after fire including *Inocybe*, *Sebacina* and *Elephomyces* species may also relate to their capacity to regenerate hyphae (Tedersoo & Smith, 2013), tolerance of broad environmental conditions (Rosinger et al., 2018) and affinities with specific root-densities that change over succession (Koide et al., 2014). For instance, increases in the relative abundance of short-distance (delicate) fungi in sites with a short time since fire (e.g. *Inocybe* species) (Figure 3b), may be because they are less carbon-dependent and therefore able to survive soils with lower organic carbon content in this time point (Pulido-Chavez et al., 2022; Figure 1 and Table S7). By contrast, medium-distance (fringe) ectomycorrhizal fungi, including *Cortinarius* species, which may be more carbon-demanding, increased with time since fire, which may relate to temporal changes in plant community composition (Clemmensen et al., 2015; Tedersoo et al., 2008), or temporal increases in organic N sources and below-ground carbon allocation (Lilleskov et al., 2011). Medium-distance (fringe) fungi include *Cortinarius* species, which are highly sensitive to disturbance but form a significant component of later-successional ectomycorrhizal fungi (Figure 3; Hart et al., 2018; Pulido-Chavez et al., 2021; Twieg et al., 2007; Visser, 1995). Over much longer chronosequences (thousands of years since the last fire), these fungi may also be more abundant in 'earlier' (hundreds of years since the last fire) successional stages, relative to 'later' (thousands of years since the last fire) successional stages driven by plant compositional changes (Clemmensen et al., 2015).

Heterogeneity within the morphological structures of ectomycorrhizal fungi such as the number of emanating hyphae or the presence of rhizomorphs can affect the uptake and transfer of nutrients and represent distinct exploration and foraging strategies (Agerer, 2001; Burgess et al., 1993; Cairney & Burke, 1996). Therefore, differences in the abundance of ectomycorrhizal fungi with different exploration strategies after fire may have functional implications in forests (Agerer, 2001; Defrenne et al., 2019; Koide et al., 2014; Tedersoo & Smith, 2013). For instance, medium-distance (fringe) ectomycorrhizal fungi (including *Cortinarius* species), which were more abundant in sites with a longer (>26 years) time since fire, can produce longer and denser mycelia than those with short-distance types, which were more abundant in recently burnt sites (e.g. *Inocybe* and *Sebacina* species; Weigt et al., 2012). These morphological differences allow medium-distance (fringe) ectomycorrhizal fungi to undertake more intensive resource exploration from further distances, increasing the supply of nutrients and water to host plants (Agerer, 2001; Defrenne et al., 2019; Koide et al., 2014; Weigt et al., 2012). This greater transfer of nutrients demands a higher carbon exchange from the plant to support the symbiosis (Weigt et al., 2012), which may subsequently increase soil carbon sequestration (Orwin et al., 2011). Increases in medium-distance (fringe) ectomycorrhizal fungi with time since fire may therefore positively affect plant growth and productivity and alter carbon dynamics.

4.4 | Inter-guild associations between saprotrophs and ectomycorrhizal fungi vary with time since fire

Consistent with our fourth hypothesis, we found strong negative inter-guild correlations between ectomycorrhizal and saprotrophic fungi with medium time (13–19 years) and long time (>26 years) since fire but not with short time (3 years) since fire (Figure 6). These negative correlations are likely explained by the higher abundance of ectomycorrhizal fungi in sites with a medium and long time since fire, relative to those with a short time since fire, which may increase competition with saprotrophs.

Competition between ectomycorrhizal fungi and saprotrophic fungi in sites with a long time (>26 years) and medium time (13–19 years) times since fire may alter carbon cycles by modifying rates of carbon mineralisation (decomposition) and carbon sequestration. For instance, the ‘Gadgil hypothesis’ (Gadgil & Gadgil, 1971) predicts that increasing competition between ectomycorrhizal fungi and saprotrophic fungi for nitrogen may reduce decomposition rates and increase carbon storage (Averill & Hawkes., 2016; Fernandez & Kennedy, 2016; Sterkenburg et al., 2018). Moreover, ectomycorrhizal fungi can also contribute large fluxes of carbon into soil organic matter through significant hyphal growth and turnover (See et al., 2022). Therefore, it is possible that reduced rates of competition between ectomycorrhizal fungi and saprotrophs with recent fire may translate to rapid decomposition and lower carbon sequestration, as indicated by low measures of soil organic carbon in our sites (Figure 1; Averill & Hawkes., 2016; Orwin et al., 2011). However, recent work challenges this paradigm by suggesting that these effects may be species-specific and context-dependent (Lindahl et al., 2021). For instance, some ectomycorrhizal fungi can act as ‘mycorrhizal decomposers’, including *Cortinarius* and *Russula* species, which possess organic-matter degrading enzymes that facilitate soil organic matter decomposition and the mobilization of nitrogen for which they compete directly with decomposing microbes (Agerer, 2001; Averill et al., 2014; Lindahl & Tunlid, 2015). Indeed, mycorrhizal fungi may utilize organic carbon: (a) as an alternate source of carbon when supplies are low from host plants, (b) as a consequence of mining for other nutrients or (c) to encourage the growth and activity of mycorrhizal fungi when photosynthate allocations are high (Talbot et al., 2008). Increases in mycorrhizal decomposers with longer times since fire may therefore increase long-term nutrient cycling and decomposition and potentially reduce carbon sequestration (Clemmensen et al., 2015; Lindahl et al., 2021).

