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A roadmap for pyrodiversity science

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Abstract

Background: Contemporary and projected shifts in global fire regimes highlight the importance of understanding how fire affects ecosystem function and biodiversity across taxa and geographies. Pyrodiversity, or heterogeneity in fire history, is often an important driver of biodiversity, though it has been largely overlooked until relatively recently. In this paper, we synthesise previous research to develop a theoretical framework on pyrodiversity–biodiversity relationships and propose future research and conservation management directions.

Theoretical Framework: Pyrodiversity may affect biodiversity by diversifying available ecological niches, stabilising community networks and/or supporting diverse species pools available for post-fire colonisation. Further, pyrodiversity's effects on biodiversity vary across different spatial, temporal and organismal scales depending on the mobility and other life history traits of the organisms in question and may be mediated by regional eco-evolutionary factors such as historical fire regimes. Developing a generalisable understanding of pyrodiversity effects on biodiversity has been challenging, in part because pyrodiversity can be quantified in various ways.

Applying the Pyrodiversity Concept: Exclusion of Indigenous fire stewardship, fire suppression, increased unplanned ignitions and climate change have led to dramatic shifts in fire regimes globally. Such shifts include departures from historic levels of pyrodiversity and add to existing challenges to biodiversity conservation in fire-prone landscapes. Managers navigating these challenges can be aided by targeted research into observed contemporary pyrodiversity–biodiversity relationships as well as knowledge of historical reference conditions informed by both Indigenous and local ecological knowledge and western science.

Future Research Directions: Several promising avenues exist for the advancement of pyrodiversity science to further both theoretical and practical goals. These lines of investigation include but are not limited to (1) testing the increasing variety of pyrodiversity metrics and analytical approaches; (2) assessing the spatial and temporal scale-dependence of pyrodiversity's influence; (3) reconstructing historical pyrodiversity patterns and developing methods for predicting and/or promoting future pyrodiversity; and (4) expanding the focus of pyrodiversity science beyond

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biodiversity to better understand its influence on ecosystem function and processes more broadly.

KEYWORDS

biodiversity, climate change, conservation, fire ecology, fire regimes, landscape ecology, pyrodiversity

1 | THE PYRODIVERSITY–BIODIVERSITY HYPOTHESIS

Fire is a fundamental ecological process that influences landscape patterns and biodiversity globally (He et al., 2019; Pickett & White, 1985; Viljur et al., 2022). Its effect on vegetation type and successional stage has long been understood to support different components of ecological communities (Whittaker, 1953). However, the recognition that variation in fire patterns, also known as pyrodiversity, is an important driver of biodiversity is relatively recent (Martin & Sapsis, 1992). Since Martin and Sapsis first proposed that 'pyrodiversity begets biodiversity', studies surrounding the topic have grown in both number and scope, as has interest in applying the concept to fire management and biodiversity conservation (Jones & Tingley, 2022). However, current support for the pyrodiversity–biodiversity hypothesis as well as the conceptual and methodological approaches to the topic have been remarkably varied. Many key scientific and applied questions remain surrounding the underlying mechanisms that link pyrodiversity and biodiversity, the implications of changing fire regimes and how pyrodiversity science can be best applied to biological conservation. Here, we provide a conceptual framework for the pyrodiversity–biodiversity hypothesis, synthesise the current scientific knowledge on the topic and suggest a roadmap for future research and application of pyrodiversity science.

Fire regimes are the collection of the temporal (fire frequency and seasonality), spatial (burned patch size and configuration), or magnitude (intensity or severity) fire attributes of a landscape. Research has commonly focused on the central tendencies of these attributes over the long term (e.g. mean fire return interval; Agee, 1996). Pyrodiversity expands upon the fire regime concept by emphasising the variation in the distributions of these fire attributes (Martin & Sapsis, 1992; Steel et al., 2021). The explicit focus on variation in fire regimes provides a complimentary lens with which to study the drivers and ecological implications of historic and changing fire regimes.

Climate, topography and vegetation type (i.e. the 'fire triangle'; Countryman, 1966) have influenced fire regimes since the origin of terrestrial plants (Pausas & Keeley, 2009). As human populations spread and grew, their manipulation of fire began to greatly influence fire regimes in many regions (Pausas & Keeley, 2009). Humans have used fire as a tool to manage resources for thousands of years, and Indigenous stewardship, in particular, has influenced

pyrodiversity historically and contemporarily (Beale et al., 2018; Hoffman et al., 2021; Trauernicht et al., 2015). With expanded recognition that most fire regimes have also been shaped by human management (Archibald et al., 2013; Iglesias et al., 2022), we thus propose the 'fire diamond' as an update to this concept of the primary drivers of both the central tendencies and variation of fire regime attributes (Figure 1).

Eco-evolutionary relationships, spatiotemporal scale and the underlying ecological mechanisms likely interact to determine the nature of pyrodiversity's influence on biodiversity. Our ability to observe the true magnitude and form of the pyrodiversity–biodiversity relationship is determined by research methodologies and limitations. Finally, the utility of pyrodiversity science for practical biodiversity conservation is shaped by socio-cultural context, including public attitudes towards fire management (Figure 1).

The pyrodiversity–biodiversity hypothesis is a growing ecological and management-oriented paradigm for understanding how fire shapes past, current and future biodiversity patterns. A recent review found that the number of papers referencing the hypothesis have increased exponentially since its conceptualisation (Jones & Tingley, 2022), with the greatest increase coincident with the growth of 'mega-fires' since 2005 (Linley et al., 2022). While the number of studies seeking to explicitly test the pyrodiversity–biodiversity hypothesis have also increased during this time—to over 40—this increase has not matched the pace of growth in studies citing or referencing the hypothesis (Jones & Tingley, 2022). This is potentially troubling, as evidence in support of the pyrodiversity–biodiversity hypothesis is decidedly mixed, with Jones and Tingley (2022) noting that there currently is not enough data to differentiate between methodological issues that may prevent the detection of an effect and any context-specific dependencies that may exist (e.g. scale, taxa and ecosystem).

The most effective way forward involves multiple research prongs: targeted tests of the hypothesis that develop mechanistic understanding, rigorous testing of methods for evaluating pyrodiversity and experimental application of the pyrodiversity concept in adaptive fire and conservation management. The need for development in these areas has been called for in previous work (Bowman et al., 2016; Jones et al., 2022; Jones & Tingley, 2022; Kelly et al., 2017). Answering these calls, we here develop a roadmap for exploring these topics, while providing the theoretical context and a framework through which the pyrodiversity–biodiversity hypothesis can be more effectively measured, tested and applied toward biological conservation.

