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Fire as a driver of fungal diversity — A synthesis of current knowledge

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ABSTRACT

Fires occur in most terrestrial ecosystems where they drive changes in the traits, composition, and diversity of fungal communities. Fires range from rare, stand-replacing wildfires to frequent, prescribed fires used to mimic natural fire regimes. Fire regime factors, including burn severity, fire intensity, and timing, vary widely and likely determine how fungi respond to fires. Despite the importance of fungi to post-fire plant communities and ecosystem functioning, attempts to identify common fungal responses and their major drivers are lacking. This synthesis addresses this knowledge gap and ranges from fire adaptations of specific fungi to succession and assembly fungal communities as they respond to spatially heterogeneous burning within the landscape. Fires impact fungi directly and indirectly through their effects on fungal survival, substrate and habitat modifications, changes in environmental conditions, and/or physiological responses of the hosts with which fungi interact. Some specific pyrophilous, or “fire-loving,” fungi often appear after fire. Our synthesis explores whether such taxa can be considered cosmopolitan, and whether they are truly fire-adapted or simply opportunists adapted to rapidly occupy substrates and habitats made available by fires. We also discuss the possible inoculum sources of post-fire fungi and explore existing conceptual models and ecological frameworks that may be useful in generalizing fungal fire responses. We conclude with identifying research gaps and areas that may best transform the current knowledge and understanding of fungal responses to fire.

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INTRODUCTION


Every year, an estimated 570 million hectares of land burns globally, altering the storage and cycling of carbon and nutrients as well as the composition and function of ecosystems (Bond-Lamberty et al. 2007; Bowman et al. 2009; Pellegrini et al. 2018). In many locations, contemporary fire regimes (e.g., fire frequency, seasonality, and intensity) have diverged from historical averages as a result of climate change, land use, and human encroachment at wildland-urban interfaces (Andela et al. 2017; Bento-Gonçalves and Vieira 2020; Dennison et al. 2014; Miller et al. 2009; Westerling et al. 2006). The impact of changing fire regimes on ecosystem function will partly be determined by the organismal fire responses. Fungal responses are likely critical, as they provision essential ecosystem services.

Fungal communities respond to fire with resultant significant effects on ecosystem functioning and nutrient cycling (Dooley and Treseder 2012; Holden and

Treseder 2013; Knelman et al. 2017). In ecosystems that rarely experience wildfires, infrequent fires can drive dramatic fungal community shifts that may take years (Gutknecht et al. 2010) or even decades (Dooley and Treseder 2012; Kipfer et al. 2011) to recover. In contrast, other ecosystems are maintained by frequent fires that may be necessary to also maintain fungal communities. Partly because of this variation in fire histories and regimes, we lack a synthetic understanding of the primary drivers of fungal fire responses. This understanding, however, is essential to better predicting how fire-induced shifts of fungal communities may alter ecosystem functions. Decoupling drivers and fungal responses, however, is not straightforward. Fire changes an array of ecosystem components (Certini 2005), many of which are inherently linked. For example, changing fire regimes drive corresponding shifts in ecosystem carbon and nutrient cycles by changing plant communities, removing plant biomass (both live and dead),

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direct combustion of soil organic legacies including carbon (C) and nitrogen (N), altering fuel loads, and impacting soil microbial communities (e.g., Baird et al. 1999; Kauffman et al. 1995; Mack et al. 2021; Muqaddas et al. 2015; Ojima et al. 1994; Pellegrini et al. 2015). Drivers that may underlie the responses of fungal communities are complex and likely include (i) direct heat-induced mortality from fire; (ii) abrupt changes to substrates and nutrient availability (Kaye and Hart 1998; Wang et al. 2012); (iii) long-lasting indirect changes in environmental conditions (Chen and Cairney 2002; Reazin et al. 2016); and (iv) altered physiology or mortality of plant hosts on which some fungi depend (Haase and Sackett 1998; Schwilk et al. 2009). Simultaneous shifts in plant responses (from individual plant

physiology to entire communities), substrates for fungal decomposers, and soil nutrient availability (including immobilization, losses through combustion and volatilization, and release through organismal mortality) all complicate generalizing fungal fire ecology, particularly across widespread variation in fire regimes and ecosystems.

Here, we identify and address the gaps in our understanding of fungi and fungal communities in the context of fire. Our central goal is to define a unifying framework that can help integrate patterns across numerous independent studies and identify generalities in fungal fire ecology. Toward this goal (see FIG. 1), we aim to (i) evaluate direct and indirect drivers for fungal responses to fire, outlining how these differ among ecosystems, fire

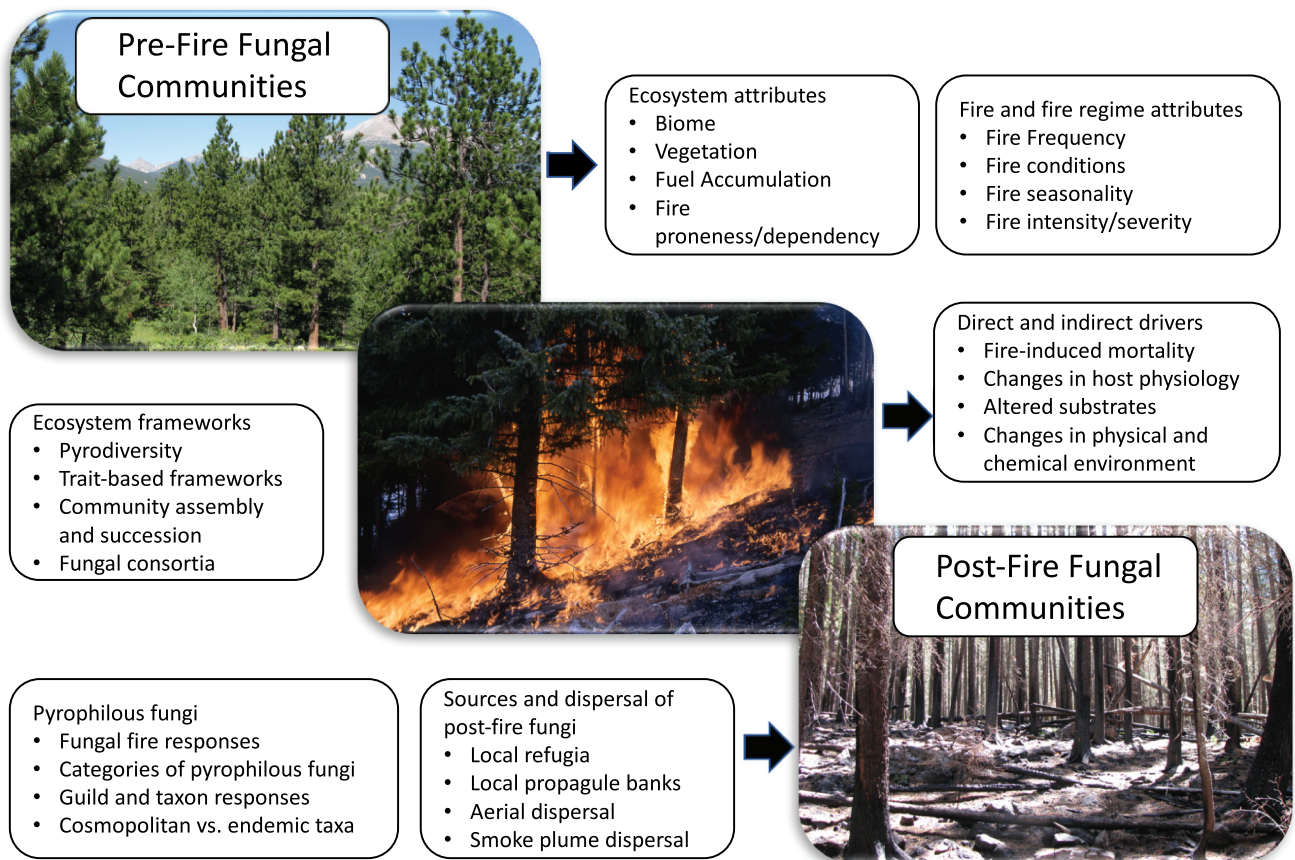


Figure 1. A conceptual model demonstrating the ecosystem and fire regime attributes that contribute to structuring the pre-fire fungal communities and to the fire behavior and its impacts on fungal community dynamics. Whereas some systems may be maintained by fires, others (e.g., temperate and boreal coniferous forests) experience fires infrequently. These ecosystem attributes are linked to fuel accumulation and fire intensity or severity, highlighting the numerous context dependencies that preclude universal general statements about fungal fire responses. This work discusses various ecological frameworks that can be applied to better understand fungal responses to fire, including trait- or consortium-based frameworks as well as those that link pyrodiversity or community assembly and succession. Only some members of the fungal communities are directly impacted by fire or fire-induced mortality. Others are impacted indirectly and may primarily respond to changes in substrates or environmental conditions, whereas others yet respond to loss hosts or changes in their physiology. Post-fire fungal communities are composed of fungi that may rely on local refugia and spore banks or newly enter aurally, perhaps even within the smoke plumes. A subset of these fungi are pyrophilous and respond positively to fire or prevailing conditions in the post-fire environment. Pre-fire and post-fire photos by Cathy Cripps. Fire photo courtesy of the Yellowstone National Park Archives.

regimes, and fungal guilds; (ii) explore existing ecological frameworks and evaluate how well they may apply to fungi and fungal communities; (iii) define fungal traits related to fire, then explore how they are reflected in key pyrophilous taxa, their distributions, and more broadly among fungal guilds; and (iv) discuss the origin of post-fire fungi—not in the evolutionary context, but rather in terms of strategies for dispersal and dormancy.

