Current Landscape Ecology Reports
https://doi.org/10.1007/s40823-022-00075-6

INTERFACE OF LANDSCAPE ECOLOGY AND CLIMATE CHANGE (B ZUCKERBERG, SECTION EDITOR)

Pyrodiversity in a Warming World: Research Challenges and Opportunities

G. M. Jones[1] · **J. Ayars**[1,2] · **S. A. Parks**[3] · **H. E. Chmura**[4] · **S. A. Cushman**[5] · **J. S. Sanderlin**[5]

Accepted: 1 August 2022
This is a U.S. Government work and not under copyright protection in the US; foreign copyright protection may apply 2022

Abstract

Purpose of Review Climate change will continue to alter spatial and temporal variation in fire characteristics, or pyrodiversity. The causes of pyrodiversity and its consequences for biological communities are emerging as a promising research area with great potential for understanding and predicting global change. We reviewed the literature related to the causes and consequences of pyrodiversity over the 3-year period 2019–2021 to identify emerging themes and innovations.
Recent Findings Key innovations include multi-scale analyses of pyrodiversity, a focus on mechanisms underlying single-species responses to pyrodiversity, investigating how pyrodiversity influences community stability and beta-diversity, and novel, integrative approaches for measuring pyrodiversity.
Summary Pyrodiversity research is still maturing, and will benefit from exploration of multi-scale, gradient analysis of integrated (multi-measure) pyrodiversity metrics, an increased focus on how climate change may influence pyrodiversity across different systems, and a stronger framework for operational pyrodiversity within the context of land management. We suggest that research focusing on pyrodiversity could be generalized to include "turbadiversity," or the cumulative patterns of heterogeneity produced by multiple types of disturbances (i.e., not just fire).

Keywords Pyrodiversity · Biodiversity · Climate change · Multi-scale · Fire management · Landscape ecology

Introduction

Fire is a natural and crucial agent of change on Earth [1, 2]. Every vegetated terrestrial system on Earth has an associated fire regime, characterized by variation in the seasonality, frequency, size, and severity of fire [3, 4]. Across all fire-prone ecosystems, fire acts as a regenerative force by releasing nutrients, resetting vegetation dynamics, and creating heterogeneity across scales of biotic organization [5]. The selective pressures that fire exerts as a natural disturbance and the landscape variability it creates helped generate Earth's biodiversity patterns [6•]. Over the course of millennia, many species and biotic communities have accumulated adaptations that allow them to persist even after fire; some vegetation communities even depend on fire and are degraded in the absence of fire [7, 8].

However, climate change is rapidly altering global fire regimes [9–12], thereby sparking concerns about fire-catalyzed vegetation transition, such as enduring conversions from forest to non-forest [13]. Of course, large, severe "megafires" are normal in some systems [14, 15], but the increasing severity (i.e., fire effects to vegetation) observed in megafires is unprecedented from both an ecological perspective and from the perspective of modern human society [10, 16, 17, 18•]. Like climate change, the

---

This article is part of the Topical Collection on *Interface of Landscape Ecology and Climate Change*

✉ G. M. Jones
gavin.jones@usda.gov

[1] USDA Forest Service, Rocky Mountain Research Station, Albuquerque, NM, USA

[2] Biology Department, University of New Mexico, Albuquerque, NM, USA

[3] Aldo Leopold Wilderness Research Institute, USDA Forest Service, Rocky Mountain Research Station, Missoula, MT, USA

[4] USDA Forest Service, Rocky Mountain Research Station, Missoula, MT, USA

[5] USDA Forest Service, Rocky Mountain Research Station, Flagstaff, AZ, USA

Published online: 16 August 2022

rate at which fire regimes are changing may be outpacing the ability of biotic communities to adapt [19]. Likewise, human society is not fully prepared to coexist with fire in an era of changing fire regimes [20, 21].

In some places, fires are becoming larger and more homogeneous in their severity, and these changes are driven in part by warmer, drier conditions associated with climate change. In the US State of California, for example, recent wildfires are more likely to contain large, blocky patches of stand-replacing fire, which contrasts with the historical norm for this bioregion [22, 23]. Moreover, increases in annual area burned and fire severity in western North America are linked to a warming climate [9, 12, 17, 24]. Similarly, in southeastern Australia, extreme drought conditions associated with climate change contributed to the most significant fire season ever recorded during 2019–2020, burning nearly 6 million hectares of temperate forest [25, 26] with a record 1.8 million hectares burning at high severity [27]. Climate-driven homogenization of post-fire landscapes resulting from extensive high-severity fire may have serious consequences for biodiversity in many ecosystems.

All fire regimes, whether historical (often influenced by Indigenous burning practices; e.g., [28]) or contemporary, produce characteristic levels of *pyrodiversity* (Fig. 1). High levels of pyrodiversity have been hypothesized to give rise to a wide range of ecological niches that support higher biodiversity (i.e., "pyrodiversity begets biodiversity") [29•, 30•, 31]. The term pyrodiversity was introduced by Martin and Sapsis (1992) [32] as the “variety in interval between fires, seasonality, dimensions, and fire characteristics, producing biological diversity at the micro-site, stand, and landscape level.” Indeed, the relationships between landscape diversity and biodiversity have been the focus of research since the inception of ecology as a discipline. The intermediate disturbance hypothesis (IDH; e.g., [33]) suggests that when disturbances occur at intermediate frequencies, they maximize habitat diversity and within-ecosystem diversity. This occurs because competitive interactions are disrupted sufficiently to prevent exclusion of less competitive species, but disturbances are not so frequent that they simplify the ecosystem and eliminate species associated with late seral development and absence of disturbance. Similarly, increasing pyrodiversity might increase landscape diversity, which in turn might lead to higher biodiversity. Research examining the link between pyrodiversity and biodiversity (i.e., the "pyrodiversity-biodiversity hypothesis") has been increasing rapidly [see 6•,29,30•], but little attention has been given to the broader context of pyrodiversity-biodiversity relationships in a changing climate, despite ongoing climate-driven changes to fire patterns and characteristics.

Perhaps, one reason for the lack of climate contextualization is that, despite well-established theoretical underpinnings (e.g., the IDH), pyrodiversity-biodiversity research is still in its early stages. Considerable gaps remain in the

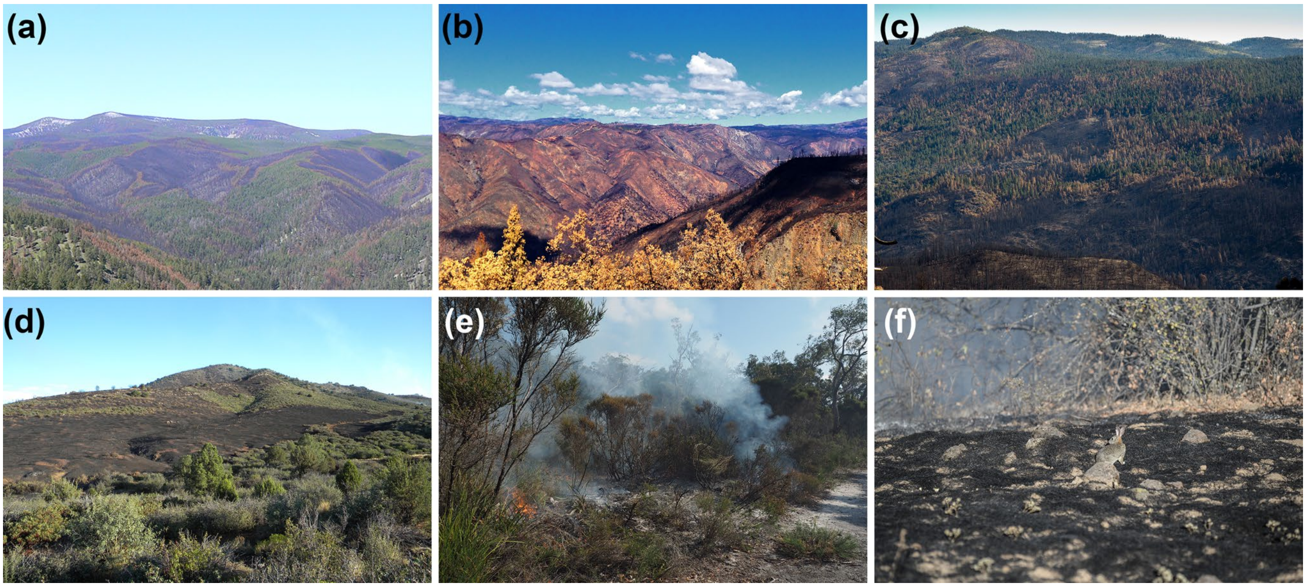

Fig. 1 What does pyrodiversity look like? Examples of real landscapes showing different degrees and qualities of pyrodiversity at various spatial scales. Panels **a**–**c** show pyrodiversity (in terms of burn severity) across relatively large landscapes, with panels **a** and **c** showing moderate to high pyrodiversity characterized by high patchiness in burn severity, and panel **b** showing low pyrodiversity, with almost all visible land having been burned at high severity. Panel **d** shows pyrodiversity at a fine spatial scale (a single hillside), and panel **e** shows pyrodiversity at an even finer spatial scale (a patch of vegetation). Panel **f** shows the fine scale juxtaposition of unburned and burned areas providing habitat for wildlife. Images **a**, **b**, **d**, **e**, and **f** are used under a CC-BY-2.0 license. Image **c** is credited to Sheila Whitmore, used with permission

theoretical development of pyrodiversity as a concept [30•] and the role it can, or should, play in conservation [31]. Indeed, the pyrodiversity paradigm has been criticized for its underdeveloped relevance to land management [34]. Moreover, thus far, researchers have failed to coalesce around exactly what pyrodiversity is and how to measure it [35••]. This has yielded an extremely wide variety of pyrodiversity metrics and mixed empirical support for pyrodiversity-biodiversity relationships that challenge broader syntheses of the hypothesis [29•]. Therefore, placing pyrodiversity-biodiversity research in a climate context requires developing and clarifying these issues further.

Here, we attempt to further develop some of these key questions and issues while placing pyrodiversity research in the context of climate change, which we hope will encourage further study and thought. We have three objectives in this paper. First, we review the recent literature (2019–2021) on pyrodiversity to identify emerging research themes and innovations. Second, we identify and discuss existing issues with pyrodiversity as a conceptual framework, including critiques of the paradigm. Third, we propose opportunities for pyrodiversity-biodiversity research to address some of the key problems we identified and allow better contextualization with climate change, and we provide direction for integrating pyrodiversity into land management to improve conservation.

The Promise of Pyrodiversity: the Cutting Edge and Recent Innovations

The conceptual introduction of pyrodiversity by Martin and Sapsis [32], while seminal, lacked empirical evidence and was sufficiently vague in definition that it left the door open for varied interpretation and application [e.g., 34–38]. In the following decades, numerous researchers have sought to identify pyrodiversity-biodiversity relationships and have done so using a remarkably wide range of approaches and techniques [29•]. While the broad original definition [32] has challenged the concept's clarity, it has also spurred innovation in quantifying and interpreting pyrodiversity metrics in recent years.

