

Pyrodiversity and biodiversity: A history, synthesis, and outlook

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Abstract

Aim: Pyrodiversity is the spatial or temporal variability in fire effects across a landscape. Multiple ecological hypotheses, when applied to the context of post-fire systems, suggest that high pyrodiversity will lead to high biodiversity. This resultant “pyrodiversity–biodiversity” hypothesis has grown popular but has received mixed support by recent empirical research. In this paper, we sought to review the existing pyrodiversity literature, appraise support for the pyrodiversity–biodiversity hypothesis, examine potential mechanisms underlying the hypothesis and identify outstanding questions about pyrodiversity and future research needs.

Location: Global terrestrial ecosystems.

Methods: We performed a systematic literature review of research related to pyrodiversity and the pyrodiversity–biodiversity hypothesis. We also examined how two individual species with distinct relationships with fire (spotted owl *Strix occidentalis* and black-backed woodpecker *Picoides arcticus*) respond to pyrodiversity as case studies to illustrate underlying mechanisms.

Results: We identified 41 tests of the pyrodiversity–biodiversity hypothesis reported from 33 studies; 18 (44%) presented evidence in support of the pyrodiversity–biodiversity hypothesis, while 23 (56%) did not. Our literature review suggested that support for the pyrodiversity–biodiversity hypothesis varies considerably with no consistent patterns across taxonomic groups and ecosystem types. Studies examining the pyrodiversity–biodiversity hypothesis often define pyrodiversity in different ways, examine effects at different scales and are conducted in ecosystems with different natural fire regimes, baseline levels of biodiversity, and evolutionary histories. We suggest these factors independently and jointly have led to widely varying support for the pyrodiversity–biodiversity hypothesis.

Main Conclusions: Clarifying the pyrodiversity–biodiversity hypothesis will be facilitated by stronger development of the different potential mechanisms underlying pyrodiversity–biodiversity relationships, which can be aided by examining how individual species respond to pyrodiversity. Future research would benefit from a closer examination of the role of scale (e.g. scale dependence) in pyrodiversity–biodiversity relationships, standardization of pyrodiversity metrics, broad-scale mapping of pyrodiversity, and macroecological study of pyrodiversity–biodiversity relationships.

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KEYWORDS

ecological mechanisms, fire management, fire mosaic, megafires, pyrodiversity, pyrodiversity–biodiversity hypothesis, scale

1 | A CONCEPTUAL HISTORY AND EVOLUTION OF PYRODIVERSITY

Pyrodiversity describes the degree of variation in post-fire landscape characteristics within or among fires. While at its core pyrodiversity is a technical descriptor of the properties of burned areas, its conceptual roots are biological and tightly linked to community ecology, niche theory and biodiversity conservation. The term was formally introduced by Martin and Sapsis (1992), who described pyrodiversity as an agent of biodiversity, whereby “pyrodiversity begets biodiversity.” The authors hypothesized that the degree of variation contained within different dimensions of a fire regime, such as fire return interval, seasonality, size or intensity, will result in an associated mosaic of successional stages and structure that would define the breadth of niche space for different species to occupy. Thus, pyrodiversity is a composite characteristic of a fire regime: certain fire regimes will have higher or lower pyrodiversity, which will in turn lead to higher or lower biodiversity, respectively.

A central concern in the contemporary pyrodiversity literature is that a variety of anthropogenic factors may be decreasing pyrodiversity across landscapes, potentially leading to biodiversity losses. Indeed, a central element of Martin and Sapsis’ work was pointing out that pyrodiversity was likely decreasing because of recent human activities—in particular, the loss of indigenous fire, which had created or sustained pyrodiversity. Supporting this claim, there is now widespread historical and contemporary evidence of people promoting pyrodiversity across large landscapes (Bird et al., 2008; Taylor et al., 2016; Trauernicht et al., 2015), which is likely to influence how contemporary biotic communities respond to pyrodiversity. Whether real or hypothesized, temporal trends in pyrodiversity have the potential to reshape biodiversity patterns across ecosystems.

Yet, complicating our study of such trends is that there is no single operational definition of pyrodiversity. Martin and Sapsis’ proposition nearly three decades ago provided a strong conceptual foundation for the study of the pyrodiversity–biodiversity hypothesis, but their original definition of pyrodiversity was broad and operationally vague. How could pyrodiversity be measured and the pyrodiversity–biodiversity hypothesis be tested in practice? Since its conceptual introduction, pyrodiversity has been defined in many ways by researchers attempting to test the pyrodiversity–biodiversity hypothesis—each describing a different dimension or “axis of variability” in fire regime characteristics (Appendix 1). In addition, pyrodiversity is etymologically related to other concepts in fire ecology (Box 1), and so, the pyrodiversity–biodiversity hypothesis has—in essence—also been tested under other names (e.g. “patch-mosaic burning hypothesis”).

What constitutes a test of the pyrodiversity–biodiversity hypothesis? Most attempts to define pyrodiversity involve selecting a single fire dimension, such as fire age, and quantifying the spatial variation in that characteristic within each sampling unit (e.g. Taylor et al., 2012). The variability in that characteristic for each sampling unit can then be linked to species diversity within that sampling unit, enabling an explicit test of the hypothesis that increased pyrodiversity correlates with increased biodiversity (typically alpha diversity, but also see studies examining pyrodiversity relationships with beta diversity, e.g. Farnsworth et al., 2014; Leavesley & Cary, 2013; McGranahan et al., 2018; Pastro et al., 2011). Yet, the broad original definition of pyrodiversity has led to some relatively permissive interpretations of the concept, as well as confusion regarding what exactly does, and does not, constitute a study of pyrodiversity and a test of the pyrodiversity–biodiversity hypothesis. In our view, a test of the pyrodiversity–biodiversity hypothesis should meet a defined set of criteria (Box 2). While there exists a vast literature on how fire and fire regimes affect various aspects of biodiversity (e.g. how fire frequency influences plant richness)—and other recent syntheses have focused on these broad questions (Kelly et al., 2020)—relatively few studies explicitly examine the pyrodiversity–biodiversity hypothesis (Box 2).

The lack of a single definition of pyrodiversity has also led to considerable innovation in how pyrodiversity can be measured. Some researchers have explored empirical support for the pyrodiversity–biodiversity hypothesis using multiple independent measures of pyrodiversity (e.g. Farnsworth et al., 2014), while others have developed integrated multi-axis metrics of pyrodiversity (e.g. Ponisio et al., 2016; Steel et al., 2021). More recently, technological advances have permitted an expansion of how pyrodiversity can be defined, particularly incorporating fine-scale heterogeneity. For example, remote sensing tools such as Landsat allow researchers to define pyrodiversity as the variability in burn severity in forest systems (e.g. variation in tree basal area or canopy mortality) following fire in each sampling area (e.g. Tingley et al., 2016). In an interesting deviation from traditional inquiry, Bowman et al. (2016) defined pyrodiversity as “the coupling of biodiversity and fire regimes in food webs” focusing on trophic feedbacks and critiquing “simple, one-way statistical linkages between biodiversity surrogates and fire regimes...” that have characterized pyrodiversity–biodiversity research to date. Bowman et al. (2016)’s renewed focus on mechanism and ecosystem processes that shape and underly the pyrodiversity–biodiversity relationship is useful, and we discuss below the importance of future research focusing on mechanisms. The variety of approaches for defining and quantifying pyrodiversity have their own strengths and weaknesses, but each is also consistent with the breadth of Martin and Sapsis’ pyrodiversity–biodiversity hypothesis. In the absence of any critical evaluation of different metrics, there has been no

BOX 1 Pyrodiversity and related ecological concepts

The term pyrodiversity is related to several other ecological concepts. All of the below concepts are themes in landscape ecology and relate in some way to the measurement of variability but have subtly different histories of use and interpretations. Here, we define several of these concepts and describe how they are intertwined with pyrodiversity.