Few of our objectives are resolved definitively but rather provide insights that fall into a variety of context dependencies, many based on fire characteristics (FIG. 2). In describing different fire characteristics, we follow the existing conventions (He et al. 2019; Keeley 2009) such that we use fire intensity to describe the energy released by a fire, whereas fire/burn severity describes the consumption of organic matter to discriminate between fire intensity and

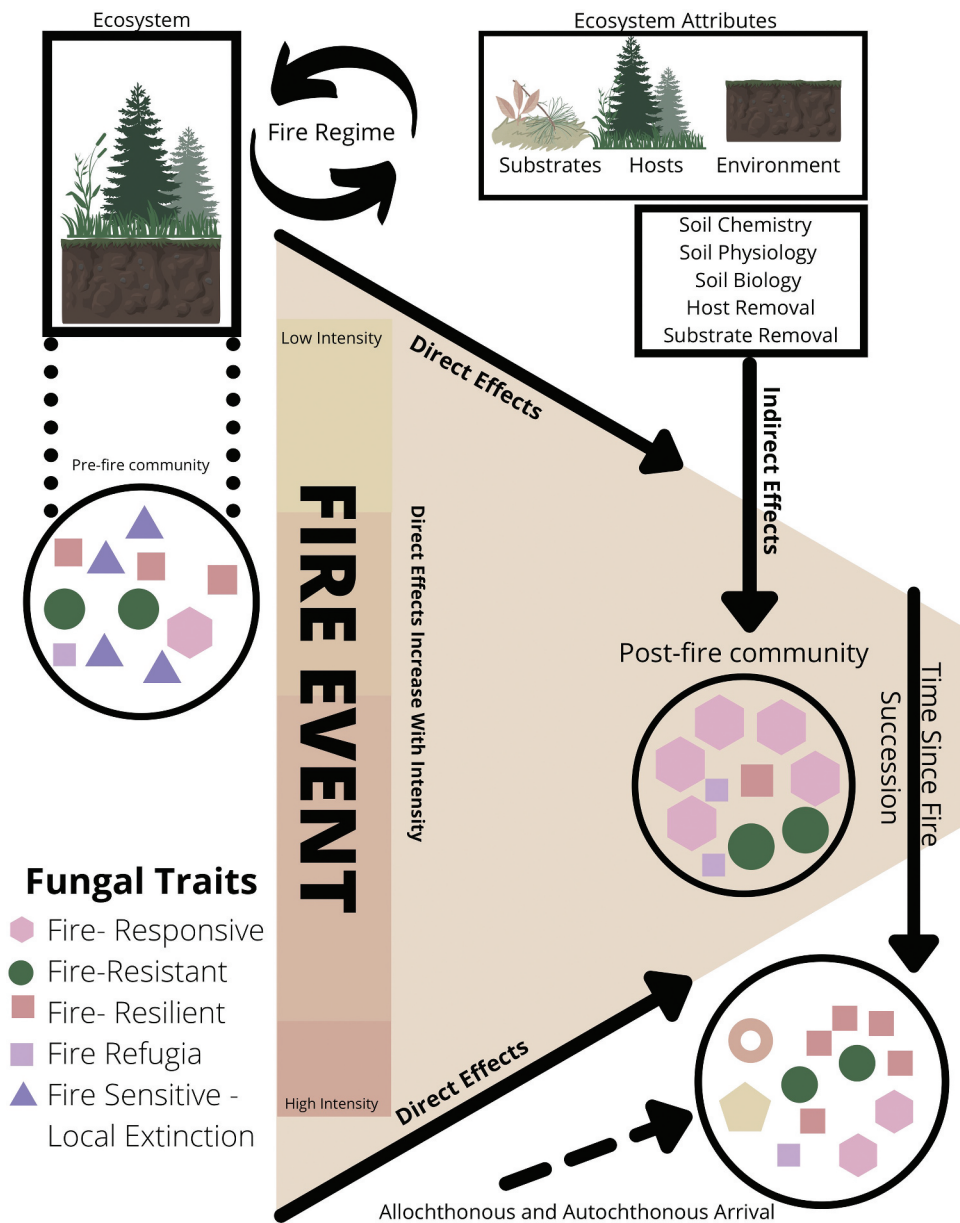


Figure 2. A conceptual model highlighting the interdependencies of system and environmental contexts and resultant variability in fungal community responses to fire. Ecosystems differ and environmental conditions vary in fire regimes and conditions. Direct fire-induced mortality as well as indirect effects, including changes in soil chemistry and structure, removal of hosts and substrates, or the altered competitive balance among the resident organisms, impact fungal communities and change their composition. Post-fire communities are a result of survival of fire-resistant fungi as well as those that are protected by refugia or those that are able to return after fire from local and distant sources. Pyrophilous fungi are often stimulated by fires and increase in abundance following a fire event. Assembly of the fungal communities in the median and long term can be considered in the contexts of successional dynamics and assembly rules or theoretical frameworks that incorporate these concepts.

burn severity—the two key “*fire regime factors*.” Not all fires are created equal, and variation in fires based on intensity are well documented (FIGS. 1–2): low-intensity fires that are common in many systems may have only minimal ecosystem effects, whereas high-intensity fires often result in substantial mortality and dramatically transform substrates. Similarly, fungal guilds experience fires differently. Biotrophic fungi (mutualists and antagonists alike) are not only affected directly by the fire but also by the responses of their host. Saprotrophic fungi and pathogens may respectively benefit from newly available, fire-generated substrates and weakened hosts that are stressed by fire. In detailing these diverse responses, this synthesis can serve as common foundation for future research, provoke debate, and ultimately stimulate a deeper understanding of fungi and their responses to fire.

DIRECT VS. INDIRECT DRIVERS

Fire characteristics (e.g., intensity, duration) and fire regime (e.g., frequency, fire return interval) vary widely and may determine the relative impact of fires on fungi (FIG. 2). We first focus on the mechanisms by which fire acts as a selective force on fungi and fungal communities. Most fires reach lethal temperatures only in the topmost soil profiles where a large portion of soil biological activity takes place (Neary et al. 1999; Smith et al. 2016). Even without direct mortality, indirect fire effects may ultimately be just as strong a selective pressure for fungi, and their importance may increase with time since fire (Hart et al. 2005), both in the short term (e.g., transient increases in availability of inorganic N and phosphorus [P]) and in the long term (e.g., loss of litter or changes in plant community composition).

Direct impacts.—Fires may kill fungi directly and can provide a strong selective pressure for fungal evolution. Some fungi can survive temperatures greater than 50 C and even up to 145 C (Kipfer et al. 2010; Seaver 1909; Suryanarayanan et al. 2011), albeit 60 C for 1 min has been commonly considered lethal for most soil organisms (Neary et al. 1999), with 100 C often discussed as an uppermost threshold (Hartford and Frandsen 1992). The food industry considers fungi heat-resistant if they can survive 75 C for 30 min (Samson et al. 2004). Clearly, simple fit-for-all thresholds require revision. A meta-analysis of biological responses to soil questioned the 60 C threshold, since thresholds severely misrepresent the great heterogeneity in soil characteristics, organismal tolerances, and the complexity of heat transfer in the substrate (Pingree and Kobziar 2019). Lethal temperatures may also depend on environmental conditions

such as soil moisture that may control heat transfer (Dunn et al. 1985). Sustained exposure to lethal temperatures is common in both wildfires and prescribed fires in forests, but less so in grasslands (Archibald et al. 2013). The maximum temperatures that fungi experience are moderated by fungal habitats, fuel accumulation, soil type, soil water content, and soil depth, as steep thermal gradients occur from the surface downward (Bruns et al. 2020; Kipfer et al. 2010). Lethal temperatures most likely occur in burning litter, as indicated by clear declines of saprotrophic fungi after fire (Pulido-Chavez et al. 2021, 2021; Semenova-Nelsen et al. 2019). In contrast, mineral soils are often better insulated from heat transfer, particularly deeper in the soil profile (Massman 2012; Smith et al. 2016), with smaller post-fire fungal community shifts in mineral than organic horizons (Hopkins et al. 2021; Semenova-Nelsen et al. 2019). Similarly, downed wood and surviving plant tissues (e.g., leaves, roots) can provide insulation that protects substrate- or tissue-inhabiting fungi from heat-induced mortality, exemplifying a “fire refugium” (see Meddens et al. 2018). In addition, some post-fire “blooms” of fungi may be due to the loss of substrate or host plants, which triggers a fruiting response (Fujimura et al. 2005; Hughes et al. 2020b; Kuo et al. 2014). Finally, repeated exposure to fires can also dictate fungal responses. For example, wood-inhabiting fungi in fire-prone habitats in the boreal systems experience half the mortality compared with fungi in similar systems that rarely burn (Carlsson et al. 2012), potentially as a result of less fuel accumulation and therefore lower burn severities. Frequent fires may also drive fungal adaptations, including heat-resistant spores and sclerotia, and even fire-induced germination and growth (see “Fire-specific fungal traits and pyrophilous fungi” below).

Fire consumption of plants and debris represent direct losses of fungal habitats and available substrates (Bowman et al. 2009). Plant mortality often results in the death of plant-associated fungi, including mycorrhizal fungi (Dove and Hart 2017), even if fungi themselves are insulated from heating. For example, mycorrhizal fungi on roots may die if host trees are killed in wildfires and new compatible hosts are unavailable. Many obligate mycorrhizal fungi will not persist in the absence of a host (Collier and Bidartondo 2009) unless they produce resistant propagules that can persist in the spore bank (Glassman et al. 2015). Fire has played a key role in plant diversification, and plant fire adaptations likely provide novel morphological structures (Keeley et al. 2011) that may host (and protect) specialized fungi. Decomposer fungi in wood, plant litter, and other substrates may similarly be lost when fire consumes them, although heat-generated convection winds

may also serve as an important dispersal mechanism (Camacho et al. 2018; Mims and Mims 2004) and as a potential means to escape fire-induced mortality. For fungi dependent upon plant hosts and substrates lost in severe fires, recolonization may not be possible until these niches recover (Hart et al. 2005). If fungi are not completely consumed by fire, environmental shifts can also drive important changes to fungal physiology, growth, and community composition.

Indirect impacts.—Fire can modify soil physical properties in a variety of ways that may impact fungi (Certini 2005; Neary et al. 1999). For example, fires can affect hydrology through decreased soil water retention, increased surface runoff, and increased sediment loading to surface water (DeBano 2000). Moderate- to high-severity fires often increase soil hydrophobicity that indirectly impacts soil fungal communities (Seaton et al. 2019) by creating a discrete and water-repellent front parallel to the surface that can decrease soil permeability for up to 2 years (Imeson et al. 1992). Fire can also modify soil color, which may influence fungi through impacts on albedo. For example, soil charring by a severe fire can blacken a layer 1–15 cm thick (Ulery and Graham 1993). By removing vegetation, fires also reduce light interception and change albedo, and combined, these effects can increase soil temperatures and alter evapotranspiration in ways that indirectly influence fungal communities (Hart et al. 2005).

Fire can also impact fungi indirectly by modifying soil chemistry and nutrient availability. Fire tends to increase soil pH, as organic acids denature during heating (Certini 2005). Increased soil pH affects the bioavailability of most cations and can also strongly modify fungal communities (Glassman et al. 2017b). Depending on severity, fires can cause immediate losses in N and C through combustion but often produce flushes of bioavailable N and P (Neary et al. 1999). A meta-analysis of 185 data sets from 87 studies between 1995 and 1999 found that fire increased soil ammonium (NH_4^+) by 94% and nitrate (NO_3^-) by 152% (Wan et al. 2001). Increase in N availability could significantly alter the compositions of both mycorrhizal and saprotrophic fungi (Cox et al. 2010; Morrison et al. 2016; Tahovská et al. 2020). Fires often result in a short-term enrichment of available P (Serrasolsas and Khanna 1995) because burning drives conversion of soil organic P to orthophosphate (Cade-Menun et al. 2000). Increased P bioavailability will likely influence fungi, particularly arbuscular mycorrhizal (AM) fungi, that are important in mobilizing P for their plant hosts

(Whiteside et al. 2019) but whose colonization declines when more P is available (Treseder 2004). Apart from fungi alone, these fire-induced stoichiometric shifts may also alter fungal symbiotic functions (Mouginot et al. 2014) and their competitive interactions with saprotrophic fungi (Frey 2019).

