Wildland fire has impacted most landscapes of the Americas, leaving evidence of its passing in the biota, soils, fossils, and cultural artifacts (Swetnam and Betancourt 1990; Delcourt and Delcourt 1997; Platt 1999; Ryan et al. 2012). Many terrestrial ecosystems reflect this long evolutionary history with fire and require periodic fire to maintain species composition and stand structure and function (Abrams 1992; Agee 1993; Pausas and Keeley 2009).

The presence of fuels and a source of ignition are necessary for wildland fires to occur. Variations in fire spread and intensity across landscapes are dependent on the physical and chemical characteristics of these fuels, with fuel moisture and fuelbed continuity being two of the most important factors. An abundance of fine (high surface area-to-volume ratio), dry fuels that are continuous or interconnected is required for fire to spread. Cold- or moisture-limited ecosystems are often fuel-limited because combustible biomass accumulates slowly and the continuity of the fuelbed takes longer to redevelop following a fire. Wet forests develop fuelbed continuity more quickly but may also be effectively fuel-limited because the fine fuels are rarely dry enough to burn. Intermediate to these extremes are a range of ecosystems that produce abundant fine fuel and are seasonally dry and susceptible to ignition from lightning or humans. Rates of fuel accumulation and prevalence of ignition sources varies by region and ecosystem across North America (Knapp et al. 2009). Within regions, fire potential also varies year to year, under the influence of global circulation patterns such as the El Niño–Southern Oscillation (ENSO; Swetnam and Betancourt 1990; Ryan et al. 2012). The southeastern US coastal plains and southwestern mountain ranges experience frequent lightning storms; when lightning strikes dry fuels, for example, in the days prior to summer monsoon rains (Figure 1; Flagstaff, Arizona and Ocala, Florida), numerous fires result (Swetnam and Betancourt 1990; Stambaugh et al. 2011). Major conflagrations commonly occur during La Niña episodes, when monsoonal rains are delayed or weak. These areas recover fuel continuity quickly and are characterized by high fire frequency. In contrast, soaking
summer rains hamper lightning ignitions in the deciduous hardwood forests of northeastern North America (Figure 1; Athens, Ohio). In this region, fuels are combustible mainly during autumn–spring dormancy, the period when sunlight can dry the newly-fallen leaf litter. Lightning is rare during this time and fires are therefore primarily human-caused (Schroeder and Buck 1970; Guyette and Spetich 2003). Lightning fires are largely restricted to ridges and sandy plains that favor the development of more open pine–oak (Pinus and Quercus spp, respectively) forests, and where more rapid drying of surface fuels is possible (Motzkin et al. 1999; Keeley et al. 2009). Much of western North America is typified by an extended summer dry season (e.g., Figure 1; Yosemite National Park, California). “Dry” thunderstorms – those that lack wetting rains – are a major source of summer fires in the western mountains, particularly during droughts. Lightning is also the dominant source of large, landscape-scale fires in the boreal forests of Alaska and northern Canada (Krezek-Hanes et al. 2011). In many areas of North America, relatively recent settlement of rural woodlands is shifting the proportion of human versus lightning ignitions (Peters et al. 2013).

Humans migrated to the Western Hemisphere at least 14,000 years before present (Goebel et al. 2008) and used fire for heat, light, food preparation, and hunting (cf. Nowacki et al. 2012; Ryan et al. 2012), but the degree to which human-caused fires were agents of land-cover change is unknown because of the spatial and temporal limitations of paleological data. Questions therefore remain about the extent to which pre-Columbian fires were of natural or human origin (Boyd 1999; Vale 2002). In areas of high lightning density, such as in the mountains of the US Southeast and Southwest, fire frequency was most likely limited by the recovery rate of fine fuels. In Pacific Coast forests and in the temperate deciduous forest biome of eastern North America, the rarity of dry-season lightning suggests that humans were a major igni-
Humans and fire after Euro–American settlement

European settlers caused major changes in fire regimes throughout North American forests. Logging was associated with land clearing for agriculture, as well as providing fuel for heating, powering steam engines, and industrial production. Unregulated forest harvesting during the 19th and early 20th centuries generated logging slash (residual coarse and fine woody debris) that contributed to catastrophic wildfires (Haines and Sando 1969; Pyne et al. 1996). In the US, the societal and legal responses to these fires made wildland fire suppression a dominant activity in federal, state, and private forest management (eg USFS 10 AM Policy of 1935). Fire factored into the creation of several federal land-management agencies (eg US Forest Service [1905], US National Park Service [1916], and the US Bureau of Land Management [1946]) and similar forest conservation agencies at the state level (Pyne 1982). Without exception, agency policies coupled with propaganda on the benefits of fire prevention (eg Smokey Bear) were designed to control the impacts of fire through active fire prevention and suppression (Pyne 1982).

Early organized efforts at fire control by fledgling government agencies were hampered by the lack of roads and fire suppression infrastructure. Airplanes and equipment freed up by the end of World War II, as well as intensified road building for logging to support post-war housing demand, helped to bring effective fire suppression to all but the most remote areas, such as the northern boreal forests.