Patch-mosaic burning is a fire management approach originally applied in some South African national parks (e.g. Kruger and Pilanesberg) in the early 1990s (Van Wilgen et al., 1998). Application of the approach has since expanded and is more or less synonymous with the term pyrodiversity. The goal of patch-mosaic burning was to establish a mosaic of vegetation structural types through prescribed burning that would allow “efficient means of conserving biodiversity” (Van Wilgen et al., 1998). Under this fire management paradigm, prescribed burns are initiated at random locations throughout the project area and allowed to burn out by themselves until an established quota of burned area is reached. The result is a heterogeneous mosaic of burn conditions that vary in extent, seasonality and other characteristics. The emergence of the patch-mosaic burning paradigm paralleled the broader cultural shift away from equilibrium thinking to recognizing the importance of non-equilibrium processes in ecology (Parr & Brockett, 1999; Pickett & White, 1985). Related concepts/terminology include vegetation mosaic, fire mosaic and successional mosaic.

Mixed-severity fire is a term commonly used to describe fires that contain a broad gradient of post-fire tree basal area or canopy mortality (i.e. severity) with some mixture of low-, moderate- and high-severity effects. Mixed-severity fire is most commonly defined as containing between 20% and 70% tree mortality (or “high-severity fire”) across a fire area (Agee, 1993) although some definitions include an even broader range (e.g. 5%–70%). Such fires could almost certainly be characterized as containing a relatively high degree of pyrodiversity in most circumstances, although the spatial pattern of burn severity and the scale at which pyrodiversity is summarized may influence this generalization. Many fire regimes, particularly those in western North America, have widely been characterized as having mixed-severity fire regimes (e.g. DellaSala & Hanson, 2015). However, Collins et al., (2017) pointed out that the term mixed-severity fire is so broad that it carries little meaning, because nearly all forest fires experience between 20% and 70% high-severity fire, and moreover, this definition ignores the role of spatial patterns of burn severity. Pyrodiversity may face a similar issue related to how it is defined and interpreted (e.g. at what point is a fire, or a landscape, considered “pyrodiverse”) and reinforces the need to consider how pyrodiversity and associated ecological effects may vary as a function of scale.

Fire regime is the typical frequency, size, seasonality, intensity, pattern and other attributes of burned areas that have been typical for a given ecosystem over a long period of time (Agee, 1993; Gill, 1975; Kilgore, 1981). Different ecosystems are characterized by different fire regimes because of broad-scale variation in climate, vegetation type and ignition frequency (Pyne et al., 1996). Pyrodiversity thus might be considered one component of fire regimes (which itself is comprised of one or more components), where fire regimes are characterized by a typical (or range of) within- or among-fire pyrodiversity. For example, frequent-fire regimes in seasonally dry forests might be characterized by relatively high pyrodiversity (i.e. they contain a more dynamic mosaic of successional stages). In contrast, infrequent-fire regimes in more mesic and high-elevation forest types might be characterized by relatively low pyrodiversity (i.e. having larger, more homogeneous fires and even-aged forest conditions). However, this dichotomy depends in part on the spatial and temporal scales being used to characterize fire regimes. Martin and Sapsis (1992) noted that fire suppression has altered fire regimes and has thereby likely reduced pyrodiversity (i.e. made fires more homogeneous), particularly at larger spatial scales, in some systems such as parts of the Pacific Northwest of the United States. Indeed, recent empirical work has confirmed that fires in California, USA, are increasingly becoming more homogeneously severe (Stevens et al., 2017; Steel et al., 2018).

The intermediate disturbance hypothesis (IDH) posits that too much or too little disturbance will favour lower species richness, but moderate levels of disturbance will maximize species richness (Connell, 1978; Karr & Freemark, 1985). For example, if disturbances that reset successional dynamics are very frequent, the community will be dominated by a smaller number of *r*-selected dispersal-adapted species and colonizers. If disturbances are too infrequent, late-successional characteristics will dominate and the community will be characterized by a smaller number of *K*-selected species and old-growth specialists. However, if disturbances are moderately frequent, the community will represent a highly dynamic mixture of *r*- and *K*-selected species that will lead to higher species richness. Fire regimes characterized by higher pyrodiversity may reflect “intermediate” levels of disturbance because low pyrodiversity could reflect either too much or too little disturbance, depending on how pyrodiversity is quantified. Thus, there is a natural connection between the IDH and the pyrodiversity–biodiversity hypothesis. Like pyrodiversity, the IDH is likely to show high sensitivity to the spatial and temporal scales at which disturbance is quantified.

Natural range of variability (NRV), also called historical range of variability (HRV), describes the range of ecological conditions that are typical of a given ecosystem or region, often prior to widespread modification by Western human society. Fire regime is thus an approach for characterizing the NRV of fire in a system. Because pyrodiversity is a metric that characterizes variation in fire conditions, there is therefore a natural linkage between these two concepts: historical patterns of pyrodiversity characterized

BOX 1 (Continued)

one axis of the natural range of variability in fire characteristics. NRV is often invoked in ecosystem restoration, where it is used to guide management and restoration targets to approximate historical and ecologically appropriate landscape conditions (Safford & Stevens, 2017; Swanson et al., 1994).

Patchiness is a concept with roots in landscape ecology that describes the degree of variability in discrete land cover or habitat classes (e.g. vegetation types) in a landscape. Patchiness can be formally quantified in a wide variety of ways, including patch density (number of patches of a given type), mean patch size, patch richness (number of different patch types) or other metrics that characterize patches in terms of their shape (e.g. fractal dimension, perimeter-to-area ratio). Fires can be characterized in terms of their patchiness (e.g. size or shape of different burn severity classes or fire age classes), and thus, there might be some predictable relationships between patchiness and pyrodiversity. For example, landscapes with high patch richness (e.g. many different burn severity or fire age classes) would be more pyrodiverse. Some studies investigating ecological effects of pyrodiversity used fire “patchiness” as a synonym for pyrodiversity (e.g. Lawes et al., 2015; McGranahan et al., 2018; Menges & Quintana-Ascencio, 2004). Patches of different fire severities or ages also imply the existence of edges between patch types, and pyrodiversity characterized at finer spatial scales will be higher at these interfaces between patches than within a given patch.

single “correct” or “best” way to define pyrodiversity, and different researchers have unsurprisingly defined pyrodiversity in different ways according to the objectives and ecological context of their studies.

One consequence of the wide variety of approaches for quantifying pyrodiversity is that different researchers have seldom asked the same question of the pyrodiversity–biodiversity hypothesis. Directly comparing support for the hypothesis among studies that apply different operational definitions of pyrodiversity might seem questionable, because the lack of a consistent definition may make broad generalizations and synthesis across studies challenging. However, this variability may also hold unexpected benefits because different approaches for quantifying pyrodiversity may allow researchers to test different ecological mechanisms underlying the pyrodiversity–biodiversity hypothesis. Among studies, pyrodiversity is not only quantified in different ways, and tests applied to different taxa in different ecosystems, but it is also quantified at different spatial and temporal scales. As is the case for all ecological phenomena (Levin, 1992; Wiens, 1989), pyrodiversity–biodiversity relationships are likely to be scale-dependent. Thus, the scale (e.g. spatial grain or extent, or temporal window) selected by the researcher will influence whether the hypothesis is supported because different scales may test different mechanisms and may be more or less relevant for different taxa.

Here, we attempt to summarize and synthesize the existing state of knowledge on the pyrodiversity–biodiversity hypothesis, provide clarity on proposed mechanisms, and search for any consistent rules or results. Additionally, we present case studies of two focal species of conservation concern in western North America for which emerging research is demonstrating that pyrodiversity plays a role in the species’ ecology, providing intriguing evidence for underappreciated mechanisms that could underlie the pyrodiversity–biodiversity hypothesis. We then identify major unanswered questions and identify research gaps in the study of pyrodiversity and the pyrodiversity–biodiversity hypothesis. In sum, we conclude that, while much

research has been conducted on pyrodiversity, rich opportunities remain to rapidly advance pyrodiversity research in the era of megafires.