Fire impacts on total C and N storage are less clear than impacts on nutrient availability and differ within the soil profile: litter and the topmost horizons are most impacted, whereas deeper mineral soils are insulated. One meta-analysis concluded that forest fires across a variety of ecosystems increased mineral soil C and N (Johnson and Curtis 2001), a response attributed to C sequestration of charcoal and post-fire colonization by N fixing vegetation. Another that focused exclusively on temperate forests, however, concluded that fires reduced soil C and N (Nave et al. 2011). These losses were largely from the organic layer, whereas mineral soil organic C was unchanged. Changes to these key components can alter stoichiometry that dictates fungal physiology, growth, and community composition. Fires can also indirectly affect fungal community composition by transforming wood and leaf litter to pyrogenic organic matter (PyOM; Knicker 2011), which may serve as a food source for particular fungi (José et al. 2018; Kymäläinen et al. 2015) or increase C storage due to its recalcitrance (Santín et al. 2015).

Finally, fires can indirectly impact fungal communities by modifying fungal food web connections and fungal habitat availability. Fires often reduce microbial biomass (Dooley and Treseder 2012), but fire-generated necromass may provide nutritional opportunities for surviving fungi (Bruns et al. 2020). Fires affect the biomass and composition of soil-dwelling invertebrates (Certini et al. 2021; Pressler et al. 2019), which may have cascading impacts on fungal communities (Lavelle et al. 1997). Broader microbial mortality from fire, including bacteria and protists, may reduce competition for surviving fungi (El-Abyad and Webster 1968a; Zak and Wicklow 1980) or represent a loss of a key members of important ecological guilds such as ectomycorrhizal symbionts (Yang et al. 2020) or saprotrophs (Semenova-Nelsen et al. 2019). Like extinctions on small islands, wildfires may also drive fungal extirpations in isolated reserves if large, high-severity fires disrupt or remove propagule sources that sustain their populations (Glassman et al. 2017a; Peay et al. 2007). For fungi restricted to fire-frequented ecosystems, however, their persistence may depend on maintaining frequent, low-severity fires, as it does for many endemic plants and animals.

ECOLOGICAL FRAMEWORKS APPLICABLE TO FUNGAL FIRE ECOLOGY

Our central goal is to help define a general ecological framework for fire fungi, and many existing frameworks may be usefully adapted. Most are derived from studies focusing on plants and have been vetted by field and empirical research over several decades. A unified conceptual framework has been recently proposed to predict and characterize temporal dynamics of microbiomes specifically (Stegen et al. 2018). Although this broad, unified framework that considers abiotic and biotic history, internal dynamics, and external forcing factors may ultimately be useful, we choose to focus on established frameworks that either are specific to fire ecology or have been widely adopted to characterize community dynamics. We explore three ecological frameworks that may provide useful comparisons: (i) fire-derived heterogeneity (i.e., pyrodiversity) as a driver of fungal biodiversity; (ii) trait-based frameworks that may predict fungal community responses to fire; and (iii) community assembly/succession frameworks that recognize fire impacts on fungal communities and their dynamics.

Fire as a driver of pyrodiversity/biodiversity.—Fire-derived heterogeneity, collectively called pyrodiversity (He et al. 2019; Martin and Sapsis 1991), facilitates niche diversity in time and space to organisms including fungi. Both plant and animal biodiversity often increase with pyrodiversity (Jones and Tingley 2021), which is driven by a variation in fire characteristics including fire type, intensity, pattern, seasonality, and fire history (He et al. 2019). For example, differences in fire severity across the landscape may help maintain a wide range of organismal traits, including those tightly linked to fire (e.g., fruiting in response to fire or extirpation with severe fire) and those only weakly impacted by fire. Further, some organisms may be only minimally affected by fire as a result of “fire refugia” (Meddens et al. 2018), protected by landscape attributes (e.g., topography) and substrate/habitat (plant tissues or position in the soil profile). Niches created by this fire variation across space and time likely increase landscape-level fungal richness, even if fire itself reduces richness within small landscape patches.

Pyrodiversity interacts with abiotic and biotic factors, including topography, moisture, and vegetation, that also shape fungal niche space, resulting in heterogeneous landscape mosaics (Hiers et al. 2009). Because these parameters interact before, during, and after a fire event, disentangling pyrodiversity and fungal diversity is difficult. Fungal diversity clearly changes in response to fire (Dove and Hart 2017; Holden et al.

2013), and these changes are not uniform across the landscape mosaic that fire creates (Agee 1998; Kong et al. 2019). A study of fire impacts in Oregon ponderosa pine forests found that fungal communities were distinct among plots that experienced different fire severities within the landscape (Reazin et al. 2016). In addition, dominance within the fungal community changes through time as burned areas recover and produce heterogeneous belowground mosaics of abiotic and biotic conditions (Huffman and Madritch 2018) or as plant communities transition through distinct post-fire successional trajectories (Hart et al. 2005; Huang et al. 2016). As with plants and other sessile organisms (He et al. 2019), it is likely that the diverse landscape mosaics created by fire provide distinct habitats (in time and space) where fungi with different and unique trait combinations can survive.

Evidence that fire-created mosaics increase heterogeneity for fungal communities varies among systems, fire attributes, and the scale of observation. Fire characteristics, and fire severity in particular, have been key in addressing the diversifying or homogenizing effects of fire on biodiversity. High-severity fires have long been considered a homogenizing force in ecosystems (Allen and Holling 2008; Holling et al. 1996; Turner et al. 1994), particularly for plants. Such individual fires are often stand-replacing, resulting in substantial plant mortality and ecosystem homogenization (“resetting the successional clock”), knocking vast areas back to a uniform successional stage (Baskin 1999), and promoting plant communities dominated by few ruderal species (Burkle et al. 2015). However, the ecosystem and scale of analyses impact the conclusions drawn about spatial variation in fire effects. Fires may homogenize the landscape, particularly at small spatial scales, killing aboveground vegetation and producing even-aged patches (Allen and Holling 2008; Velle et al. 2014). Following the 1988 Yellowstone National Park fire, however, different burn intensities “reset” the dominant pre-fire vegetation and landscape units to different successional stages, such that post-fire landscape was as patchy and as variable as the pre-fire landscape (Baskin 1999). Wildfire effects on both vegetation and fungi likely depend on pre-fire heterogeneity itself, with more homogenous systems such as the Yellowstone lodgepole pine (*Pinus contorta*) system showing less homogenization from fire. In contrast, frequent low-severity fires are essential to maintaining ecosystem attributes and plant diversity in many grassland and savanna ecosystems. Fire characteristic impacts on fungal community heterogeneity and diversity, however, remain less clear.

The few studies that can directly assess fungal community heterogeneity following fires suggest that fire regimes and ecosystem differences are important. Large fuel quantities and subsequent severe fires lead to decline in fungal richness but also to communities distinct from surrounding areas with less severe burns (Reazin et al. 2016), therefore adding to fungal community variation across the landscape. It is still uncertain how long communities responding to severe fires remain distinct and whether they represent unique successional trajectories, although chronosequence studies suggest that the fire-generated landscape units likely persist for years and perhaps even decades (Holden et al. 2013; Pérez-Valera et al. 2018; Sun et al. 2015). In other cases, fire severity differences in fungal communities may arise over time, even when initially absent following fires of different severity (Rincon and Pueyo 2010). Apart from fire severity, lower fungal richness in experimental tallgrass prairie units that burned more frequently (Carson et al. 2019) would suggest fungal sensitivity to repeated burning (e.g., Dooley and Treseder 2012; Pressler et al. 2019) and thus less pyrodiversity on a landscape level. In contrast, prescribed burning in both pine savanna (medium severity) and tallgrass prairie (low severity) changed soil fungal communities as well, but plots were no more or less similar to one another when burned than when not burned that year (Hopkins et al. 2021). Frequent prescribed fires in these systems (i.e., every 1–3 years) may maintain heterogeneity. As with other ecosystem components (Kowal et al. 2014; Ligon et al. 1986; Steen et al. 2013a, 2013b), varying fire intervals may affect fungal communities (Oliver et al. 2015) and help maintain landscape-level heterogeneity and high fungal beta-diversity (Carson et al. 2019). In some systems and scales, fires can maintain ecosystem heterogeneity, and that of fungal communities, but more data are clearly needed.

In addition to landscape-scale heterogeneity, soil is inherently heterogeneous (Cardinale et al. 2000). Fires may promote fungal community heterogeneity across the soil profile as a result of the rapid heat attenuation with depth. Fire-generated heat pulses are greatest near the surface, and the heat pulses gradually decline with soil depth (Campbell et al. 1994; Massman 2012). Importantly, heat penetration also depends on soil water content (dry soils conduct heat poorly compared with wet soils) and on the depth and combustibility of the organic layer (Kreye et al. 2016; Reardon et al. 2007; Valette et al. 1994). While severe fires likely eliminate much of the soil biota—including fungi—from the upper few centimeters of soil (Semenova-Nelsen et al. 2019), dormant organisms residing in deeper soil strata

can be stimulated by moderate heat (Massman 2012)—the so-called “goldilocks zone,” wherein the fire temperature/duration is within “optimal range” for stimulation (Bruns et al. 2020; Kipfer et al. 2010). Fungal community shifts following prescribed fires were much greater in litter compared with the soil layer just below (to 2 cm) in sandy, pine savanna soils (Semenova-Nelsen et al. 2019). Following wildfires in mixed forests of the Great Khingan Mountains in Mongolia, ectomycorrhizal fungi declined in richness (<40%) in the organic soil horizon but not in the deeper mineral layers, whereas saprotrophic fungi had no depth-dependent fire responses (Yang et al. 2020). More work is clearly needed to generalize these patterns, which likely reflect both direct and indirect fire effects.

Fire impacts on soil properties, and plants may also indirectly drive diverse fungal responses to fire across the soil profile. High temperatures can combust large proportions of the lignocellulosic biomass near the surface, transforming some into partially burned PyOM (Keiluweit et al. 2010). Substrate removal and transformation are not homogeneous, and the governing factors vary even at small, local scales (Kreye et al. 2016). Fuel accumulation, landscape and ecosystem attributes, as well as fire history and characteristics likely dictate the generation of heterogeneous mosaics of unburned and pyrogenic substrates across the soil profile. Fire generates and deposits alkaline ash that modifies pH, particularly in the surface soils (Certini 2005). At the landscape scale, increased pH seems to interact with fire severity to determine fungal community responses to boreal wildfires (Day et al. 2019; Whitman et al. 2019), but differential pH impacts on fungi across the soil profile remain unexplored. Other fire-responsive soil attributes (soil inorganic N, soil organic matter) tend to shift most at the soil surface, with effects declining with depth. Plant rooting strategies are also diverse and create heterogeneous niches throughout the soil profile. Fire-caused plant mortality may remove specific habitats for plant-associated fungi, resulting in replacement by saprotrophic fungi. For example, tree mortality following a boreal wildfire had a greater impact on fungal communities than the surface fire severity (Pérez-Izquierdo et al. 2021). In many fire-frequented systems, plants have key belowground adaptations to fire that may create additional habitat heterogeneity for fungi across the soil profile. To our knowledge, little research has addressed whether fungi can specialize on fire-adapted belowground plant organs. More explicit belowground research that parse fire effects on soil layers, plant tissues, and fungal niches may help better explain resultant fungal biodiversity and their responses after fire.