A Review of the Recent Literature (2019–2021)

We reviewed the scientific literature on pyrodiversity and the pyrodiversity-biodiversity hypothesis during the period 2019–2021 to identify emerging themes and innovations. We searched Web of Science on 10 January 2022 for "pyrodivers*" for 2019-01-01 to 2021-12-31, which yielded 54 results. We read through the abstracts to determine whether the paper conducted an analysis relating to pyrodiversity or the pyrodiversity-biodiversity hypothesis. Papers that did not address pyrodiversity within the text were excluded, as were review papers. We found eight papers that dealt with the causes of pyrodiversity or ways to quantify pyrodiversity and 29 papers that addressed the consequences of pyrodiversity in biotic systems. Of the eight papers that dealt with the causes of pyrodiversity, five considered pyrodiversity as it related to Indigenous cultural burning practices. Of these studies, which could be characterized as anthropological in their focus, only one formally quantified pyrodiversity [39], while the others used it as a framing idea, in that cultural or anthropogenic burning was expected to increase pyrodiversity.

Pyrodiversity was not quantified in all papers, and when it was, it was rarely quantified in a consistent manner. Of the 29 papers concerned with the consequences of pyrodiversity, 15 quantified pyrodiversity directly (Table 1), 12 made indirect inferences about the impacts of pyrodiversity by examining among-sample variation in other fire variables (e.g., time-since-fire) or using pyrodiversity as a concept to interpret findings in the discussion [29•], and two did not actually quantify pyrodiversity. Additionally, one paper proposed a new pyrodiversity metric [35••] and one quantified pyrodiversity outcomes from Indigenous burning [39]. We identified 10 unique pyrodiversity metrics, not accounting for the spatial scale over which metrics were summarized. These were as follows: diversity of post-fire stand age classes ($n=5$), variance or standard deviation of burn severity ($n=3$), diversity of burn severity ($n=2$), number of unique fire histories ($n=2$), diversity of unique fire histories ($n=1$), number of unique values of years since fire ($n=1$), evenness of discrete burn severities ($n=1$), diversity of fire frequencies ($n=1$), Simpson's diversity index of fire histories, weighted for similarity between the unique fire histories ($n=1$), and a convex hull of fire return interval, burn severity, burn season, and patch size to represent functional diversity ($n=1$).

All of the papers that addressed the consequences of pyrodiversity in biotic systems ($n=29$) represent geographic areas where fire is a major source of disturbance. Fifteen were in dry forests of the American West, five in arid regions of Australia, four in savannas and grasslands of South Africa and Zimbabwe, two in the Mediterranean region of Europe, two in the American Midwest, and one in a South American savanna. Interestingly, previous work reviewing the pyrodiversity literature over a broader period (1992–2020) was heavily biased toward Australia [29•], perhaps indicating a recent uptake of the concept in other regions, particularly the American West. This literature (2019–2021) was also taxonomically diverse. There were six studies of mammalian diversity, four of plant diversity, five of insects, four of bat diversity, three of bird diversity, five of individual bird species, one of gray long-eared bats (*Plecotus austriacus*), and one covering multiple taxa.

Table 1 Publications quantifying the consequences of pyrodiversity in biotic systems. All research publications from 01–01-2019 to 12–31-2022 which directly quantified pyrodiversity and its effects are included. Spatial scale is ordered (patch < landscape < meta-landscape < region), where a patch is in the 100 s of hectares or less, a landscape is in the 1000 s of hectares, a meta-landscape describes a design where replicates are large enough to be landscapes, and a region encompasses an entire bioregion. More detail is provided where available

Publication	Topic	Pyrodiversity metric	Relevant explanatory variables	Spatial scale	Key conclusions	Management advice
Stillman et al. [44•]	Age-specific habitat relationships (stand selection) for black-backed woodpeckers (*Picoides arcticus*) in Californian coniferous woodlands (USA)	Variance of continuous burn severity within a selected stand	Live tree density, snag density, burn severity	Landscape	Fledglings and adult woodpeckers used different habitats, as fledglings require unburned nurseries for predation protection before they can forage alongside parents in stands with higher snag density and burn severity	Promoting pyrodiversity might reduce the risk of megafires forming large homogenous patches of high severity burns
Steel et al. [128]	Effects of wildfire severity and pyrodiversity on bat species occupancy in fire-suppressed forests of the Sierra Nevada, USA	Variation in continuous burn severity at four spatial scales: 50, 100, 250, and 500 m	Time since fire	Landscape	Bat richness increased with burn severity and pyrodiversity. Forest disturbance improves navigability for some species, while clutter-specialists prefer low and unburned forest. Forest densification from fire suppression decreased habitat quality for most bats	None given
Ponisio [46]	Responses of a pollinator community (in terms of pollinator community resistance, community functionality, population resistance, species richness, and functional redundancy) to extreme drought in a valley in Yosemite National Park, USA, and the influence of the site's fire history diversity on these effects	Simpson's diversity index for fire diversity around a monitoring plot, treating each unique fire history as a species	No others	Landscape	Fire history and community network properties both contributed to resistance to drought. Pyrodiversity was unrelated to community-level drought resistance but did promote population resistance and community functionality	None given, research was done in a wilderness area that is not managed

Table 1 (continued)

Publication	Topic	Pyrodiversity metric	Relevant explanatory variables	Spatial scale	Key conclusions	Management advice
Swan et al. [127]	How ground-dwelling mammal richness, alpha-diversity, beta-diversity, and gamma-diversity responds to habitat heterogeneity in mountain ranges in southeastern Australia	Fire age class diversity in landscape	Presence of recent fire, vegetation heterogeneity index, and vegetation type diversity	Meta-landscape	Prescribed fire increased landscape-scale structural heterogeneity, supporting the mechanism that pyrodiversity leads to landscape heterogeneity, providing more niche space for species richness. However, while they did find increased beta-diversity among sites, pyrodiversity had a weak negative effect on alpha-diversity, and no effect on landscape-scale species richness	None given
Jorge et al. [129]	Pyrodiversity and restoration effort effects on predator abundance in longleaf pine ecosystems of Florida, USA	Number of unique values of years since fire in a 500 m, 1000 m, and 1500 m buffer around each camera trap	Years since fire, vegetation type	Meta-landscape, 227 km^2	Predators tended to be more abundant closer to hardwood sites and at sites with higher pyrodiversity. Hardwood removal and patch-mosaic burning (3–5 yr rotation) would decrease predator abundance	To conserve white-tailed deer, continue restoration efforts by removing hardwoods and doing prescribed burns
Furnas et al. [130]	Pyrodiversity effects on forest carnivore occupancy in northern California, USA public and private forest lands	Simpson's measure of evenness of four burn category proportions (none, low, moderate, high) at 10-yr and 25-yr timeframe, for a 10 km buffer around each camera trap	Cumulative amount of area in each burn class for 10 or 25 years preceding within 10-km buffer	Meta-landscape	Carnivore richness was highest with intermediate pyrodiversity for both time frames. More specifically, carnivore richness peaked at a certain proportion of low severity burn. There was no independent effect of time since fire	Maximizing pyrodiversity is not the best course for forest carnivore conservation. Low severity prescribed burns may provide ecological services to wildlife in this area that are not provided by other management
Docherty et al. [47]	Response of avian species richness, dispersion, and functional redundancy to patch-mosaic burning in a South African semi-arid savanna	Shannon habitat diversity index, which incorporates the number of age classes in a landscape and their proportional area	Edge contrast index, fire frequency, proportion of newly burned habitat, proportion of unburned habitat	Landscape of 100-ha patches	Certain types and configurations of fire histories promote avian diversity and ecological functioning, not pyrodiversity per se	In savannas, maintain some late-seral habitat unburned, since this feature is required by some specialist birds
Senior et al. [131]	Large scale response of mammals (in terms of species occupancy) to pyrodiversity in fire-prone woodlands of semi-arid Australia	Diversity of post-fire age classes within 9 × 9 or 19 × 19 m buffers depending on mammal size	Area of post-fire age classes and configuration of post-fire age classes, summarized over the applicable buffer	Regional	Pyrodiversity is associated with biodiversity on a regional scale. Long-term unburned areas are necessary for some species	Managers are recommended to use their conclusions and maps to plan fire management around conserving multiple mammal species

Table 1 (continued)

Publication	Topic	Pyrodiversity metric	Relevant explanatory variables	Spatial scale	Key conclusions	Management advice
Gordijn and O'Connor [126]	Fire regime effects on grassland plant species richness, beta-diversity, and functional group richness in an study area in South Africa that had plots with 1-, 2-, 5-, and 12-year fire return intervals	Quantified by selecting permutations of non-contiguous quadrats of varying sizes with different fire histories, to simulate a larger landscape	Seasonality was included for the more frequent return intervals	Patch, 8 ha	The effects of pyrodiversity vary with plant functional groups and with biodiversity metric	Recommend supplementing biennial burning systems with some patches with longer fire-return intervals
Stillman et al. [45]	Influence of fire characteristic variation on black-backed woodpecker fledgling selection and survival in the Sierra Nevada and Washington state, USA	Simpson's diversity index for 100 m buffer around location points where a "species" is a discrete burn severity class at 30×30 m resolution	Binary variable for whether a fledgling spent more than 50% of its time in high-severity burn during a foraging interval, years since fire	Meta-landscape, seven fire footprints	Survival to independence was four times higher for fledglings that avoided high-severity patches compared to those that used high severity patches. There was no relationship with pyrodiversity, but this provides evidence of a need for habitat complementarity for black-backed woodpeckers	None given
Blakey et al. [40]	Response of bat richness to burn extent, configuration, and diversity in the Plumas National Forest, USA	Standard deviation of continuous burn severity across all pixels within each of 10 buffer sizes (circles radius 1–10 km around each acoustic monitor)	Edge between high severity fire and canopy cover, edge between burned and unburned areas, mean patch area, patch density, and edge density, for each of the 10 buffers	Meta-landscape of 83 sites with variable buffers	Bat richness was related to extent and configuration of forest cover and pyrodiversity with no variability in the relationship across scales. Unexpectedly, bat richness was not related to forest structural diversity. Overall bat communities appear to be resilient to fire, heterogeneous forests, and shorter-interval fire regimes	Maintaining late-seral forest for clutter specialists and doing vegetation treatments in mid-seral forests could maintain habitat for all bats
Ulyshen et al. [125]	Pollinator community response to pyrodiversity in the Florida coastal plain (USA), a high-frequency fire regime pine forest, in terms of bee and butterfly richness, diversity, and abundance	Number of unique fire histories within a 250-m buffer around each pollinator sampling site	Burn frequency in past 10 years, percent burned during year of sampling, canopy openness, all for the same 250-m buffer	Landscape, 1100-ha study site	Bee and butterfly richness, diversity, and abundance were all positively related to pyrodiversity. However, butterfly richness was reduced at high burn frequency	Idiosyncratic responses of individual species means that there is no one fire management approach that will benefit all pollinators