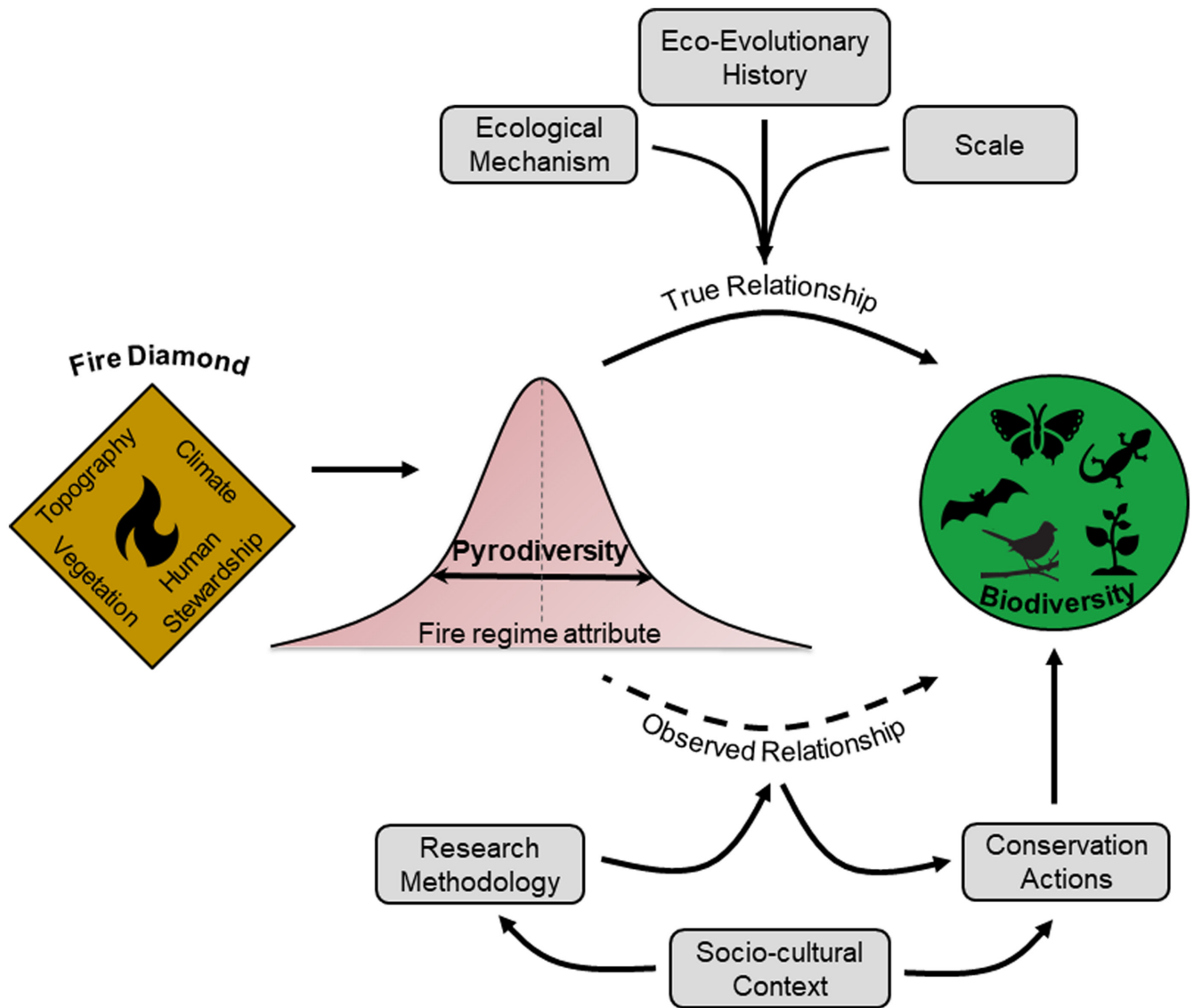


FIGURE 1 A conceptual framework for pyrodiversity's influence on biodiversity. Pyrodiversity, or the variation in fire regime attributes (e.g. burn severity or return interval), is influenced by vegetation, topography, climate and human stewardship/management (the 'Fire Diamond'). Here, pyrodiversity is represented as the dispersion (horizontal two-sided arrow) of an attribute's frequency distribution, which contrasts with the mean value of that distribution (vertical dashed line). The influence of pyrodiversity on biodiversity patterns is determined by one or more ecological mechanisms and mediated by eco-evolutionary history and the scale at which organisms and fire interact. Our ability to observe the true pyrodiversity–biodiversity relationship is dependent on methodological choices and limitations. Ultimately, our ability to take effective conservation actions to support biodiversity in flammable ecosystems is shaped by our understanding of pyrodiversity's influence as well as societal goals and values.

2 | ECOLOGICAL MECHANISMS AND MEDIATING FACTORS

Following Martin and Sapsis' (1992) original hypothesis, numerous mechanisms have been offered to explain the observed pyrodiversity–biodiversity relationship. We consider three broad mechanistic hypotheses whereby pyrodiversity: (1) increases niche availability and heterogeneity; (2) stabilises community networks; and/or (3) supports colonisation and persistence dynamics for a diverse species pool following disturbance. The expression of these mechanisms (i.e. the strength and functional form of the relationship) may be mediated by the eco-evolutionary context of an ecosystem and the scale

at which species perceive and respond to pyrodiversity (Figure 1). A better understanding of how and under what conditions these mechanisms and mediating factors are influential may help better describe the variability in the observed effects of pyrodiversity on biodiversity in the existing literature.

2.1 | Niche heterogeneity

The niche heterogeneity hypothesis of pyrodiversity posits that pyrodiversity generates and maintains different habitat types or patches within the same landscape, thus generating high levels of

spatial niche heterogeneity and allowing a greater number of species with disparate resource needs to coexist (Kelly et al., 2017; Martin & Sapsis, 1992). Variability in fire regimes promotes the evolution of fire-dependent and fire-resilient traits from serotiny to post-burn resprouting in plants (He et al., 2019) to pyrocarivory and smoke-dependent mating cues in animals (Pausas & Parr, 2018). Niche heterogeneity can be created by temporal, spatial and/or magnitude (i.e. severity or intensity) components of the fire regime and can support both specialist species that require narrow fire-created habitat conditions and generalist species accommodated by a wide range or a mix of habitats. For example, variation in burn severity in dry forests of western North America can simultaneously create patches of fire-killed trees (snags) used by beetles, woodpeckers and bats, as well as patches of lightly burned mature forests needed for late-successional specialists such as the spotted owl and fisher (Jones & Tingley, 2022; Steel et al., 2019; Stillman, Siegel, Wilkerson, Johnson, & Tingley, 2019). Likewise, post-fire succession creates continually changing habitat conditions suited for different species. Variation in fire frequency or time since fire supports plant and insect species adapted to different successional stages within the same landscape (Brown & York, 2017; Wilkin et al., 2021).

