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Spatial scale in prescribed fire regimes: an understudied aspect in conservation with examples from the southeastern United States

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Abstract

The idea that not all fire regimes are created equal is a central theme in fire research and conservation. Fire frequency (*i.e.,* temporal scale) is likely the most studied fire regime attribute as it relates to conservation of fire-adapted ecosystems. Generally, research converges on fire frequency as the primary filter in plant community assembly and structure, which is often critical to conservation goals. Thus, conservation success is commonly linked to fire frequency in fire regimes.

The spatial scale of fire may also be vital to conservation outcomes, but this attribute is underrepresented in the primary literature. In our global, contemporary literature search, we found 37 published syntheses concerning the effects of prescribed fire in conservation over the last decade. In those syntheses, only 16% included studies that reported data-based inferences related to the spatial scale of the fire, whereas 73% included discussion of empirical studies on the temporal scale. Only one of the syntheses discussed studies that explicitly tested the effects of spatial extent, and none of those studies were experiments manipulating spatial scale. Further, understanding spatial-scale-dependent patterns may be relevant because two databases of fire-occurrence data from the United States indicated that spatial scale among lightning-ignited and prescribed fires may have been mismatched over the past few decades.

Based on a rich ecological literature base that demonstrates pervasive scale-dependent effects in ecology, spatial-scale-dependent relationships among prescribed fire regimes and conservation outcomes are likely. Using examples from the southeastern United States, we explored the potential for scale-dependent ecological effects of fire. In particular, we highlighted the potential for spatial scale to (a) influence wildlife populations by manipulating the dispersion of habitat components, and (b) modulate plant community assembly and structure by affecting seed dispersal mechanics and spatial patterns in herbivory. Because spatial-scale-dependent outcomes are understudied but likely occurring, we encourage researchers to address the ecological effects of spatial scale in prescribed-fire regimes using comparative and manipulative approaches.

Keywords: burn severity, fire attributes, fire intensity, fire season, prescribed burn, prescribed fire, pyric herbivory, pyrodiversity, seed dispersal, spatial scale

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Resumen

La idea de que no todos los regímenes de fuego se generan de la misma manera es un tema central en la investigación de fuegos y conservación. La frecuencia de incendios (*i.e.*, su escala temporal) es probablemente el atributo más estudiado del régimen de fuegos, dado que se relaciona con la conservación de ecosistemas adaptados al fuego. En general, las investigaciones coinciden en que la frecuencia del fuego es el filtro primario en el ensamble y estructura de una comunidad, lo que es frecuentemente crítico para lograr metas de conservación. Por lo tanto y en distintos regímenes de fuego, el éxito en la conservación está frecuentemente ligado a la frecuencia del fuego.

La escala espacial de un fuego puede ser también vital para los resultados de la conservación, aunque este atributo está subrepresentado en la literatura básica. En nuestra revisión global y contemporánea de la literatura, encontramos 37 síntesis de trabajos concernientes a los efectos de las quemas prescriptas en temas de conservación en la última década. En esas síntesis, sólo el 16% incluyeron estudios que reportaban inferencias basadas en datos relacionados con la escala espacial del fuego, mientras que el 73 % incluyeron discusiones de estudios empíricos sobre la escala temporal. Sólo una de esas síntesis discutió estudios que testeaban explícitamente los efectos de extensión espacial, pero ninguno de estos estudios fueron experimentos donde se manipuló la escala espacial. Además, el entendimiento de los patrones escala-espacio-dependientes puede ser relevante, pues dos bases de datos de ocurrencia de fuegos en los EEUU indican que la escala espacial entre los fuegos iniciados por rayos y por quemas prescriptas han sido asimétricas en algunas décadas pasadas.

Basados en la rica literatura ecológica de base que demuestra la persistencia de efectos escala-dependientes en ecología, son probables las relaciones espaciales escala-dependientes entre los regímenes de quemas prescriptas y resultados de conservación. Usando ejemplos del Sudeste de los EEUU, exploramos el potencial de los efectos ecológicos de incendios escala-dependientes. En particular, destacamos el potencial de la escala especial para (a) influenciar las poblaciones de fauna silvestre mediante la manipulación de dispersión de los componentes del hábitat, y (b) modular el ensamble y estructura de la comunidad mediante la afectación de los mecanismos de dispersión de semillas y los patrones espaciales de herbívoría. Dado que los resultados de la escala espacio-dependiente han sido sub- estudiadas pero que probablemente ocurran, recomendamos a los investigadores considerar los efectos ecológicos de la escala espacial en regímenes de quemas prescriptas usando aproximaciones comparativas y manipulativas.

Introduction

Scale-dependent patterns are pervasive across ecological processes and ecosystems. For the past few decades, scale dependence has been considered the central problem in understanding observed spatial patterns in biodiversity and ecosystem function (Levin 1992). The species–area relationship might be the closest thing to a scientific law in ecology and is perhaps the most informative pattern to fire ecologists considering spatial scale in fire regimes (May 1975; Rosenzweig 1975; Connor and McCoy 1979). According to the species–area relationship, as area increases, species-richness predictably increases (Connor and McCoy 1979). This concept is central to island biogeography theory, which predicts species richness based on the size of an island and the distance to the source of colonizing organisms (Simberloff 1974). In island biogeography theory, an island is a patch that is dramatically different from its surroundings, like an island in the ocean. From a fire ecologist's perspective, an island could be the burn unit at whatever spatial scale it differs from its surroundings. Two notable issues arise when considering such scale-dependent patterns.

First, the relationship between biodiversity and area is functioning at many scales simultaneously. Species richness increases with island size, but islands with more heterogeneity, such as rapid elevation changes, have a steeper slope of species accumulation (Hortal et al. 2009). The same multi-spatial scale patterns may be fundamental to conservation success in areas subjected to burning, where an island may be an individual burn unit, an entire property, or a collection of properties. Although spatial scale may be a major factor determining overall biodiversity contained within the fire island, heterogeneity within the fire regime likely augments the slope of change. This concept, referred to as pyrodiversity, is defined by diversifying attributes within fire regimes, such as fire-return interval, fire intensity, and fire season, to promote a mosaic of community structure across patches with different fire histories (Martin and Sapsis 1992; Ponisio et al. 2016; Tingley et al. 2016; Kelly and Brotons 2017; Beale et al. 2018). Similarly, firing techniques that promote heterogeneity in fire spread can accomplish the same goal within a burn unit. This mosaic in community structure is more likely to support

greater beta diversity within the entire managed area than a homogeneous burning approach.