Table 1 (continued)

Publication	Topic	Pyrodiversity metric	Relevant explanatory variables	Spatial scale	Key conclusions	Management advice
Radford et al. [41]	Northern Australian savanna mammal community richness and abundance response to fire history, cat presence, dingo activity, feral livestock presence, and weeds, analyzed at several scales	Diversity of post-fire age classes within each buffer around mammal survey sites (1, 3, 5, and 10 km)	Fire frequency, fire intensity, distance to unburnt, percent unburnt, percent burnt in previous year, area of long unburnt vegetation, and ratio of late dry season burns to total burns	Meta-landscape	Site scale (1 km) was more informative for mammal richness and abundance than landscape (5 km) or meta-landscape (10 km) scales. There was a strong local influence of cats where they were present. Pyrodiversity was negatively related to mammal abundance and richness at local and meta-local (3 km) scales	To improve mammal richness/abundance, reduce fire extent, use low intensity burns to maintain shrub cover, maintain more and larger patches of long unburnt vegetation, reduce fire frequency in less fire-prone areas, and reduce the impacts of livestock, cats, and weeds
Wilkin et al. [132]	Influence of pyrodiversity and other landscape factors on understory plant percent cover, richness, evenness, and diversity in Sierra Nevada mixed conifer forests, USA	Simpson's diversity index weighted to account for similarity between unique fire history "species."	Time since last fire, fire severity, times burned	Meta-landscape, 2 valleys in Yosemite, USA	Understory plant richness was strongly affected by the interaction of plot fire history and plot-neighborhood pyrodiversity. Pyrodiversity also indirectly influenced understory plants by controlling canopy cover	They recommend reducing tree canopy cover to increase understory plant cover and diversity and fostering pyrodiversity as well
Jones et al. [42]	Large severe fire impacts on California spotted owl (*Strix occidentalis*) territory occupancy in the Sierra Nevada, USA	Variation in categorical burn severity at four spatial scales: 300, 700, 1100, and 1500 m, using the Shannon diversity index	Proportion of area experiencing post-fire logging, proportion which experienced stand-replacing fire (> 75% canopy mortality)	Landscape	Megafire causes persistent loss of spotted owl habitat. Post-fire logging is irrelevant since spotted owls leave sites with high proportions of stand replacing fire (where post-fire logging occurs). Pyrodiversity promotes territory persistence	Forest treatments are likely necessary to avoid large areas of stand-replacing fire and the displacement and/or death of spotted owls

Emerging Themes in Pyrodiversity Research (2019–2021)

Recent research has been characterized by several promising innovations that advance our understanding of the causes and consequences of pyrodiversity. First, many studies are embracing a multi-scale analytical paradigm to understand the scale at which pyrodiversity operates on biotic communities. Second, an increasing number of studies are investigating the relationship between pyrodiversity and the occupancy, demography, and behavior of individual species to uncover mechanisms. Third, some studies have taken a broader view of biodiversity, investigating the effects of pyrodiversity on axes of diversity beyond species richness, including beta-diversity and functional redundancy.

Most studies summarize their explanatory variables over one scale, but several studies from 2019–2021 analyzed pyrodiversity-biodiversity relationships over multiple scales. Blakey et al. [40] assessed the response of bat species richness to burn extent, configuration, and diversity of fire severity in a northern California dry forest. Each fire variable was summarized across ten spatial scales (1–10 km radii) around each sampling unit, consisting of a passive acoustic recorder. Bat richness was positively related to pyrodiversity across all scales. Similarly, Radford et al. [41] studied northern Australian savanna mammal community response to fire history across multiple scales. They summarized their explanatory variables over 1, 3, 5, and 10 km scales and found that site scale (1 km) was more informative to mammal assemblages than landscape (5 km) or meta-landscape (10 km) scales, and that pyrodiversity was negatively related to mammal abundance and richness at local and meta-local (3 km) scales. Finally, Jones et al. [42] addressed California spotted owl occupancy after megafires at 300, 700, 1100, and 1500 m scales. Sampling units characterized by higher pyrodiversity were more likely to support continued post-fire spotted owl site occupancy, but this effect was only apparent at finer spatial scales (300 and 700 m). The importance of scale differed greatly among these studies, likely reflecting differences in how each taxon interacts with its environment (e.g., mobility, body size; see [29•]). Collectively, these results underscore the importance of multi-scale analyses, even in cases where there may be a priori reasons to think specific spatial scales are important.

Different species prefer habitat exhibiting different post-fire characteristics, providing the foundation for the pyrodiversity-biodiversity hypothesis [32]. An emerging theme in recent literature has been to examine how individual species interact with pyrodiversity, thereby allowing deeper exploration of mechanisms that may underlie the pyrodiversity-biodiversity hypothesis. While several papers we reviewed took this approach [e.g., 42, 43], one of the strongest examples has been a series of papers on the movement ecology and demography of black-backed woodpeckers in post-fire landscapes [44•, 45]. Researchers found that both adult and fledgling woodpeckers fitted with radio-tracking equipment generally favored using forests stands with greater pyrodiversity (measured as the standard deviation in burn severity). However, fledglings and adult habitat use varied strongly in other ways, as fledglings preferred using areas with more live trees, fewer dead trees (snags), and lower burn severity compared to adults [44•]. These space-use patterns were hypothesized to minimize predation risk to fledglings by providing greater cover in green forest, supporting both the “habitat-complementation” (e.g., configuration of fire elements supporting life history needs) and “habitat-refuge” (e.g., configuration of fire elements influencing immediate survival) mechanistic sub-hypotheses of the pyrodiversity-biodiversity hypothesis suggested by Kelly et al. [30•]. Subsequent work confirmed lower survival rates by fledgling woodpeckers in high-severity burn patches compared to moderate- or low-severity burned patches [45]. We encourage further studies that illuminate these underlying mechanisms of the pyrodiversity-biodiversity hypothesis.

In some pyrodiversity-biodiversity studies, the use of species richness (alpha-diversity) as a response variable implies some connection between biodiversity and community and/or ecosystem stability. However, two recent pyrodiversity-biodiversity analyses have investigated community stability directly as a response variable. Ponisio [46] examined the responses of a pollinator community to extreme drought and whether those responses were influenced by fire history diversity, using pollinator community resistance, community functionality, population resistance, species richness, and functional redundancy as response variables. In a similar vein, Docherty et al. [47] used functional richness, evenness, and dispersion as response variables evaluating the pyrodiversity-biodiversity hypothesis for an avian community in a South African semi-arid savanna. Using community functional metrics as response variables is an emerging approach that may give better inferences to the long-term persistence of ecosystems than using simpler richness metrics.

The Problem of Pyrodiversity: Critiquing the Concept of Pyrodiversity and Its Use

While the recent literature demonstrates exciting advances in pyrodiversity research, the pyrodiversity paradigm is not without its issues. In addition to issues raised previously (e.g., pyrodiversity is difficult to operationalize, not all fire mosaics are ecologically meaningful; see [34]), we briefly discuss three critiques of pyrodiversity as a concept and research area and offer some constructive ways that these critiques could be addressed to advance the field.

Pyrodiversity Is an Unnecessarily Abstract Way to Measure Vegetation Diversity

Fire burns vegetation, and after it has burned, regrowth on the landscape reflects the legacy of fire. Why do we care about measuring and understanding pyrodiversity when, really, post-fire vegetation conditions determine the variety of habitat niches available for animal communities to occupy? In fact, we predict that, in some cases, measuring pyrodiversity will underestimate vegetation diversity in an area, given that effects of fire on vegetation are highly variable within a fire perimeter or even within a single burn severity class. Furthermore, the effect of fire on biotic communities depends in part on pre-fire vegetation conditions [48, 49]; a mature forest and a young forest plantation that both experience fire are likely to host divergent post-fire biotic communities. Traditional approaches for measuring pyrodiversity (e.g., diversity of fire age or burn severity classes) will gloss over much of this variation.

We think this critique of the pyrodiversity concept has merit, but also believe that pyrodiversity brings a focus on the disturbance agent that is revealing beyond the information provided by resulting vegetation patterns [50]. The primary distinction between examining the diversity of post-fire vegetation vs. the diversity of burn severity (or some other fire characteristic) is a distinction of pattern vs. process. Fire is a mechanism—a process—that drives vegetation change. In a highly dynamic world, we are increasingly interested in understanding the processes driving change rather than just quantifying the patterns themselves. Mechanistic understanding of these processes improves prediction, too. For example, understanding how disturbance processes shape biodiversity can inform process-based predictive models, which allow modeling of conditions outside of the range of those previously observed [51]. Fire also initiates changes in ecosystems that are unique to the combustion process (e.g., nutrient release and cycling, [52]) and cannot, for example, be reproduced by mechanical vegetation removal. Better integration of fire mapping (i.e., the process) and pre- and post-fire vegetation conditions (i.e., the pattern) could improve understanding of post-fire landscape heterogeneity to better explain biodiversity patterns. Simply put, it is difficult or impossible to understand an ecological pattern without understanding the scale and dynamics of the processes that drive it [53, 54].

Pyrodiversity Must Be Considered in a Broader Disturbance Context

While fire is a major agent of change in many ecosystems, it is not always the dominant disturbance and is likely never the only one. In addition to fire, avalanches [55], windthrow [56], hurricanes [57], landslides [58], flooding [59], insects [60], drought [61], and timber harvest [62] affect patterns of vegetation, increase heterogeneity at multiple scales, and influence patterns of biodiversity. Moreover, such disturbances occur across underlying variation in the physical template (e.g., landform, soils) which itself influences biodiversity [63]. Considering pyrodiversity in isolation ignores this context. A fire that burns an area that has recently experienced multiple other disturbance types will not only burn differently [64, 65], but will also interact with those other disturbances and the underlying physical template to produce vegetation and habitat heterogeneity in ways that are not well understood (Fig. 2).