Trait-based frameworks for fungal fire responses.—In many fire-frequented ecosystems, animals (see Smith and Lyon 2000) and plants (see Brown et al. 2000) possess a diversity of adapted fire traits that may be paralleled in fungi. Arthropods and nematodes share many of the same environments (and scale) with fungi. These organisms generally exhibit fire intensity- and burn severity-dependent mortality, including biodiversity shifts resulting from these and other fire regime factors (Certini et al. 2021). Although still poorly understood, some of these organisms are fire-responsive (Certini et al. 2021) and many of their responses are driven by fire-related changes in substrates also used by fungi. However, because many animals can move to escape the worst fire effects, we may expect that plant adaptations are most relevant to fungal fire adaptations. Plant fire adaptations include resprouting from epicormic buds, fire-induced seed release (i.e., serotiny), heat-triggered germination, and fire-resistant structures such as thick bark (Keeley et al. 2011). These adaptations generally focus either on surviving fire or on releasing offspring that can take advantage of the post-fire environment. Thermotolerant fungi (Fergus 1964; Redman et al. 1999; Rippon et al. 1980; Suryanarayanan et al. 2011) parallel fire-resistant plants and include fire-adapted plant-fungal associations (Baynes et al. 2011). Ecosystems defined by fire-adapted plants also appear to host fire-resistant fungi, likely representing parallel evolution (Pérez-Izquierdo et al. 2020; Smith et al. 2021). Thermotolerant fungi can also produce heat-resistant compounds (Sharkey et al. 2001; Singsaas 2000), including laccases (Hildén et al. 2007) and trehalose (Tereshina 2005). Further, some species, such as those in the genera *Anthracobia* and *Pyronema* (Pyronemataceae), fruit frequently and in great abundance after fires (Petersen 1970; Seaver 1909). Although less well described mechanistically than plant reproductive adaptations to fire, this suggests that fire-induced reproduction is likely an important fire strategy for fungi.

Grime's trait-based model, originally developed for animals and later applied to plants, considered disturbance, stress, and competition the main drivers of life history evolution (Grime 1977, 2002) and ultimately succession. In this model, disturbance-responsive organisms are r-selected strategists (ruderal taxa) that rapidly access nutrients, quickly colonize and reproduce, are noncombative, and therefore ephemeral on the disturbed landscape. Stress-tolerant or s-selected strategists colonize more slowly but persist under conditions most other organisms cannot tolerate; they too possibly occur soon after disturbance. As succession proceeds, combative or c-strategists with superior competitive abilities defend their territory and dominate in the crowded

niche space when resources are scarce. Grime (1988) identified CSR parallels between plants and fungi, and adaptations of the model have been successfully applied to mycorrhizal fungal communities (Chagnon et al. 2013) and carbon traits of microbes (including fungi; Malik et al. 2020). The CSR framework has been adapted in an attempt to generalize fungal responses to disturbance (Pugh and Boddy 1988) and to fire specifically (Enright et al. 2021; Whitman et al. 2019). Pyrophilous fungi may follow CSR, combining the attributes of taxa that thrive in the post-fire environment because of traits that either permit survival through the fire (e.g., heat-resistant/tolerant spores), facilitate rapid growth (e.g., rRNA gene copy numbers), or allow utilization of the post-fire substrates (e.g., metabolic pathways that permit aromatic C degradation) (Enright et al. 2021; Whitman et al. 2019). These and other contemporary trait-based approaches seek to avoid density dependence and acknowledge complex and diverse life cycles (Andrews 1992; Crowther et al. 2014; Reznick et al. 2002). Fungi have unique life histories and developmental phases that can differ in function and dispersal, so the whole organism (throughout its entire life) may not fit a single trait category (i.e., CSR; Zanne et al. 2020). Still, r-selected *traits* or r-selected *life phases* may yet prove useful for describing fungi that respond to fire and establish expediently in post-fire environments and systems, whereas s-selected *traits* or s-selected *life phases* may be more applicable to organisms that persist in the post-fire environments. It is also of note that no single characteristic or trait may apply generally to dynamic communities that occupy post-fire environments. Early bacterial communities establishing soon after a fire in pine forests were dominated by spore-forming, easily dispersing taxa, whereas later post-fire communities were dominated by oligotrophs in an environment characterized by sparsely available soil organic matter (Ferrenberg et al. 2013). Moreover, some empirical evidence supports fire facilitation of opportunistic, fast-growing, and readily dispersed ruderal, r-selected fungi, which are slowly replaced by competitive, slower-growing, k-selected specialists (Peay et al. 2009; Reznick et al. 2002).

Fungal adaptations to fire may be more akin to general adaptations to disturbance (Griffiths and Philippot 2013; Shade et al. 2012). Although lacking a synthetic review, fungi respond to many different disturbances, including earthquakes (Lin et al. 2019), lava (Nara et al. 2003), glacial movement (Dresch et al. 2019; Jumpponen et al. 2002), mining (Crognale et al. 2017; Zak 1992), air pollution (Arnolds 1991), and agriculture (Miller and Lodge 2007). Rapid growth is advantageous after these disturbances and is a strategy shared by many

pyrophilous fungi. For example, species in the Pyronemataceae genera *Pyronema* and *Anthracobia* have been documented to quickly overgrow burned areas (Claridge et al. 2009). Growth is a measure of species performance in a particular environment but is difficult to standardize for comparisons (Bárcenas-Moreno and Bååth 2009) and could eventually be tied to metabolic activity (Zanne et al. 2020). Pyrophilous fungi may also allocate resources to escape post-fire environments through reproduction or transitioning to other life history phases. For example, homothallic *Pyronema* spp. can produce ascocarps within a week in the laboratory (Traeger et al. 2013) and rapidly after natural (Seaver 1909) or experimental (Bruns et al. 2020) fires. Some pyrophilous fungi rapidly produce and disperse asexual mitospores (El-Abyad and Webster 1968b) while fruiting bodies can produce large numbers of meiospores, both of which may accumulate over time into spore banks in fire-prone areas (Warcup and Baker 1963). Thus far, such spore banks following fire have been documented for mycorrhizal fungi (Glassman et al. 2016) but may not be present for other (e.g., saprotrophic) fungi. We posit that an effective fire adaptation is for spores to lie dormant until cued by fire, whether by heat, smoke, chemicals, reduced toxins, released compounds, or pH change (Wicklow 1988). The trade-off is that without fire or a comparable trigger, the dormant propagules remain inactive and these fungi could risk local extinction. Many fungi that respond to fire may be a subset of a broader disturbance-adapted fungal group; therefore, models that focus on disturbance may be useful for understanding fungal fire traits and post-fire community changes.

Community assembly/succession frameworks.—

Community assembly models (Cole 1983; Diamond 1975; Hunt 1991) have also been adopted for fungal communities (Jumpponen and Egerton-Warburton 2005) and may be useful in predicting fungal community responses to fire, similar to their use for bacterial post-fire dynamics (Ferrenberg et al. 2013). Assembly rules outline the constraints—or series of filters—that select community members from local or regional species pools (Weiher and Keddy 2001) and identify ecological processes that lead to assembled communities (Drake et al. 1993). These “filter models” incorporate organismal dispersal and/or residence and constraints of organismal establishment and persistence in the communities (Keddy 1992). Fire may be a key “filter” with fungal dispersal, establishment, and persistence traits determining post-fire community assembly. The application of community assembly to fungi has already

helped explain community patterns in fungal wood decomposers (Fukami et al. 2010) and AM fungi (Maherali and Klironomos 2012). In addition, priority effects, where early arrival of some taxa alters the success of later arriving taxa, occur in nectar yeasts inhabiting insect-pollinated flowers (Peay et al. 2012) and fungal endophytes following disturbance (Sikes et al. 2016). Trait-based assembly models may be useful in determining post-fire fungal communities, as fire-associated mortality (severity dependent) reduces fungal competition in ways that also shape post-fire community assembly. Further, abiotic and plant host changes from fire also may be important filters for the post-fire fungal assembly (Hart et al. 2005), and most of this research has focused on fungal community succession.

Succession describes the process of community assembly, and post-fire fungal succession has been considered extensively. Following a fire, fungal communities respond rapidly within days or few weeks (Reazin et al. 2016), albeit the post-fire communities may remain distinct from those present before fire for years or decades (Dooley and Treseder 2012; Pulido-Chavez et al. 2021). Fire alters fungal successional dynamics (e.g., Lombao et al. 2020; Pressler et al. 2019; Smith and Wan 2019) that may be related to a number of factors, including (i) population mortality and differential community recovery driven by dispersal, colonization probabilities, and priority effects; (ii) shifting edaphic conditions that facilitate emergent niche partitioning in surviving fungi; (iii) differential utilization of pyrogenic substrates (e.g., biochar or fire-generated necromass); or (iv) perhaps, collections of taxa that act in concert as interacting fire-resilient subcommunities (i.e., consortia; Paerl and Pinckney 1996). All of these may be operating simultaneously, and it seems certain that their relative importance to post-fire fungal succession differs based on fire regime, ecosystem, and a range of related environmental factors. However, successional models may be useful in generalizing the combined effect of these factors on fungal community changes after fire.

It is tempting to view post-fire community shifts as deterministic (e.g., Clements 1916; Petersen 1970) within the context of a temporal system recovery, but the relative importance of different community assembly processes (e.g., neutral and niche- or filter-based processes) may shift with time since a fire (Ferrenberg et al. 2013). Early assembly of post-fire fungal communities may also strongly influence subsequent trajectories, potentially paralleling “initial floristics” succession models for plants (Drury and Nisbet 1973). For example, when fungal communities differed in the absence of fire, fires did not create similar pyrophilous fungal communities on distinct and isolated landscape units (sky islands), despite having similar

climate, soils, and hosts (Bowman et al. 2021). Evidence for fungal priority effects following fire, to our knowledge, however, has not been specifically experimentally explored. Distinct fire traits (e.g., heat-stimulated spores or heat-resistant [pseudosclerotia]) and “refugia” habitats (Meddens et al. 2018) almost certainly provide nonrandom “initial” taxa for post-fire fungal communities. Together, these provide additional functional, temporal, and spatial complexity to the successional dynamics that result in distinct potential post-fire successional trajectories.

Most commonly, fungal succession following wildfires in infrequently burned systems is treated simply as community “recovery,” interlocked with other ecosystem properties. The regrowth of vegetation and rebuilding of substrates can limit the pace of fungal succession (Duhamel et al. 2019; Hart et al. 2005) and drive contrasts between systems where these processes occur slowly (e.g., forested, colder biomes) and those where vegetation can recover rapidly (e.g., temperate grasslands) after fires. With vegetation regrowth come organic legacies, such as the accumulation of litter and organic matter on which saprotrophic fungi rely and which promotes mycorrhizal acquisition of nutrients (Alem et al. 2020; Sun et al. 2015). In contrast, many have pointed out that mycorrhizal fungi often facilitate post-disturbance vegetation recovery (e.g., Cazares et al. 2005; Read 1989). A key factor still to unravel is how feedbacks between fungi, plant communities, and soil nutrients operate to govern fungal succession after fire. Fire-frequented systems may provide important experimental systems in which fire itself can be manipulated but may prove conservative models because recurrent fires represent a strong selective force. In these systems, nutrients are often scarce and fire is not a disturbance but a necessity for ecosystem stability. Vegetation and fungi are often fire-resistant, fire-resilient, both, or even depend on fire for reproduction and completion of their life cycles (see “Categories of pyrophilous fungi” below). Two key areas for future research are to target the temporal dynamics of fungal communities at short time scales immediately after fire as well as time series that incorporate fire regime, pre-fire conditions, short-term fungal dynamics, and successional dynamics that occur over longer time frames.