The second issue, which practitioners often have more control over, is the size of burn units within the area actively managed with fire. In general, the same principles at the property scale should apply to beta diversity at the individual burn-unit scale. Burn-unit alpha diversity increases with unit size, but this relationship's slope becomes steeper with increasing fire spread heterogeneity. For conservation, a burn unit's size may influence community interactions at the local scale with consequences that scale up to affect system-wide processes.

While fire ecologists often acknowledge the importance of the spatial scale of fire, we show herein that this may be the least studied fire-regime attribute in research concerning the conservation of fire-adapted ecosystems.

We discuss syntheses from a global search focusing on prescribed fire. For the entire USA, we compare the spatial extent of lightning-generated fires to prescribed burns lit for conservation from two databases. Also, we discuss the relevance of our findings in the context of ecological theory related to scale-dependent processes and patterns. Because we work in the southeastern USA, and to focus on this special issue, we use examples involving commonly targeted species from this region to discuss the potential for spatial-scale dependence of fire on essential ecological processes and conservation goals. Finally, we conclude with recommendations to stimulate discussion concerning the role of spatial scale in fire ecology. With these recommendations, we hope to inspire future fire research that will elucidate the ecological effects of spatial scale that have meaningful conservation implications.

Lack of focus on spatial scale

To explore the discussion of spatial scale of prescribed burns, we surveyed syntheses in the fire ecology literature. For this survey, we looked for syntheses published within the last 10 years (*i.e.,* 2009 to 2018) that reviewed research concerning prescribed burns ignited for conservation. We defined conservation burning as burns conducted to maintain vegetation in a desired seral stage to create or preserve wildlife and plant habitat components or populations. We set the literature search criteria *a priori* and used any peer-reviewed manuscript meeting our standards as a data point. We searched Web of Science (https://webofknowledge.com/WOS) for "fire" in the title, which returned 26 352 publications. Then, we refined the search to include syntheses in the subject areas of forestry, ecology, zoology, and biodiversity and conservation, yielding 138 publications. Next, we screened the abstracts of these looking for evidence that the reviews discussed prescribed burns, resulting in 37 reviews (Additional file 1). We then searched the remaining reviews for keywords related to fire attributes (*e.g.,* scale, severity, intensity, frequency, season) and their synonyms. In publications covering both wildfires and prescribed burns, we ensured that the authors described the attribute in the context of prescribed burns before proceeding. Finally, we tallied the number of publications discussing attributes and data-based inferences.

We assumed that these syntheses, created from exhaustive reviews of empirical evidence from multiple decades, would indicate current knowledge related to spatial scale of fire regimes. We focused on prescribed-fire publications because they included research on using fire to achieve conservation outcomes. We surveyed reviews, not to exhaustively synthesize the literature, but instead to use these syntheses as an indicator of how often contemporary fire ecology addressed spatial scale with data-driven discussions. We restricted the time frame to the last decade *a priori* to indicate relatively current discussion in the discipline. This span also provided the minimum amount of time to detect trends in research (McCallen et al. 2019).

Sixty-five percent (24 of 37) of the syntheses discussed the spatial scale of the fires studied, which was approximately as often as other attributes were mentioned (Fig. 1). Those publications included a range of statements, from merely mentioning spatial scale to the inclusion of citations from empirical work on spatial-scale effects. If the percentage of papers that discuss a particular fire attribute indicates how relevant authors believe that attribute to be, then the spatial scale of fire is equally important as other attributes. However, the disconnect between spatial scale and other attributes emerged when we focused on data-based inferences. Reviews rarely presented data-based inferences regarding the effects of spatial scale (16%), whereas all other fire attributes that we tallied used data-based inference at least more than twice as often. Authors most often presented data-based inferences concerning fire frequency (more than four times as much as spatial scale in the surveyed reviews).

Our findings concerning data-based inferences related to the spatial scale of fire are conservatively high because of the criteria we used to delineate a data-based inference. We defined a data-based inference as a statement citing research that measured anything that could be considered an ecological effect of spatial scale. Indeed, no reviews discussed the effects of manipulating spatial scale, and only one review presented research that explicitly explored the effects of spatial scale on the focal metric of the study. Much of the spatial-scale discussion was from authors calling for future researchers to investigate spatial scale. Few authors explicitly called for experiments designed to ascertain the mechanisms driving spatial-scale-dependent ecological effects.