2 | SYNTHESIS OF EXISTING TESTS OF THE PYRODIVERSITY–BIODIVERSITY HYPOTHESIS

We performed a systematic literature review of pyrodiversity research via Web of Science using the workflow outlined in Grames et al. (2019) and the associated R package litsearchr version 1.0.0. First, we conducted a naive search using the search string (“pyrodiversity” AND “biodiversity”) across three databases: Biological Abstracts, BIOSIS Citation Index and Zoological Record. Then, we used the litsearchr package to consolidate and de-duplicate records from the naive search results and build a keyword co-occurrence network to capture themes related to, but not included in, our original search string. We manually reviewed keywords and generated an expanded Boolean search for a refined literature review. The final search string was ((pyrodivers* OR "fire* mosaic*" OR "burn* pattern*" OR "mosaic* burn*" OR "patch* mosaic*" OR "pyrodivers* landscap*") AND (biodivers* OR "beta* divers*" OR "communiti* composit*" OR "speci* composit*" OR "speci* divers*" OR "speci* rich*" OR "alpha* divers*" OR "communiti* divers*" OR "disturb* hypothesi*" OR "intermedi* disturb*")). We conducted this refined search across the three above-mentioned databases and assembled a final de-duplicated database on 5 October 2020.

Here, we summarize the results of the literature search. The search returned 176 results, 95 of which we determined to be relevant to the present paper (other studies were largely unrelated to fire and biodiversity). In addition, we searched through references of two recent fire-related review papers (He et al., 2019; Kelly et al., 2017) to identify papers that our literature search might have missed; this yielded an additional three papers that clearly examined

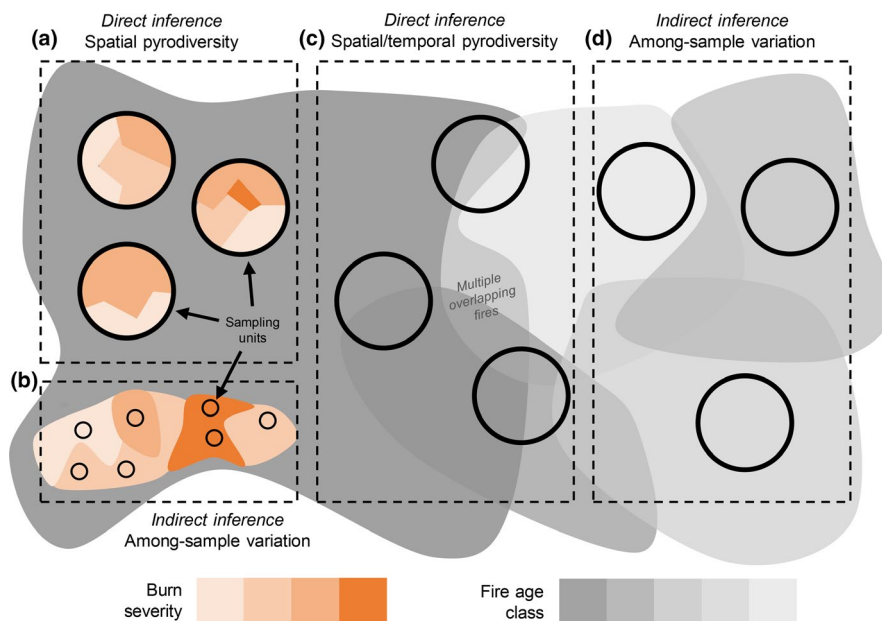
BOX 2 Testing the pyrodiversity–biodiversity hypothesis

Pyrodiversity was originally conceived as an inherently spatio-temporal concept. Martin and Sapsis (1992) described pyrodiversity as “variety in interval between fires, seasonality, dimensions, and fire characteristics, producing biological diversity at the microsite, stand, and landscape level.” This broad (and somewhat vague) definition has led to a proliferation of approaches for testing the pyrodiversity–biodiversity hypothesis in practice. Yet, in our view, simply examining how biodiversity responds to a chosen element of a fire regime does not provide the required elements for a direct test of the pyrodiversity–biodiversity hypothesis.

We propose that a direct test of the pyrodiversity–biodiversity hypothesis should include a metric of variation (e.g. coefficient of variation, Shannon diversity index) to be quantified on a fire characteristic (e.g. fire age, burn severity) *within* spatially replicated sampling units or a buffered area surrounding each sampling unit (insets a and c below). Variation should occur *within* sampling units, not strictly *among* sampling units. The *within*-sample variation in fire characteristics (i.e. pyrodiversity) is then linked to a *within*-sample measure of biodiversity (e.g. alpha diversity), and standard procedures such as regression or other models can be used to determine whether a linear or nonlinear relationship between the two variables exists (e.g. Tingley, et al., 2016).

The pyrodiversity–biodiversity hypothesis is sometimes examined in indirect ways as well. This situation often arises when variation in fire characteristics (e.g. time since fire, fire severity) occur *among* sampling units (see insets b and d below), and variation in species richness or community composition is then linked to *among*-sample variation in fire characteristics. Often, studies taking this approach will then infer that because different species are associated with different fire characteristics, it follows that landscape variation in these characteristics will support higher biodiversity (e.g. Taillie et al., 2018). We refer to this situation as an indirect inference about the pyrodiversity–biodiversity hypothesis. Indirect approaches may also go one step further by using optimization analyses of among-sample variation to more formally assess combinations of fire characteristics expected to promote biodiversity (e.g. Kelly et al., 2015).

Individual studies testing the pyrodiversity–biodiversity hypothesis may quantify either *spatial* or *temporal* components of pyrodiversity, or a combination of both (see below figure). Spatial pyrodiversity is the spatial variation in a fire characteristic (e.g. burn severity) within a sampling unit (see inset a). Temporal pyrodiversity is the spatial variation in a temporal fire characteristic (e.g. fire age/successional stage) within a sample unit (see inset c), which we note is inherently spatio-temporal. If no variation occurs within sampling units (insets b and d), then pyrodiversity has not been measured and a direct test of the pyrodiversity–biodiversity hypothesis is not possible. For example, sampling in inset b would simply yield a test of how biodiversity responds to burn severity, and inset d would test how biodiversity was affected by time since fire; neither would be considered a direct test of the pyrodiversity–biodiversity hypothesis.



the pyrodiversity–biodiversity hypothesis. We reviewed all 98 papers and noted the publication date, geographic location, ecosystem type, taxa studied, whether a test of the pyrodiversity–biodiversity

hypothesis appeared to have been performed and whether support for the hypothesis was inferred by the authors, how pyrodiversity was defined or conceptualized, and other key points and conclusions