We think that examining pyrodiversity in isolation from other disturbance agents still holds value, especially if effects on biodiversity are relatively clear and if the interest is in examining hypotheses related specifically to fire. However, we hypothesize that in some systems (particularly

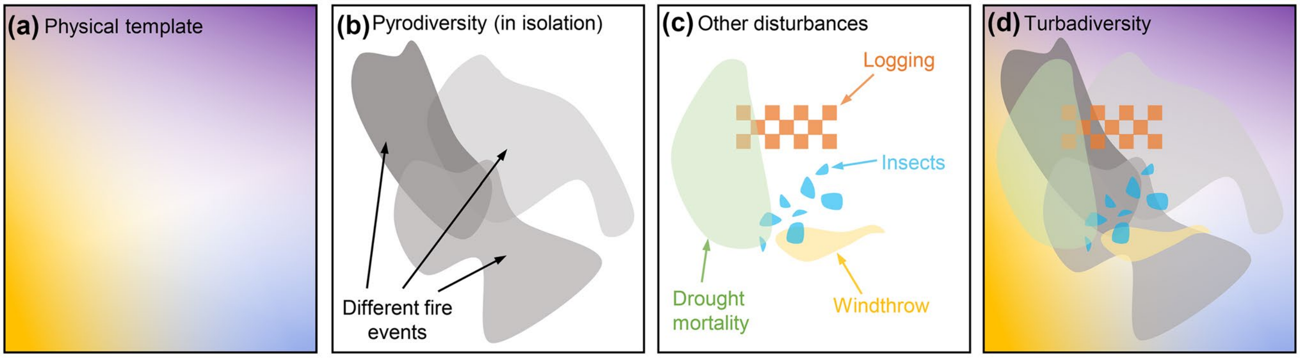

Fig. 2 Various sources of landscape heterogeneity may produce spatial and temporal patterns of biodiversity including (**a**) spatial variation in the physical template (i.e., soils, vegetation, topography), (**b**) pyrodiversity, characterized by heterogeneity in fire characteristics across a landscape, and (**c**) a broader mosaic of other natural and anthropogenic disturbances. The cumulative variation produced by multiple types of overlapping disturbances (**d**), or "turbadiversity," is likely to influence patterns of biodiversity. These patterns may be further varied depending on how turbadiversity interacts with the underlying physical template

those in which fire is less dominant and/or frequent), the vegetation diversity generated by other disturbances will influence biodiversity patterns more than fire, and it is essential that these other agents be examined critically. We suggest that the pyrodiversity-biodiversity hypothesis could therefore be generalized to include any disturbance type, not just fire. The Greek pyro- (relating to "fire") could be exchanged for the Latin turba- (the root of "disturb") to form the "turbadiversity-biodiversity" hypothesis, which would postulate that diversity of disturbances (of any kind) might influence patterns of biodiversity (Fig. 2). Connections to the habitat diversity hypothesis (HDH; [66]) and the intermediate disturbance hypothesis (IDH; [33, 67]) are obvious (see above discussion), but compared to these existing frameworks, the turbadiversity-biodiversity hypothesis focuses more on the diversity and relative impacts of disturbance agents and the cumulative effects such agents might have on biodiversity than either the HDH or IDH.

Pyrodiversity Is Difficult to Interpret Because It Can Be Non-directional

One of the more common approaches for quantifying pyrodiversity is using a diversity index (e.g., Shannon or Simpson) to measure variation in fire age class (i.e., time-since-fire), burn severity, or some other variable related to fire characteristics across a defined area [e.g., 42, 68–71]. This yields an axis of variation in fire characteristics ranging from low to high pyrodiversity. High pyrodiversity is easy enough to conceptualize; this would be an area with a relatively equal mixture of different fire characteristics (e.g., burn severity classes). Low pyrodiversity is more complicated; it reflects areas with homogenous fire characteristics, but this could mean predominately (or entirely) low or high severity effects across an area, for example (Fig. 3). Yet, these extremes might be expected to support very different biotic richness and/or different community composition. In this way, pyrodiversity as a variable—in its current usage—is often a blunt tool.

In our experience, this is indeed problematic and has meant that when interpreting pyrodiversity, additional post hoc steps are required to understand low pyrodiversity (as its meaning will vary among studies). However, such solutions—even if illuminating [e.g., 62]—are not ideal and post hoc checks will become prohibitive with large datasets. Perhaps we need to start thinking about pyrodiversity as occurring along more than one axis. Non-metric multidimensional scaling (NMDS) or principal components analysis (PCA) ordination approaches could offer one solution by clustering unique qualities of pyrodiverse landscapes into multiple axes of variation (Fig. 4). Multiple fire variables could inform an ordination that would produce two axes for each sampling unit. Other approaches could draw on methods used to measure beta diversity (differences in unique species composition) in biological communities [72]; metrics of "beta-pyrodiversity" might offer some interesting opportunities for maintaining the identity of fire characteristics in areas of low pyrodiversity.

The Future of Pyrodiversity: Needs, Solutions, and Directions

Considering emerging themes in the recent literature and critiques of the pyrodiversity paradigm, we highlight three opportunities to improve pyrodiversity research and its practical application to land management in a warming world. First, we need to evaluate pyrodiversity within a multi-scale, gradient paradigm to improve linkages to its effects on biotic communities at the relevant scale. Second, we consider how pyrodiversity might change as the climate warms and identify related research needs. Third, we consider pyrodiversity as a potentially unifying management paradigm (that is, unifying multiple resource management objectives that may traditionally be at odds) in a changing climate.

Multi-scale, Gradient, and Integrated Analysis of Pyrodiversity

The sensitivity of pattern-process relationships to scale has emerged as an organizing principle in landscape ecology [53, 66, 73]. Patterns vary in different ways at different scales [74, 75]. Likewise, ecological processes operate at different scales and interact with landscape patterns to drive, limit, and influence them [76, 77]. Fire is a dominant disturbance process at landscape scales. Furthermore, fire events, behavior, and regimes are all influenced by and, in turn, influence landscape patterns. Thus, a scale-dependent and multi-scale approach is needed to evaluate pyrodiversity.

Within any extent of a landscape, pyrodiversity metrics will be influenced by the grain at which the fire characteristic is mapped (e.g., pixel size of burn severity), the thematic content of its mapping (a continuous index, categories, or other depiction), and the thematic resolution (how finely the index or categories are delineated) [76, 78, 79]. Ideally, pyrodiversity assessments should evaluate a range of grain, thematic content, and thematic resolution, or, at the very least, be explicit in defining these landscape parameters and justifying them based on the goals, objectives, and processes under investigation.

Pyrodiversity will also vary with extent of analysis. Analysis extent has been shown to strongly influence landscape patterns and the ecological processes that create and are moderated by them (e.g., [80]). Therefore, in some contexts such as mapping, one might consider computing pyrodiversity across a range of extents with a focal moving window (e.g., [81•]) using a sensitivity analysis approach. In such

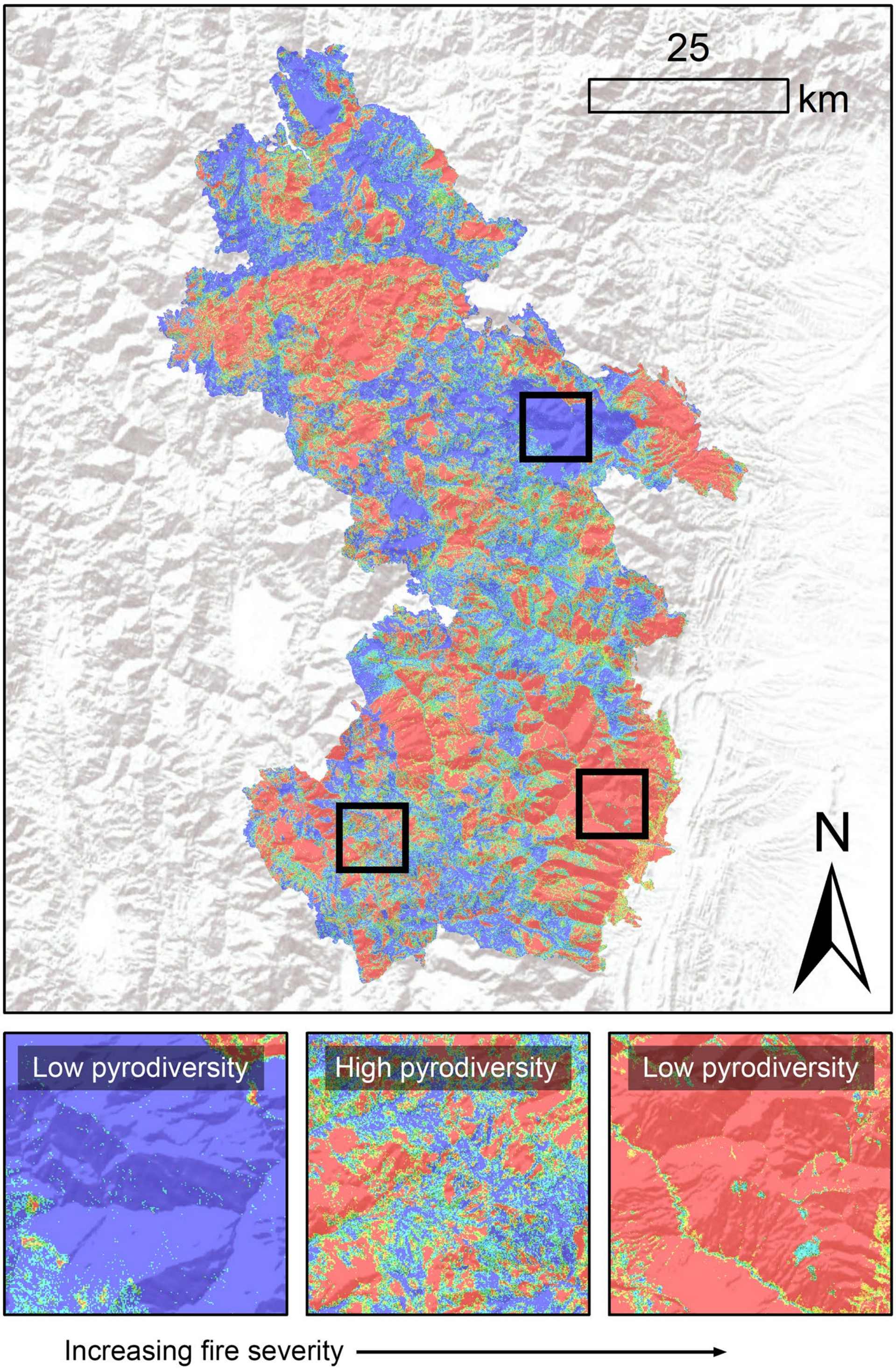

Fig. 3 Examples of pyrodiversity from the 2020 August Complex fire in northern California, USA, using remotely sensed burn severity metrics. Areas characterized by low pyrodiversity might be characterized by homogenous areas of either low or high severity fire, whereas high pyrodiversity is always characterized by a mosaic of burn severities. Blue represents lower severity fire and red represents higher severity fire

an approach, the mean and variance of these pyrodiversity surfaces can be plotted as a function of extent to visualize the scale-dependency of pyrodiversity. Subsequently, the variance-to-mean ratios (also known as dispersion index or coefficient of dispersion) can also be plotted across the range of extents. The variance-to-mean ratio has additional value in measuring a component of landscape pattern: for spatially random processes, the variance is equal to the mean of a variable ($\sigma^2 = \mu$), while it is greater than the mean when the process is spatially aggregated ($\sigma^2 > \mu$) and lower than the mean when the process is spatially dispersed ($\sigma^2 < \mu$). These approaches provide a means to directly incorporate and account for scale dependency and landscape pattern in measuring pyrodiversity.