Niche heterogeneity theory of pyrodiversity parallels the long-established intermediate disturbance hypothesis (IDH), which predicts that a moderate level of disturbance maximises species diversity (Connell, 1978; He et al., 2019). While IDH expects intermediate levels of disturbance to be optimal because too little or too much disturbance excludes specialist species, pyrodiversity theory stresses maintaining a wide range of niches within the same landscape, which could facilitate specialist species adapted to the extremes. In many cases, the two theories will create similar predictions (e.g. Figure 2A—when average burn severity peaks at intermediate levels and variation in severity is also high). However, if the mean landscape condition is characterised by intermediate levels of disturbance but with little variation around that mean (Figure 2B—no unburned or high-severity patches), IDH would predict higher levels of biodiversity than the pyrodiversity hypothesis. Conversely, a burned landscape dominated by severity extremes with limited intermediate levels would be predicted to produce much lower levels of biodiversity under IDH than the pyrodiversity hypothesis (Figure 2C). This distinction has important implications for fire management, including biodiversity objectives.

2.2 | Community network stabilisation

A central tenet of biodiversity-ecosystem function theory is the idea of species functional redundancy, whereby multiple species provide the same ecosystem function, promoting community resistance (Allan et al., 2011; Mouillot et al., 2013; Oliver et al., 2015). In redundant communities, if a particular species goes extinct, the ecosystem functions provided by that species would still be maintained

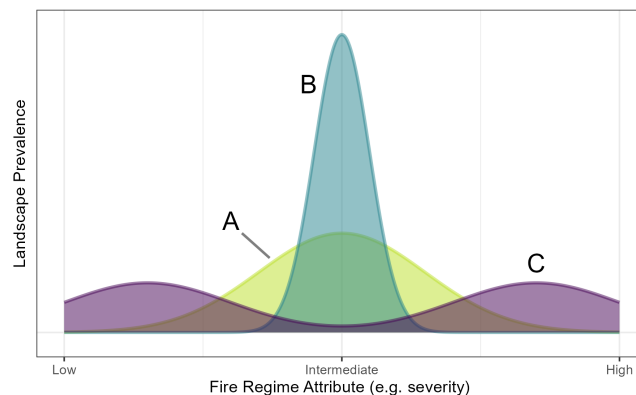


FIGURE 2 Hypothetical density distributions of a fire regime attribute (e.g. severity) illustrating different predictions of the intermediate disturbance hypothesis (IDH) and pyrodiversity hypothesis (PH). (A) In instances where the dominant disturbance is at intermediate levels but with high variation around the mean, IDH and PH will predict similar levels of biodiversity. (B) Where a moderate level of disturbance dominates the landscape with little variation, predictions of biodiversity will be high under IDH but low under PH. (C) Where a landscape contains highly contrasting levels of disturbance, IDH will predict much lower levels of biodiversity than PH.

by the remaining species in the community. The loss of species in such a community would not impact overall function provision (i.e. 'Biodiversity insurance hypothesis'; Yachi & Loreau, 1999). Functional redundancy is inherently limited by the species richness of a community. Depending on the relationship between species richness and the accumulation of functional redundancy, pyrodiversity may therefore enhance community resistance. However, the only study directly examining this effect found that pyrodiversity increased functional complementarity (the opposite of functional redundancy) in plant-pollinator networks (Ponisio, 2020). This apparent conflict between theory and the observations by Ponisio (2020) highlights the need for further study into pyrodiversity-complementarity versus pyrodiversity-redundancy relationships.

In addition to functional redundancy at the community-level, pyrodiversity has the potential to increase population-level resistance by enabling flexible behavioural strategies that promote an individual's survival (Hofmann & Todgham, 2010; Oliver et al., 2015). This ability to 're-wire' interactions, or interaction flexibility, is known to increase species persistence over years (Gaiarsa et al., 2021; Ponisio et al., 2017) and over thousand-year time scales (Yeakel et al., 2014). Ponisio (2020) found that bees that could shift floral partners and network niches are better able to take advantage of the heterogeneity generated by pyrodiversity, thereby buffering their populations against drought-induced changes in floral abundance. Similarly, in woodpeckers, Stillman et al. (2019) found that pyrodiversity enabled woodpeckers to interact more flexibly with different habitat types to both forage and avoid predators. Studies on species interactions, such as food webs, are key to understanding the potential of pyrodiversity to enable flexible behaviours, though as of yet, few studies go beyond species occurrence (Bowman et al., 2016).

2.3 | Colonisation and establishment dynamics

Heterogeneity in both the spatial and temporal components of fire history has the potential to influence the pool of species available to colonise and establish following a wildfire. The size and configuration of high-severity burn patches may filter the species available for ex situ (from outside) colonisation post-fire. Obligate seeding plants and wildlife species with limited dispersal ability can be slow to return to the interiors of large, high-severity patches (Pausas et al., 2004; van Mantgem et al., 2015). In this way, post-fire community assembly may display dynamics predicted by island biogeography theory, where colonisation of more isolated habitat patches (or their interiors) may be limited (Brown & Kodric-Brown, 1977; Diamond et al., 1976; MacArthur & Wilson, 2016). For example, Steel et al. (2022) found that large high-severity burn patch interiors contain subsets of, rather than complements to, edge bird communities, potentially due to trait filtering and/or a reduction in habitat availability. In contrast, landscapes that include unburned or lightly burned fire refugia can support within-fire pools for re-colonisation by fire-intolerant species. Pyrodiversity may also enhance spatial variability or in situ (from within) species pools such as soil seed banks or resprouting plants, as well as animals able to shelter in place in their adult (e.g. burrowers) or larval (e.g. through diapause) forms and quickly recolonise following a fire (Pausas & Keeley, 2014; van Mantgem et al., 2015). Over longer time periods of a decade onwards, pyrodiversity can improve metapopulation stability. For example, in eastern collared lizard (*Crotaphytus collaris collaris*) populations, fires promote dispersal among glades, and the temporal and spatial variability in these fires promotes asynchrony among populations, an important factor for population persistence (Templeton et al., 2011).