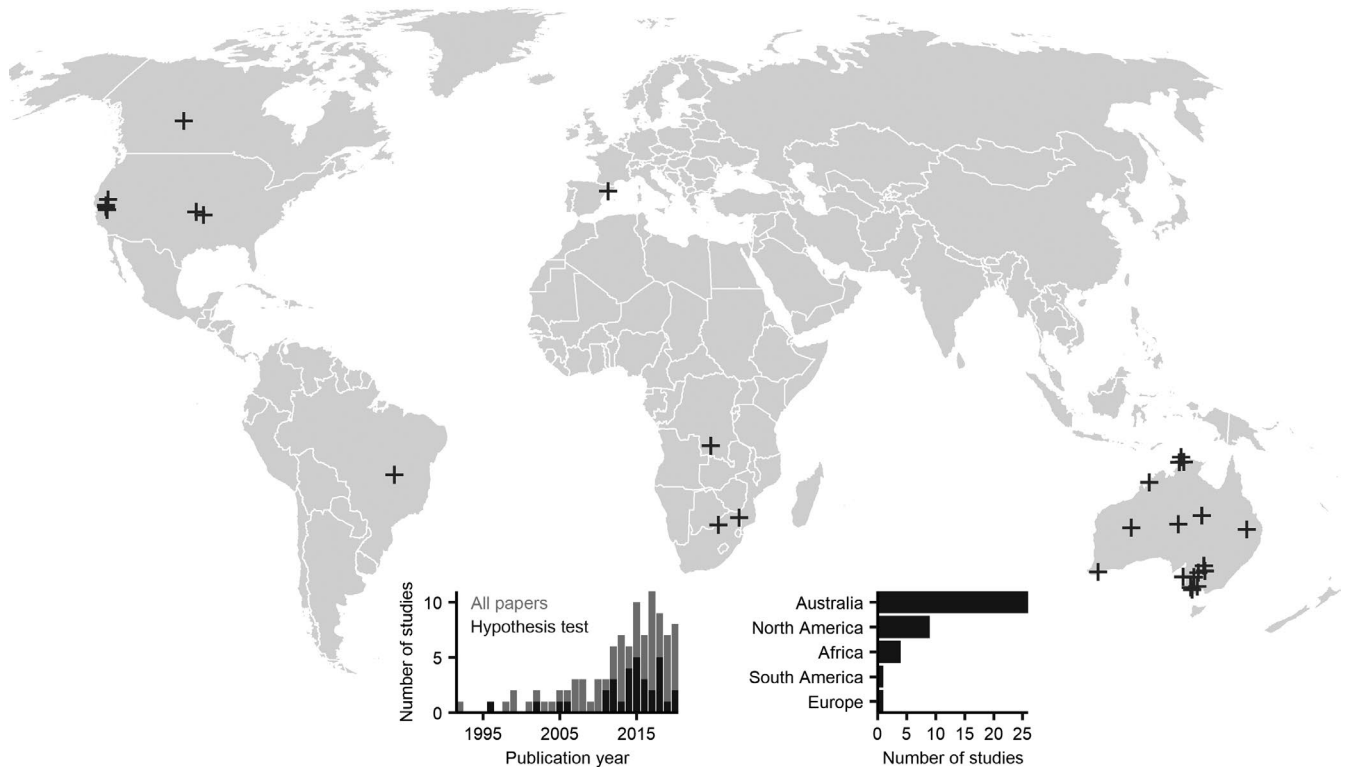


FIGURE 1 Global distribution of pyrodiversity-biodiversity research. Each grey “+” represents the approximate spatial location of studies that tested the pyrodiversity-biodiversity hypothesis (or, for broader-scale studies, the “+” shows the approximate geographic centre of the study area). The inset bar graph on the left shows trends in pyrodiversity-related research over the period 1992–2020; dark grey bars represent studies that tested the pyrodiversity-biodiversity hypothesis, while light grey bars show the total number of relevant studies from our literature search. The inset bar graph on the right shows the number of studies per continent. Our literature search did not reveal existing pyrodiversity-biodiversity research in Asia (there are no wildfires in Antarctica)

reached by the authors. Thirty-three studies appeared to have performed a test of the pyrodiversity-biodiversity hypothesis, and five of those studies reported effects across more than one broad taxonomic group (for a total of 41 study-taxa combinations that we treat as independent units) (see Appendix 1). We identified a distinction between *direct* and *indirect* inferences about the pyrodiversity-biodiversity hypothesis, which relates to whether the selected fire characteristic varied *within* or *among* sampling units, respectively (Box 2, Appendix 1).

Because of high variability in study design and how pyrodiversity was defined, we did not feel there was enough consistent information to compute standardized effect sizes in a meta-analytic framework. Therefore, effects from studies were tallied using a simplified “vote-counting” approach (Bushman, 1994). Vote-counting approaches have noted shortcomings, including but not limited to failing to account for sample and effect sizes. Moreover, tallying of studies in the “vote-counting” approach may be more likely to mask different kinds of pyrodiversity-biodiversity relationships, such as nonlinear (or “hump-shaped”) relationships (e.g., Steel et al., 2021). We acknowledge these caveats and point out that here our aim is to provide a broad summary of the pyrodiversity-biodiversity literature, with a focus on support for positive associations between pyrodiversity and biodiversity. However, there are many ways that spatio-temporal variation in fire regimes can shape biodiversity.

As further evidence accumulates and studies of pyrodiversity-biodiversity relationships become more standardized (see “Synthesis and research gaps,” as well as Box 2), additional types of evidence synthesis may be possible.

Studies examining the pyrodiversity-biodiversity hypothesis have been conducted on four continents with the majority of studies occurring in Australia (26 studies), followed by North America (9), Africa (4), South America (1) and Europe (1) (Figure 1). We observed a recent increase in research on the pyrodiversity-biodiversity hypothesis, with an initial increase beginning in 2006 (perhaps motivated by the seminal work by Parr & Andersen in 2006 that popularized and critiqued the hypothesis) followed by a rise in tests of the hypothesis after 2011 (Figure 1). The pyrodiversity-biodiversity hypothesis has been examined in birds (12 studies), invertebrates (11), mammals (7), reptiles (5), plants (4), plant-pollinator interactions (1) and bats (1) (Figure 2a). These studies have occurred in grasslands (7 studies), scrub/shrublands (9), savannas (10) and forests/woodlands (15) (Figure 2b).

Our literature review suggests that support for the pyrodiversity-biodiversity hypothesis varies considerably across taxonomic groups and ecosystem types. Of the 41 tests reported from 33 studies, 18 presented evidence in support of the pyrodiversity-biodiversity hypothesis, while 23 did not indicate support for the hypothesis. All taxonomic groups containing more than one study examining the

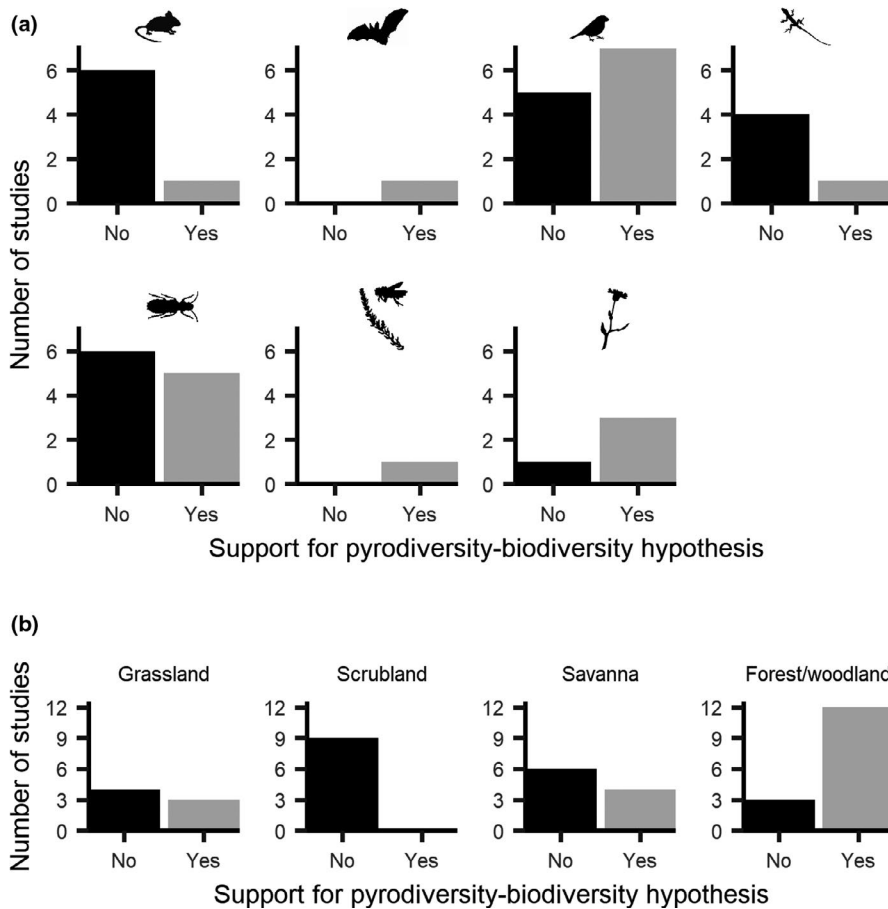


FIGURE 2 Summary of studies examining the pyrodiversity–biodiversity hypothesis grouped by broad taxonomic group and ecosystem type. (a) Support for the pyrodiversity–biodiversity hypothesis (from top left) terrestrial mammals, bats, birds, reptiles, invertebrates, plant–pollinator interactions, and pollinators (b) Support for the pyrodiversity–biodiversity hypothesis among four broad ecosystem types

pyrodiversity–biodiversity hypothesis showed mixed support: different studies suggested support either for or against the hypothesis (Figure 2a). The same pattern of mixed support was apparent when results were grouped by ecosystem type, except for scrub/shrubland ecosystems in which all existing studies have reported no support for the pyrodiversity–biodiversity hypothesis. Therefore, it does not appear that the pyrodiversity–biodiversity hypothesis is consistently supported or not supported within particular taxonomic groups or ecosystem types, suggesting that variation in the literature may be due to other factors. Thus, we must consider what factors may influence whether the pyrodiversity–biodiversity hypothesis is supported in empirical study.