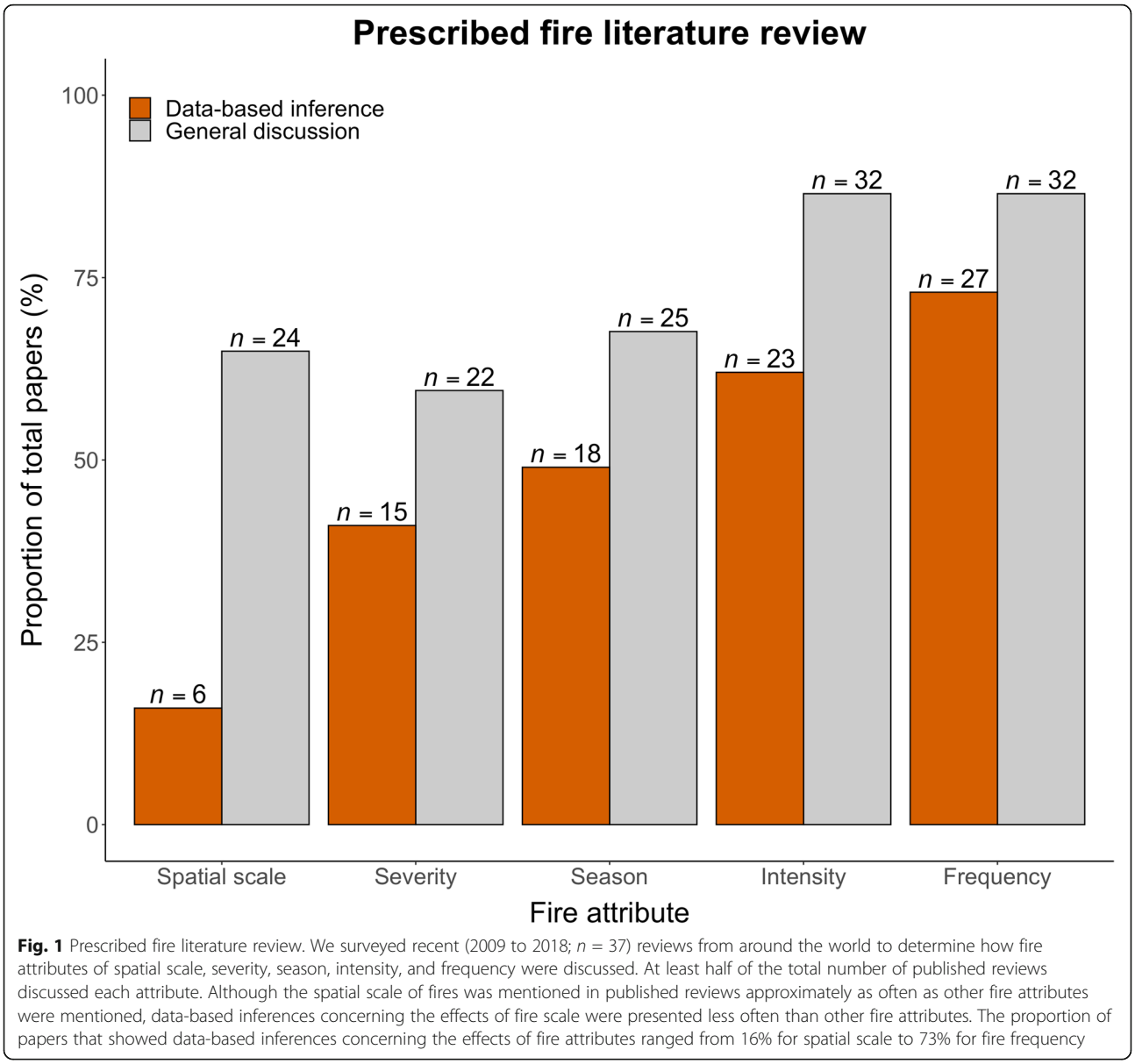

Fig. 1 Prescribed fire literature review. We surveyed recent (2009 to 2018; n = 37) reviews from around the world to determine how fire attributes of spatial scale, severity, season, intensity, and frequency were discussed. At least half of the total number of published reviews discussed each attribute. Although the spatial scale of fires was mentioned in published reviews approximately as often as other fire attributes were mentioned, data-based inferences concerning the effects of fire scale were presented less often than other fire attributes. The proportion of papers that showed data-based inferences concerning the effects of fire attributes ranged from 16% for spatial scale to 73% for fire frequency

Spatial scale mismatch in lightning and prescribed fire

We thought it would be useful to understand how the size of prescribed fires compares to size of lightning-ignited fires to determine if there is need to understand the role of spatial scale. The primary purpose of exploring available data sets for this reason was to derive a meaningful comparison between the two ignition types and not necessarily to present the most accurate mean fire size. Also, we wanted to make sure that the data sets were not being biased by differences in systems, policies, or other factors that may differ across regions of the USA. Understanding that there are limitations to each data set (discussed later), we extracted data concerning fires in the United States from the Monitoring Trends in Burn Severity (MTBS; Eidenshink et al. 2007) and Federal Wildland Fire Occurrence (FWFO; Goodman 2016) databases. We assumed that the data sets had similar issues between ignition type and region and, thus, could provide meaningful relative comparisons. Landsat data of fires occurring between 1984 to 2017 represents the MTBS data (Hawbaker et al. 2020). This database includes fires greater than 202 ha in the eastern US and 404 ha in the western US. Given that smaller fires are excluded, this data set likely skews averages high. Federal fire reports from 1980 to 2016 constitute the FWFO data (Goodman 2016). We chose the FWFO data set for the comparison between prescribed and lighting-ignited fires. This data set was the only one available that distinguishes lightning from other fire