Consortium-based framework.—Some fungi clearly thrive in fire-impacted systems, yet it remains poorly understood whether fire-responsive consortia that include fungi exist. Consortia are collections of taxa that coincide temporally, coexist spatially, and interact functionally (Koenig et al. 2011). These consortia represent organismal subcommunities within a larger community but include only members that respond interdependently

and synergistically. If such fire-responsive consortia existed, they may be adapted to respond to fire through cooperation and/or nutritional interdependencies (i.e., syntrophisms). Evidence and examples of syntrophism include communities wherein members directly or indirectly facilitate access to resources otherwise unavailable to some consortium members (Zhang et al. 2018; Wei et al. 2019). For example, post-fire communities may include fungal specialists capable of using the biochar or other pyrogenic substrates (Anderson et al. 2011; Warnock et al. 2007) that thereby facilitate other consortia members unable to use these resources directly. A challenge is to disentangle whether whole communities are driven by defined processes following fire or whether observed responses are merely the sum of individual responses. Despite the potential value of incorporating consortium frameworks in ecology, this is not routinely done (but see Tian et al. 2014; Weber et al. 2006). Where groups of fire fungi are considered together, analyses and inference generally rely on phylogenetic frameworks (e.g., shifts in abundances of fungal genera or families in response to fire) (Enright et al. 2021) or functional categories (e.g., saprobes, symbiotrophs) (Brown et al. 2019; Semenova-Nelsen et al. 2019). Although such analyses are important for better understanding fungal fire responses, they do not account for consortia, whose members likely represent different lineages, functional groups, or even kingdoms. As a result, these approaches likely overlook syntrophic or other interdependent associations. Ecologically relevant, engineered consortia can facilitate detailed mechanistic understanding of community dynamics and function (Erbilgin et al. 2017; Zhang et al. 2018), and pure-cultured community members from fire-affected ecosystems may afford a detailed understanding that can inform system-wide processes and post-fire dynamics.

Many questions remain on fungal fire ecology, and rigorous consideration of existing models for other organisms and their fire responses seems fruitful. Assessing whether these models—be they pyrodiversity, trait-based, or focused on assembly processes—are appropriate for fungi in multiple ecosystems is critical in trying to generalize fungal fire responses and dynamics. Fungi are unique, diverse, and interconnected with other organisms and substrates, making this task complicated. Identifying general fire-adapted traits in fungi is fundamentally complicated by the many simultaneous abiotic and biotic post-fire changes as well as the diversity of fungal lifestyles, life stages, and dormancy. For plant-associated fungi, decoupling the fungal responses to altered host physiology and to the direct effects of fire is a challenge that will likely require ingenious experimental arrangements or laboratory studies that allow us to determine their changing relative

importance across hosts, fire gradients, and soils. Models that explicitly consider multidimensional fungal traits seem the most likely to advance generalizable frameworks to understand fungal fire adaptations, life history, community structure, and ultimately function. Finally, simplified manipulative pyrocosm systems that have recently been developed (Bruns et al. 2020) may permit detailed investigations of fungal communities—or consortia if such exist—and their responses to fire. Renewed experimentation with individual fungi and fungal consortia in laboratory and mesocosms can provide key data to better generalize fungal responses to fire.

FIRE-SPECIFIC FUNGAL TRAITS AND PYROPHILOUS FUNGI

Organisms respond to fires in many ways. Although nearly exclusive to burned areas, some fire-responsive species may also fruit in unburned habitats but flush in large numbers after a fire. However, it is often unclear what are the traits that define fire-resistant, fire-tolerant, fire-responsive, or fire-adapted fungi—or how these broad categorizations differ. We approach these questions through carefully selected examples and consider whether lifestyles that include dormant propagules that may persist through fires should be incorporated. Much of what we currently know about fungi and their fire adaptations or fire-related traits comes from records of fungal fruiting or, more recently, from molecular analyses of substrates exposed to fire. As a result, the fire-related traits are usually indirectly inferred from such data and direct observations of morphological and/or physiological adaptations are few.

Fungal adaptations to fire cannot be examined without explicit consideration of maximum temperatures and duration of heating in the substrate—soil or living plant tissues and litter—or organismal differences in their heat tolerance. A recent meta-analysis of biological responses to soil heating suggests use of duration-temperature models to explore fungal inactivation to better represent the selective pressure such that the cumulative and additive effects of substrate heating could better identify fire-adapted taxa (Pingree and Kobziar 2019). Regardless of how organismal heat tolerances are described, the pyrophilous fungi that we discuss below can survive or even thrive in the post-fire conditions, even though fire duration, intensity, or severity are rarely measured in their immediate surroundings or substrates.

Defining fungal responses to fire.—A number of terms (phoenicoid, pyrophilous, anthracophilous, carbonicolous, fireplace fungi, post-fire fungi) have been applied to those

specialized fungi that appear after wildfires, in autoclaved soils, or on volcanic ash (Carpenter and Trappe 1985; Carpenter et al. 1987; Dix and Webster 1995; Fujimura et al. 2005; Petersen 1970). For most of these fungi, the life history traits that allow long-term survival in the absence of fire but trigger the sudden initiation of post-fire growth or reproduction remain elusive. However, a prerequisite is that pyrophilous fungal mycelia and/or propagules must either be resistant to heat, have propagules in the “goldilocks zone,” (Bruns et al. 2020), or rapidly invade burned soils from an external source (Kobziar et al. 2018). Many pyrophilous species that fruit and proliferate rapidly after a fire are in the ascomycete order Pezizales (*Anthracobia*, *Geopyxis carbonaria*, *Morchella*, *Peziza*, *Pyronema*, *Scutellinia*, *Sphaerospora*, *Tricharina*; Fujimura et al. 2005; Hughes et al. 2020b, 2020a; FIG. 3), although some pyrophilous basidiomycetes exist (e.g., *Pholiota carbonicola* = *Pholiota highlandensis*, *Lyophyllum atratum*; Matheny et al. 2018; Steindorff et al. 2021). In some cases, the fungal lifestyle may shift from mycorrhizal to saprotrophic following fire (Greene et al. 2010) and often from basidiomycete- to ascomycete-dominated communities (Cairney and Bastias 2007). Fire-derived changes to substrates, including pH, nutrient availability, or competitor mortality, can stimulate fungal species that respond positively across post-fire landscapes for days, weeks, and months. The traits that associate with these responses are inferred for fungi on burns, but empirical data remain limited to a few traits for a few taxa.

Categories of pyrophilous fungi.—Building from previous efforts (Moser 1949; Raudabaugh et al. 2020), we aim to categorize pyrophilous fungi. Here, we categorize pyrophilous fungi as fire-resistant, fire-responsive, and fire-adapted—fully acknowledging that these classifications overlap, that some taxa may belong in more than one category, and that the traits we use to define these categories may apply to more than one category.

Fire-resistant

We define fire-resistant fungi as those that are heat-resistant for some aspect of their life cycle. However, fire resistance may also occur as a consequence of buried propagules that are insulated from excessive heat by substrates. For example, buried sclerotia of some *Morchella* spp. (FIG. 3B) can survive wildfires (Baynes et al. 2011; Greene et al. 2010), and some fungi likely have persistent, heat-resistant spores, for example, *Rhizopogon olivaceotinctus* (FIG. 3K; Baar et al. 1999; Glassman et al. 2016; Bruns et al. 2019), *Ascobolus carbonarius*, and *Trichophaea abundans* (conidia and ascospores; Msh and Webster 1968b). Others may survive as mycelia in mycorrhizae or soil, as exemplified by

