Conservation of Earth's biodiversity is embedded in Indigenous fire stewardship

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Increasingly, severe wildfires have led to declines in biodiversity across all of Earth's vegetated biomes [D. B. McWethy *et al.*, *Nat. Sustain.* 2, 797–804 (2019)]. Unfortunately, the displacement of Indigenous peoples and place-based societies that rely on and routinely practice fire stewardship has resulted in significant declines in biodiversity and the functional roles of people in shaping pyrodiverse systems [R. Bliege Bird *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* 117, 12904–12914 (2020)]. With the aim of assessing the impacts of Indigenous fire stewardship on biodiversity and species function across Earth's major terrestrial biomes, we conducted a review of relevant primary data papers published from 1900 to present. We examined how the frequency, seasonality, and severity of human-ignited fires can improve or reduce reported metrics of biodiversity and habitat heterogeneity as well as changes to species composition across a range of taxa and spatial and temporal scales. A total of 79% of applicable studies reported increases in biodiversity as a result of fire stewardship, and 63% concluded that habitat heterogeneity was increased by the use of fire. All studies reported that fire stewardship occurred outside of the window of uncontrollable fire activity, and plants (woody and nonwoody vegetation) were the most intensively studied life forms. Three studies reported declines in biodiversity associated with increases in the use of high-severity fire as a result of the disruption of Indigenous-controlled fire regimes with the onset of colonization. Supporting Indigenous-led fire stewardship can assist with reviving important cultural practices while protecting human communities from increasingly severe wildfires, enhancing biodiversity, and increasing ecosystem heterogeneity.

Indigenous fire stewardship | pyrodiversity | cultural burning | habitat heterogeneity | global fire synthesis

Humans have used fire as a tool for resource management, community protection, and cultural purposes for millennia; however, changes to fire regimes as a result of more recent human actions have exacerbated incidents of large and destructive wildfires (1–3). This new era of wildfire has altered the behavior of fire activity and is threatening biodiversity at a global scale such that identifying and implementing human–fire interactions that support a variety of social and ecological values is becoming increasingly urgent (3, 4). Fortunately, the revitalization of Indigenous fire stewardship (IFS) is demonstrating the value of routinely applying controlled fire to adapt to changing environments while promoting desired landscapes, habitats, and species and supporting subsistence practices and livelihoods (5). Documenting the impacts of IFS on global patterns of biodiversity and ecosystem heterogeneity can support strategies aimed at increasing the use of fire as a cultural practice and as a tool for enhancing biodiversity and ecosystem conservation (6).

Fire was one of the first tools used by humans to shape their environments, and this relationship has been fundamental in the development of ecosystem structure, species diversity, and the global distribution of biomass (7). IFS systems have developed independently around the globe and across a multitude of biomes, but all control specific aspects of fire (severity, timing, behavior, and seasonality) to influence ecosystem structure, biomass, and community assemblages (8). IFS can shape community composition by increasing or decreasing the abundance and/or productivity of specific plants, animals, fungi, and insects (6). In some cases, IFS is used to change the abundance of several target species across a variety of taxa (9). Although evidence for widespread IFS exists, how Indigenous peoples used fire to shape their surroundings and the frequency and extent of contemporary use is still debated in many parts of the world (10–13). This debate is in part driven by colonialism, fire suppression policies, and public perceptions of wildfire, which can be in direct opposition to scientific evidence and Indigenous Ecological Knowledge (IEK) that fire is a necessary and healthy component of functioning ecosystems (3, 4, 6, 14).

Over a century of widespread fire suppression related to colonization and land-use change has shifted human relationships with and reliance on fire. Not surprisingly, this has resulted in changes in community structure and composition and declines in pyrodiversity (the diversity and characteristics of fires in a region) (15, 16). New and fundamentally different human–environment interactions are rapidly displacing human–fire linkages that have existed for millennia, and contemporary changes in human–fire

Significance

Large and severe wildfires are becoming increasingly common worldwide and are having extraordinary impacts on people and the species and ecosystems on which they depend. Indigenous peoples comprise only 5% of the world's population but protect approximately 85% of the world's biodiversity through stewardship of Indigenous-managed lands. Much of this is attributed to long-term and widespread relationships with and dependence on fire, which has been applied as a tool for managing landscapes for millennia. Fortunately, the revitalization of Indigenous fire stewardship is demonstrating the value of routinely applying controlled fire to adapt to changing environments while promoting desired landscapes, habitats, and species and supporting subsistence practices and livelihoods.