We suggest that there are at least three interacting factors that may drive variation in support for the pyrodiversity–biodiversity hypothesis among studies: mechanism, history, and scale. In this context, mechanism refers to different studies asking different questions of the pyrodiversity–biodiversity hypothesis by defining pyrodiversity in different ways (see Appendix 1). As an example, examining how species richness is affected by the diversity of fire age classes across a landscape is asking a question related inherently to temporal processes—how different species accumulate and replace one another through time across different successional stages initiated by fire (e.g. Nimmo et al., 2013). In contrast, examining how species richness is affected by diversity in burn severity is asking a question inherently about spatial processes—how species

accumulate and partition resources across space based on structural heterogeneity produced by a single fire event (e.g. Steel et al., 2019). Questions related to the pyrodiversity–biodiversity hypothesis can thus vary in terms of exploring temporal versus spatial mechanisms, but spatial and temporal processes can also interact to influence strength of a pyrodiversity–biodiversity effect (e.g. Tingley et al., 2016).

Many specific spatial and temporal mechanisms grounded in ecological theory have been proposed (He et al., 2019; Kelly et al., 2017). For example, Kelly et al. (2017) discuss several hypotheses based on ecological mechanisms that may give rise to observed pyrodiversity–biodiversity relationships, including habitat complementation (spatial variation in fire effects fulfils multiple habitat needs of an individual species), habitat heterogeneity (spatial variation in fire effects enhances multispecies coexistence through creation of diverse habitats), habitat refuge (spatial variation in fire effects produces refuges and alters predator–prey interactions) and fire season (temporal variation in fire seasonality influences fire effects and alters multispecies coexistence). Different approaches for quantifying pyrodiversity may allow the above hypotheses to be further parsed. Studies examining these mechanisms and other spatial and temporal mechanisms in different systems should not necessarily be expected to arrive at the same conclusions about the pyrodiversity–biodiversity hypothesis when quantifying pyrodiversity in different ways.

The second factor that may drive variation in support for the pyrodiversity–biodiversity hypothesis among studies is history. In this context, history refers to the evolutionary environment and ecological regimes that have characterized different systems over time, and which may constrain the development of pyrodiversity–biodiversity relationships. For example, we may not expect the pyrodiversity–biodiversity relationship to look the same in boreal forests as in temperate or tropical forests. These ecosystems vary greatly in their overall species diversity (generally increasing from boreal to temperate to tropical) (Gaston, 2000) and limiting factors that influence fire ignitions and behaviour (ranging from fuel-limited dry ecosystems to climate-limited wet ecosystems) (Krawchuk & Moritz, 2011).

Fire regimes are a significant evolutionary force in both plants and animals (Bond & Keeley, 2005; Pausas & Parr, 2018). As such, there is an interplay between fire regimes over evolutionary time and accumulation of adaptive traits by species to those fire regimes. For example, conifer species associated with frequent-fire regimes have thick bark, tall crowns and flammable litter, while species associated with infrequent-fire regimes have thin bark, shorter crowns and less flammable litter (Stevens et al., 2020). These adaptations then produce stabilizing feedbacks that reinforce the fire regime (He et al., 2019). Because fire can reset community dynamics (He et al., 2019), there may be an expectation that ecosystems with more frequent-fire and low- to moderate-severity regimes might support more opportunities for evolutionary forces to rapidly give rise to biodiversity. In contrast, infrequent-fire systems might more often be characterized by climax communities dominated by a smaller number of species, and fewer opportunities for fire-related disturbances to open evolutionary pathways. Thus, the same degree of pyrodiversity (however defined) may never be observed in frequent- versus infrequent-fire systems; even if it was, the same degree of pyrodiversity might be associated with different levels of biodiversity and thus a different expected “shape” to the pyrodiversity–biodiversity relationship (e.g., Steel et al., 2021).

The third factor that may drive variation in support for the pyrodiversity–biodiversity hypothesis among studies is scale. In this context, scale may refer to several components of a given study, but we are referring to the spatial and temporal extent and grain of the analysis and to what extent these scales relate to relevant ecological scales for the organism(s) or taxa under study. For example, pyrodiversity at larger scales (e.g. larger spatial extent and grain) may be more relevant for larger-bodied mammalian assemblages than for terrestrial invertebrates because often the scale of effect varies positively with characteristics such as body size and dispersal ability (Jackson & Fahrig, 2012). Thus, relevant spatial scales for studying pyrodiversity–biodiversity relationships might scale with body size or other traits. Larger spatial and temporal scales of measurement may also be required to capture sufficient variability to detect a pyrodiversity–biodiversity relationship in infrequent-fire systems in comparison with frequent-fire systems.

In general, our review revealed that little attention is paid to the problem of scale in the study of pyrodiversity–biodiversity

relationships, with some exceptions. For example, while studying avian communities in dry mixed-conifer forests of California, Tingley et al. (2016) explored whether support for the pyrodiversity–biodiversity relationship was scale-dependent (e.g. pyrodiversity measured at the plot level or fire level). In this case, the authors found support for this relationship at both spatial scales—although slightly stronger at the larger scale—and similar support for this relationship being time-dependent (and thus scale-dependent in the temporal sense). In general, we advocate for future research to explicitly consider a multi-scale perspective in which support for the pyrodiversity–biodiversity hypothesis is tested at multiple spatial and temporal scales when possible, avoiding assumptions about the correct scale of effect (McGarigal et al., 2016).

In addition to operating independently on apparent pyrodiversity–biodiversity relationships, these three factors are also likely to interact with one another in complex ways. Certain definitions of pyrodiversity may represent mechanisms that more naturally operate at certain spatial or temporal scales, whose relative importance could vary based on the ecological and evolutionary history of the system under study. For example, consider defining pyrodiversity as the spatial variability in burn severity (e.g. Steel et al., 2019). This definition—which provides a mechanism for how species accumulate and partition resources across space based on structural heterogeneity produced by fire—might be more relevant in systems where stronger spatial gradients in burn severity exist because of higher spatial variation in fuel conditions (e.g. fuel-limited dry forest ecosystems). Within-fire variation in burn severity inherently occurs at finer spatial scales than any among-fire measures of pyrodiversity, and therefore might be more relevant for smaller-bodied organisms because of scaling of effects with body size as discussed above. In summary, all three of these factors—mechanism, history and scale—should be considered together when designing and interpreting studies that examine the pyrodiversity–biodiversity hypothesis.

3 | MECHANISMS UNDERLYING A DIVERSE RESPONSE TO PYRODIVERSITY

The high degree of variability in studies testing diversity responses to pyrodiversity gives rise to numerous questions about the mechanisms underlying such a phenomenon and whether a pyrodiversity–biodiversity effect is real. At the same time, there is widespread evidence that environmental heterogeneity broadly drives variation in species richness (Stein et al., 2014) and that this is a consequence of heterogeneity in species’ responses to environmental variation. This diversity in species’ environmental affinities is the foundational mechanism proposed for why biodiversity should respond positively to pyrodiversity (He et al., 2019; Kelly & Brotons, 2017).

Although beyond the scope of our review, a large and growing literature demonstrates support for species-specific responses to the heterogeneity of habitats and conditions that exist following fire. This literature is much older than the newer phenomenon

of explicitly testing pyrodiversity–biodiversity (Figure 1) and has roots in the classic “habitat heterogeneity hypothesis” (Lack, 1969; MacArthur & Wilson, 1967; Simpson, 1949). Given how long this question has captivated ecologists, there now exists a wide variety of studies that convincingly demonstrate that species-specific responses to post-fire conditions exist, at least, in bats (Blakey, Webb, et al., 2019; Buchalski et al., 2013) and other mammals (Bliege Bird et al., 2018), birds (Hutto, 2008; Smucker et al., 2005), herptiles (Rochester et al., 2010; Russell et al., 1999), pollinators (Carbone et al., 2019) and plants (Pausas & Ribeiro, 2017). Moreover, this species-specific variation arises from how different species’ traits benefit or hinder establishment along the spectrum of post-fire environments (Blakey, Webb, et al., 2019; Pausas & Keeley, 2014; Pausas & Lavorel, 2003).