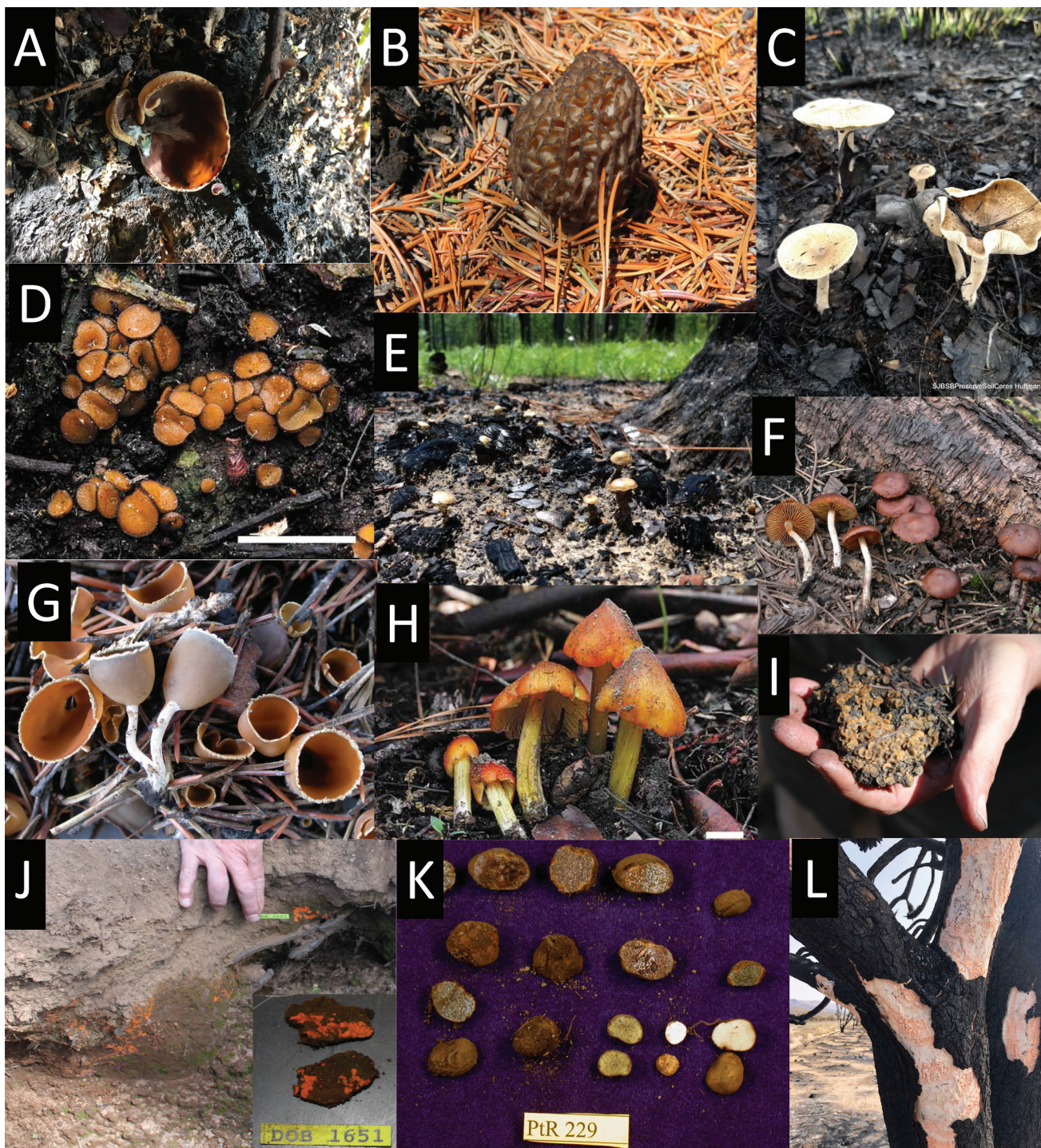


Figure 3. Examples of ascomota and basidiomata commonly found after fire, including prescribed burns and wildfires in the eastern and western United States. A. *Peziza echinospora* following 2016 wildfire in Great Smoky Mountains National Park; photo by K. Hughes. B. *Morchella* cf. *septimelata* (CLC3670(MONT)) following 2017 Meyers Fire, Montana; photo by C. Cripps. C. Flush of undescribed *Clitocybe* spp. following 2018 prescribed fire at St. Joseph Bay State Buffer Preserve, Florida; photo by J. Huffman. D. *Anthracobia* cf. *melaloma* (TENN-F-071502) following 2016 wildfire at Great Smoky Mountains National Park; photo by B. Matheny. E. *Pholiota carbonaria* following 2017 prescribed fire at Wade Tract near Thomasville, Georgia; photo by B. Sikes. F. *Pachylepyrium carbonicola* following 2001 Fridley Fire, Montana, wildfire; photo by C. Cripps. G. *Geopyxis carbonaria* (CLC2304(MONT)) following 2006 Jungle Fire, Montana, wildfire; photo by C. Cripps. H. *Hygrocybe conica* (TENN-F-071517) following 2016 wildfire at Great Smoky Mountains National Park; photo by B. Matheny. I. *Tricharina praecox* following 2013 Rim Fire (wildfire), California; photo by T. Bruns. J. *Pyronema omphalodes* following 2014 Rim Fire, California; photo by T. Bruns. K. *Rhizopogon olivaceotinctus* following 2013 Vision Fire in Pt. Reyes, California; photo by T. Bruns. L. *Neurospora* cf. *crassa* (via Pierre Gladieux) on eastern Joshua trees (*Yucca jaegariana*) immediately following 2020 Dome Fire in Mojave Desert National Preserve, California, wildfire; photo by S. Glassman.

Rhizopogon roseolus, *Cenococcum geophilum*, and *Wilcoxina rehmi* (Kipfer et al. 2010, 2011; Pulido-Chavez et al. 2021). The basidiomycetes *Basidioascus* and *Geminibasidium*, isolated from soil samples, are both heat-resistant and xerotolerant (Enright et al. 2021; Hopkins et al. 2021; Nguyen et al. 2013). The first fungi to fruit after a wildfire are often those with large fire/heat-resistant sclerotia or pseudosclerotia (McMullan-Fisher et al. 2011). Without specific fire resistance experiments, the term “fire-tolerant” is also used, albeit less frequently, to describe fungi found in fire-dependent ecosystems (Dooley and Treseder 2012; Hansen et al. 2019). Such fungi may even be symbionts and have a cooperative tolerance with their plant host (Baynes et al. 2011). While there is some literature devoted to fungal heat tolerance, fewer studies exist on other chemical and edaphic fire-driven changes in the soil (Pingree and Kobziar 2019).

Fire-responsive

Fire-responsive taxa are those triggered to grow and/or fruit by heat or by chemical changes caused by heat (e.g., *Anthracobia*, *Neurospora*, *Pyronema*). Fire events also tend to increase airborne spore counts in general, with numbers peaking after more than a week after such events (Camacho et al. 2018). However, it remains unclear whether this indicates fire responsiveness. Fire-induced convections of heated air mass and environmental conditions that are favorable for fires may promote the spore release. Alternatively, fire events and conditions favorable for fires may simply disperse spores that would have been released regardless of the fire. Be that as it may, the greater airborne spore abundance after fires is an interesting dispersal mechanism, as is the potential stimulation of spore germination by heated air. Such combined effects might provide an explanation for the rapid appearance of many pyrophilous fungi soon after fire. For example, in moist tropical areas, deserts, and grasslands, *Neurospora* (FIG. 3L) appears quickly on burned vegetation (Dix and Webster 1995; Emerson 1948) and appear to respond rapidly (20-fold increase) after fire based on molecular data in tallgrass prairie system (Mino et al. 2021). Similarly, in temperate climates, the operculate Pezizales (e.g., *Anthracobia*, FIG. 3D; *Pyronema*, FIG. 3J) rapidly fruit after severe fires. However, dispersal and stimulation by heated convection air mass is likely not the only process at work. Soil sampling suggests that *Pyronema* is normally present in soils at low frequencies but increases rapidly after a fire in soil (Bruns et al. 2020). In this case, spores are not only heat-resistant, but their rapid growth appears to be triggered in heat-treated soils (El-Abyad and Webster

1968b). Similarly, heat stimulates spore germination for *Anthracobia melaloma* (FIG. 3D) and some species of *Aspergillus* and *Penicillium* (Warcup and Baker 1963). Many of these fire-responsive species may also be fire-resistant—some may have been locally insulated from fire-generated heat pulses and respond to other indirect stimuli such as nutrient release or reduced competition. Although evidence strongly suggests that some fungi are fire-responsive and stimulated by fire, it remains unclear whether spores can be stimulated to germinate by the heated air mass, thus resulting in positive fire response.

Fire-adapted

Fire-adapted fungi are those with specific traits related to fire and that may require fire to complete their life cycle (e.g., *Pholiota carbonicola*, FIG. 3E; *Sphaerospora* spp.). Several fungi discussed above also possess clear fire adaptations, including heat-stimulated spore production/germination or heat-resistant sclerotia or spores. Fungal traits parallel those of many fire-adapted plants where frequent fires enable some part of their life cycle. Serotinous pines, for example, release seeds after a fire, many *Eucalyptus* spp. produce epicormic buds from the protected vascular cambium tissues (Burrows 2002), and *Quercus suber* (cork oak) protects buds with its thick bark (Burrows and Chisnell 2016). Recent studies with the pyrophilous basidiomycete *Pholiota carbonicola* (FIG. 3E) demonstrated that it may persist as an endophyte of mosses and fruit only when the host is burned (Raudabaugh et al. 2020). In like manner, *Sphaerospora* spp. endophytes and/or mycorrhizal partners of *Pinus pungens*, a fire-adapted Appalachian endemic tree, are undetectable in unburned soils but after a fire increase in abundance in burned soil and fruit (Hughes et al. 2020a). More work is needed to identify the traits that allow fungi to either resist or respond to fire, including whether such adaptations are to direct fire effects or the many abiotic and biotic changes fire causes in ecosystems.

Fire responses of fungal guilds and taxa.—Fire can affect fungi differently depending on their ecological guild. For fungi in tight associations with their plant hosts, fire responses can depend mainly on the host responses. Mycorrhizal fungi (Dove and Hart 2017) and many decomposers often decline substantially following fire (Brown et al. 2013; Day et al. 2019; Semenova-Nelsen et al. 2019), albeit these responses depend on fire severity and position in the soil profile. As detailed above, landscape-scale variation in fire severity likely plays an important role in determining the mosaic of hosts for many fungi. In turn, host availability can impact fungal community dynamics by determining inoculum sources that maintain or reestablish the fungal

community, whether it be from spore banks, living mycelium that survives in refugia, or new propagules arriving from outside the burn.

Most studied are mycorrhizal fungal responses, which vary widely and likely reflect their diversity. Fires tend to decrease overall mycorrhizal fungal richness (Dove and Hart 2017); a decline that can persist a decade or more in systems impacted by high-severity fire (Kipfer et al. 2011; Pulido-Chavez et al. 2021). The dependence of mycorrhizal responses on fire characteristics and ecosystem attributes is another key factor that makes broad generalizations so difficult. Certain ectomycorrhizal taxa dominate soon after fire. The ascomycete *Pustularia*, for example, was a dominant ectomycorrhizal fungus 2 years after high-severity fires in Washington ponderosa pine stands (Pulido-Chavez et al. 2021). Several other ectomycorrhizal genera clearly colonize roots shortly after fire, including *Thelephora*, *Phialophora*, *Pustularia*, *Amphinema*, and *Wilcoxina* (Bent et al. 2011; Kalucka and Jagodzinski 2016; Pulido-Chavez et al. 2021). In Pinaceae-dominated systems, *Suillus* and *Rhizopogon* species often colonize young seedlings on both unburned and burned sites where they may arise early from spore banks or via animal vectors (Ashkannejhad and Horton 2006; Glassman et al. 2016; Kipfer et al. 2011). Similarly, *Hebeloma anthracophilum* appears restricted to fire-impacted sites, although its ectomycorrhizal status needs confirmation, as do some putatively ectomycorrhizal ascomycetes on burns (e.g., species of Pezizales in Fujimura et al. 2005). Fire also reduces the overall richness of AM fungi in many systems, yet several taxa increase in abundance (spores or sequences) following fire (Dove and Hart 2017), responses potentially linked to those of their hosts.

Although less researched following fire, changes in fungal pathogens may reflect the loss of either available hosts or opportunities to infect hosts with compromised disease resistance and/or damaged by fire (Brown et al. 2019; Dove et al. 2021; Semenova-Nelsen et al. 2019). Most surveys provide evidence for the latter. Several taxa in the plant pathogen genus, *Teratosphaeria*, were key indicators of burned plots (Semenova-Nelsen et al. 2019) in pine savannas. Potential fungal pathogens in aspen leaves resprouting after fire were 4-fold higher compared with similarly aged leaves in unburned sites (Dove et al. 2021). In western North America, fungal forest pathogens often disperse to damaged trees via insects (Parker et al. 2006). Just as with insect defoliation (Saravesi et al. 2015), defoliation by fire likely alters plant host C allocation, leading to fungal community responses belowground of many different functional groups. Fungal parasites of other taxa (e.g., animals,

insects, other fungi) may also shift after fire but are even more poorly studied than plant pathogens. Nonpathogenic endophyte responses to fire are also poorly understood. In southwestern US systems that periodically burn, however, fire increases foliar endophyte diversity and produces consistent community shifts, even if they are rare overall (Huang et al. 2016). Almost certainly the responses of pathogens and foliar or root-associated, nonmycorrhizal endophytes are not homogeneous and likely depend on the dispersal limitations or the fire regimes (e.g., frequency, severity) of the systems in which the fungi have coevolved with their hosts.

Finally, some presumed saprobes (post-fire ascomycetes such as *Anthracobia* [FIG. 3D] and *Pyronema* [FIG. 3J]) appear unique to burned environments. Fire responses of saprobic fungi are likely complex, because of the many abiotic and biotic factors that rapidly and simultaneously shift because of a fire. Fire results in a heat pulse and may lead to sterilization of soil—at least in the topmost layers, if large volumes of fuel have accumulated (e.g., slash piles, large down wood) (Busse et al. 2010; Smith et al. 2016). Some wood-inhabiting fungi reportedly have heat-resistant mycelia, which can favor them in fire-prone or post-fire environments (Carlsson et al. 2012). The heat pulse can also change the nutrient and substrate environment (Certini 2005) and produce necromass that may serve as a substrate for a number of specialized saprobes, such as *Pyronema domesticum*, that metabolizes PyOM (Fischer et al. 2021). Clearly, there is a need to distinguish between the taxa that use pyrogenic materials and opportunists that exploit resources made available by the death of others. Differentiating these may help us better generalize saprobic fungal responses to fire. Although variation within these functional guilds challenges our ability to generalize, these examples highlight fungi in different functional guilds that all thrive after fire. We suggest that these functionally different fungi may be central players in fire-adapted fungal consortia.