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relationships are occurring during a period of unprecedented environmental change (9). Decades of warmer temperatures and greater instances of drought have lengthened wildfire seasons around the globe, and uncharacteristically severe wildfires have negatively impacted biodiversity in all of Earth's biomes (4, 17). Unfortunately, the displacement of Indigenous peoples and place-based societies that rely on and routinely practice fire stewardship has resulted in significant declines in biodiversity and the functional roles of people in shaping pyrodiverse systems (8, 9, 18).

IFS supports intergenerational teachings of fire-related knowledge, beliefs, and practices among fire-dependent cultures regarding fire regimes (including the relationship between intentional and lightning ignitions), fire effects, and the role of cultural burning in fire-prone ecosystems and habitats (5). Identifying how humans have and continue to utilize fire and for what specific purposes is key to understanding the direction and magnitude of change (increase or decrease) and the impact (benefit or detriment) of fire on biodiversity (19–21). With the aim of assessing the effects of IFS on biodiversity and species function across Earth's major terrestrial biomes, we conducted a review of relevant primary data papers published from 1900 to present day (Fig. 1). We examined fire regime attributes regarding the frequency, seasonality, and severity of cultural burning (one aspect of IFS) and how it relates to (improves or impairs) reported metrics of biodiversity. We also assessed changes in landscape heterogeneity and species composition across a range of taxa and spatial and temporal scales. Further, we focused on the intended use of fire and under what conditions IFS can revitalize or erode pyrodiversity.

Results

Our findings incorporate millennia of IEK and decades of research on the relationship between IFS, biodiversity, and heterogeneity in all continents except Europe and Antarctica and across all terrestrial biomes except the tundra (Fig. 1). A total of 53 of the 861 (6%) reviewed articles met all criteria for inclusion in our analysis and were published between the years 1994 and 2020 (*SI Appendix*, Table S1). The savanna/tropical grassland biome was best represented in the review with 38% (20/53) of studies occurring there, primarily in Australia (*SI Appendix*, Fig. S1). Most studies considered more than one site in their research (33/53) and generally considered processes occurring at historic (0 to 150+ y; 18 studies) or short (0 to 10 y; 19 studies) timescales (Fig. 2*A*). Based on our definitions (*SI Appendix*, Table S2), the vast majority of research considered processes occurring at regional scales (42/53) (Fig. 2*B*). In more recently published articles (since 2000), authors tended to use multiple, cross-discipline approaches to study the effects of fire on biodiversity, blending IEK with vegetation sampling and remote sensing techniques (Fig. 2*C*). Importantly, our search criteria identified literature reviews examining elements, purposes, and objectives of IFS and fire knowledge but no global-scale analyses of the direct or indirect effects of IFS on measures of biodiversity and habitat heterogeneity were identified in our review.

Of the relevant studies, 85% (45/53) reported the use of low-severity fire, and 23% (12/53) reported the use of mixed-severity fire (Fig. 3). Three studies that cited historical increases in biodiversity associated with low-severity fire also reported contemporary decreases in biodiversity associated with changes to the fire regime as a result of colonization and the use of high-severity fire as a tool for land clearing (Fig. 3). One study did not report or provide related details from which fire severity could be inferred. A total of 31 studies directly analyzed or inferred the relationship between IFS on biodiversity and heterogeneity across life forms ranging from microbes to small mammals and a diverse taxa of plants (Fig. 4). Similar to findings published in systematic reviews by Huffman (2013) (14), Trauernicht et al. (2015) (22), and Scherjon et al. (2015) (23), fire effects on vegetation (woody and nonwoody vegetation) were by far the most intensively studied life forms, followed by fire effects on reptiles, mammals, and birds (Fig. 2*D*).