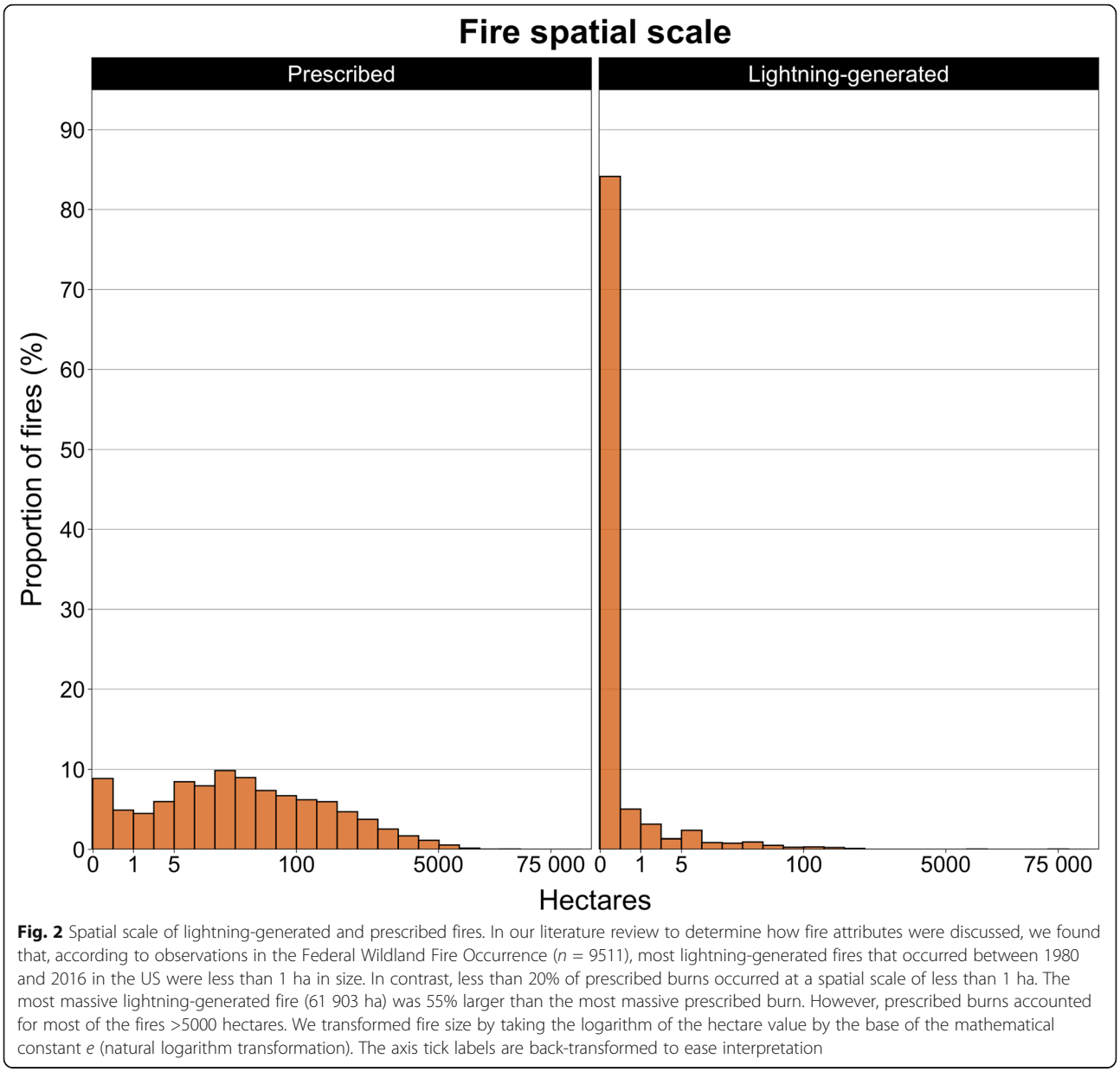

Fig. 2 Spatial scale of lightning-generated and prescribed fires. In our literature review to determine how fire attributes were discussed, we found that, according to observations in the Federal Wildland Fire Occurrence (*n* = 9511), most lightning-generated fires that occurred between 1980 and 2016 in the US were less than 1 ha in size. In contrast, less than 20% of prescribed burns occurred at a spatial scale of less than 1 ha. The most massive lightning-generated fire (61 903 ha) was 55% larger than the most massive prescribed burn. However, prescribed burns accounted for most of the fires >5000 hectares. We transformed fire size by taking the logarithm of the hectare value by the base of the mathematical constant *e* (natural logarithm transformation). The axis tick labels are back-transformed to ease interpretation

ignition sources. The FWFO data set also describes whether lightning-ignited fires were extinguished naturally or by fire-suppression efforts, allowing us to minimize biases associated with fire suppression by not including fires that were suppressed. Incomplete location information is present in the FWFO data, so the MTBS database was included to provide additional verification of prescribed fire sizes even though these data sets likely include some proportion of the same fires. We did not use the MTBS data for natural fires due to size class restrictions and the inability to distinguish the cause. Instead, we used this data simply to compare average prescribed burn size in states.

We filtered the FWFO database to attain naturally extinguished, lightning-generated fires and prescribed fires ignited for a conservation purpose, resulting in 9511 fires. Prescribed and lightning-generated fires accounted for 6919 and 2592 of the observations, respectively. In all possible years, fires were observed in 39 states or territories and ranged in size from 0.1 to 61 903 ha. The distribution of lightning-generated fires was more left truncated and positively skewed than prescribed burns (Fig. 2). In addition, the average spatial scale of fire was less for lightning-generated natural fires (μ = 30 ha, σ = 1225 ha) than for prescribed burns (μ = 226 ha, σ = 839 ha). We filtered the MTBS data to

include only prescribed burns (n = 5650) and created a combined scatterplot and boxplot depicting the distribution of prescribed fire size by state (Additional file 2).

If these data sets had included burning on private lands, the average prescribed burn size would likely be smaller, especially considering that MTBS data does not include smaller fires. While not inclusive of all cases, trends on public lands are a significant indicator of general conditions for wildlife species in the United States (Gergely and McKerrow 2013; Vincent et al. 2019). Public lands (*e.g.,* federal, state, and local) constitute 329 million hectares (35%) of the United States. Although private lands comprise a greater total of land area in the United States, the gap in the relative importance of private and public lands for conservation does not reflect this disparity in area. Approximately half of the total land area in the United States is developed or dedicated to agriculture, and most land dedicated to these purposes predominantly occurs on private property (Bigelow and Borchers 2017; World Bank 2020). Except for programs such as the Conservation Reserve Program (https://www.fsa.usda.gov/programs-and-services/conservation-programs/conservation-reserve-program/), conservation is not the primary objective of most private agricultural land. Public lands may, therefore, represent roughly 50% of the total area available for conservation. Many resources and much literature are devoted to convincing private landowners to alter fire frequency for conservation and management purposes. Thus, while the issue of large spatial scales may be primarily restricted to public lands, we believe that this does not indicate that spatial scale is not a relevant topic to explore in fire ecology.

These data sets have weaknesses and should be interpreted with caution. For example, MTBS data may overrepresent the size of fires by calculating perimeter, which ignores unburned areas within the perimeter (Kolden et al. 2015). Also, Nowell et al. (2018) presented a combination of government fire records and data from several satellites, showing that most burn sizes occurring in Florida, USA, were substantially smaller than the average size that we calculated with the MTBS database. Satellite-based databases, such as MTBS, also only track larger fires, thereby ignoring much of the prescribed burn activity in Florida (Nowell et al. 2018). Similarly, Gunderson and Snyder (1994) collated data from several government agencies and publications, finding prescribed burn sizes in Florida's southern Everglades between 1942 and 1992 were approximately 43% less than we reported for the entire state. Gunderson and Snyder (1994) also described similar averages for prescribed burns and lightning-ignited fires. However, the southern Everglades fire averages have two limitations. First, this region may not reflect conditions in other parts of the state. Second, the authors noted that prescribed and lightning-generated fires were likely underreported or misreported in the early parts of the century (Gunderson and Snyder 1994). Whether the evidence from Florida represents fires in other parts of the country is unknown, but readers should view our presented prescribed burn averages with these issues in mind. Moreover, our intent of providing the averages was not to provide a precise mean of size, but instead to determine if the two types of fire ignitions differ in spatial extent. We believe that the issues with these data sets have comparable inconsistencies across ignition type and, thus, provide a useful relative comparison.