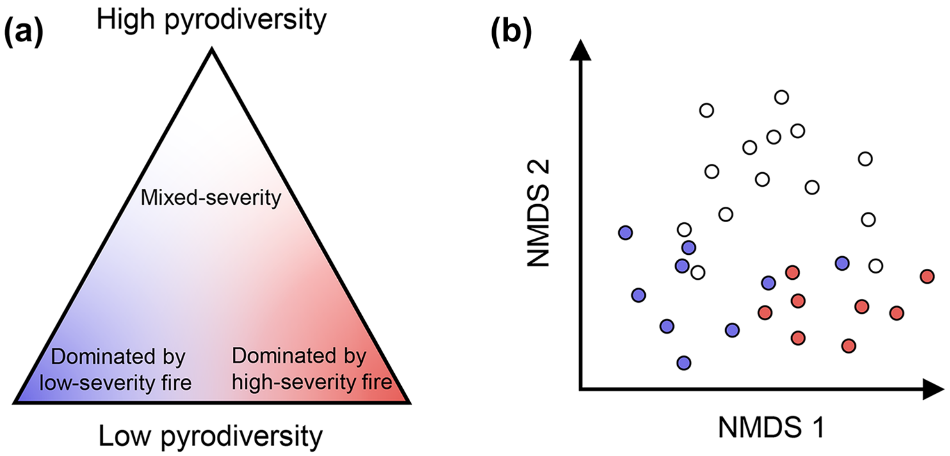

Fig. 4 Conceptual depictions of pyrodiversity that expand on the directional gradient of "low to high pyrodiversity." In panel **a**, we recognize that low pyrodiversity can arise from homogeneity in fire effects, but that the biodiversity outcome is different for low- vs. high-severity fire. In panel **b**, various metrics that define pyrodiversity (e.g., time since fire, patch size of low, moderate, and high severity, time since fire, number of times burned) could be used in a nonmetric multidimensional scaling (NMDS) or other ordination frameworks to define axes and differentiate pyrodiversity "clusters" in terms of the distinct fire characteristics they contain

In addition to adopting a multi-scale approach to measuring pyrodiversity, in some contexts, adopting a "gradient paradigm" [82–84], as opposed to a patch-mosaic paradigm, may be useful. Certain data types such as fire severity are naturally represented as continuously varying quantitative variables. Often such variables are categorized into classes (which may be arbitrarily defined) and subsequent mapping and analysis is applied to the patches in this classified output [85]. However, information is lost and biases are introduced when continuous data are binned into categories [86, 87]. Thus, it is often more informative to keep continuous variables in their original form and analyze them as scale-dependent gradient processes. Doing so retains all information in the spatial pattern of variation and allows flexible multi-scale analysis of those patterns. Numerous metrics may be appropriate in multi-scale gradient analyses of pyrodiversity, including variance-to-mean ratios, a multitude of surface metrics [84], or measures of configurational entropy (e.g., [88–90]). However, we acknowledge that the patch-mosaic paradigm has its place; when it makes sense to quantify pyrodiversity in a way that involves patches (e.g., patch sizes of burn severity classes), then a gradient paradigm cannot always be used.

Yet, recent approaches have been developed that combine multiple fire characteristics to create integrated measures of pyrodiversity [35••], which could accommodate conceptualizations in both gradient and patch-mosaic paradigms. After all, pyrodiversity, as first conceptualized by [32], is much more than variation in burn severity—as admittedly has been a strong focus of this review—or any other single characteristic. The variation in numerous fire characteristics, such as time-since-fire, number of times burned, burn severity, patch size, and others are all important. The generalizable functional diversity approach, introduced by Steel et al. [35••], offers a promising opportunity for integrating multiple fire metrics in a unified framework for measuring pyrodiversity.

Climate Change and Pyrodiversity

Over the last several decades, warmer and drier conditions associated with climate change have resulted in longer fire seasons [91], increased annual area burned [9, 24], and increased annual area burned at high severity [17]. These changes to the fire regime will continue to alter pyrodiversity across spatial and temporal scales. Assuming we can adequately measure pyrodiversity and do so at the appropriate scale, how might we expect climate change to influence pyrodiversity?

The effect of climate change on pyrodiversity is highly contextual and depends on the bioclimatic setting (i.e., vegetation and climate) and the timeframe of inference (Fig. 5). In regions that have rarely burned historically, such as the tussock tundra or cold, high-elevation forests, climate change may actually increase pyrodiversity by shortening the fire return interval [92]. Yet, it is increasingly being recognized that climate change has short- and long-term consequences for fire and vegetation (and by extension, pyrodiversity) and that the short-term consequences may differ in direction and magnitude compared to the longer-term. In some bioclimatic settings, for example, annual area burned is expected to increase in the short-term (approximately the next few decades) as climate change results in more fire-conducive weather and drier fuels but may actually decrease over longer timeframes because warming climate conditions

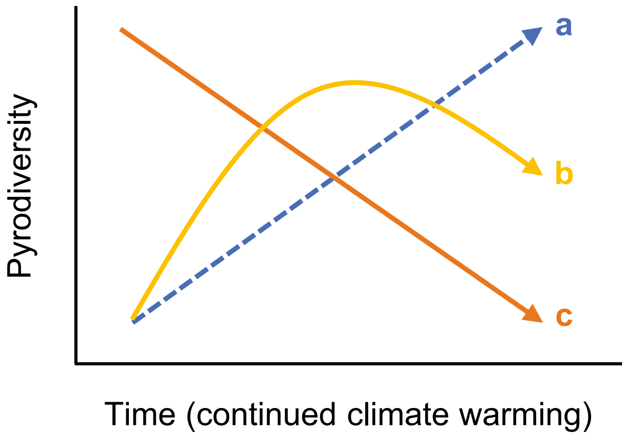

Fig. 5 How will pyrodiversity change as the climate warms? In systems that rarely burn, increased fire activity associated with climate change might increase pyrodiversity (**a**). In systems with historically frequent fire, climate change might reduce pyrodiversity by generating more homogenous, severely burned landscapes (**c**). With climate-vegetation feedbacks, nonlinear changes in pyrodiversity might also be expected to occur in ways that are difficult to predict (**b**). How pyrodiversity changes with climate likely will vary depending on ecosystem type, the reference period being used for comparison (e.g., recent vs. deep past), and the spatial scale being considered (i.e., trajectories might be scale-dependent)

reduce productivity and therefore available fuel to burn [93, 94]. Indeed, evidence for recent increases in annual area burned is mounting [95, 96]. The longer-term consequences in terms on annual area burned have yet to play out, but it is worth noting that projected longer-term *decreases* in annual area burned are limited to the drier bioclimatic settings (those at the climatic margin between forest and shrubland that are expected to be less productive) [12, 97]; regions with less moisture stress are projected to experience more frequent fire in both the short and long term (cf. [98]).

Climate also influences fire severity and, by extension, pyrodiversity. Warmer and drier fire seasons are more conducive to high-severity fire [17, 99], but climate can also indirectly influence fire severity through controls on fuel amount (i.e., productivity) and vegetation type [100]. Consequently, the short- and long-term consequences of climate change on fire severity may differ, in that the short-term consequence is higher severity fire, but the longer-term consequence is either lower or higher severity fire, depending on the bioclimatic context [97].

The longer-term patterns and trends we have discussed so far are extremely general and based on expected biogeographic shifts in fire regime characteristics associated with climate change. However, non-climatic factors (oftentimes interacting with each other and climate change) are also going to drive changes in pyrodiversity, namely excessive fuel loads in forested ecosystems associated with fire exclusion, invasive species, and insect-induced tree mortality. For example, excessive biomass in many dry forest ecosystems in the western US is contributing to higher-severity fire that often exceeds that of what is considered characteristic for a given ecosystem (e.g., [101, 102]). When these forests inevitably burn, the resulting pattern may reflect high pyrodiversity initially, but in fact, the resulting burn mosaic may put the site on a trajectory toward landscape homogenization and low pyrodiversity in future decades. There are several examples of such fires, particularly if sites burn again, that have converted forested landscapes to homogenous non-forested states that will exhibit extremely low pyrodiversity when they burn again (e.g., [13, 103]). Invasive species are also leading to altered vegetation and homogenization of landscapes with low pyrodiversity. For example, the invasive species cheatgrass has invaded the Great Basin and now covers large swaths of former sagebrush ecosystems (historically infrequent fire); many areas are now in a frequent fire state with low pyrodiversity [104]. Lastly, insect-induced tree mortality, which has affected millions of acres of forest in the western US over the last few decades [105, 106], appears to set the stage for higher-severity fire [107]. While such areas may exhibit high pyrodiversity as a result of an initial fire, their resilience to future fire events is diminished and an overall reduction of pyrodiversity can be expected over longer time periods. Cumulatively, as climate change interacts with uncharacteristically severe fire as a result of excessive fuels, invasive species, and insect-induced drought mortality, we can expect homogenization of vegetation and fire effects through time [108, 109], and as a result, lower pyrodiversity will manifest in many ecosystems.

Pyrodiversity: a Unifying Landscape Conservation Paradigm in a Warming World?

As we witness the effects of changing wildfire regimes on biodiversity, ecosystems, and society, we seek tractable conservation and management solutions. How do we mitigate the adverse effects of changing fire regimes? Pyrodiversity, as a general framing concept, might form a key piece of the solution by acting as a unifying conservation paradigm. The application of a pyrodiversity paradigm in landscape management and conservation might naturally resolve challenging problems that have led to conflict and inaction under existing paradigms.

A greater understanding of the relationships between pyrodiversity and biodiversity might unify the divide between coarse-grain ecosystem management and fine-grain species habitat conservation. This divide is characterized by the scale at which conservation resources should be focused: species, ecosystems, or landscapes [110, 111]. On the one hand, there are too many species to manage each individually, so ecosystem- and landscape-level management approaches (coarse-grain) are the only tractable, cost-effective conservation solution [110]. Yet, such coarse-grain approaches might end up harming individual species with unique habitat requirements (fine-grain) that help support ecosystem integrity [112]. In some systems, moderate to high pyrodiversity generally may be associated with more favorable features (from a conservation perspective) at the ecosystem- and landscape-level, including structural variability that is associated with resilience [113, 114•]. These same diverse landscape features produced by multi-scale pyrodiversity have the potential to support overall wildlife diversity [31, 51] as well as individual species of conservation concern with ecological associations as disparate as the black-backed woodpecker and spotted owl in dry western US forests [29•, 42, 45]. This is because pyrodiversity generates a juxtaposition of various habitats that can fulfill life-history needs of individual specialists (i.e., habitat complementation) [30•].