All studies reported that fire stewardship took place outside of the window of uncontrollable fire activity (spring/winter/fall or wet season or night). This pattern was identified across biomes and fire regimes, highlighting how Indigenous fire knowledge is embedded in quantitative and qualitative assessments of fire weather, fuel flammability, fire spread, and associated fire severity impacts to biodiversity and ecosystem function. In total, 28% (15/53) of studies reported an increase in biodiversity associated with high frequency (<1 y) and low-severity fire, while 57% of studies (30/53) reported increases in biodiversity with fire frequencies of <5 y (Fig. 3 and *SI Appendix*, Fig. S2). A total 17% (9/53) of studies reported increases in biodiversity as a result of mixed-severity fire

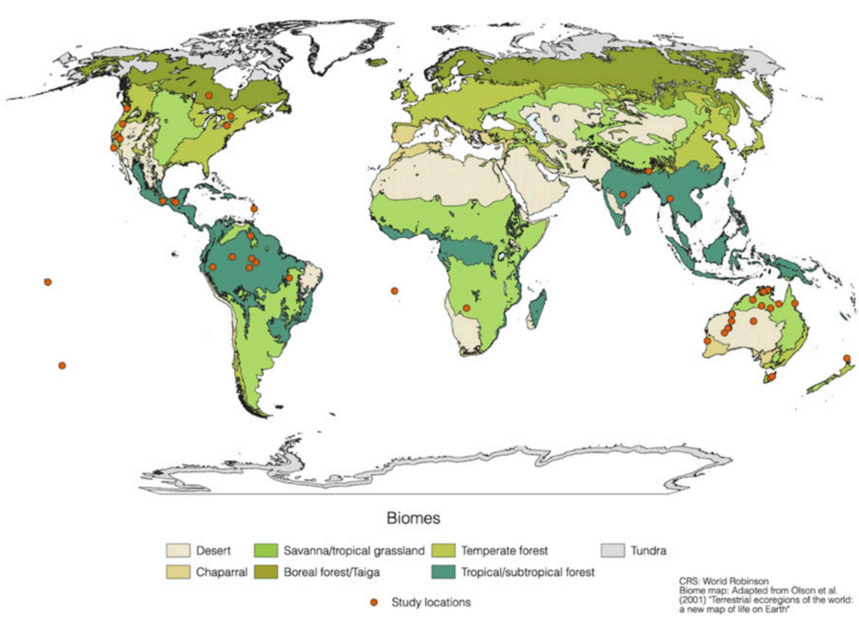

Fig. 1. Map of study locations included in the analysis in each of seven major biomes.