Cosmopolitan vs. endemic pyrophilous fungi.—

Wildland fires are globally prevalent (Scott 2008). Yet, it remains unclear whether particular taxa of pyrophilous fungi have a widespread distribution or individual fungal lineages have arisen in different ecosystems. Many fungal taxa that respond positively to fire were also observed after the volcanic eruptions of Mount St. Helens, 1981–1983 (Carpenter et al. 1987), perhaps because of similarities to fire: increased soil pH, altered soil chemistry, and abundant necromass. Across different fire events, however, the same taxa are not

consistently present, highlighting the variety of uncertainties and unknowns about fungal fire ecology and fungal responses to fire. For example, *Pyronema* spp. are often considered pyrophilous (Bruns et al. 2020; Petersen 1970), yet they are not always present after a fire (Brown et al. 2019; Hopkins et al. 2021; Semenova-Nelsen et al. 2019). It remains uncertain whether these differences stem from biome and system distinctions or mere absence of communities or propagules that strongly and positively respond to fire.

Many pyrophilous fungi are thought to be widely distributed (Larson et al. 2016), but distribution data are sparse. Limited post-fire collections among ecosystems and following fires of different severities compromise our ability to assess distributions of post-fire fungi. The problem is exacerbated by three key issues: (i) geographic sampling that is biased toward Australia, North America, and Europe; (ii) the paucity of molecular data for pyrophilous fungi and inaccurate or uncertain identifications in the literature and GenBank; and (iii) the lack of expertise to accurately identify pyrophilous fungi, especially within the Pezizales, that dominate early post-fire fruiting. Sampling itself can often be challenging. Wildfires are unpredictable and the specific timing of prescribed fires depends on weather. Further, burns are heterogenous and the timing of responding pyrophilous fungi varies as a direct result. Even obtaining permits to sample recently burned areas can be difficult because these landscapes may be dangerous or inaccessible for long periods of time. Given these challenges, it is difficult to ascertain which pyrophilous taxa are truly cosmopolitan. Below, we exploit existing literature and highlight three genera of pyrophilous fungi that contained the most morphological and DNA sequence data to determine whether there is evidence of ubiquity (SUPPLEMENTARY TABLE 1). We aim to err on the side of caution, as we fully acknowledge that “absence of evidence is not evidence of absence”—a note particularly fitting here.

***Anthracobia* (Pyronemataceae; Ascomycota).**—Widely considered an obligate pyrophilous taxon (Larsen 1975), *Anthracobia*'s life cycle (like many post-fire fungi) in the absence of fire is largely unknown and may involve saprotrophic or endophytic stages. All *Anthracobia* spp. seem pyrophilous with the exception of “taxonomic species B,” which fruits on cow dung (Larsen 1975). *Anthracobia* spp. have been reported fruiting in North America following the Washington State Mount St. Helens eruption (Claridge et al. 2009) and wildfires in the western (Claridge et al. 2009; Fujimura et al. 2005) and eastern (Hughes et al. 2020b) United States. They have also been observed fruiting after wildfires in

Australia (Sjm et al. 2011; Warcup 1990), the United Kingdom (Wilberforce 2005), and Denmark (Dix and Webster 1995). From this limited evidence, we conclude that the genus *Anthracobia* may have a cosmopolitan distribution. The details on the distribution of species within the genus *Anthracobia* are included in Supplementary Material (SUPPLEMENT 1).

***Morchella* (Morchellaceae; Ascomycota).**—Field guides tend to treat the true morels as a few widely distributed species and frequently use incorrect European names for North American taxa (O'Donnell et al. 2011). Certainly, the genus *Morchella* appears to have a cosmopolitan distribution, with reports from North America and Europe (Richard et al. 2015), South and Central America (Baroni et al. 2018), Israel (Masaphy and Zabari 2013; Masaphy et al. 2008), Turkey (Taşkın et al. 2012), China (Du et al. 2012), and Australia (Elliott et al. 2014). It remains less certain whether this is true for congeneric species—particularly so for those considered pyrophilous. Most *Morchella* spp. are not fire-responsive (Kuo et al. 2012). Of those that are pyrophilous, some may be obligately so (fruiting only after a fire, fire-adapted), whereas others are facultative (fruiting enhanced by fire, fire-responsive) (O'Donnell et al. 2011). Reported pyrophilous *Morchella* spp. include (but are not limited to) *M. tomentosa* (Kuo et al. 2012; Stefani et al. 2010), *M. sextelata* (Kuo et al. 2012), *M. septimelata* = *Mel-7* of O'Donnell 2011 (Kuo et al. 2012), *M. capitata* (*M. exuberans*; Kuo et al. 2012), and *M. eximia* (*M. anthracophila*; Richard et al. 2015). In the eastern United States, *M. exuberans* fruited in a *Pinus pungens* forest following a wildfire (Miller et al. 2017), and *M. importuna* was collected after a fire in a burned pine forest in Sichuan, China (Li et al. 2017). Li et al. (2017) consider *M. importuna* as a fire-responsive taxon “involved in nutrient acquisition,” but Kuo et al. (2012) describe this species as growing in planters and on wood chips in landscaping. *Morchella conica* was observed in pine plantations in Israel 5 months after a fire (Masaphy et al. 2008). These reports highlight the broad interest in pyrophilous *Morchella* as well as the taxonomic challenges that are inherent in generalizing their fire responses.

It is likely that fire adaptation is convergent in *Morchella* (O'Donnell et al. 2011). Current estimates of the evolution of a clade of fire-adapted morels date to the Oligocene, 25 million years ago (O'Donnell et al. 2011). Three species from this clade observed in Turkey (*Mel-7*, *Mel-9*, *Mel-10*) appear to be endemic to western North America (Taşkın et al. 2012), perhaps transferred with pine plantings in Turkey. The *M. elata* subclade provides

key examples of the diversity of fire responses within a subclade (O'Donnell et al. 2011). Two species, *Mel-7* and *Mel-9*, are obligate post-fire species, whereas *Mel-10* appears to be facultatively fire-responsive. In contrast, *Mel-6* and *Mel-12* are *Bromus tectorum* endophytes able to increase host seed production and biomass. Interestingly, infected plants produced seed that was better adapted to fire (Baynes et al. 2011). Overall, we conclude that the genus *Morchella* is cosmopolitan, but only some of the congeneric species seem pyrophilous. Known pyrophilous *Morchella* spp. seem not cosmopolitan but instead limited in distribution to specific ecosystem(s).

Pyronema (Pyronemataceae; Ascomycota).— Evidence that the genus *Pyronema* is pyrophilous dates back more than a century (Seaver 1909). Like *Anthracobia* and *Morchella*, several *Pyronema* spp. are globally distributed and appear rapidly after fires. High-throughput sequencing (HTS) data in the western United States, for example, suggest that *Pyronema* spp. are highly abundant as mycelium in soils immediately post-fire (Bruns et al. 2020; Reazin et al. 2016). *Pyronema* species were nearly undetectable via HTS of unburned soils, but *Pyronema domesticum* surged to 58% and *P. omphalodes* to 7% of ITS1 sequences after experimental fires in laboratory pyrocosms (Bruns et al. 2020). *Pyronema* spp., however, were not detected with HTS of ITS2 amplicons (Ihrmark et al. 2012) after wildfire in the Southern Appalachians (Brown et al. 2019) or prescribed fires of longleaf pine savannas (Semenova-Nelsen et al. 2019) and prairies (Hopkins et al. 2021), even when other Pyronemataceae were present. Available evidence suggests that the genus *Pyronema* is spotty in its distribution even in relation to fire and likely requires a threshold of fire severity to bloom.

Pyronema omphalodes (FIG. 3J) and *P. domesticum* are the two most likely candidates for cosmopolitan fire fungi. Both have been reported to be fireplace fungi in northern Europe (Petersen 1970). A *Pyronema* sp. (reported as *P. omphalodes* in Warcup 1990) fruited in high abundance after wildfires in *Eucalyptus* forests in Australia (Warcup 1990), and *P. omphalodes* (= *P. confluens*) has been reported to fruit after fires across the United States in Iowa, New York, and North Dakota (Seaver 1909). After a 2016 wildfire in Tennessee, *P. omphalodes*, but not *P. domesticum*, was recovered both as ascomata on burned soil (Hughes et al. 2020b) and as ITS2 sequences from severely burned soils but not in great abundance and only in hemlock/pine areas (Hughes, unpublished data). Other studies report that *P. domesticum* and *P. omphalodes* accounted for approximately 60% of ITS1 sequences after a mega-fire burned down a *Pinus ponderosa* forest in the California

Sierra Nevada (Pulido-Chavez et al. 2021) and after a high-severity fire burned a California chaparral shrubland (FIG. 4). *Pyronema domesticum* ITS1 sequences also increased 100-fold in frequency after experimental fires in an Oregon *P. ponderosa* forest (Reazin et al. 2016). From available literature and molecular data, we conclude that *P. domesticum* occurs in Europe and western North America, whereas *P. omphalodes* may have a broader distribution including eastern and western North America, Europe, and Australia. Thus, *P. omphalodes* may be a true cosmopolitan dominating post-fire landscapes ranging in host diversity (eucalyptus and pine forests, chaparral) and globally from Australia to Europe to western North America. Details on the distribution of species within the genus *Pyronema* is included in SUPPLEMENT 1.

Available data and literature strongly suggest that while pyrophilous genera are likely globally distributed, congeneric species may often have much more limited ranges. Admittedly, our conclusions are based on limited data and likely biased toward Europe, North America, and Australia. We posit that it is likely that there are also locally adapted and endemic pyrophilous taxa. For example, *Rhizopogon olivaceotinctus* (Rhizopogonaceae, FIG. 3K) is a hypogeous, putatively pyrophilous basidiomycete that forms ectomycorrhizae with western North American pines and appears to be endemic to these forested systems. *Rhizopogon olivaceotinctus*-dominated root colonization after the 1995 Vision Fire burned down a *Pinus muricata* forest (Baar et al. 1999) and after the 2013 Rim Fire burned down a *Pinus ponderosa* forest (Glassman et al. 2016), both in California. Its great abundance in the roots of juvenile trees is likely due to its ability to produce and maintain

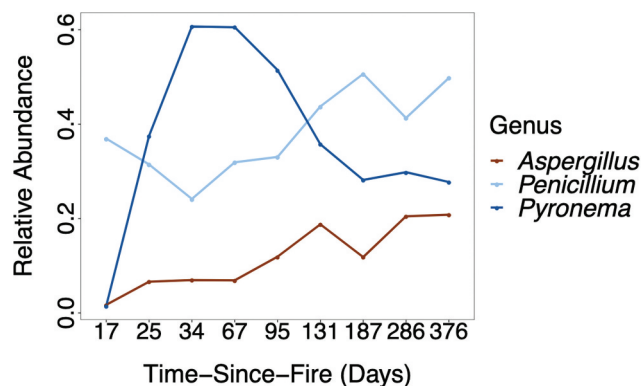


Figure 4. Relative ITS2 sequence abundance (using Illumina MiSeq) of three of the most abundant genera after the 2018 Holy Fire burned down a manzanita (*Arctostaphylos* sp.)-dominated chaparral in Southern California. Sampling occurred nine times between 2 weeks and approximately 1 year post-fire. Pulido-Chavez et al. 2021.

prolific thermotolerant spore banks in soil (Bruns et al. 2019). Many more endemic pyrophilous fungi may exist that are thus far at best known only as sequences in community surveys or, more likely, wholly undescribed.