The spatial pattern or timing of fire may also influence post-fire colonisation order and the resulting community composition. Specifically, such patterns may drive 'priority effects' (Fukami, 2015), whereby the first species to establish after fire may inhibit or facilitate the colonisation of additional species. Priority effects operate both within and across seasons (Wainwright et al., 2012) through niche preemption or niche modification (Fukami, 2015). In instances of low pyrodiversity due to very large, high-severity burn patches, species that (re)establish rapidly after fire may become dominant (D'Antonio et al., 2001), sometimes creating taxonomically and functionally homogenous landscapes. Niche preemption may limit subsequent colonisation of new species in the same niche. For example, in high-severity burn patches in conifer forests in California, USA, tree propagule availability can determine whether forest stands regenerate or whether the landscape is converted to a shrubland dominated by species that exhibit fire-cued seed generation (Welch et al., 2016). Such shrublands can persist for decades in areas that were formerly forest by outcompeting less established tree seedlings (Weeks et al., 2023). Further, the seasonality of fire events may influence the survival and availability of propagules for immediate colonisation. Communities with diverse survival (e.g. ability to

resist or flee) and colonisation (in situ or ex situ) adaptations may maximise post-fire biodiversity when both spatial and temporal pyrodiversity is high.

2.4 | Mediating factors: eco-evo history and scale

The strength and magnitude of the pyrodiversity–biodiversity relationship may be contingent upon the eco-evolutionary history of a region, including its historical fire regime (Jones & Tingley, 2022; Steel et al., 2021). Communities that assembled under conditions of high historical pyrodiversity may see biodiversity loss when fire is excluded or homogenised (e.g. due to wide-spread fire suppression). Indeed, many fire-adapted temperate forests where fire suppression has reduced pyrodiversity can see biodiversity boons from restoring pyrodiversity (Bliège Bird et al., 2008; Steel et al., 2019). In contrast, communities composed of species that evolved in the absence of fire may see biodiversity loss with increased fire activity. This may be particularly true for groups of species that require large patches of undisturbed habitat (e.g. some large mammals) if high levels of pyrodiversity result in landscape fragmentation (Figure 3; He et al., 2019). In non-fire-adapted systems such as the rainforests of New Zealand, which historically experienced exceptionally low pyrodiversity and 'fire naïve' ecological communities (Nimmo et al., 2021), even a small but sudden introduction of fire and associated pyrodiversity could result in catastrophic biodiversity loss (McWethy et al., 2010; Whitlock et al., 2015). Even in ecosystems that likely supported moderate levels of pyrodiversity historically, shifts in one or more dimensions of pyrodiversity could have detrimental effects. For example, in California chaparral, the increased fire frequency and corresponding increased range of time since fire have led to non-native plant invasions, type conversion and loss of habitat for shrubland-dependent organisms (Miller et al., 2022; Syphard et al., 2019). A key area of future research is to identify optimal levels or desirable ranges of pyrodiversity for different ecosystems and taxa of conservation concern (Kelly & Brotons, 2017), particularly in regions (e.g. Asia) and ecosystems (e.g. tropical forests) that have thus far seen little pyrodiversity research (Jones & Tingley, 2022).

The spatial scale at which pyrodiversity affects organisms is likely based on individual mobility, dispersal ability and/or perceptual characteristics relative to the scale of landscape heterogeneity created by pyrodiversity (Figure 4). Sessile taxa, such as plants, respond to pyrodiversity at fine scales (Wilkin et al., 2021). Lichens and fungi or near sessile (e.g. soil microbes) communities are also likely sensitive to fine-scale variations in fire but are understudied. At intermediate scales, bees were influenced by pyrodiversity within 150m of survey locations (Poniso et al., 2016). For more mobile taxa such as bats and birds, pyrodiversity can influence diversity at multiple scales ranging from 250m to 10km (Blakey et al., 2021; Steel et al., 2019; Tingley et al., 2016). Individual species of birds, such as the black-backed woodpecker, show age-dependent pyrodiversity relationships that

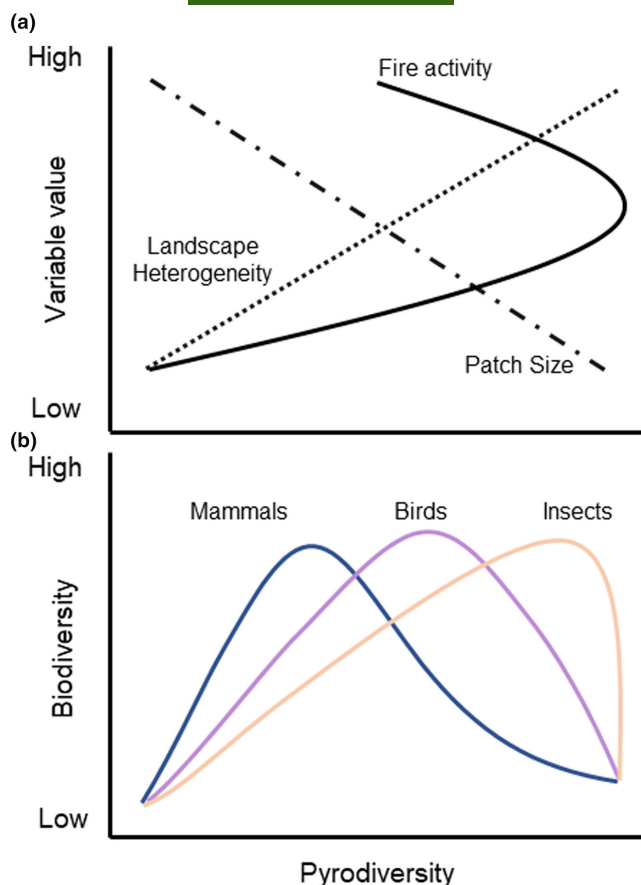


FIGURE 3 Theoretical relationships between biodiversity and variables of landscape pattern and process. (a) Pyrodiversity is expected to increase landscape heterogeneity and decrease patch size linearly. It's relationship with fire activity is expected to be non-linear where both the absence of fire and regular fire patterns (e.g. burning every season) can reduce pyrodiversity. (b) Hypothetical response curves illustrating that taxa with different sensitivities to fragmentation or communities associated with different fire regimes may show unique threshold-specific patterns of biodiversity with pyrodiversity.

emerge at the home-range scale (between 20 and 300ha) based on daily movements and nest site choices (Stillman et al., 2021; Stillman, Siegel, Wilkerson, Johnson, Howell, & Tingley, 2019; Tingley et al., 2014). Carnivore richness, measured at home range scales of 10km was highest at intermediate levels of pyrodiversity (Furnas et al., 2022). Based on these observations, pyrodiversity at many scales is needed to foster diversity across taxons but additional multi-scale research is needed to identify scale optimums for different taxa and environmental conditions and help explain the apparent variability in responses to pyrodiversity among taxa.

Additional factors beyond the eco-evolutionary history and scale are also important to consider in studies of pyrodiversity. Studies that tease apart when factors are indirect drivers, additive effects or when they mediate the effect of pyrodiversity itself would further our understanding of ecological mechanisms at play. Environmental conditions such as climate, topography, soils, anthropogenic alteration and interactions with other disturbances

(e.g. drought mortality) can all influence biodiversity, but they may do so indirectly by determining the amount of pyrodiversity that occurs or by affecting biodiversity independently. For example, the micro-hydroclimatic difference between wet meadows and upland conifer forests can drive differential burn severity and resulting pyrodiversity along the meadow-forest ecotone, as well as differences in soil productivity that can determine suitability for different plant species (Wilkin et al., 2021).