Given the preponderance of evidence that species broadly show heterogeneity in response to post-fire ecosystems and that pyrodiversity increases heterogeneity in post-fire landscapes, it is perhaps surprising that direct evidence for a pyrodiversity–biodiversity relationship is so limited and equivocal (Figure 2). In addition to the reasons discussed in the previous section, a challenge in interpreting empirical research to date is that fire is very difficult to experimentally reproduce, lending limited opportunities for mechanism testing. Until many more pyrodiversity–biodiversity studies can be replicated across landscapes, taxa and dimensions of fire variability, such phenomenological studies of species assemblages will likely remain inherently ambiguous in their overall conclusions. In addition, some species might successfully occupy landscapes across a gradient from low to high pyrodiversity but may vary greatly in their abundance across that same gradient. Therefore, there exists the possibility that studies based on presence/absence measures (i.e. species richness) could underestimate the effects of pyrodiversity on generating patterns in biodiversity.

But another approach to learning about the mechanisms underlying pyrodiversity–biodiversity is to decompose the effect from an aggregate impact on biodiversity, to a component effect on individual species. We can thus ask does pyrodiversity benefit individual species? Alternatively, does pyrodiversity harm or inhibit individual species? Depending on the frequency with which species fall into one category or another, we can assemble a bottom-up picture of how pyrodiversity impacts communities. To this end, single-species studies on pyrodiversity impacts can contribute positively to our developing understanding of its effects on biodiversity.

One way to investigate whether there are species that benefit from—or, alternatively, are hindered by—pyrodiversity is to examine species that seemingly exist at opposite ends of the spectrum of affinity for disturbance. Put another way, we should pick a “fire-reliant” species that is attracted to recent patches of severely burned habitat and compare its relationship with pyrodiversity (in this case, spatial variation in burn severity) relative to a species that is known to be intolerant of disturbance, such as an “old-growth” forest indicator. To be clear, neither type of species is expected to respond positively to pyrodiversity: the old-growth species eschews large-scale disturbance of any kind, while the fire-reliant species benefits from

recent, severe fire, but not necessarily a diversity of fire characteristics. With no strong expectations of affinity for pyrodiversity from either species, any such discovery to the opposite would effectively change our perceptions of the range of mechanisms underlying a proposed pyrodiversity–biodiversity effect.

4 | CASE STUDY OF AN “OLD-GROWTH” SPECIES, THE SPOTTED OWL

We begin this thought experiment by highlighting recent research conducted on the spotted owl (*Strix occidentalis*), a flagship “old-growth” species of far western North America. We here focus specifically on the California spotted owl (*S. o. occidentalis*), and so, hereafter reference to the “spotted owl” refers to this subspecies. The spotted owl primarily occurs in mid-elevation mixed-conifer montane forest, and many studies and syntheses have demonstrated the species’ reliance on late-seral forests characterized by large trees and a relatively closed overstorey canopy (Jones et al., 2018; North et al., 2017; Tempel et al., 2016). Conservation strategies focused on spotted owls have therefore suggested delineating large blocks of undisturbed habitat to meet the needs of the species (Verner et al., 1992). While “old-growth” conditions are considered important for supporting nesting, roosting and foraging activities, spotted owls are known to use a broader range of forest conditions for foraging (Blakey, Siegel, et al., 2019; Roberts, 2017). However, because nesting habitat is considered to be more limited in landscape availability, human and natural disturbances that significantly alter forest structure such as clear-cutting and large, severe fires have long been considered a threat to owl habitat and long-term population persistence (Peery et al., 2017; Verner et al., 1992).

Recent research has indeed shown that large, severe fires are detrimental to spotted owls and their habitat (e.g. Jones et al., 2016), but has also uncovered significant nuance in how spotted owls respond to a range of post-fire conditions and has shed light on potential mechanisms that may underlie owls’ response to pyrodiversity. Within fires, spotted owls continue to occupy and reproduce in territories that have experienced relatively high pyrodiversity—as characterized by a mixture of unburned, and low- and moderate-severity fire, with smaller patches of high-severity fire (Jones et al., 2016; Schofield et al., 2020). Over the short term, spotted owls may even continue to occupy and nest in territories that burned extensively at high-severity as long as there is sufficient residual late-seral habitat (e.g. in riparian areas) (Lee & Bond, 2015), but it is unclear how persistent these apparent neutral effects may be. Demographic analysis has suggested that although some spotted owls may continue to occupy territories that have experienced extensive severe fire, these territories show lower survival and increased recruitment rates suggesting that occupied territories within severe fire represent population “sinks” (Rockweit et al., 2017).

Studies of the movement and foraging ecology of owls that persist in burned landscapes have perhaps revealed the most about how pyrodiversity may shape spotted owl habitat. It has long been

known that spotted owls will forage in forest habitat that has experienced different burn severities and may even prefer foraging in severely burned forest (Bond et al., 2009). Two recent papers (Jones et al., 2020; Kramer et al., 2021) together suggest that a complex interplay between forest heterogeneity, pyrodiversity, and severe fire patch size may better explain how and why spotted owls use burned landscapes the way that they do. Owl use of severely burned forest appears to be mediated by severe fire patch size. In general, spotted owls select smaller patches of severely burned forest for foraging activities, avoid larger patches (Jones et al., 2020; Kramer et al., 2021) and tend to stay within 100m of “green” forest when foraging in severely burned areas (Jones et al., 2020). Both Jones et al., (2020) and Kramer et al., (2021) tested whether owls selected or avoided areas with higher pyrodiversity (in this case, defined as the Shannon diversity of burn severity classes), and the two studies reached opposite conclusions. Jones et al. (2020) provided some evidence that owls *selected* more pyrodiverse areas for foraging, while Kramer et al., (2021) suggested they *avoid* more pyrodiverse areas.

This apparent contrasting result makes more sense when overlaid on the two study landscapes: Jones et al. (2020) found that owls used more pyrodiverse areas within the context of a broadly homogeneous, fire-suppressed landscape (i.e. U.S. National Forests, a mixed-use landscape); Kramer et al., (2021) found owls avoided more pyrodiverse areas within the context of an already structurally heterogeneous landscape with a long history of managed and prescribed fire use (i.e. U.S. National Parks, a preservation-based landscape). Thus, the relative importance of pyrodiversity in creating owl foraging habitat may depend on the existing degree of surrounding landscape heterogeneity in forest structure. It is clear that spotted owls use more heterogeneous landscapes for foraging activities (Atuo et al., 2019), and in some cases (e.g. in homogeneous fire-suppressed forests), pyrodiversity may introduce some of that important variability to the benefit of spotted owls. Moreover, this observation suggests that in single-species studies, the effect of pyrodiversity on behaviour or vital rates may be related to pyrodiversity creating some minimum, or threshold level of structural diversity in otherwise homogeneous landscapes that provides required resources for the species. Thus, the effects of pyrodiversity on the ecology of single species could be highly nonlinear.

As for the driver of this pyrodiversity relationship, there is some evidence that cross-trophic interactions are the mechanism underlying spotted owls' preference for the structural heterogeneity that can be introduced through pyrodiversity. In the Sierra Nevada of California, spotted owl territories are less likely to go extinct when owls occupying those territories consume more woodrats and fewer flying squirrels (Hobart et al., 2019). Woodrats tend to be associated with open, early-seral forest, while flying squirrels tend to be associated with late-seral, closed-canopy forest (Roberts et al., 2015). Therefore, in fire-suppressed forests, pyrodiverse areas characterized by smaller patches of severely burned forest may introduce forest conditions that either recruit woodrats or increase local densities of flying squirrels (Sollmann et al., 2016), and both outcomes could improve spotted owl hunting efficiency (Hobart et al., 2021).

Pyrodiverse areas may also give owls access to “open” forest patches for hunting while maintaining concealment in surrounding green forest from predators such as great horned owls (Gutiérrez et al., 1995; Johnson, 1992).