It is increasingly clear that detection and identification of pyrophilous fungi, including defining their endemism, depends on the timing of the fire and subsequent fungal surveys because pyrophilous fungi follow distinct temporal trajectories. For example, the intensive temporal sampling in the year following the 2018 Holy Fire in Southern California demonstrates marked shifts in soil fungal abundance over time (FIG. 4; Pulido-Chavez et al. 2021). Within the first several weeks post-fire, the basidiomycete yeast *Geminibasidium* dominated (data not shown) but then quickly declined as the ascomycete *P. domesticum* spiked in abundance. After a month, other ascomycetes (*Aspergillus* and *Penicillium*; Aspergillaceae) increased in abundance (FIG. 4). Although we do not wish to argue that all these taxa are pyrophilous, soil heating experiments suggest thermotolerance of some aspergilli and penicilli (Warcup and Baker 1963) as well as *Rhizopogon roseolus* and *Cenococcum geophilum* (Kipfer et al. 2010), *Geminibasidium* (Nguyen et al. 2013), and *Pyronema* (Bruns et al. 2020). Similar post-fire taxa were also reported in approximately monthly sampling following prescribed fires in both longleaf pine savanna (Florida) and tallgrass prairie sites (Kansas), including Aspergillaceae, Pyronemataceae, and *Geminibasidium* (Hopkins et al. 2021). It remains uncertain whether these taxa occur following a fire because of their thermotolerance or whether they have alternate strategies such as fast post-fire colonization, response to fire-generated necromass, or release of cytoplasmic contents after organismal death. More time series data—both on finer temporal scales as well as over longer periods post-fire—are necessary to help identify and determine the ubiquity of pyrophilous taxa.

In conclusion, a few cosmopolitan pyrophilous taxa likely exist, but more sampling is necessary in Africa, South America, and Asia to confirm whether they are truly cosmopolitan. Most data are limited to single post-fire sampling of fruiting bodies or HTS data based on short ITS fragments with limited taxonomic resolution. Thus, it remains a challenge to validate distribution based on the available data. To better understand the pyrophilous taxon distribution, molecular data including nrITS sequences must be linked to morphological descriptions for vouchered pyrophilous fungi worldwide. Such data and collections would also facilitate detailed studies aiming to resolve whether putative species are cryptic complexes that may include endemic taxa.

SOURCES AND DISPERSAL OF PYROPHILOUS FUNGI

Sparse empirical data currently limit our understanding of the early post-fire dynamics of fungal communities (but see Hopkins et al. 2021). Instead, most post-fire fungal successions rely on space for time substitutions (e.g., chronosequences), or sample collection after enough time has passed that important fungal responses may have been missed (Dove and Hart 2017; Pressler et al. 2019; Yang et al. 2020). While providing critical data on which our understanding (and much of this paper) is based, these data so far all fail to identify inoculum sources in the post-fire landscape. These sources may determine immediate fungal fire responses and, if priority effects are important, longer-term community assembly.

Fungi must either survive fire or recolonize soon after to establish the diverse and functionally important post-fire communities. Fungal spores can and likely do arrive aerially any time after the fire. Several well-known ascomycetes can be transported long distances by smoke plumes (Mims and Mims 2004), and recent evidence suggests that this may be a common vector for colonization into burned sites (Kobziar et al. 2018; Moore et al. 2021). Low-density propagule pools likely exist that are stimulated by heat and/or the resultant changes in soil chemistry. Additional mycelial reservoirs are possible in unburned roots (Dighton 2003; Vrålstad et al. 1998), other plant tissues (Wang et al. 2016), and bryophytes (Raudabaugh et al. 2020) or may survive as sclerotia or tubers (Sjm et al. 2011). However, the relative importance of these sources—whether from external sources (i.e., allochthonous) or dormant propagules and/or surviving mycelia already at the site (i.e., autochthonous)—remains uncertain (FIG. 2). Post-fire communities establish rapidly after a fire (Bruns et al. 2020; Reazin et al. 2016), suggesting that the initial community likely includes a large component of resident, resistant propagules. Even at small scales—in mesocosms or campsite fire pits—pyrophilous fungi either establish vegetative mycelia or fruit abundantly (Adamczyk et al. 2012; Bruns et al. 2020), providing additional support for the importance of local propagule pools in the establishment of pyrophilous fungal communities. The importance of other mycelial reservoirs may be important as well.

What reservoirs may be present within the system after fire? Soil heating reduces vegetative mycelium, particularly in the organic and upper mineral soil layers (Cairney and Bastias 2007; Dooley and Treseder 2012). However, mycelial inocula can be derived from cryptic life stages in unburned plant parts (Raudabaugh et al.

2020) or in roots of dying trees (Dighton 2003). Within plants, fire causes declines in colonization that coincide with compositional changes in mycorrhizal associates. When measured in situ, mycorrhizal colonization often declines following fire, whereas colonization measured in bioassays does not (Dove and Hart 2017). This difference may indicate shifts in pools of organisms that survive to colonize new roots versus those that establish from resident propagule pools. Many post-fire fungi may form new mycorrhizal associations soon after a fire (Dahlberg 2002; Egger and Paden 1986; Vrålstad et al. 1998), and we posit that these are more likely to establish from resident spore banks rather than from surviving mycelia in soil (Baar et al. 1999; Glassman et al. 2016). Some ectomycorrhizal fungi already in soils clearly produce heat-resistant spores (Kipfer et al. 2010; Peay et al. 2009), explaining the increase in their abundance after experimental or natural soil heating (Glassman et al. 2016; Izzo et al. 2006; Kipfer et al. 2011; Peay et al. 2010).

Early colonization may be from autochthonous reservoirs, but recent work has confirmed the importance of fire to fungal dispersal and showed clear pathways for post-fire dispersal into fire-impacted sites. Fires in the Mediterranean increased airborne fungal spores, with a peak ~10 days after fires (Camacho et al. (2018), and abundant fungal propagules aerosolized within smoke plumes that followed prescribed fires in Florida pyrogenic ecosystems (Kobziar et al. 2018). Smoke from the Yucatan Peninsula in Mexico carried several known plant pathogenic fungi as far as central Texas (Mims and Mims 2004). These studies suggest that pathogenic and nonpathogenic fungal dispersal may be fire-stimulated. More work is clearly needed on microbial aerobiology in relation to fire (Moore et al. 2021). Small mammals (Johnson 1995; Trappe et al. 2005) and invertebrates (Vašutová et al. 2019) may also carry fungal spores to and from burned sites. Pyrophilous mycophagous insects are attracted to recently burned areas (Wikars 2002) and, as noted above, are important in the post-fire spread of fungal tree diseases (Parker et al. 2006). Beyond specific forest pests, however, how important these insects are as fungal vectors for dispersing spores remains unknown.

Current understanding of pyrophilous fungi is based mainly on records of fruiting. Undeniably, vegetative establishment and mycelial resource exploitation must precede the observed fruiting, further highlighting the expedient pyrophilous fungal responses. The “Fire-specific fungal traits and pyrophilous fungi” section above details how fire stimulates sporulation, growth, and fruiting in several different species. Based on this

rapid fruiting and mycelial expansion inferred from molecular data, we posit that most pyrophilous fungi recorded as fruiting bodies emerge from resident inocula. More broadly, sources that establish the distinct post-disturbance fungal communities following fire are largely unresolved. Post-fire species may survive as mycelium (Vrålstad et al. 1998), have inactive spores present in soil that germinate only after exposure to fire (e.g., Jalaluddin 1969; El-Abyad and Webster 1968b), or may establish from airborne propagules (Chen and Cairney 2002) or from plant reservoirs (Raudabaugh et al. 2020). We speculate that post-fire communities, now overwhelmingly characterized using molecular tools, are most likely a combination of airborne sources and—to a larger extent—a rapid vegetative expansion from either heat-resistant or deep-buried propagule banks and perimeters of the intensely burned areas that lead to the community turnover resulting from the rapid responses to fire. These speculations are consistent with observations of low-frequency detection of the post-fire dominants in the pre-fire communities and the very fast establishment of the post-fire community. Many open questions remain about the necessary morphological, genomic, and physiological adaptations that underlie the fungal responses to fire-generated stimuli.

CONCLUSIONS

Fire effects on ecosystem properties and biodiversity are increasingly important research areas as fire frequencies and burn severities increase in many areas because of climate change and an expansion of the wildland-urban interface. Our synthesis explores the impacts of fire on fungal communities and their diversity. It is important to improve our understanding of fire in the Earth system by focusing on nonplant organisms, which are generally overlooked in fire ecology. Our goal was to highlight fungal fire traits, key pyrophilous fungi, and fungal community dynamics initiated by fire, identifying key research gaps along the way. Applying existing frameworks for fungal fire responses is challenging because of the many unique life history traits fungi possess. Developing matrices of trophic, dispersal, and metabolic traits may serve as an effective tool to characterize the largely unknown diversity of pyrophilous fungi (Zanne et al. 2020). Although this synthesis shows how much we have learned about fungi that commonly appear in fire-impacted systems, the temporal component is often lacking from our research. Experiments that combine pre-fire conditions and repeated sampling in time series are sorely needed. Combining sequencing approaches with

vouchered specimen collections in this research is also critical in order to better link DNA-based community responses to specific cosmopolitan pyrophilous taxa. Such studies can also help differentiate immediate community dynamics from longer-term successional trajectories to distinguish fungi that exploit fire-impacted systems and provide essential ecosystem functions at different time scales. Such experiments might best be combined with mechanistic tests that help explain how specific fungi proliferate in post-fire environments. Another key area that is lacking data is fungal community functional responses to fire. Are shifting communities functionally distinct or redundant? Do fire-resultant changes in substrates lead to novel functional attributes in these communities? In individual pyrophilic systems, post-fire fungi appear poorer at decomposition (Semenova-Nelsen et al. 2019, Hopkins et al. 2020) and have reduced enzyme activities following high-frequency (compared with low-frequency) fires (Pérez-Izquierdo et al. 2020), but are these general phenomena? The current explosion of environmental meta-omics tools may permit substantial insight into how to better tackle these challenging questions (e.g., Nelson et al. 2021). Ultimately, we argue that much progress can be made by relatively simple laboratory experiments that focus on identifying crucial pyrophilous traits. This is particularly the case if such minimalistic experiments are combined with carefully designed experiments in mesocosm systems or in field manipulations.

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