3 | METHODOLOGICAL CHOICES AND LIMITATIONS

Why support for the pyrodiversity–biodiversity relationship differs so greatly among studies remains an open question. Understanding whether and how the strength of the underlying mechanism(s) varies among ecosystems and with respect to taxa would be very useful to fire management and biodiversity conservation, yet our understanding is confounded by the many ways in which pyrodiversity has been measured and by data limitations. When attempting to test the underlying mechanisms of the pyrodiversity–biodiversity relationship, careful consideration of methodological options and limitations is necessary.

3.1 | Pyrodiversity metrics

Conclusions about pyrodiversity–biodiversity relationships depend on methodological choices by investigators and limitations in data availability and precision (Figure 1). As studies into pyrodiversity proliferate, so have the approaches to quantifying pyrodiversity and assessing its relationship with biodiversity (Jones et al., 2022). Among the various methodological decisions, researchers must choose which fire regime attributes to assess, which diversity metrics to apply, and whether to assess pyrodiversity directly or indirectly (Figure 5). To date, the predominant approach is to measure variation in a single fire regime attribute, such as severity (e.g. Steel et al., 2019; Tingley et al., 2016) or frequency (e.g. Brown & York, 2017; Taylor et al., 2012), often using simple and well-established statistical measures (e.g. standard deviation; Figure 5C). The single-attribute approach implicitly assumes that this aspect of fire history is the primary driver of biodiversity for a given system. Some recent studies have moved beyond the single-attribute approach by treating unique combinations of multiple fire regime attributes (e.g. time since last fire and severity class) as distinct 'species' in order to calculate diversity metrics such as Simpson's diversity index (Figure 5d,h; Ponisio et al., 2016; Wilkin et al., 2021). Still others have treated different components of a fire regime as functional traits (sensu biological traits such as wing length or body mass) and applied multidimensional analyses to measure pyrodiversity using functional diversity metrics (Figure 5d,h; Hempson et al., 2018; Steel et al., 2021; Wilkin et al., 2021).

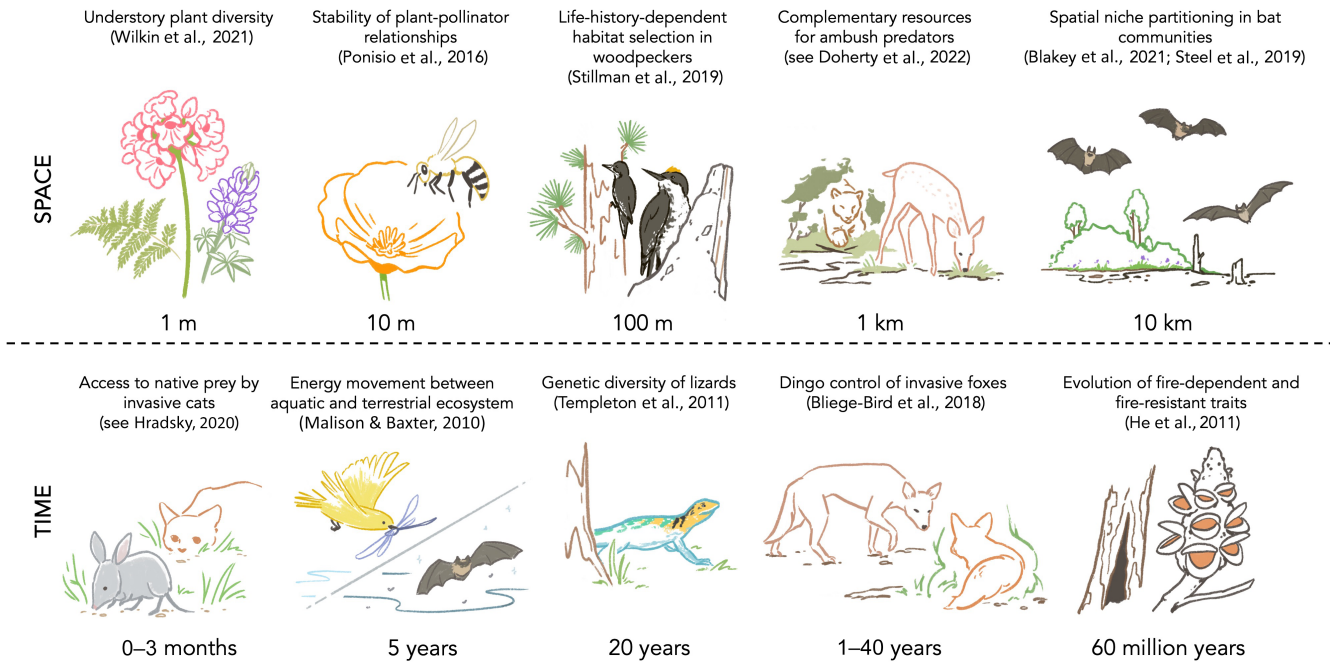


FIGURE 4 A variety of evidence exists supporting the pyrodiversity–biodiversity over a range of both spatial and temporal scales, indicating a potential pervasive influence of this ecological phenomenon on community structure and ecosystem function.