Species-specific changes in ectomycorrhizal dominance and the capacity of these species to be ‘mycorrhizal decomposers’ might explain the negative correlations between ectomycorrhizal fungi and soil organic carbon found in our study. However, the causal reasons for this association remain unclear and could also reflect competitive dynamics between ectomycorrhizal fungi with saprotrophs, which were positively associated with organic carbon (Bowd et al., 2022a). Such positive associations between saprotrophs and soil organic carbon may reflect pathways through which litter decomposition can contribute to soil organic matter formation via microbial incorporation of dissolved organic matter (Cotrufo et al., 2015). Further research, including direct experimental manipulations, would be required to quantify how declines in ectomycorrhizal fungi and changes in their associations with saprotrophs influence carbon sequestration and decomposition after fire in our study system.

5 | CONCLUSION

Globally, forest ecosystems face a myriad of ecological pressures, which may compromise their value for biodiversity and the ecosystem services they provide to humans (Watson et al., 2018). These pressures include widespread increases in the occurrence of large-scale, high-severity wildfire (Abatzoglou & Williams, 2016; van Oldenborgh et al., 2021; Williams et al., 2019). Understanding the temporal responses of biodiversity to fire is therefore critical to inform adaptive management and to predict how ecosystems will respond to potential increases in the frequency of severe fires. This is especially important for fungal communities, which are grossly under-documented (Hawksworth & Lücking, 2017), yet have key ecological functions that facilitate the recovery of forests after fire.

Our results advance the understanding of how fungal communities respond to fire in forests by providing novel insights into community responses across functional groups, morphological structures of ectomycorrhizal fungi and fungal inter-guild associations. In summary, our findings indicate that fire is likely to be a major driver of fungal community composition in dry-sclerophyll forests in the short-medium term (3–19 years), with very recent fires disproportionately negatively affecting ectomycorrhizal fungi. With increases in the frequency and intensity of fire predicted across many temperate forests including those in our study (Bradstock et al., 2009; Canadell et al., 2021; Smith et al., 2020), adaptive management may be required to conserve sensitive fungi and curtail the potential functional implications of altered fungal communities (e.g. plant growth, seedling survival, decomposition, nutrient cycles). For instance, land managers should consider the temporal effects of fire on fungal communities when implementing prescribed burning at short intervals (<13 years). However, while our findings suggest burning at short intervals (<13 years) may be deleterious to ectomycorrhizal fungi, spatial heterogeneity in postfire abiotic conditions resulting from differences in fire severity and fuel loads require further consideration to refine management recommendations. Where prescribed burning at short intervals is necessary to meet other important management outcomes (e.g. fuel-load reduction), strategies that limit the effect of fire on ectomycorrhizal fungi may be helpful for their conservation. These include burning patch mosaics and leaving unburnt patches of vegetation among those burnt to act as refugia for ectomycorrhizal fungi and allow for re-colonization. Broadscale mulching applications may also help to facilitate the recovery of some communities where organic C is limited (Figure 1; Dove et al., 2022). We also suggest the integration of fungal communities in biodiversity assessments and ecological monitoring to assess their long-term responses to fire and identify potential functional implications.

AUTHOR CONTRIBUTIONS

EJB led the paper conception, writing and statistical analysis. CF established the experimental design of this project. EE conducted the bioinformatics analyses underpinning the microbial data and contributed to writing the paper. DBL, DAW, PK and CF also contributed to writing the paper.

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CONFLICT OF INTEREST STATEMENT

The authors declare no potential sources of conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available on dryad via https://datadryad.org/stash/share/49mAGwV1IqAPRI-PSHvgfujMJvMkbrryYkU2HJ0Ej2o for private peer-review access (Bowd et al., 2022b). Sequencing data are permanently archived on NCBI SRA (Bioproject: PRJNA926791).

BENEFIT-SHARING STATEMENT

Benefits Generated: Benefits from this research accrue from the sharing of our data and result on public databases as described above.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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