In addition to differences related to the data source, actual variation in fires could cause discrepancies in reported average prescribed-fire size. Gunderson and Snyder (1994) indicated that prescribed fire in Florida increased in number and area in the latter half of the century. Nowell et al. (2018) showed that wildfire and prescribed fire differ annually in Florida due to fluctuations in rainfall and reduced fuel loads from prescribed burns. As indicated by differing reported values in the National Prescribed Fire Reports, total area burned may also vary in any given state (Melvin 2018). Similarly, regions also vary in the relative proportion of prescribed and naturally occurring fires (Eidenshink et al. 2007; Goodman 2016). These ignition sources are interrelated; differences in the relative frequency of either type of fire can affect the rate and extent of the other (Nowell et al. 2018). This variability in the extent of fires is relevant because spatial-scale effects are not fully understood. Again, our intent was to provide a relative comparison, and we assumed that the issues were similar across ignition type and region.

We note two final assumptions in our methods concerning the spatial scale of the lightning-ignited fires. First, we assumed that the spatial scale observed in lightning ignitions provided insight into the evolutionary history of spatial scale in fire regimes. Second, we assumed that the spatial scale observed was representative of what would occur naturally. Even though we only included lightning-generated fires in the FWFO data that were not actively extinguished by human efforts, these data may still underestimate the average lightning-generated fire size. Fuel management, landscape characteristics, and climate are potential factors obscuring actual historical lightning-generated fire size. However, we are unaware of a better data set to determine the historical spatial scale of fires lit by lightning or otherwise. Notwithstanding the issues above, our results are consistent with the findings of other contemporary accounts of the relative size of lightning-generated fires (*e.g.,* Cumming 2001; Reed and McKelvey 2002; Stocks et al. 2003; Wotton and Martell 2005). Whether this trend has a meaningful conservation consequence is unknown, but the observed differences between lightning-generated

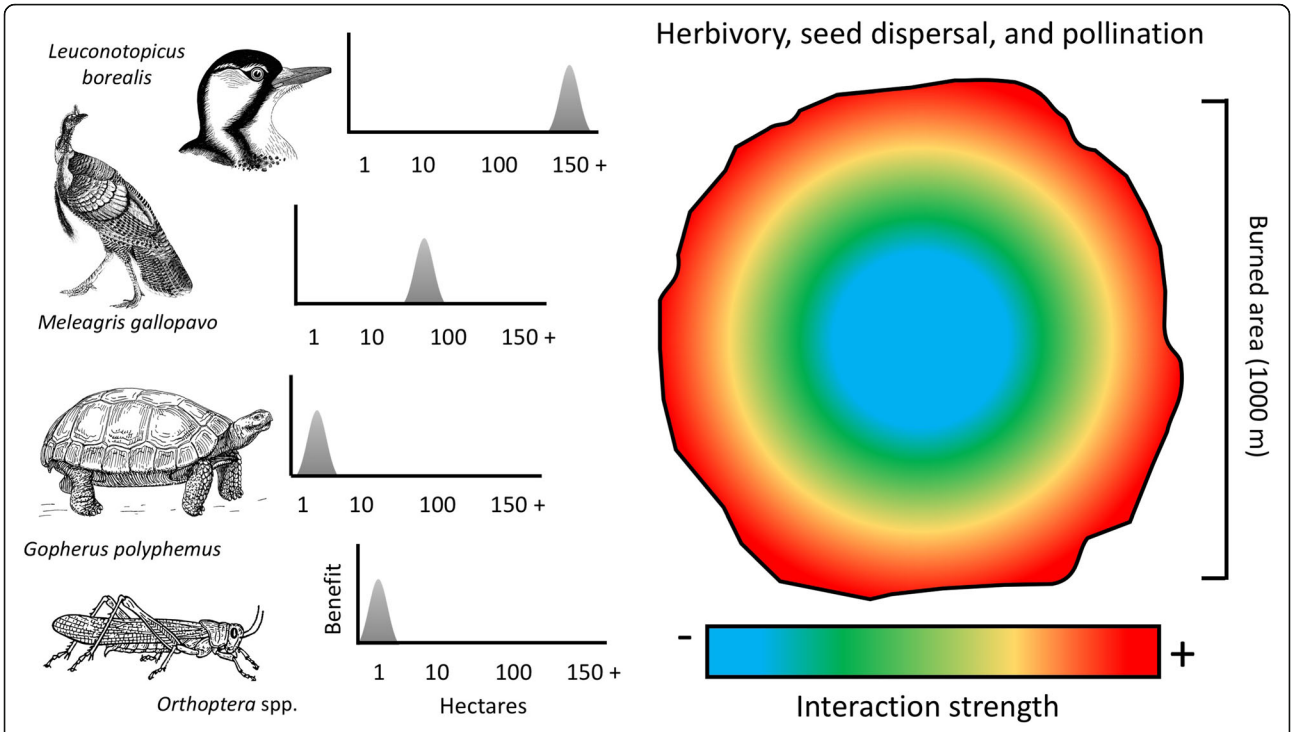

Fig. 3 Projected response to fire. To contextualize the role of fire size in conservation in the southeastern US, we created a conceptual diagram depicting how species and ecological interactions may respond to fires of varying sizes. Optimal burn size is contingent upon the projected response of individual species, target populations, or ecological interactions of concern. On the left side of the figure, we focus on individuals and present the hypothetical benefit of burns for animals belonging to four species common to forests of the southeastern United States. For *Leuconotopicus borealis* and *Gopherus polyphemus,* home-range size determines the projected benefit (DeLotelle et al. 1987; Yager et al. 2007). For *Meleagris gallopavo,* the average burn compartment size used by managers determines the anticipated benefit (Wann et al. 2020). Evidence of decreased herbivory with distance from edge establishes the expected benefit to *Orthoptera* spp. (Knight and Holt 2005). On the right side of the figure, we present a hypothetical gradient of interactions (*e.g.,* herbivory, seed dispersal, and pollination) that decreases in strength with distance from the edge of the burn. Evidence of reduced interactions at the center of burns informed our thinking when developing this gradient (Davis and Cantlon 1969; Gross and Werner 1982; Frelich and Lorimer 1991; Romme et al. 1998; Vickery 2002; Turner et al. 2003; Knight and Holt 2005; Brown et al. 2017). Homogeneous burns would likely increase the effect of distance on this gradient in comparison to more heterogeneous burns or those with frequent refugia. *M. gallopavo* image (https://owips.com/sites/default/files/clipart/turkey-clipart-clipart/151130/turkey-clipart-clipart-wild-turkey-151130-2931421.gif) is the property of owips.com (https://owips.com.cutestat.com/), used in accordance with the web site's requirements

and prescribed burns means that it may be a relevant discussion for fire ecologist to have.