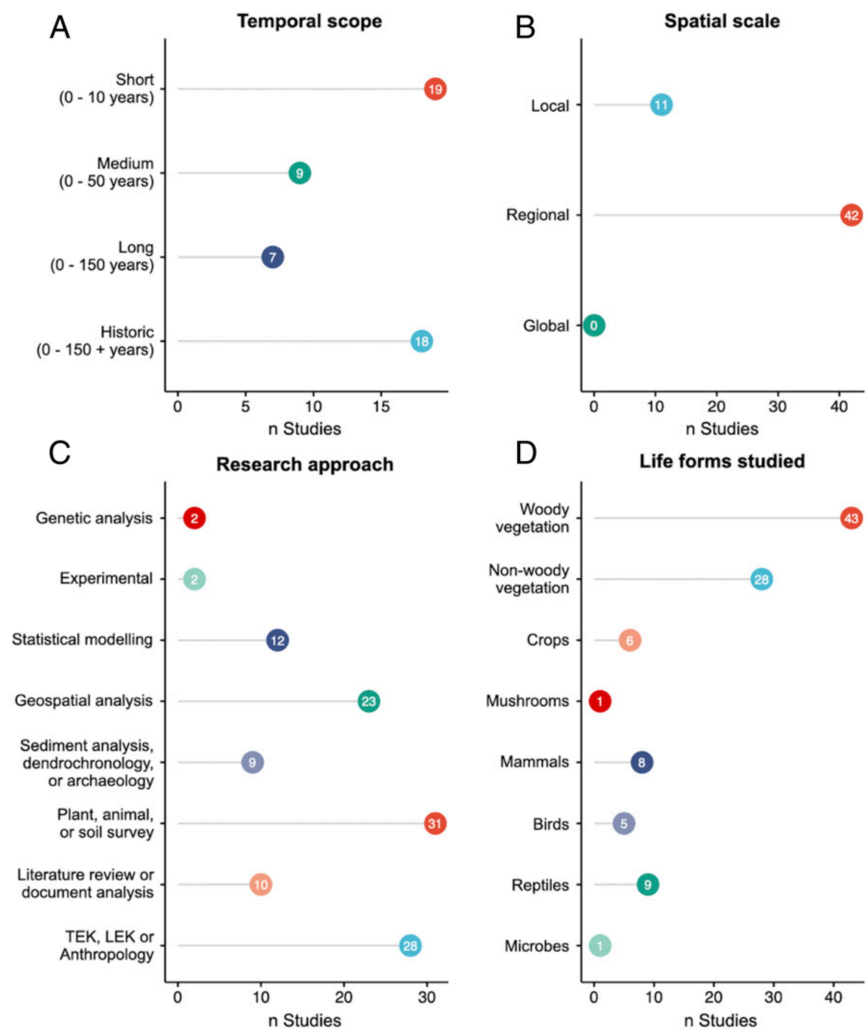

Fig. 2. Number of studies addressing the impacts of fire on biodiversity, species composition, or habitat heterogeneity at various temporal (*A*) and spatial (*B*) scales; the frequency of various approaches used by study authors (*C*); and the frequency at which various life forms were studied (*D*). Note that several studies applied more than one research approach and studied more than one life form.

regimes with fire frequencies of 5 to 10 y, and 6% (3/53) of studies reported fire frequencies of >10 y (Fig. 3). A total 4% of studies (2/53) reported no change, and 17% (9/53) did not report biodiversity metrics related to fire.

A total of 44 studies analyzed species composition; of those, 79% (42/53) concluded that species composition was altered by the use of fire (Fig. 4). Of the studies that assessed the impacts of Indigenous use of fire on habitat heterogeneity, 57% (31/54) concluded that habitat heterogeneity was increased by the use of fire, 6% (3/53) noted a decrease in habitat heterogeneity, and the remainder of the studies concluded that heterogeneity changed but it was not clear in which direction (Fig. 4). References for all papers reviewed are included in Dataset S1.

Discussion

Recent global reviews of protected areas reveal that Indigenous-managed (owned, governed, titled, or unceded) lands have higher levels of biodiversity than parks and protected areas under conventional management (24, 25). Much of this is attributed to long-term and widespread relationships with and dependence on fire, which has been applied as a tool for managing landscapes for millennia (7, 8, 18, 26). Although IFS may seem counterintuitive to stabilize or increase biodiversity in dry biomes where fire naturally occurs, IFS can greatly decrease the severity of wildfires (both lightning and human ignitions) when they do occur by reducing the abundance of available fuels and increasing the fire resistance of vegetation (27–29) (Fig. 3).

Applying controlled fire allows humans to press an ecological "reset button" or maintain an ecosystem at a specific or more desired state (20, 27). Plants, animals, fungi, and insects have all adapted to fire regimes (fire frequency, intensity, seasonality, and type [ground/surface fires or crown]) depending on their location across the globe (11) (*SI Appendix*, Table S3). Life histories (growth, dispersal, and senescence) are often synchronous with, and reliant on, predictable fire cycles, and the majority of these fire cycles are either fully or partially controlled by humans (albeit fire stewardship has decreased dramatically as a result of widespread fire suppression) (16, 30). Despite abrupt changes to both cultural and lightning fire regimes at the beginning of the 20th century, IFS exerts a strong evolutionary force on the distribution and attributes of biomes globally (9).