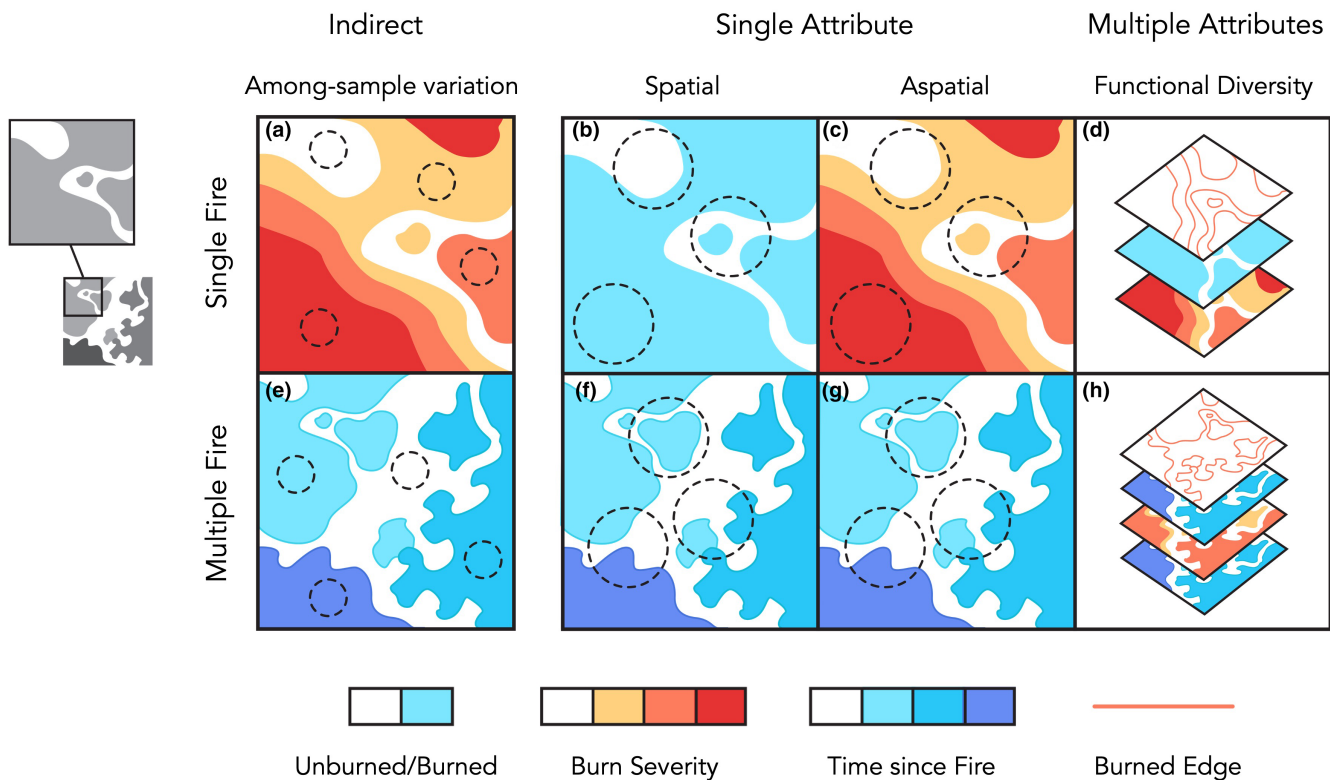


FIGURE 5 A classification of pyrodiversity metrics, based on single fire and multiple fire categories (rows), as well as indirect single fire attributes (spatial and aspatial) and multiple fire attributes (columns). Metrics that examine pyrodiversity–biodiversity relationships using indirect inference (a, e) are differentiated from direct measures because they do not quantify variability within or around a sample unit. Single attribute approaches can consider explicitly spatial (e.g. patch density; b and f) or aspatial (e.g. severity or time since fire; c and g). Multi-attribute approaches that use unique combinations of fire attributes or functional diversity metrics can be applied to individual fires (d) or to the full fire history of a landscape (h). Fire regime attributes illustrated include: burn severity (a, c, d and h), patch density (b, d), time since fire (e, g) and patch density weighted by time since fire (f). Note that the single fire illustrated in the top row is a subset of the multiple fire landscape in the bottom row (see inset).

Investigators must also choose whether to assess the pyrodiversity of individual fires (e.g. within-fire severity or patch size variation) or use the full fire history of a landscape, which may also include measuring the variation in fire frequency and/or seasonality. Jones and Tingley (2022) further differentiate between direct and indirect assessments of pyrodiversity, where direct tests link biological samples within a spatial unit to variation in fire attributes within or immediately surrounding the same spatial unit. In contrast, some have taken an indirect approach where variation in fire attributes is assessed among sample units and inference is made by the degree of difference in biological diversity among areas with different fire histories (e.g. Taillie et al., 2018; Figure 5a,e). The diversity of methodological approaches provides opportunities to better understand the nuanced ecological role of pyrodiversity but also poses challenges when trying to draw broad scientific conclusions or make practical management and policy recommendations (Jones & Tingley, 2022).

The selection of a pyrodiversity metric is dependent on whether the pyrodiversity–biodiversity relationship is being studied as an aggregate effect on biodiversity or a component effect on individual species (Jones & Tingley, 2022). At the scale of a community or ecosystem, pyrodiversity metrics that incorporate multiple fires and multiple attributes may be preferred (Figure 5h). However, when studying the response of a single species to pyrodiversity, the variability of a single attribute that is most likely to produce a specific functional response may be useful. For example, species may require landscapes with different burn severities for different age classes (Stillman, Siegel, Wilkerson, Johnson, & Tingley, 2019), and some predators may be able to capitalise on the hunting benefits provided by burned edges (Broken-Brow et al., 2019; Parkins et al., 2018). Spatial measures of heterogeneity such as edge density and patch density are likely to be particularly important for mobile and long-lived organisms, which require complementary resources within the landscape (Figure 5b,f; Bradstock et al., 2005; Nimmo et al., 2018).

3.2 | Data limitations

Limited data availability or quality can constrain our ability to observe the true pyrodiversity–biodiversity relationship of a system and apply that knowledge for conservation (Figure 1). Comprehensive data on spatially explicit fire occurrence and frequency is dependent on institutional fire records, whose quality and temporal span vary across the globe. The development of satellite-borne sensors has greatly advanced our ability to collect consistent fire data. Most notably, imagery from the Landsat family of satellites allows for spatially explicit estimates of burn severity back to the mid-1980s. These data have been invaluable for pyrodiversity research, but their utility is limited to ecosystems where we have calibrated severity models (e.g. North American conifer forests; Parks et al., 2019). These data challenges are especially acute where only part of the historic range of pyrodiversity is represented in the contemporary record. For example, a researcher's ability to test variation in fire frequency is

limited when fire events are rare due to a naturally infrequent-fire regime or aggressive fire suppression. These limitations can be mitigated somewhat as advances in remote sensing and modelling continually improve our ability to measure recent pyrodiversity among ecosystem types and at finer spatial resolutions. There are active and ongoing efforts by the broader fire ecology and biogeography community to resolve many of the data challenges underlying these limitations (e.g. Hagmann et al., 2021; Haugo et al., 2019; Morgan et al., 2017), which promise to open new avenues for pyrodiversity research in the years ahead.

4 | PYRODIVERSITY AND SHIFTING FIRE REGIMES

Each ecosystem has its own historical fire regime that arose through the interaction of native vegetation co-evolved with fire and influenced by topography, climate and humans over thousands to millions of years (Figure 1; Bond & Keeley, 2005). In many locations, however, contemporary fire-human interactions have pushed ecosystems far from historical norms (Flannigan et al., 2009; Hagmann et al., 2021; Haugo et al., 2019; Higuera et al., 2021; Williams et al., 2023), likely including changing levels of pyrodiversity with consequences for biodiversity (Jager et al., 2021). Thus, in different ecosystems, pyrodiversity has either increased or decreased, sometimes rapidly. For example, in frequent-fire forests of the western United States, fire suppression and exclusion have led to a decline in pyrodiversity (Martin & Sapsis, 1992), while the arrival of Polynesians and human-driven fire to the South Island of New Zealand approximately 800 years ago resulted in the rapid increase in fire activity and biodiversity loss of the native fire-intolerant flora (Bond et al., 2004; McWethy et al., 2010).