Why is spatial scale rarely considered in fire regimes?

We focused on two avenues to explore the lack of spatial scale consideration. From the practitioner's point of view, the amount of area successfully burned may be a measure of management success. However, time, personnel, and equipment limitations also may exist. These conditions may force practitioners into using a fire-regime model incorporating (a) the largest and most efficient burn blocks possible, and (b) the burning of adjacent blocks collectively. From the researcher's point of view, four realities likely contribute to the lack of focus on spatial scale in fire research. First, spatial-scale research may not be actionable because of the same practical considerations facing practitioners. Second, demand and funding may be lacking. Third, well-replicated manipulative experiments are also challenging to design and implement. And fourth, other factors that are affected by or correlated to spatial scale (*e.g.,* fire severity, higher variability in communities within a burn unit, etc.) make isolating spatial-scale effects particularly difficult. Perhaps exploratory research is needed to understand the ramifications of inappropriate spatial scale before these challenges can be overcome.

Reasons spatial scale of fires may matter to conservation outcomes

Dispersion of wildlife habitat

The spatial scale of a fire can influence the physical location and geographical arrangement of habitat components by manipulating the structure and composition of plant communities and dead plant material (Harper et al. 2016). Wildlife require all habitat components to survive, and

species have different spatial limitations in acquiring or locating those components. Insects, reptiles, mammals, and birds may have varying capabilities of utilizing burn units based on the size of the burn unit relative to their movement ability (Fig. 3). Whereas species capable of flight can track resources at a relatively greater distance, habitat features restrict the resource tracking behavior of other species (Brommer and Fred 1999; García et al. 2011). Similarly, an animal's ability to reach disparate habitat components may also differ depending on the life stage (Hagstrum and Subramanyam 2010). These differences are also observable on islands in the ocean, where the effect of distance on observed species richness is steeper for less mobile organisms (Lawlor 1986).

Interior and edge species are likely to have an inverse pattern in response to spatial scale. As larger homogeneous burn blocks reduce edge effects, interior species should have a positive association with spatial scale. However, edge species are likely to have some threshold in burn-block size where habitat components within the burn block interior are too far from those provided in unburned areas, rendering the interior portion of the burn block unusable. For example, Cohen et al. (2019) demonstrated that eastern wild turkeys (*Meleagris gallopavo,* Linnaeus 1758) were unlikely to use the interior of burn blocks when greater than 250 m from an unburned edge, and Sullivan et al. (2020) found that turkey use was highest in smaller burn blocks (23 ha). Even so, this species is capable of traveling much longer distances, and fire consistently produces desirable plant community structure for that species (Chance et al. 2019).

Understanding the influence of spatial scale is complicated because of animal behavioral plasticity and dispersion of wildlife habitat that is inherently temporally dynamic. For example, variance in Blanford fox (*Vulpes cana,* Blanford 1877) daily movement depends on the distance between denning sites and locations with high prey availability (Geffen et al. 1992). Similarly, red-cockaded woodpecker (*Leuconotopicus borealis,* Vieillot 1809) movement is least when habitat quality is highest (Engstrom et al. 1996). The same space may also potentially provide different habitat components at different times, or component quality may vary with time since some event (*e.g.,* rainfall, fire, or resource pulse). For example, a wild turkey may select a recently burned patch to forage. As time since fire and understory vegetation biomass increases, turkeys may use the same area for nesting (Martin et al. 2012). In this example, habitat component quality changes with time since fire. Forage quality decreases, and cover increases, but not indefinitely.

Spatial-scale-dependent dispersal processes

Plants, varying in vagility and dispersal mechanism, may have differing success in penetrating or escaping the interior of burned areas. When able to adequately reach all disturbed areas—whether by seed banks, far-reaching wind-dispersed seeds, or resprouting—plant response to a fire can be scale independent (Romme et al. 1998). However, plant assemblages in disturbed areas may be scale dependent if only a subset of species can reach the interior, or resident plants in the interior are released from competition from those unable to reach the interior (Davis and Cantlon 1969; Gross and Werner 1982; Frelich and Lorimer 1991; Romme et al. 1998; Turner et al. 2003). Because of these scale-dependent relationships, plant recovery after a fire depends on biotic interactions that may be dictated exclusively by distance.

Animals may face similar challenges when moving through recently burned areas. For example, animals with lower vagility, such as gopher tortoises (*Gopherus polyphemus,* Daudin 1801), may require frequent fire to create viable habitat, but may not be able to reach and utilize interior areas of newly burned areas if source populations are too distant. Invertebrate populations may decline after large or rapidly progressing fires, and die-offs may occur at particular life stages such as recent egg-laying or mating periods (Swengel 2001; Ferrenberg et al. 2006; Hagstrum and Subramanyam 2010). However, there is little evidence of direct vertebrate mortality associated with dispersal away from fire (Harper et al. 2016). Still, animals that could physically penetrate or escape burned areas may choose not to for behavioral reasons (Cohen et al. 2019). White-tailed deer (*Odocoileus virginianus,* Zimmermann 1780) avoid larger patches due to fear of predation in low cover but intensively select recently burned areas at smaller spatial scales even when extremely small (*e.g.,* <0.25 ha; Lashley et al. 2015a, Westlake et al. 2020). Whether driven by movement ability or behavior, differences among animals may lead to differing responses to fires of varying scale.

Scale-dependent dispersal processes are relevant in prescribed burns, which are often homogeneous in intensity and severity (Ryan et al. 2013). In these conditions, dispersal may reach thresholds at which the spatial scale of fire limits some organisms from colonizing the interior. This theoretical threshold is not necessarily negative, as colonization by some species may be problematic. In such cases, larger burn blocks may prevent invasion by non-native species or protect species favored by land managers from herbivores and seed predators. Increasing the spatial scale could be an effective way to promote some species by utilizing the reductions in top-down pressure or competition within the burn block interior. However, even in homogeneous prescribed burns, the spatial scale is not the only factor influencing scale-dependent processes.

Landscape context and burn history should theoretically also modulate scale-dependent dispersal processes. Blocks burned in different years may compose a heterogeneous landscape when considered in aggregate. Still, plants and invertebrates with lower vagility or smaller home ranges may be unable to access other patches in the heterogeneous mosaic (Davis and Cantlon 1969; Swengel 2001). These scale-dependent dispersal processes are also inherently temporal scale dependent because the recovery of plant community structure may allow the eventual colonization of the interior by animals. However, consistently short fire-return intervals may restrict some animals from colonizing the interior areas of larger burn blocks if populations that are vulnerable to direct mortality also recolonize slower than the return interval. Consistent homogeneity in fire behavior may also simplify plant communities over more extended periods, leading to conditions that make animal movement more difficult (Lashley et al. 2014). Because the surrounding landscape and burn history have such consequences on dispersal, the effects of the spatial scale of fire are likely contextual.