Yet, high pyrodiversity will not be desirable in all systems. Whether pyrodiversity is "good" or "bad" for biodiversity, individual species, and/or ecosystem processes is likely to depend on the system and its ecological history, context, and characteristics, as well as the spatial and temporal scales being considered (see [29•]). Systems that historically experienced low pyrodiversity would not necessarily be expected to benefit from management that promotes increases in pyrodiversity, such as in ecosystems in which fire was historically relatively rare (e.g., temperate rainforests in the Pacific Northwest of North America). In systems with higher historical pyrodiversity, understanding the nature of "good" pyrodiversity is critical. For example, some dry forest types may have had relatively high historical pyrodiversity (e.g., moderate to frequent fire return interval, small patches of high-severity fire), but low pyrodiversity over the past century because of fire exclusion. Increasing fire activity in these areas may be increasing pyrodiversity relative to the past century, but the specific variety of pyrodiversity may not be appropriate for the system (e.g., very large patches of high-severity fire; [22]). Further research is needed to quantify "reference" pyrodiversity for a variety of systems, which could help compute the degree to which modern pyrodiversity is departed from historical baselines (i.e., novelty in pyrodiversity; [115]). We encourage a continued thoughtful exploration of a pyrodiversity paradigm within the context of land management, and caution against applying the paradigm where it may not be warranted [34].

The integration of the pyrodiversity paradigm into land management is not new. But there is a new interest and momentum surrounding its application. For millennia, Indigenous people in biomes across the globe have used fire to generate landscape heterogeneity to support subsistence hunting, local economies, communication, and other natural resource needs [28]. Moreover, evidence suggests that past and ongoing Indigenous fire use yields patterns of fire characteristics across the landscape that would be considered "pyrodiverse" [116]. Similarly, patch-mosaic burning (PMB)—a management approach based on pyrodiversity—was a concept applied in South African national parks beginning in the early 1990s that focused on rotating prescribed fires throughout the park area to produce the landscape heterogeneity that would support habitat for many species [117]. PMB burning in South Africa is conducted primarily in grassland/savannah systems and is intended to provide forage of different ages over space and time; we note that in many of our examples, we use burn severity, which is not applicable in grassland. In this context, though, PMB has been critiqued as having been applied without sufficient empirical evidence to support the objectives it claims to achieve, and little clear guidance for operational use [34].

Operational Pyrodiversity: Future Research Needs

We think that developing rules for "operational pyrodiversity" is one of the concept's most urgent needs moving forward. While we do not resolve this issue here, we raise some questions that we hope will lead to future research. What is the appropriate scale at which to apply a pyrodiversity paradigm? Specifically, should managers aim to promote pyrodiversity across tens of hectares, thousands, or tens of thousands? Above we argued for multi-scale assessments of pyrodiversity impacts to biodiversity. In the same way, pyrodiversity should also be managed at multiple scales, and relevance of different scales to management will vary across ecosystems. Should managers aim for promoting certain pyrodiversity "targets," i.e., a specified minimum degree of variation in fire characteristics that is associated with their objective? Can you produce "too much" pyrodiversity in a given ecosystem and, if so, how do we identify this threshold? What is the optimal amount of pyrodiversity, and scale at which it must occur, and how does this vary among ecosystems? Developing reference frameworks for ecological systems based on historical, ecological, management, and other considerations is needed; these frameworks can then be used to help define desired conditions with respect to pyrodiversity [118–120].

Perhaps the most relevant to the question of developing an operational pyrodiversity is whether the concept (as it is currently used and measured in the literature) is even meaningful or realistic as a prescriptive objective within the context of land management. For example, when instructing a prescribed fire team to produce "pyrodiversity," what does this look like on the ground? What are the levers (i.e., specific management actions and decisions at different scales) that can be used to control pyrodiversity given other stated resource management objectives? And how much control do operators really have in producing desired patterns? Presumably, some aspects of pyrodiversity can be controlled better than others with prescribed fire (fire intervals/seasonality vs. variation in severity), but it is unclear what variability in control could mean for implementing desired patterns in pyrodiversity. Fire has always been a "blunt" tool for management because it is difficult to control and impossible to predict the patterns it will yield with precision. Beyond prescribed fire operations, should unplanned wildfires managed for resource benefit be guided to produce pyrodiversity? If so, how? Often, managed wildfires naturally generate pyrodiversity (e.g., [121]), so does the concept add any value in this context?

Developing an operational pyrodiversity will also require developing "reference" targets that are system-specific and describe the deviation of desired conditions from current conditions [115, 118]. This deviation of desired conditions from current conditions informs resource managers ability to "resist, accept or direct" ecological changes (RAD framework; [122]). Ecosystem types vary in their historical fire regimes and will differ in their trajectory when fire is applied to the system. Biodiversity patterns arising from pyrodiversity could be expected to respond differently based on if current and historical fire regimes are consistent or divergent, regardless of if there is a fire deficit or fire surplus [123]. For example, an area that historically experienced infrequent, high-severity fire (i.e., cold, high-elevation forests) but is now experiencing a fire surplus because of increasing fire frequency [124] may lose biodiversity due to a mismatch between historical and contemporary fire regimes.

In general, we think that the concept of pyrodiversity could engender creativity and flexibility in fire management, but better guidelines are needed. We are not the first to express concern about our current inability to develop guidance for operational pyrodiversity. Several studies we reviewed noted that a goal of pyrodiversity may be too vague a directive for management [41, 47, 125], echoing one of the early critiques of the pyrodiversity paradigm [34]. Studies that call for management using pyrodiversity often place bounds on pyrodiversity in some way, such as limiting high-severity fire [35••] or setting aside unburned areas [126]. We are a long way off from operationalizing the concept of pyrodiversity, and doing so will require close feedback between scientists and land managers moving forward.

Concluding Remarks

Research on the causes of pyrodiversity and its consequences for biotic communities is entering a period of rapid growth, with promising innovations in the most recent literature. Those that stand out to us include the application of multi-scale analyses (e.g., [40]), the exploration of pyrodiversity effects on single species (e.g., [45]), measurement of beta-diversity (e.g., [127]), functional redundancy (e.g., [47]) and related community metrics (e.g., [46]), and research developing novel, integrative methods for measuring pyrodiversity (e.g., [35••]). These works push the boundaries of the concept and illuminate unknowns, and we encourage more similar work. Yet like any emerging, still-immature research topic, the pyrodiversity paradigm has several theoretical and practical "rough spots." Future research will address these issues over time. Nevertheless, the pyrodiversity idea has the potential to be a unifying conservation paradigm—a paradigm that achieves multiple resource objectives and resolves previously intractable resource management problems—and particularly so in a warming world that will be characterized by more fire.

Acknowledgements We thank B. Zuckerberg for inviting us to submit this review paper. This research was supported in part by the USDA Forest Service, Rocky Mountain Research Station. The findings and conclusions in this publication are those of the authors and does not necessarily represent any official USDA or US Government determination or policy.

Compliance with Ethical Standards

Conflict of Interest The authors declare no competing interests.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

References

Papers of particular interest, published recently, have been highlighted as:
• Of importance
•• Of major importance

1. Bowman DMJS, Balch JK, Artaxo P, Bond WJ, Carlson JM, Cochrane MA, et al. Fire in the earth system. Science. 2010;481:481–5.
2. Krawchuk MA, Moritz MA, Parisien MA, Van Dorn J, Hayhoe K. Global pyrogeography: the current and future distribution of wildfire. PLoS One. 2009;4:e5102.
3. Pausas JG, Ribeiro E. Fire and plant diversity at the global scale. Glob Ecol Biogeogr. 2017;26:889–97.
4. Archibald S, Lehmann CER, Gómez-Dans JL, Bradstock RA. Defining pyromes and global syndromes of fire regimes. Proc Natl Acad Sci USA. 2013;110:6442–7.
5. Bond WJ, Keeley J. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends Ecol Evol. 2005;20:387–94.
6.• He T, Lamont BB, Pausas JG. Fire as a key driver of Earth's biodiversity. Biol Rev. 2019;94:1983–2010. **This review paper provides a comprehensive, theory-driven review of research showing how plant and animal evolution is shaped by fire regimes.**