Changes in fire frequency, timing (seasonality) and severity are three common ways in which pyrodiversity is directly manipulated by humans. For thousands of years, Indigenous peoples strategically set fires or incorporated lightning-ignited fires to manage ecosystem structure for hunting, farming and foraging opportunities, which in part drove pyrodiversity (Bird et al., 2018; Hoffman et al., 2021; Trauernicht et al., 2015). However, disagreements exist on the historical scale, timing and extent of human-set fires around the globe (Bowman et al., 2011; Ryan et al., 2013). In ecosystems where human-fire relationships have existed since the late Pleistocene and where plants and animals have co-evolved with fire, it can be difficult to separate historical lightning and human ignitions (Bowman et al., 2022). Throughout much of the 20th century, policies of fire suppression and exclusion decreased fire frequency in many parts of the world, as attempts were made to eliminate fire from landscapes. This decline in fire frequency decreased pyrodiversity (Martin & Sapsis, 1992), but also increased fuel levels and coupled with industrial forest management ultimately resulted in greater burn severity when fire eventually returned (Levine et al., 2022; Steel et al., 2015; Stephens et al., 2014). In contrast, fire frequency has often increased in the wildland-urban interface (WUI), where human-caused ignitions (e.g. powerlines, cars,

cigarettes and camp fires) are plentiful (Fusco et al., 2022; Higuera et al., 2023; Syphard et al., 2017). In some regions, low-severity fire has been reintroduced in the form of prescribed fire to emulate the historic fire regime (Miller et al., 2017). This is in contrast to area that historically had largely mixed-severity fires such as the dry interior forests of British Columbia, Canada. In such fire regimes, the application of low-severity prescribed fire does not fully reflect the variability of previous fire activity and may not be informed by Indigenous knowledge on historic cultural burning (Chavardès et al., 2020; Levy et al., 2022).

Changing fire regimes can be exacerbated by or interact with other global change factors to influence biodiversity. Climate change is causing warmer weather, which, when combined with declining or more infrequent precipitation events, can lead to vegetation drying that extends fire seasons and increases flammability, ignitions and severity (Moritz et al., 2012; Parks & Abatzoglou, 2020; Parks et al., 2015; Westerling, 2016). Although we do not yet have a clear understanding of how climate change is influencing pyrodiversity worldwide, in certain landscapes, such as Mediterranean-type ecosystems and boreal conifer forests—climate change is expected to decrease pyrodiversity, creating conditions conducive to frequent, and more impactful, high-severity fires (Jones & Tingley, 2022; Whitman et al., 2022). In some ecosystems where invasive species have an outsized impact on native biota, shifts in fire regimes may have notable indirect impacts on biodiversity. For example, increasingly frequent and severe fires in Australia could lead to predation pinch points where, shortly after the fire and prior to vegetation regeneration, introduced predators have increased access to native prey (Hradsky, 2020). Given that many native prey species require fire for their persistence, it follows that more heterogeneous fire regimes, including patchy, lower-severity vegetation refuges, are likely to improve the survival of some species immediately after fire (Davies et al., 2018). These effects carry over into intermediate time scales, where pyrodiversity maintained through cultural burning promotes diverse niches for native animals while seemingly giving native predators a competitive advantage over invasive predators (Bird et al., 2018).

5 | ADVANCING PYRODIVERSITY RESEARCH AND APPLICATION

5.1 | Future pyrodiversity research

Pyrodiversity is now recognised as an important aspect of how fire affects ecological communities, but there are many unanswered questions surrounding when and how pyrodiversity drives biodiversity. The effects of pyrodiversity are reported to vary substantially among different species, taxonomic groups and ecosystems, and this variability likely reflects life history and eco-evolutionary differences among organisms and ecological contexts (Jones & Tingley, 2022). To some extent, however, inconsistent results regarding pyrodiversity effects on biodiversity may reflect the numerous ways to conceptualise and quantify pyrodiversity. Here,

we suggest best practices and future research directions that can advance the understanding of the ecological and cultural role of pyrodiversity and better apply the concept to fire management and biological conservation.

The many approaches to testing the pyrodiversity–biodiversity hypothesis have both provided innovations in pyrodiversity science and challenged generalisations in the literature. We do not advocate for strict standardisation of methods but offer some guidelines to facilitate cross-study comparisons and future syntheses. When initiating future tests of the hypothesis, we recommend scientists consider the following:

1. *Define the mechanism(s) being assumed and/or tested:* Explicit consideration of the causal relationships will help the field move beyond simple documentation of correlations. Where possible, large manipulative (e.g. using prescribed fire programmes) or natural experiments (e.g. contrasting watersheds with restored vs. fire-suppressed fire regimes) can help isolate the process of interest.
2. *Be explicit about the spatial and temporal scale being considered:* Does the scale at which pyrodiversity is measured match the process or life histories of the organisms of interest (Figure 4)? Are there limitations on how pyrodiversity can be quantified (e.g. resolution of satellite imagery or temporal extent of fire history maps) that affect the inference drawn from a study's results? Further, investigations explicitly focused on the scale-dependence of pyrodiversity–biodiversity relationships for different groups of organisms will advance the field.
3. *Consider the assumed and modelled form of the pyrodiversity–biodiversity relationship:* Often, discussions of the pyrodiversity–biodiversity relationship implicitly assume a monotonic relationship whereby greater pyrodiversity indefinitely increases available niche space and ecological opportunities for new species (Martin & Sapsis, 1992). However, others have suggested that the relationship between pyrodiversity and biodiversity is non-linear, with biodiversity maximising and then declining at high levels of pyrodiversity due to increasing habitat fragmentation (He et al., 2019) or the generation of novel niches (i.e. through vegetation type conversion) to which the native species pool is not adapted (Figure 3; Steel et al., 2021).
4. *Consider the historical and contemporary contexts:* Has the ecosystems' fire regime significantly departed from historical conditions under which native species evolved and/or communities assembled? How might this departure or likely future departure under climate change influence the pyrodiversity–biodiversity relationship for the study system and taxa of interest?
5. *Take care to select pyrodiversity and biodiversity metrics that align with the goals of the analysis:* Testing multiple metrics of pyrodiversity within the same dataset may also provide useful comparisons that help resolve confusion caused by the numerous pyrodiversity metrics. Ideally, chosen metrics would match those in the existing literature for direct comparison among studies and subsequent synthetic analyses (Figure 4).