Although the timing, frequency, and severity of fire is specific to cultural groups and biomes, comparable practices of fire stewardship exist around the globe and significantly impact biodiversity, heterogeneity, and human connections to place (27). For example, global ethnographic reviews of traditional fire knowledge by Huffman (2013) (14) and traditional fire management by Trauernicht et al. (2015) (22) and Scherjon et al. (2015) (23) cited

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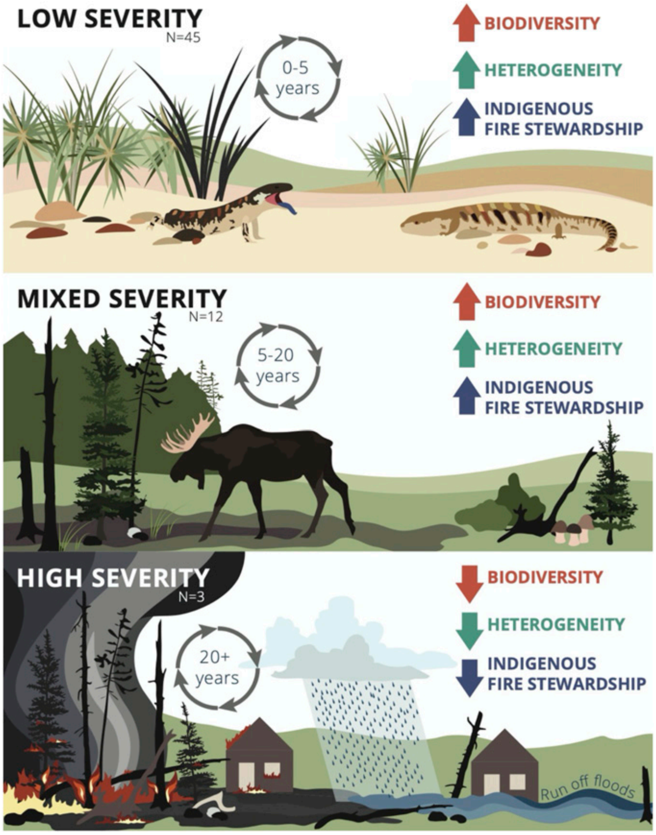

Fig. 3. Visualization of studies recording impacts related to low-, mixed- and high-severity fires with approximate corresponding fire frequencies. Note that the mixed-severity fire category included both low- and moderate-severity fire activity. Studies reporting more than one type of fire activity were counted twice.

multiple immediate and long-term management objectives achieved through cultural burning. Similar to our findings, clearing landscapes or fire effects on vegetation (to produce desired food plants) was the most common reason for fire (Fig. 5). Whereas our analyses were more ecologically focused to fire effects on biodiversity, cross-referencing of the three prior data sets revealed that our review captured 8% of the papers reviewed by Huffman (2013) (14), 19% of the paper review by Trauernicht et al. (2015) (22), and 21% of the papers reviewed by Scherjon et al. (2015) (23). The amalgamation of these data sets expands our understanding of the relationship between IFS, biodiversity, and heterogeneity outside of more narrowly focused biodiversity literature.

Our global review found similarities in the functional application of mixed-severity fire to create habitat in Canadian boreal forests, the savanna grasslands of Australia, and the chaparral oak forests of California (21, 31, 32). We also noted several examples of Indigenous groups occupying the same ecosystem but applying different fire stewardship practices related to distinct diet requirements. For instance, Indigenous groups that rely on woodland caribou (an old growth forest obligate; *Rangifer tarandus*) as a primary food source do not apply fire as frequently or as widely as neighboring Indigenous groups that hunt moose (*Alces alces*, which prefer recently disturbed forests (Fig. 5) (31, 33). IFS has many names (including swidden agriculture, slash and burn, fire stick farming, and shifting cultivation) but is consistently a system of ecosystem succession management that influences structural and functional biodiversity.

Fire stewardship can also have profound effects on ecosystems that lack resilience to fire. For example, New Zealand experienced almost no human-ignited fires until the arrival of Polynesians (Māori) ~800 y ago, which resulted in several mixed- and high-severity fire events due in part to the flammability of fire intolerant closed-canopy forests, which had little resilience to fire (34). In New Zealand, fire was a novel disturbance that in a few decades resulted in rapid deforestation and significant losses in biodiversity (35). Contrary to this, applying frequent fire to fire-resilient ecosystems helps ecosystems function and retain ecological memory to buffer against future wildfire and other disturbances (20).