5 | CASE STUDY OF A “FIRE-RELIANT” SPECIES, THE BLACK-BACKED WOODPECKER

As a counterexample to the spotted owl, we highlight the black-backed woodpecker (*Picoides arcticus*), a species that is emblematic of burned forests in western North America. The black-backed woodpecker occurs broadly across North America, from its southernmost range in the Sierra Nevada of California, eastward across the boreal belt to Québec and the Adirondack and White Mountains of New England and the Maritimes. Everywhere, it is associated with dense pockets of disturbed conifer trees, particularly those killed by fire (Tremblay et al., 2016). The black-backed woodpecker is frequently described as the most fire-associated species of bird in North America, possibly the world (Hutto, 2008). It is also closely associated with recent fires, often colonizing forests within the first year since burning, and declining in density 4–5 years after fire (Tingley et al., 2020). The reason for its strong post-fire affinity derives from its natural history. Black-backed woodpeckers excavate their nests preferentially in recently killed, undecayed snags (i.e. standing dead trees: Saab et al., 2009; Seavy et al., 2012). Foraging also occurs nearly exclusively on dead or dying trees, from which beetle larvae—particularly that of woodboring beetles (e.g. *Cerambycidae*)—are extracted. As the woodboring beetles primarily lay their eggs in the undecayed wood of recently killed trees (Powell, 2000), the primary food source, and thus the woodpecker itself, is tightly constrained to recent post-fire areas.

The literature surrounding black-backed woodpeckers' post-fire affinity describes a species that should greatly benefit from large, extensive areas of forest burned at high severity (Hutto, 2008). Nest sites are preferentially located in the highest density stands of small- to medium-sized conifer snags (Saab & Dudley, 1998; Seavy et al., 2012). Of North American woodpeckers found in the east, black-backed woodpeckers are considered the most specialized for foraging on dead wood (Nappi et al., 2015), and home range size (as a proxy for resource availability) scales inversely with the density of fire-killed snags within a home range (Tingley et al., 2014). Broadly, black-backed woodpeckers are more likely to be found closer to high-severity burned patches with high snag densities and farther from the fire perimeter (Saracco et al., 2011; Tingley et al., 2020; White et al., 2019).

Yet, new research is highlighting the potentially critical role that pyrodiversity—specifically, spatial heterogeneity in burn severity—plays in structuring the habitat use and selection of black-backed woodpeckers. A critical first observation has come from studies following recent “megafires” in California, where exceptionally large forested areas burned quickly over a matter of days, leaving large

expanses of high-severity burned forest (e.g. Coen et al., 2018). Such fires were expected to be ideal breeding grounds for black-backed woodpeckers, yet surveys found surprisingly few individuals (White et al., 2019) and models overpredicted observed abundances (Tingley, Wilkerson, et al., 2016). Tracking studies have helped clarify the reasons behind this discrepancy. In one study following black-backed woodpeckers in six fires of northern California, adult woodpeckers chose to forage in areas of medium and high burn severity, but that were proximal to low-severity or unburned forest (Stillman et al., 2019). Similarly, in the choice of nest location, black-backed woodpeckers were very unlikely to choose to build a nest in a tree that was >500 m from the closest patch of live forest (Stillman, Siegel, Wilkerson, Johnson, Howell, et al., 2019). In both cases— foraging and nest site placement—adult black-backed woodpeckers selected areas with higher heterogeneity in burn severity (i.e. greater pyrodiversity; Stillman, Siegel, Wilkerson, Johnson, Howell, et al., 2019; Stillman, Siegel, Wilkerson, Johnson, & Tingley, 2019).

The mechanism underlying this surprising pyrodiversity affinity in black-backed woodpeckers appears to be predation risk of juveniles. Tracking observations revealed that juveniles—particularly recent fledglings—equally prefer live trees to snags and spend significantly more time in low-severity and unburned forest than adults (Stillman, Siegel, Wilkerson, Johnson, & Tingley, 2019). As juvenile black-backed woodpeckers are often dependent on parents for provisioning for approximately 35 days after fledging, juveniles and adults concentrated in edge areas where live forest abutted high-severity patches with large concentrations of snags (Stillman, Siegel, Wilkerson, Johnson, & Tingley, 2019). The dangers to juvenile black-backed woodpeckers of entering the high-severity burned areas were significant—survival of that 35-day window is only 13% for fledglings in a high-severity patch, but rises to 53% for fledglings in unburned to medium-severity patches (Stillman et al., 2021). Juvenile mortality was primarily due to predation by raptors—hunters that find prey primarily through visual cues. As a result, an age-specific trade-off between predation and starvation (Houston et al., 1993) may drive a species-level habitat affinity for areas with greater pyrodiversity.

6 | SYNTHESIS AND RESEARCH GAPS

The extent to which the pyrodiversity–biodiversity hypothesis is supported depends on a variety of factors, indicating a highly context-specific phenomenon. The strength of the pyrodiversity–biodiversity relationship has been shown to vary by taxa, spatial scale, temporal scale, geographic region and biome (Figure 2). Critically, the strength of the relationship also varies by how pyrodiversity itself has been measured and defined, which widely varies in the literature. Despite more than 40 published examples to date that explicitly test the pyrodiversity–biodiversity hypothesis (Figure 2), the extreme heterogeneity in design, approach, and scale of these studies complicates evidence synthesis. Plainly, we still know far too little about how pyrodiversity impacts biodiversity in most systems in most parts of the world.

Yet, the spotted owl and black-backed woodpecker case studies present an intriguing, alternative path to gaining ecological understanding of pyrodiversity. Here are two iconic species co-occurring in western North American conifer forests that have long been seen to occupy distinct and largely non-overlapping habitats within the same landscape. As scientists dig deeper into how heterogeneity in fire impacts these two species, we learn that the “old-growth specialist” owl can benefit from diverse post-fire landscapes, while the “fire-reliant” woodpecker selects for burned forest patches that are close to living, green forest. The mechanisms underlying these two single-species pyrodiversity–biodiversity relationships seem convergent: severe fire brings a boon of resources (nesting for the woodpecker, food for both the owl and woodpecker), but severe fire also brings danger (predation risk for the woodpecker and possibly the owl, and loss of limiting nesting habitat for the owl). Consequently, a pyrodiverse forest presents sufficient areas with elevated resources that are also adjacent to locations for protection and cover. Pyrodiversity, thus, stands to facilitate the creation of patch diversity that satisfies predictions from predation foraging risk optimization theory (Brown, 1999; Brown et al., 1999).

The amalgam of mixed global support for pyrodiversity–biodiversity relationships, combined with emerging mechanism-based support within individual species, assists in clarifying the existing gaps in our composite understanding of the pyrodiversity–biodiversity hypothesis. To best move forward in testing this hypothesis, we present the following six key research gaps:

1. *Stronger development of the different potential mechanisms underlying the pyrodiversity–biodiversity relationship.* Mechanistic understanding, to date, has been weak to non-existent and was vague in the original conceptualization. Evidence suggests that multiple, non-exclusive mechanisms may impact pyrodiversity–biodiversity relationships (e.g. Kelly et al., 2017), and a stronger inferential approach in the future will result in specific studies designed to test for particular mechanisms within the composite framework.
2. *Testing for sensitivity to different pyrodiversity metrics and scale dependence.* Examining whether the pyrodiversity–biodiversity relationship is sensitive to different approaches for quantifying pyrodiversity (Appendix 1) could illuminate underlying mechanisms and help explain why some studies do not find support to the relationship. Moreover, the pyrodiversity–biodiversity relationship is likely to be scale-dependent, but general rules for such scale dependence are unknown.
3. *Standardization of metrics for pyrodiversity.* Pyrodiversity has been measured in many different ways, even when describing diversity within a single axis of fire regimes (e.g. variation in burn severity). A strong mechanism-based foundation and further empirical research (examining the relative importance of different pyrodiversity metrics; see #2 above) will help provide a foundation for the superiority of certain metrics over others, while still recognizing that definitions may require adjustments based on data availability or study objectives. Broad adoption of particular metrics

among researchers (and testing of multiple independent metrics) could aid future synthesis and meta-analysis.