Beyond expanded studies of the direct relationship between pyrodiversity and biodiversity, pyrodiversity science would also benefit from exploration of the drivers of pyrodiversity, how pyrodiversity varied among ecosystems historically and how to apply the pyrodiversity concept in management and conservation. Some progress has been made in assessing the ultimate drivers of pyrodiversity in Africa and the forests of western North America (Hempson et al., 2018; Steel et al., 2021), but these studies are conducted at coarse spatial scales and/or encompass a limited number of ecosystem types. Most pyrodiversity research focuses on contemporary patterns of pyrodiversity, which can be readily analysed through remote sensing approaches. Although great progress has been made in reconstructing the central tendencies of historical fire regimes, historical pyrodiversity patterns are rarely quantified and remain poorly understood. Similarly, there have been few efforts to predict future pyrodiversity using fire simulations. Considering historical fire regimes is critical for understanding the contemporary effects of fire on biodiversity. A better understanding of historical pyrodiversity and predicting future patterns are both important frontiers for pyrodiversity–biodiversity research. Finally, additional research into the practical application of pyrodiversity science—importantly supporting Indigenous-led ecological knowledge and applications—can aid efforts to conserve biodiversity, including in areas with multiple ecological and cultural management objectives. For example, in addition to supporting biodiversity, pyrodiverse landscapes have been linked to reduced fire hazard and increased hydraulic function (Stephens et al., 2021), although the explicit assessment of pyrodiversity on non-biological resources remains rare.

5.2 | Considerations for pyrodiversity management

As a growing framework, pyrodiversity is both implicitly and explicitly incorporated in management strategies. While the term is often omitted, in many cases, existing Indigenous stewardship, prescribed fire and other fire management programmes already produce landscape variation in fire characteristics by design. The recent proliferation of pyrodiversity research provides an opportunity to hone fire management practices using emerging scientific and traditional ecological knowledge (TEK). When Western science and TEK align, they can inform optimal levels of pyrodiversity that support various management objectives or whether managers should aim to increase or decrease different dimensions of pyrodiversity (e.g. variation in severity or frequency) relative to existing approaches.

The concept of pyrodiversity has been formalised as a prescriptive practice in some management plans, most notably patch-mosaic burning of subtropical savannas located in some South African national parks (Wilgen et al., 1998). The patch-mosaic-burning approach includes the initiation of prescribed burns at random locations on the focal landscape where fires are allowed to burn until a target threshold is reached. The result is a patchwork of post-fire conditions that vary in extent, seasonality, time since fire and other characteristics. However, this pyrodiversity-driven management

paradigm has been critiqued for lacking substance in terms of its operational guidelines, including the total percentage of area burned, desired patch size frequency distribution and seasonal distribution of fires (Parr & Andersen, 2006).

An emerging management approach in North America known as 'pyrosilviculture' attempts to address multiple forest and fire management goals through the strategic use of prescribed burning, mechanical thinning and managed wildfire to restore fire-dependent forests at the landscape scale (North et al., 2021). This synergistic approach indirectly impacts pyrodiversity by operationalising wildfire to decrease fuel loads within strategic areas of a landscape. However, to fully restore pyrodiversity and its potential benefits, increasing capacity for Indigenous-led fire stewardship is necessary to directly increase the abundance and composition of specific plant and animal species. Depending on fire practices, both Indigenous fire stewardship and Western fire management can restore pyrodiverse landscapes by intentional selection or removal of flammable plant species, promoting patch mosaics and creating dynamic forest structure (Hoffman et al., 2021).

These approaches and their critiques highlight a larger challenge when using pyrodiversity science to inform land management: fire is a blunt and unpredictable tool. Even if the science suggests an optimal level or configuration of pyrodiversity, precision prescriptions of pyrodiversity are unlikely to be met even under the most ideal burning conditions. Such an observation might lead one to conclude that pyrodiversity science has limited use in on-the-ground fire management. Rather, the observation should point to the need for further research on linking pyrodiversity science to management through an adaptive learning cycle. Furthermore, unpredictability in fire behaviour will lead to variation, and variation is at the heart of the pyrodiversity concept. Thus, there is potential for the pyrodiversity concept to provide great utility in land management, but further targeted research is needed.

Here, we suggest several guidelines for applying the pyrodiversity paradigm within an adaptive management cycle that includes research, learning and co-production of knowledge with fire practitioners.

1. *Do not reinvent the wheel:* All fire management programmes generate variation in fire characteristics, and these programmes have existing terminologies to describe the concept that researchers call pyrodiversity. Pyrodiversity science would benefit from learning these terminologies, and practitioners would benefit from learning about existing pyrodiversity science. Additional research is needed to understand the extent to which concepts loosely related to pyrodiversity are already implemented in management and how existing systems should be adapted to incorporate pyrodiversity science.
2. *Recognise that high pyrodiversity may not always be desirable:* It is critical to remember that 'increasing' or 'decreasing' pyrodiversity does not necessarily have consistent consequences for all components of biodiversity (Figure 3). Natural ecosystems are adapted and co-evolved to historical fire regimes that produce a certain amount of pyrodiversity. Optimal levels of pyrodiversity for

biodiversity are likely highly context- and ecosystem-dependent, requiring increased research into the pyrodiversity–biodiversity relationship for a given ecosystem or fire regime.

3. *Support Indigenous-led fire stewardship*: The original concept of pyrodiversity as articulated by Martin and Sapsis (1992) was linked to the hypothesised beneficial burning practices of Indigenous peoples that generated abundant habitat for wildlife. Subsequent research has indeed demonstrated that cultural burning practices executed by Indigenous peoples around the world provide enormous benefits for biodiversity (Hoffman et al., 2021). It follows that prudent application of fire management to benefit biodiversity should rely on TEK and support Indigenous communities in their use of cultural fire. Understanding linkages between Western pyrodiversity science and Indigenous burning practices (e.g. Greenwood et al., 2022) could further the potential success of pyrodiversity as a legitimate management paradigm.

6 | CONCLUSION

The relationship between pyrodiversity and biodiversity is increasingly recognised as an important driver of ecological communities' composition and function. While progress has been made, there remains much to learn about the underlying mechanisms driving pyrodiversity–biodiversity relationships, how they vary among ecosystems and across scales, and how best to incorporate our growing understanding into the application of pyrodiversity science. Among the current knowledge gaps is a need to better understand how global change affected pyrodiversity in the past and how ongoing changes in fire regimes are likely to influence pyrodiversity in the future. The development of a more general understanding of the ecological role of pyrodiversity will benefit from greater consistency in its conceptualisation and quantification and facilitate the practical application of the concept. By incorporating insights from pyrodiversity science, TEK and adaptive management, we can improve fire management for biodiversity and promote the conservation of ecological communities.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data was created or analysed in this study.

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BIOSKETCH

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