As warmer and drier conditions lead to increasingly severe fire behavior and the lengthening of wildfire seasons, there is a renewed call to fight fire with fire. For example, the Savanna biome contributes ~62% of annual gross global mean fire emissions, and early dry season Savanna fires have been proposed as a way to mitigate greenhouse gas emissions (36). Although increased investments in capacity and preventative (rather than reactive) fire management are critical, it is important to note that prescribed burning is distinct from cultural burning primarily in the burn objectives, techniques used to burn, and who is conducting the burning (5). Indigenous peoples, whose fire management practices have co-evolved with landscapes for millennia, are revitalizing fire stewardship practices after decades or even centuries of fire suppression (19). However, many Indigenous groups face significant barriers to revitalizing fire stewardship initiatives within their territories, such as risks associated with burning dead and dense fuels, the presence of highly flammable invasive species, laws prohibiting the cultural use of fire, and in some cases the loss of knowledge associated with cultural fire practices (6, 8, 14, 17). In many places, returning or reviving ecosystems to their formerly fire-driven biodiverse states can take decades and may not be successful as ecosystems are undergoing rapid environmental and land-use change (3).

It is noteworthy that the studies reviewed did not involve Indigenous peoples engaging in fire stewardship to increase biodiversity per se, but increased biodiversity or landscape heterogeneity was instead an indirect result of IFS. Other benefits of IFS include strengthening of social networks and increased community physical and mental health (Fig. 5) (5, 6). Using fire as a tool for ecosystem restoration is distinct from Indigenous peoples' knowledge of and reliance on fire, which is grounded in worldviews, beliefs, and understandings that have been passed down through generations (6). Ignoring or attempting to replace relationships between humans, fire, and biodiversity while failing to recognize and support IFS has altered wildfire behavior around the globe (9). Conserving global biodiversity is possible through integrating, valuing, and supporting Indigenous-led approaches to fire stewardship and ecosystem management.

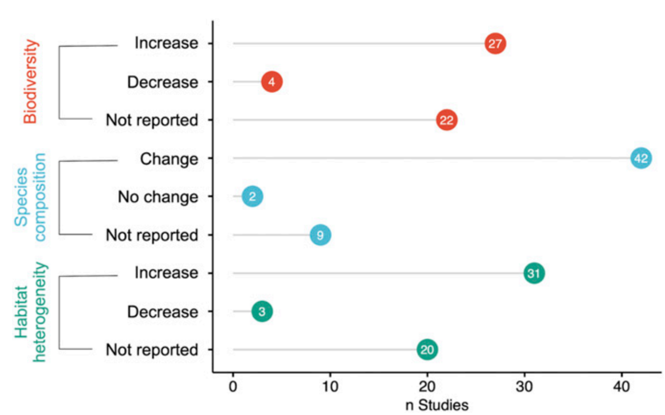

Fig. 4. Number of studies reporting a change in biodiversity (red), species composition (blue), and/or habitat heterogeneity (green).

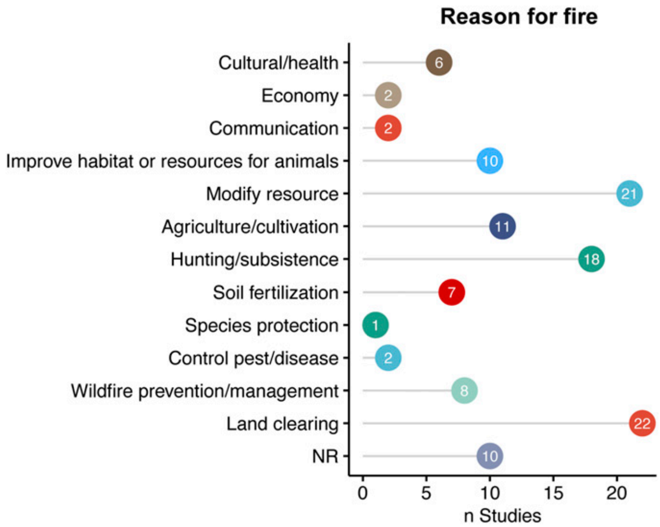

Fig. 5. Out of 68 studies, 63 (93%) reported the reason for IFS. IFS was reported for more than one purpose in over half of the studies. Note that landscape clearing refers to clearing, cleaning, and reducing fire risk. Fertilization refers to soil fertility, biochar, and *terra preta*. Agriculture refers to raising and/or managing livestock and cultivation. Modifying resource refers to increasing or decreasing the abundance of specific plant and animal species. Hunting refers to using fire to increase forage for prey, easing hunting effort, or driving prey for hunting. If the reason for IFS was not reported, it was documented as (NR).