7. Pausas JG, Parr CL. Towards an understanding of the evolutionary role of fire in animals. Evol Ecol. 2018;32:113–25.
8. Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA. Fire as an evolutionary pressure shaping plant traits. Trends Plant Sci. 2011;16:406–11.
9. Westerling AL. Increasing western US forest wildfire activity: sensitivity to changes in the timing of Spring. Philos Trans R Soc Lond B Biol Sci. 2016;371:20150178.
10. Stephens SL, Burrows N, Buyantuyev A, Gray RW, Keane RE, Kubian R, et al. Temperate and boreal forest mega-fires: characteristics and challenges. Front Ecol Environ. 2014;12:115–22.
11. Nimmo DG, Carthey AJR, Jolly CJ, Blumstein DT. Welcome to the Pyrocene: animal survival in the age of megafire. Glob Chang Biol. 2021;27:5684–93.
12. Littell JS, McKenzie D, Wan HY, Cushman SA. Climate change and future wildfire in the western United States: an ecological approach to nonstationarity. Earth's Futur. 2018;6:1097–111.
13. Coop JD, Parks SA, Stevens-Rumann CS, Crausbay SD, Higuera PE, Hurteau MD, et al. Wildfire-driven forest conversion in western North American landscapes. Bioscience. 2020;70:659–73.
14. Romme WH, Despain DG. Historical perspective on the Yellowstone fires of 1988. Bioscience. 1989;39:695–9.
15. Margolis EQ, Swetnam TW, Allen CD. A stand-replacing fire history in upper montane forests of the southern Rocky Mountains. Can J For Res. 2007;37:2227–41.
16. Gill AM, Stephens SL, Cary GJ. The worldwide "wildfire" problem. Ecol Appl. 2013;23:438–54.
17. Parks SA, Abatzoglou JT. Warmer and drier fire seasons contribute to increases in area burned at high severity in sestern US forests From 1985 to 2017. Geophys Res Lett. 2020;47:e2020GL089858.
18.• Bowman DMJS, Kolden CA, Abatzoglou JT, Johnston FH, van der Werf GR, Flannigan M. Vegetation fires in the Anthropocene. Nat Rev Earth Environ. 2020;1:500–15. **This paper reviews the recent past and discusses the likely near-term future of vegetation fires and their impacts to natural resources and society.**
19. Araújo MB, Ferri-Yáñez F, Bozinovic F. Marquet P a, Valladares F, Chown SL. Heat freezes niche evolution Ecol Lett. 2013;16:1206–19.
20. Moritz MA, Batllori E, Bradstock RA, Gill AM, Handmer J, Hessburg PF, et al. Learning to coexist with wildfire. Nature. 2014;515:58–66.
21. Schoennagel T, Balch JK, Brenkert-Smith H, Dennison PE, Harvey BJ, Krawchuk MA, et al. Adapt to more wildfire in western North American forests as climate changes. Proc Natl Acad Sci. 2017;114:4582–90.
22. Stevens JT, Collins BM, Miller JD, North MP, Stephens SL. Changing spatial patterns of stand-replacing fire in California conifer forests. For Ecol Manage Elsevier. 2017;406:28–36.
23. Safford HD, Stevens JT. Natural range of variation for yellow pine and mixed-conifer forests in the Sierra Nevada, Southern Cascades, and Modoc and Inyo National Forests, California, USA. Albany, CA: PSW-GTR-256; 2017.
24. Abatzoglou JT, Williams AP. Impact of anthropogenic climate change on wildfire across western US forests. Proc Natl Acad Sci. 2016;113:11770–5.
25. Boer MM, Resco de Dios V, Bradstock RA. Unprecedented burn area of Australian mega forest fires. Nat Clim Chang. 2020;10:171–172.
26. Nolan RH, Boer MM, Collins L, Resco de Dios V, Clarke H, Jenkins M, et al. Causes and consequences of eastern Australia's 2019–20 season of mega-fires. Glob Chang Biol. 2020;26:1039–41.
27. Collins L, Bradstock RA, Clarke H, Clarke MF, Nolan RH, Penman TD. The 2019/2020 mega-fires exposed Australian ecosystems to an unprecedented extent of high-severity fire. Environ Res Lett. 2021;16:044029.
28. Hoffman KM, Davis EL, Wickham SB, Schang K, Johnson A, Larking T, et al. Conservation of Earth's biodiversity is embedded in Indigenous fire stewardship. Proc Natl Acad Sci U S A. 2021;118:e2105073118.
29.• Jones GM, Tingley MW. Pyrodiversity and biodiversity: a history, synthesis, and outlook. Divers Distrib. 2022;28:386–403. **This paper reviews and synthesizes empirical support for the pyrodiversity-biodiversity hypotheses and proposes future directions to strengthen pyrodiversity research.**
30.• Kelly LT, Brotons L, McCarthy MA. Putting pyrodiversity to work for animal conservation. Conserv Biol. 2017;31:952–5. **This paper describes some of the mechanistic hypotheses that might underlie pyrodiversity-biodiversity relationships.**
31. Kelly LT, Brotons L. Using fire to promote biodiversity. Science. 2017;355:1264–5.
32. Martin RE, Sapsis DB. Fires as agents of biodiversity: pyrodiversity promotes biodiversity. Proc Symp Biodivers Northwest Calif. 1992;150–157.
33. Connell JH. Diversity in tropical rain forests and coral reefs. Science. 1978;199:1302–10.
34. Parr CL, Andersen AN. Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. Conserv Biol. 2006;20:1610–9.
35.•• Steel ZL, Collins BM, Sapsis DB, Stephens SL. Quantifying pyrodiversity and its drivers. Proc R Soc B Biol Sci. 2021;288:20203202. **This paper proposes a novel, generalizable functional diversity approach for quantifying pyrodiversity that integrates multiple fire characteristics.**
36. Andersen AN, Hoffmann BD. Conservation value of low fire frequency in tropical savannas: ants in monsoonal northern Australia. Austral Ecol. 2011;36:497–503.
37. Nimmo DG, Kelly LT, Spence-Bailey LM, Watson SJ, Taylor RS, Clarke MF, et al. Fire mosaics and reptile conservation in a fire-prone region. Conserv Biol. 2013;27:345–53.
38. Tingley MW, Ruiz-Gutierrez V, Wilkerson RL, Howell CA, Siegel RB. Pyrodiversity promotes avian diversity over the decade following forest fire. Proc R Soc B Biol Sci. 2016;283:20161703.
39. Greenwood L, Bliege Bird R, Nimmo D. Indigenous burning shapes the structure of visible and invisible fire mosaics. Landsc Ecol. 2022;37:811–27.
40. Blakey RV, Webb EB, Kesler DC, Siegel RB, Corcoran D, Cole JS, et al. Extent, configuration and diversity of burned and forested areas predict bat richness in a fire-maintained forest. Landsc Ecol. 2021;36:1101–15.
41. Radford IJ, Corey B, Carnes K, Shedley E, McCaw L, Woolley L-A. Landscape-scale effects of fire, cats, and feral livestock on threatened savanna mammals: unburnt habitat matters more than pyrodiversity. Front Ecol Evol. 2021;9:739817.
42. Jones GM, Kramer H, Berigan W, Whitmore S, Gutiérrez RJ, Peery M. Megafire causes persistent loss of an old-forest species. Anim Conserv. 2021;24:925–36.
43. López-Baucells A, Flaquer C, Mas M, Pons P, Puig-Montserrat X. Recurring fires in Mediterranean habitats and their impact on bats. Biodivers Conserv. 2021;30:385–402.
44.• Stillman AN, Siegel RB, Wilkerson RL, Johnson M, Tingley MW. Age-dependent habitat relationships of a burned forest specialist emphasise the role of pyrodiversity in fire management. J Appl Ecol. 2019;56:880–90. **This paper shows the importance of pyrodiversity in shaping habitat characteristics that fulfill multiple life history needs for a single species, the black-backed woodpecker.**
45. Stillman AN, Lorenz TJ, Fischer PC, Siegel RB, Wilkerson RL, Johnson M, et al. Juvenile survival of a burned forest specialist

in response to variation in fire characteristics. J Anim Ecol. 2021;90:1317–27.

46. Ponisio LC. Pyrodiversity promotes interaction complementarity and population resistance. Ecol Evol. 2020;10:4431–47.
47. Docherty TDS, Hethcoat MG, MacTavish LM, MacTavish D, Dell S, Stephens PA, et al. Burning savanna for avian species richness and functional diversity. Ecol Appl. 2020;30:e02091.
48. Kuenzi AM, Fulé PZ, Sieg CH. Effects of fire severity and pre-fire stand treatment on plant community recovery after a large wildfire. For Ecol Manage. 2008;255:855–65.
49. Muñoz A, Felicísimo ÁM, Santos X. Analysing how pre-fire habitat legacy and post-fire management influence the resilience of reptiles to fire. Forests. 2021;12:1487.
50. White PS. Pattern, process, and natural disturbance in vegetation. Bot Rev. 1979;45:229–99.
51. Kelly LT, Giljohann KM, Duane A, Aquilué N, Archibald S, Batllori E, et al. Fire and biodiversity in the Anthropocene. Science. 2020;370:eabb0355.
52. Boerner REJ. Fire and nutrient cycling in temperate ecosystems. Bioscience. 1982;32:187–92.
53. Turner MG. Landscape ecology: the effect of pattern on process. Annu Rev Ecol Syst. 1989;20:171–97.
54. Turner MG, Gardner RH, O'Neill RV. Landscape ecology in theory and practice: pattern and process. New York, NY: Springer-Verlag; 2001.
55. Bebi P, Kulakowski D, Rixen C. Snow avalanche disturbances in forest ecosystems-State of research and implications for management. For Ecol Manage. 2009;257:1883–92.
56. Ulanova NG. The effects of windthrow on forests at different spatial scales: a review. For Ecol Manage. 2000;135:155–67.
57. Wang W, Qu JJ, Hao X, Liu Y, Stanturf JA. Post-hurricane forest damage assessment using satellite remote sensing. Agric For Meteorol. 2010;150:122–32.
58. Garwood NC, Janos DP, Brokaw N. Earthquake-caused landslides: a major disturbance to tropical forests. Science. 1979;205:997–9.
59. Swanson FJ, Johnson SL, Gregory SV, Acker SA. Flood disturbance in a forested mountain landscape. Bioscience. 1998;48:681–9.
60. Hlásny T, König L, Krokene P, Lindner M, Montagné-Huck C, Müller J, et al. Bark beetle outbreaks in Europe: state of knowledge and ways forward for management. Curr For Reports. 2021;7:138–65.
61. Corlett RT. The impacts of droughts in tropical forests. Trends Plant Sci. 2016;21:584–93.
62. Cushman SA, McGarigal K. Landscape-level patterns of avian diversity in the Oregon Coast Range. Ecol Monogr. 2003;73:259–81.
63. Anderson MG, Comer PJ, Beier P, Lawler JJ, Schloss CA, Buttrick S, et al. Case studies of conservation plans that incorporate geodiversity. Conserv Biol. 2015;29:680–91.
64. Stephens SL, Collins BM, Fettig CJ, Finney MA, Hoffman CM, Knapp EE, et al. Drought, tree mortality, and wildfire in forests adapted to frequent fire. Bioscience. 2018;68:77–88.
65. Lydersen JM, Collins BM, Brooks ML, Matchett JR, Shive KL, Povak NA, et al. Evidence of fuels management and fire weather influencing fire severity in an extreme fire event. Ecol Appl. 2017;27:2013–30.
66. Wiens J. Spatial scaling in ecology. Funct Ecol. 1989;3:385–97.
67. Paine RT. Food Web Complexity and Species Diversity. Am Nat. 1966;100:65–75.
68. Taylor RS, Watson SJ, Nimmo DG, Kelly LT, Bennett AF, Clarke MF. Landscape-scale effects of fire on bird assemblages: does pyrodiversity beget biodiversity? Divers Distrib. 2012;18:519–29.
69. Ponisio LC, Wilkin K, M'Gonigle LK, Kulhanek K, Cook L, Thorp R, et al. Pyrodiversity begets plant-pollinator community diversity. Glob Chang Biol. 2016;22:1794–808.
70. Davis H, Ritchie EG, Avitabile S, Doherty T, Nimmo DG. Testing the assumptions of the pyrodiversity begets biodiversity hypothesis for termites in semi-arid Australia. R Soc Open Sci. 2018;5:172055.
71. Avitabile SC, Nimmo DG, Bennett AF, Clarke MF. Termites are resistant to the effects of fire at multiple spatial scales. PLoS ONE. 2015;10:e0140114
72. Whittaker RH. Evolution and measurement of species diversity. Taxon. 1972;21:213–51.
73. Levin SA. The problem of pattern and scale in ecology. Ecology. 1992;73:1943–67.
74. Wu J, Loucks OL. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. Q Rev Biol. 1995;70:439–66.
75. Schneider DC. The rise of the concept of scale in ecology. Bioscience. 2001;51:545–53.
76. Turner MG, Dale VH, Gardner RH. Predicting across scales: theory development and testing. Landsc Ecol. 1989;3:245–52.
77. Peters DPC, Bestelmeyer BT, Turner MG. Cross-scale interactions and changing pattern-process relationships: consequences for system dynamics. Ecosystems. 2007;10:790–6.
78. Turner MG, O'Neill RV, Gardner RH, Milne BT. Effects of changing spatial extent on landscape pattern analysis. Landsc Ecol. 1989;3:153–62.
79. Turner MG. Spatial and temporal analysis of landscape patterns. Landsc Ecol. 1990;4:21–30.
80. Saura S, Martínez-Millan J. Sensitivity of landscape pattern metrics to map spatial extent. Photogramm Eng Remote Sensing. 2001;67:1027–36.
81. • McGarigal K, Wan HY, Zeller KA, Timm BC, Cushman SA. Multi-scale habitat selection modeling: a review and outlook. Landsc Ecol. 2016;31:1161–75. **This paper reviews the prevalence of multi-scale analyses of habitat selection and offers a roadmap to their successful implementation.**
82. McGarigal K, Cushman SA. The gradient concept of landscape structure. In: Wiens J, Moss M, editors. Issues Perspect Landsc Ecol. Cambridge University Press; 2005;112–9.
83. Cushman SA, Gutzweiler K, Evans J, McGarigal K. The gradient paradigm: a conceptual and analytical framework for landscape ecology. In: Cushman SA, Huettmann F, editors. Spat Complexity, Informatics, Wildl Conserv. Springer; 2010;83–108.
84. McGarigal K, Tagil S, Cushman SA. Surface metrics: an alternative to patch metrics for the quantification of landscape structure. Landsc Ecol. 2009;24:433–50.
85. Kolden CA, Smith AMS, Abatzoglou JT. Limitations and utilisation of monitoring trends in burn severity products for assessing wildfire severity in the USA. Int J Wildl Fire. 2015;24:1023–8.
86. McKelvey KS, Noon BR. Incorporating uncertainties in animal location and map classification into habitat relationships modeling. In: Hunsaker C, Goodchild M, Friedl M, Case T, editors. Spat Uncertain Ecol. New York: Springer; 2001. p. 72–90.
87. Feilhauer H, Zlinszky A, Kania A, Foody GM, Doktor D, Lausch A, et al. Let your maps be fuzzy!—class probabilities and floristic gradients as alternatives to crisp mapping for remote sensing of vegetation. Remote Sens Ecol Conserv. 2021;7:292–305.
88. Cushman SA. Thermodynamic consistency of the cushman method of computing the configurational entropy of a landscape lattice. Entropy. 2021;23:1420.
89. Cushman SA. Generalizing Boltzmann configurational entropy to surfaces, point patterns and landscape mosaics. Entropy. 2021;23:1616.