4. *Bridging from species to communities.* Biodiversity responses to pyrodiversity have been measured broadly at the aggregate level—for example tallies of species richness—yet biodiversity is composed of many species, each with their own traits and preferences. With evidence that individual species may benefit from pyrodiversity, it is important to know how widespread this phenomenon is, and whether other species (and how many) show opposite responses. Analysis of functional traits and phylogeny may help build generalizable predictions of pyrodiversity–biodiversity strength that can be translated into less data-rich systems.
5. *Broad-scale spatial and temporal mapping of pyrodiversity.* Pyrodiversity has been assumed to have decreased because of human landscape modification and fire suppression (Martin & Sapsis, 1992). However, little empirical work has explored how pyrodiversity has changed through time across global ecosystems. Quantifying pyrodiversity across large (regional, global) spatial extents (e.g. Hempson et al., 2018; Steel et al., 2021), spatial scaling of pyrodiversity, and evaluating consistency of these patterns using different definitions of pyrodiversity will go a long way in understanding its fundamental ecological role across ecosystems.
6. *Macroecological studies of pyrodiversity–biodiversity relationships.* Most studies of pyrodiversity–biodiversity relationships have focused on study areas with a relatively small spatial extent. Large-scale mapping of pyrodiversity (see #5 above) will facilitate linking measures of pyrodiversity to regional, continental, or global biodiversity datasets that could facilitate a valuable macroecological perspective of pyrodiversity–biodiversity relationships.

Research that focuses on the above needs will improve our understanding of pyrodiversity and the pyrodiversity–biodiversity hypothesis. In an era of unprecedented changes to fire regimes because of climate change and past land use, a better understanding of pyrodiversity–biodiversity relationships across global ecosystems could improve forecasts of biodiversity change and bolster conservation and fire management planning. In some systems and at certain scales, a pyrodiversity paradigm may help maintain biodiversity, promote conservation of focal species with different life histories and permit flexibility and creativity in the implementation of fire management. However, the current literature does not illuminate those relevant systems and scales. Additional research and syntheses are urgently needed in this era of megafires.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

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BIOSKETCHES

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APPENDIX 1

Summary of studies that examined the pyrodiversity–biodiversity hypothesis (PBH). Each row corresponds to a study–taxa combination because some studies examined support for the hypothesis across multiple taxonomic groups.

Reference	Support inferred for PBH	Direct test or indirect inference	How “pyrodiversity” was defined or conceptualized	Variation within or among sampling units	Continent	Ecosystem	Taxa
Masters (1996)	Yes	Indirect	“Fire mosaic”; variation in time since fire	Among	Australia	Grasslands	Reptiles
Stuart-Smith et al. (2002)	Yes	Direct	“Patchy mosaic”; implicit structural heterogeneity within burned plots	Within ^a	North America	Forest/ woodland	Birds
Brotons et al. (2005)	Yes	Direct	Variation in habitat type composition and configuration created by fire	Within	Europe	Forest/ woodland	Birds
Cook and Holt (2006)	No	Direct	“Mosaic burning”; vegetation heterogeneity	Within	North America	Grasslands	Beetles
Pastro et al. (2011)	No	Direct	Mixture of successional stages; implicit structural heterogeneity within prescribed burn plots	Within ^a	Australia	Grasslands	Plants
Pastro et al. (2011)	No	Direct	Same as above	Within ^a	Australia	Grasslands	Reptiles
Pastro et al. (2011)	No	Direct	Same as above	Within ^a	Australia	Grasslands	Mammals
Andersen and Hoffmann (2011)	No	Direct	Implicit successional heterogeneity present in frequent-fire versus long-unburned areas	Within ^a	Australia	Savanna	Ants
Langlands et al. (2012)	Yes	Indirect	Variation in post-fire ages, scale or intensity of fire	Among	Australia	Grasslands	Spiders
Davies et al. (2012)	No	Indirect	Variation in seasonality and frequency of fire	Among	Africa	Savanna	Termites
Kelly et al. (2012)	No	Direct	Shannon diversity of fire age classes	Within	Australia	Scrubland	Mammals
Taylor et al. (2012)	No	Direct	Shannon diversity index of fire age classes within sampling units	Within	Australia	Scrubland	Birds
Nimmo et al. (2013)	No	Direct	Shannon diversity index of the proportional cover of three fire age classes	Within	Australia	Scrubland	Reptiles
Maravalhas and Vasconcelos (2014)	Yes	Indirect	Variation in fire frequency and timing	Among	South America	Savanna	Ants
Andersen et al. (2014)	No	Indirect	Variation in fire frequency and seasonality	Among	Australia	Savanna	Ants
Farnsworth et al. (2014)	No	Direct	Shannon diversity index of fire age classes	Within	Australia	Scrubland	Reptiles
Sitters et al. (2014)	Yes	Direct	Variation in age class diversity and configuration	Within	Australia	Forest/ woodland	Birds
Avitabile et al. (2015)	No	Direct	Shannon diversity index of fire age classes	Within	Australia	Scrubland	Termites
Cohn et al. (2015)	Yes	Direct	Number of fire age classes in a sampling unit	Within	Australia	Forest/ woodlands	Plants
Radford et al. (2015)	No	Direct	Number of fire age classes in a sampling unit	Within	Australia	Savanna	Mammals
Kelly et al. (2015)	No	Indirect	Variation in time since fire; optimization of a mixture of successional stages	Among	Australia	Scrubland	Birds
Kelly et al. (2015)	No	Indirect	Same as above	Among	Australia	Scrubland	Reptiles

APPENDIX 1 (Continued)

Reference	Support inferred for PBH	Direct test or indirect inference	How "pyrodiversity" was defined or conceptualized	Variation within or among sampling units	Continent	Ecosystem	Taxa
Kelly et al. (2015)	No	Indirect	Same as above	Among	Australia	Scrubland	Mammals
Lawes et al. (2015)	No	Direct	"Patchiness"; average distance to unburned area over the sampling unit	Within	Australia	Savanna	Mammals
Burgess and Maron (2016)	No	Direct	Simpson diversity index of fire-mediated patch types	Within	Australia	Forest/woodlands	Birds
Tingley et al., (2016)	Yes	Direct	Standard deviation of continuous burn severity (per cent canopy mortality) in a sampling unit	Within	North America	Forest/woodlands	Birds
Poniso et al. (2016)	Yes	Direct	Simpson's diversity of unique fire history classes	Within	North America	Forest/woodlands	Bees
Poniso et al. (2016)	Yes	Direct	Same as above	Within	North America	Forest/woodlands	Flowering plants
Poniso et al. (2016)	Yes	Direct	Same as above	Within	North America	Forest/woodlands	Plant:pollinator inxn
Prowse et al. (2017)	No	Indirect	Variation in time since fire	Among	Australia	Forest/woodlands	Birds
Brown and York (2017)	Yes	Direct	Variation in post-fire age classes and number of fires	Within	Australia	Forest/woodlands	Flies
Brown and York (2017)	Yes	Direct	Same as above	Within	Australia	Forest/woodlands	Wasps
Taillie et al. (2018)	Yes	Indirect	Variation in burn severity, time since fire and their interaction	Among	North America	Forest/woodlands	Birds
McGranahan et al. (2018)	Yes	Direct	Variation in number of patches in a sampling unit, fire return interval and burn season	Within	North America	Grasslands	Prairie plants
Davies et al. (2018)	No	Indirect	Variation in fire frequency	Among	Australia	Savanna	Mammals
Davis et al. (2018)	No	Direct	Shannon diversity index of fire age classes within sampling unit	Within	Australia	Scrubland	Termites
Beale et al. (2018)	Yes	Direct	Volume of the minimum convex hull of the four-dimensional space described by all the fires within a sampling unit	Within	Africa	Savanna	Birds
Beale et al. (2018)	Yes	Direct	Same as above	Within	Africa	Savanna	Mammals
Bliege Bird et al. (2018)	Yes	Indirect	Shannon diversity of successional stages within sampling units	Within	Australia	Scrubland	Mammals (and one species of Reptile)
Steel et al. (2019)	Yes	Direct	Heterogeneity in burn severity within a sampling unit, corrected for mean severity	Within	North America	Forest/woodlands	Bats
Docherty et al. (2020)	Yes	Direct	Multiple measures including Shannon diversity in age class, shape complexity, edge contrast index and fire frequency	Within	Africa	Savanna	Birds
Wills et al. (2020)	No	Direct	Variation in fire age class/vegetation succession	Within	Australia	Forest/woodlands	Birds

^a Study inferred pyrodiversity effects from assumed (unmeasured) heterogeneity within sampling units experiencing certain fire regimes.