Spatial-scale-dependent ecological interactions

The scale of a fire may affect spatial-scale-dependent herbivory and predation due to the movement ability and behavior of a species. Low vagility results in decreased grasshopper (*Orthoptera,* Latreille 1793, species) herbivory with distance from the burn's edge (Vickery 2002; Knight and Holt 2005). Likewise, snake species with low vagility may have difficulty finding unburned areas with more cover, which leads to higher predation from avian predators (Wilgers and Horne 2007). On the other hand, seed predation rates are higher near edges because granivorous rodents avoid predators in sparse understory plant communities (Ostfeld et al. 1997; Willis et al. 2019). This behavior may generate a spatial pattern of seed depredation pressure with implications for subsequent plant establishment (Fig. 3). Although the trophic level and pathways affected differ, the scale of fire modulates ecological interactions in these examples by changing interactions among species in the food web.

Likewise, mutualistic interactions, such as seed dispersal and pollination, may decrease in large burns as penetrating the interior of more extensive burns becomes physically difficult or risky in terms of predation. In theory, these interactions should manifest in a gradient of interaction strength that ultimately influences plant community structure and composition similar to the pattern represented in Figure 3. The magnitude of animal-mediated seed dispersal, herbivory, pollination, and seed predation should weaken with distance from the edge of a burn since most species engaged in these processes are fire-edge species. At large enough scales, these interactions may even be absent in the interior, especially if those interactions involve fire-edge species. Although, when the fire burns heterogeneously, the unburned patches within may serve as refugia from which animals can more easily access the burn interior. When the species can respond to increased resource availability within burned areas, as with pollinators (*e.g.,* Mola et al. 2020), the strength of the interaction may be more influenced by temporal than spatial scale. Indeed, as time since fire increases and the structural characteristics constraining penetration by species ameliorate, temporal scale affects all animal-driven ecological interactions in the interior areas of burns.

While virtually no data exist to help us to understand the role of a fire's spatial scale on animal-mediated seed dispersal and depredation, a relatively rich literature base is available for herbivory. Herbivory often has a negative connotation when associated with forest regeneration. However, the fire–herbivory interaction is essential to the conservation of fire-dependent ecosystems (Zamora et al. 2001; Levick et al. 2009). When fire removes aboveground biomass of perennial plants, the regenerating vegetation is high quality and attractive to herbivores (Fulbright et al. 2011; Ramirez et al. 2012). This high-quality plant material generates a magnet effect for herbivores, intensifying herbivory pressure (Archibald et al. 2005). Intense herbivory pressure continues to set back regeneration, perpetuating the high-quality plant material (a grazing lawn, *sensu* McNaughton 1984). This grazing lawn continues until a new fire occurs, again attracting herbivores.

In grassland, savanna, and forest ecosystems, interactions between fire and herbivory often generate desirable conservation outcomes. Combined fire and herbivory may suppress woody encroachment or cause a bottleneck in tree demography (*i.e.,* reducing the number of woody species reaching larger size classes). Fire and herbivory also interact to generate heterogeneity in structure and composition in plant communities, which has cascading effects on other species and processes. Westlake et al. (2020) reported that the fire–herbivory interaction promoted a unique outcome, compared with either force alone, of more heterogeneity in understory composition, even on 0.2 ha burn units. This interaction between fire and herbivory is likely operating at multiple spatial scales and influenced by the spatial scale of burning.

The relative importance of small- or large-scale processes to the fire–herbivory interaction may differ between fire-interior and fire-edge herbivores. The majority of data on fire–herbivore interactions concerns interior species, which are often large grazers in grassland and savanna systems. At large spatial scales, the fire–herbivory interaction generates heterogeneity because herbivory from interior species is intense in some

areas but weak in others within the same burn unit. This heterogeneity occurs because the large spatial scale of resources effectively inundates the herbivore, and variation in herbivory pressure produces variation in the plant community. On the other hand, herbivory pressure from edge species is likely to be highest near the edge of burn blocks. Herbivory pressure from edge species should weaken as the distance from edge increases, similar to that depicted in Figure 3. For example, Lashley et al. (2015b) reported that white-tailed deer in their study avoided using relatively large burn blocks (>200 ha). Still, fire causes a magnetic effect at smaller scales on the same species in other studies (Westlake et al. 2020). At these smaller-fire spatial scales, the influence of herbivory is likely to be more homogeneous because herbivores can utilize a large portion of a burn during the window of heightened plant quality. In all cases, strengthening herbivory associated with the attractive quality of post-fire vegetative regrowth generates the desirable conservation outcome.

How do we determine the optimal scale?

When determining the optimal burning scale for a species and conservation goal of concern, understanding the ecology of the species and how fire scale may influence habitat components is essential. Most fire-adapted species require recently burned areas in their home range for at least some phase of their life history, but these species may vary in home-range size. Optimal burn size may scale linearly with home-range size, partially because larger animals require more resources (Jenkins 1981; Lindstedt et al. 1986). However, Griffiths and Brook (2014) demonstrated that the effects of fire on mammal demographic parameters depend more upon habitat requirements than body size. Theoretically, any potential relationship between optimal burn and home-range size should plateau at the burn size at which animals are unable to escape mortality or cannot effectively use the interior.

Some animals require burning over most of their home range, while others need only a proportion burned. The red-cockaded woodpecker spends most of its time in burned areas, likely because these areas have reduced predation risk and increased foraging opportunity (DeLotelle et al. 1987; Walters 1991; Garabedian et al. 2018). Gopher tortoises concentrate activity at burrows and construct new burrows in burned areas more often in comparison to unburned areas (Yager et al. 2007). Snowshoe hares (*Lepus americanus,* Erxleben 1777) in North American conifer forests benefit from larger wildfires associated with crown replacement, even as these outpace their dispersal abilities (Hutchen and Hodges 2019). In contrast, wild turkey only requires burning on a proportion of its home range (Martin et al. 2012). Wild turkey use of the interior of a burn diminishes once >250 m from the edge, and researchers have suggested using burn compartments averaging 90 ha to manage wild turkey populations (Cohen et al. 2019; Wann et al. 2020). Because of the differences among species, the benefits of fire to species or conservation goals may vary with the spatial scale of implementation.