90. Cushman SA. Calculating the configurational entropy of a landscape mosaic. Landsc Ecol. 2016;31:481–9.
91. Jolly WM, Cochrane MA, Freeborn PH, Holden ZA, Brown TJ, Williamson GJ, et al. Climate-induced variations in global wildfire danger from 1979 to 2013. Nat Commun. 2015;6:7537.
92. Higuera PE, Brubaker LB, Anderson PM, Brown TA, Kennedy AT, Hu FS. Frequent fires in ancient shrub tundra: Implications of paleorecords for arctic environmental change. PLoS ONE. 2008;3:e0001744.
93. Rocca ME, Brown PM, MacDonald LH, Carrico CM. Climate change impacts on fire regimes and key ecosystem services in Rocky Mountain forests. For Ecol Manage. 2014;327:290–305.
94. Kennedy MC, Bart RR, Tague CL, Choate JS. Does hot and dry equal more wildfire? Contrasting short- and long-term climate effects on fire in the Sierra Nevada, CA. Ecosphere. 2021;12:e03657.
95. Singleton M, Thode A, Sanchez Meador A, Iniguez P. Increasing trends in high-severity fire in the southwestern USA from 1984–2015. For Ecol Manage. 2019;433:709–19.
96. Williams AP, Abatzoglou JT, Gershunov A, Guzman-Morales J, Bishop DA, Balch JK, et al. Observed impacts of anthropogenic climate change on wildfire in California. Earth's Futur. 2019;7:892–910.
97. Parks SA, Holsinger LM, Miller C, Parisien MA. Analog-based fire regime and vegetation shifts in mountainous regions of the western US. Ecography. 2018;41:910–21.
98. Abatzoglou JT, Battisti DS, Williams AP, Hansen WD, Harvey BJ, Kolden CA. Projected increases in western US forest fire despite growing fuel constraints. Commun Earth Environ. 2021;2:227.
99. Keyser A, Westerling AL. Climate drives inter-annual variability in probability of high severity fire occurrence in the western United States. Environ Res Lett. 2017;12:065003.
100. Parks SA, Miller C, Abatzoglou JT, Holsinger LM, Parisien M-A, Dobrowski SZ. How will climate change affect wildland fire severity in the western US? Environ Res Lett. 11:035002.
101. Mallek C, Safford H, Viers J, Miller J. Modern departures in fire severity and area vary by forest type, Sierra Nevada and southern Cascades, California. USA Ecosphere. 2013;4:153
102. Haugo RD, Kellogg BS, Cansler CA, Kolden CA, Kemp KB, Robertson JC, et al. The missing fire: quantifying human exclusion of wildfire in Pacific Northwest forests, USA. Ecosphere. 2019;10:e02702.
103. Coppoletta M, Merriam KE, Collins BM. Post-fire vegetation and fuel development influences fire severity patterns in reburns. Ecol Appl. 2016;26:686–99.
104. Balch JK, Bradley BA, D'Antonio CM, Gómez-Dans J. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Glob Chang Biol. 2013;19:173–83.
105. Chapman TB, Veblen TT, Schoennagel T. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. Ecology. 2012;93:2175–85.
106. Meigs GW, Kennedy RE, Gray AN, Gregory MJ. Spatiotemporal dynamics of recent mountain pine beetle and western spruce budworm outbreaks across the Pacific Northwest Region, USA. For Ecol Manage. 2015;339:71–86.
107. Wayman RB, Safford HD. Recent bark beetle outbreaks influence wildfire severity in mixed-conifer forests of the Sierra Nevada, California, USA. Ecol Appl. 2021;31:e02287.
108. Cassell BA, Scheller RM, Lucash MS, Hurteau MD, Loudermilk EL. Widespread severe wildfires under climate change lead to increased forest homogeneity in dry mixed-conifer forests. Ecosphere. 2019;10:e02934.
109. Hagmann RK, Hessburg PF, Prichard SJ, Povak NA, Brown PM, Fulé PZ, et al. Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests. Ecol Appl. 2021;31: e02431.
110. Franklin JF. Preserving biodiversity: species, ecosystems, or landscapes? Ecol Appl. 1993;3:202–5.
111. Simberloff D. Flagships, umbrellas, and keystones: Is single-species management passe in the landscape era? Biol Conserv. 1998;83:247–57.
112. Wurtzebach Z, Schultz C. Measuring ecological integrity: history, practical applications, and research opportunities. Bioscience. 2016;66:446–57.
113. Koontz MJ, North MP, Werner CM, Fick SE, Latimer AM. Local forest structure variability increases resilience to wildfire in dry western U.S. coniferous forests. Ecol Lett. 2020;23:483–94.
114.• Stephens SL, Westerling ALR, Hurteau MD, Peery MZ, Schultz CA, Thompson S. Fire and climate change: conserving seasonally dry forests is still possible. Front Ecol Environ. 2020;18:354–60. **This paper discusses how increasing landscape heterogeneity through fire use (i.e., pyrodiversity) and forest management can support multiple resource management objectives.**
115. Radeloff VC, Williams JW, Bateman BL, Burke KD, Carter SK, Childress ES, et al. The rise of novelty in ecosystems. Ecol Appl. 2015;25:2051–68.
116. Trauernicht C, Brook BW, Murphy BP, Williamson GJ, Bowman DMJS. Local and global pyrogeographic evidence that indigenous fire management creates pyrodiversity. Ecol Evol. 2015;5:1908–18.
117. Van Wilgen BW, Biggs HC, Potgieter ALF. Fire management and research in the Kruger National Park, with suggestions on the detection of thresholds of potential concern. Koedoe. 1998;41:69–87.
118. Cushman SA, McGarigal K. Metrics and models for quantifying ecological resilience at landscape scales. Front Ecol Evol. 2019;7:440.
119. Swetnam TW, Allen CD, Betancourt JL. Applied historical ecology: using the past to manage for the future. Ecol Appl. 1999;9:1189–206.
120. Seidl R, Spies TA, Peterson DL, Stephens SL, Hicke JA. Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. J Appl Ecol. 2016;53:120–9.
121. Meyer MD. Forest fire severity patterns of resource objective wildfires in the southern Sierra Nevada. J For. 2015;113:49–56.
122. Schuurman GW, Cole DN, Cravens AE, Covington S, Crausbay SD, Hoffman CH, et al. Navigating ecological transformation: resist–accept–direct as a path to a new resource management paradigm. Bioscience. 2022;72:16–29.
123. Villarreal ML, Iniguez JM, Flesch AD, Sanderlin JS, Cortés Montaño C, Conrad CR, et al. Contemporary fire regimes provide a critical perspective on restoration needs in the Mexico-United States borderlands. Air, Soil Water Res. 2020;13:1–18.
124. Westerling AL, Turner MG, Smithwick EAH, Romme WH, Ryan MG. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. Proc Natl Acad Sci. 2011;108:13165–70.
125. Ulyshen MD, Hiers JK, Pokswinksi SM, Fair C. Pyrodiversity promotes pollinator diversity in a fire-adapted landscape. Front Ecol Environ. 2022;20:78–83.
126. Gordijn PJ, O'Connor TG. Multidecadal effects of fire in a grassland biodiversity hotspot: does pyrodiversity enhance plant diversity? Ecol Appl. 2021;31:e02391.
127. Swan M, Christie F, Steel E, Sitters H, York A, Di Stefano J. Ground-dwelling mammal diversity responds positively to productivity and habitat heterogeneity in a fire-prone region. Ecosphere. 2020;11:e03248.
128. Steel ZL, Campos B, Frick WF, Burnett R, Safford HD. The effects of wildfire severity and pyrodiversity on bat occupancy and diversity in fire-suppressed forests. Sci Rep. 2019;9:16300.

129. Jorge MH, Garrison EP, Conner LM, Cherry MJ. Fire and land cover drive predator abundances in a pyric landscape. For Ecol Manage. 2020;461:117939.
130. Furnas BJ, Goldstein BR, Figura PJ. Intermediate fire severity diversity promotes richness of forest carnivores in California. Divers Distrib. 2021;28;493–505.
131. Senior KL, Giljohann KM, McCarthy MA, Rainsford FW, Kelly LT. Predicting mammal responses to pyrodiversity: from microbats to macropods. Biol Conserv. 2021;256:109031.
132. Wilkin K, Ponisio L, Fry DL, Collins BM, Moody T, Stephens SL. Drivers of understory plant communities in Sierra Nevada mixed conifer forests with pyrodiversity. Fire Ecol. 2021;17:30.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.