Materials and Methods

A Web of Science search was conducted on April 20, 2020, to identify research articles addressing relationships between the use of fire by Indigenous peoples and biodiversity, species composition, and/or habitat heterogeneity. The search string included 19 terms (*SI Appendix*, Table S1) and spanned literature from 1900 to present day. The search yielded 840 articles that were randomly divided among the 10 coauthors for review. A total of 21 articles that were opportunistically encountered through the review process (e.g., reference lists) as being possibly relevant to the research topic were also reviewed by the group (*N* articles reviewed = 861). Reviewers were responsible for determining whether the articles were applicable to the research topic and for extracting a predefined set of relevant data (see data collection table in *SI Appendix*, Table S2). To be included in the final review, each article had to meet the following criteria:

1) At least one of the following topics had to be addressed: changes in biodiversity, species composition, or habitat heterogeneity associated with the Indigenous use of fire. If impacts of fire on biodiversity, species composition, or habitat heterogeneity were not addressed directly but the study authors concluded that they were altered in some way by the use of fire, these conclusions were noted as being inferred by the authors and included in the final review.
2) The article had to present primary data relevant to the research topic. Review papers were only included if they presented primary data based on literature.
3) A comparative element had to be present in the article. For example, the impacts of the use of fire by Indigenous peoples could be compared to unburned areas, lightning fires, and/or areas impacted by colonial fire management. Comparisons could be either direct or implied.

This first review resulted in a list of 67 articles that were then verified by one team member to ensure consistency in meeting the required criteria and in how data were extracted. This review resulted in 53 articles that met the criteria for inclusion. Several data categories were later reclassified into more general categories by review team members to facilitate comparisons across studies (see reclassification details in *SI Appendix*, Table S2). Inferences by the review team were made when only one of the following (fire severity, intensity, and frequency) were reported. Inferences were only made by the review team when other supporting information (regional studies or well documented fire regimes) were available. For example, if a fire frequency was reported as less than 1 y, sufficient evidence was available to infer a low-severity fire regime if over a specific scale and temporal (interannual or decadal) period.

We recognize that Europe is underrepresented in this review, likely due to the use of the search term "Indigenous," which applies to the majority of ethnic groups that are Indigenous to a region and have occupied it for millennia. Terms such as "biodiversity" are widely used at present but were not as common in the past, such that relevant publications from earlier decades may have been inadvertently excluded. Other locations such as boreal Canada, sub-Saharan Africa, China, and the middle east are not as well represented in this review as they are understudied due to their remoteness or political situation. Some regions are not well represented because they have historically been perceived as too wet or too cold to have human–fire–biodiversity relationships (such as temperate rainforests and tundra biomes); however, emerging research has shown millennia of IFS in several of these environments (26, 37, 38). Lastly, the search terms in this review likely do not adequately capture historical and paleo-ecological data streams (such as archaeology and palynology) as terms such as "biodiversity," "Indigenous," and "fire" are less commonly used and are often implicit in these research fields. These fields of research can provide important global context to our understanding of ancient socio-cultural, environmental, and climatic change (18, 39).

Statement of Positionality. The coauthors of this paper are primarily of settler descent (non-Indigenous) with one coauthor identifying as Indigenous. Our formal university-based training and experiences as ecologists embedded in socio-ecological systems is strengthened by long-term relationships with Indigenous communities situated in the temperate coastal rainforests of British Columbia, in boreal northern British Columbia, and across the eastern Canadian Arctic. With this paper, it is our intention to highlight global patterns and relationships of humans and fire over millennia, but we acknowledge that we are not in a position to address values and intentions related to specific indigenous management and stewardship practices.

Data Availability. All study data are included in the article and/or supporting information.

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