Even within a single species, assessing the optimal burning scale may include considering metapopulations beyond individuals directly targeted or affected by a fire. Although not immediately exposed to a burn, other populations could be positively or negatively impacted depending on connectedness, ecological interactions, and source–sink dynamics. For example, a burn may positively or negatively impact an herbivore population, generating effects on adjacent populations through increased or decreased intraspecific competition (Svanbäck and Bolnick 2007). On the other hand, burning could negatively impact one herbivore population, which could negatively impact other populations by reducing genetic diversity in the metapopulation (Svanbäck and Bolnick 2007; Vandewoestijne et al. 2008). An overarching assessment of the effect of spatial scale of a fire may depend on the temporal and spatial scope considered because most populations and landscapes exist within larger populations and landscapes.

Because optimal burning scale may vary with species and the metapopulation context, the management of entire communities may require fire regimes with burns of varying spatial scale to accommodate a wider variety of species. The goal of burning for conservation is to regenerate or maintain vegetation composition and structure as a component of habitat, and prescribed burns are often homogeneous. Although some species may require more area burned, large homogeneous fires could impair herbivory, seed dispersal, and pollination in the interior. Because animal vagility and behavior determine the theoretical size threshold governing this impairment, the organisms in the community will determine the optimal burn size. In such cases, burn units of differing size may maximize beneficial ecological interactions or be beneficial for more species.

Moving forward

Our work revealed that the spatial scale of fire is relevant to fire ecologists; researchers acknowledged this importance but rarely studied it from a conservation perspective. A shift in focus toward spatial scale may be warranted if fire regimes indeed mismatch spatial scales realized in historic burning patterns. Thus, for both current and future conservation goals, we encourage fire ecologists to empirically address the role of prescribed-fire spatial scale.

With global fire regimes changing as a result of shifting climatic conditions and land-use changes

(Prentice 2010), the need to understand these scale-dependent relationships will continually increase in importance. If the distribution of size classes shifts toward larger fires with the changing global climate, the apparent difference we report between the average size of lightning-ignited and prescribed fires may decrease. In this case, average fire size may outpace the ability for a subset of organisms to adapt, which is already occurring with other aspects of climate change (Huey et al. 2012). Also, fire regime changes may affect plant and animal evolutionary trajectories, which are already being documented in plants and animals experiencing changes in other disturbance types (Waples et al. 2009; Gómez-González et al. 2011). These are important considerations for fire ecologists interested in tailoring fire regimes to increase the resilience of ecosystems to climate change (Trumbore et al. 2015).

We suggest that researchers conduct experiments to explore the ecological effects of spatial scale. Comparative experiments with prescribed burns conducted along a gradient of size representing several orders of magnitude (*e.g.,* 1, 10, 100, 1000, and 10 000 ha) and manipulative experiments with organisms operating at smaller scales (0 to 100 ha) would provide a useful framework in which to understand the role of spatial scale in fire regimes. These experiments could complement future work that integrates other facets of fires, such as shape, perimeter length, the proportion of edge, and burn heterogeneity, thus providing a sophisticated and more thorough comparison of natural lightning-generated fires and prescribed burns. However, if scale dependence is evident, our current literature base for ecological inference may have inherent biases driven by spatial-scale-dependent patterns. This bias may be especially true in our most experimental and replicated studies (*i.e.,* often <1 ha plots) because the size of burn units may not represent the scale at which fire regimes operate in a management context. In any case, we hope this paper provokes interest from fire ecologists in understanding if, how, and to what magnitude spatial scale in fire regimes is relevant. We believe this knowledge will equip fire managers with the tools necessary for maximizing the benefits of prescribed burning for conservation.

Supplementary Information

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Additional file 1. Recent (2009 to 2018) reviews and syntheses (n = 37) from around the globe used in our literature review to determine how fire ecologists addressed fire spatial scale. The most recent papers are listed first. Shaded cells indicate whether each paper contained discussion (Discuss) or data-based inferences (Data) concerning fire attributes (References not cited in the article main text but included in the literature review and in Additional file 1 are: Abella and Springer 2015; Adams et al. 2013; Bentley and Penman 2017; Beringer et al. 2015; Brose 2014; Brown et al. 2016; Campbell 2012; Cannon et al. 2017; Cawson et al. 2012; Contreras et al. 2011; Darracq et al. 2016; Dey and Schweitzer 2018; Driscoll et al. 2010a; Driscoll et al. 2010b; Engstrom 2010; Fernandes 2013; Freeman et al. 2017; Frelich et al. 2017; Fulé et al. 2012; Geiser et al. 2018; Hessburg et al. 2015; Hesseln 2018; Hunt et al. 2014; Hutchen et al. 2017; McIver et al. 2013; Meador et al. 2017; Miesel et al. 2012; Page et al. 2014; Parkins et al. 2017; Prichard et al. 2017; Ratajczak et al. 2014; Robinson et al. 2013; Slapcinsky et al. 2010; Taudiére et al. 2017).

Additional file 2. Summary statistics of prescribed burns in each state of the United States, from our literature review to determine how fire attributes were discussed. We transformed fire sizes listed in the Monitoring Trends in Burn Severity database between 1984 and 2017 by using the natural logarithm. Boxplot hinges represent 25th and 75th percentiles, and the middle line depicts the median value. Whiskers extend to the highest and lowest values past the hinge within 1.5 multiplied by the interquartile range. The distribution of prescribed burns varied among states (n = 5650). Several states in the southern and midwestern regions had a relatively continuous distribution of prescribed burn sizes (Alabama, Georgia, Florida, Kansas, Louisiana, Mississippi, South Carolina, and Texas). In contrast, other states had fewer fires closer to the maximum and minimum values found in the data set (Alaska, Oklahoma, Iowa, and Wyoming). Also, states varied in the total number of prescribed burns in the database, with southern and western states overrepresented compared with midwestern or eastern states, except for Florida.

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Author's contributions

DSM: conceptualization, formal analysis, data curation, investigation, writing–original draft, writing–review and editing. MLL: conceptualization, investigation, writing–original draft, writing–review and editing. Both authors read and approved the final manuscript.

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