The combination of fire suppression and the decrease in burning by Native Americans dramatically altered the fire regime across much of North America. The eastern US experienced a steep decline in fire occurrence (Nowacki and Abrams 2008). In the western US, the total area burned declined sharply for some decades, reaching its minimum during the 1970s (Agee 1993; Leenhouts 1998). Since then, the trend has been toward increasing wildfire activity (Westerling et al. 2006; Littell et al. 2009), despite extensive suppression efforts. In Canada, yearly burned area increased from 1959 to the 1990s, then declined somewhat, except in the western provinces (Krezek-Hanes et al. 2011). Regardless of regional differences, the land area being burned today across much of North America is far less than what was burned historically. Leenhouts (1998) estimated that in the conterminous US, burning in the late 20th century was 7–12 times less prevalent than in pre-industrial times. In California, Stephens et al. (2007) estimated that 18 times less area was burned annually between 1950 and 1999 than had burned prior to that time. A compilation of studies of Canadian boreal forests indicated an average modern burn rate approximately five times less than the historical burn rate (Bergeron et al. 2004). Similar statistics for Mexico and Central America are not as well developed; here, fires continue to burn across large areas in some years, and ecosystems vary between experiencing less than and more than historic levels of fire (Rodríguez-Trejo and Fulé 2003; Martínez Domínguez and Rodríguez-Trejo 2008).

Ecological consequences of fire exclusion

Excluding fire from previously fire-frequent ecosystems results in major changes in ecosystem structure, composition, and function across a variety of scales (Covington and Moore 1994; Keane et al. 2002; Varner et al. 2005). The consequences of suppression-altered fire regimes include a reduction in or loss of ecosystem services, and vastly altered fuels and potential future fire behavior. Without the disturbance of periodic fire, tree density increases (Figure 2) and landscape structure homogenizes (Taylor 2004; Hutchinson et al. 2008; Nowacki and Abrams 2008). The influx of fire-sensitive species alters community composition, stand structure, and ecosystem processes (Keane et al. 2002; Rodewald and Abrams 2002; McShea et al. 2007; Alexander and Arthur 2010; Maynard and Brewer 2012). Canopy infilling by shade-tolerant, fire-sensitive trees and accumulated litter in unburned forest floors can lead to reduced cover and diversity (Hiers et al. 2007; Engber et al. 2011). Plant species that benefit from disturbance and exposed bare soil typically decline (Harvey et al. 1980; Gilliam and Platt 1999; Knapp et al. 2007). The effects of fire exclusion also affect animal communities. Loss of herbaceous species in long-unburned forests has been associated with
Reduced butterfly diversity compared to more recently burned forests (Huntzinger 2003). In southeastern pine savannas and woodlands, avian, herpetofauna, and mammalian diversity have declined substantially. The rarity of many endangered wildlife species, including the red-cockaded woodpecker (*Picoides borealis*) and gopher tortoise (*Gopherus polyphemus*), is thought to be largely due to the alteration of habitat caused by the lack of fire (Means 2006).

In drier portions of western North America, greater surface fuel continuity in combination with the influx of conifer seedlings and saplings contributes to higher fire intensity and severity, and an increased probability of crown fires (Agee and Skinner 2005). In contrast, fire exclusion in fire-prone landscapes of eastern North America (particularly oak, southern pine, and oak–pine ecosystems), is associated with the invasion of fire-sensitive species with less flammable litter, more shaded and moister microclimatic conditions, and reduced fire activity. The result is a positive feedback cycle, termed “mesophication” by Nowacki and Abrams (2008), with lower potential for burning reinforcing the advantage for the invading shade-tolerant, fire-sensitive species.

**Restoring fire as a landscape process**

In North America, recognition of the ecological benefits of prescribed burning was slow in coming and varied geographically. Fuel accumulation and loss of upland game habitat occurred especially quickly in productive southern pine forests and woodlands and ecologists in the southeastern US promoted the use of fire in land management from early on (eg Stoddard 1931; Chapman 1932). In spite of their convincing arguments, fire in the southeastern US (and elsewhere) was still frequently viewed as incompatible with timber production due to the potential for injury to mature trees and the inevitable loss of tree seedlings. Since then, research in numerous ecosystems has helped shape greater public recognition of fire’s integral role in maintaining “fire-dependent” plant communities. However, contemporary fires fueled by biomass that accumulated in the absence of fire now pose a greater risk of damage to private property, public infrastructure, and ecosystems. Numerous studies have documented the capacity for prescribed burning to mitigate extreme wildfire behavior and uncharacteristically severe fire effects (Agee and Skinner 2005; Finney et al. 2005; Prichard et al. 2010; Cochrane et al. 2012), further reinforcing the importance of fire management (Ryan and Opperman 2013). Nevertheless, the tension between risks and recognized benefits remains.

The extent to which fire has been incorporated into management protocols varies across regions. In the US, approximately one million ha are burned annually as a result of prescribed fire (NIFC 2013a). Between 1998 and 2008, US federal agencies also actively managed an average of 327 lightning-caused wildfires for the purpose of restoration, and these burned an additional 75 000 ha annually (NIFC 2013b). US federal fire managers still have latitude to allow some lightning fires to burn to provide resource benefits, but since a 2009 policy change, hectares treated in this way are no longer counted separately from total wildfire hectares. In Canada, a small percentage of wildfires in remote areas are allowed to burn or are not aggressively suppressed; these account for the majority of acres burned (Taylor 1998). Parks Canada and some First Nations conduct prescribed burns on a limited basis (Weber and Taylor 1992), but landscape-scale prescribed burning for ecosystem restoration is still relatively uncommon (Taylor 1998). While statistics for Mexico and Central America indicate a preponderance of human-caused fires, most are either escaped agricultural and pastoral burns or intentional burns that lack clear ecological objectives (Rodríguez-Trejo and Fulé 2003;
Rodríguez-Trejo 2008). Despite successes in the development of robust prescribed burning programs, especially in the southeastern US (Stephens 2005), almost nowhere has the use of fire kept pace with or even approached historic levels (Leenhouts 1998; Stephens et al. 2007). The reasons for this “fire deficit” are numerous and can be attributed to lingering questions about the comparability of prescribed or managed burning to pre-industrial fire, as well as legal, political, and operational challenges that accompany burning in the modern era.

Is prescribed fire an ecological surrogate for historical fire?

Where restoration or maintenance of ecological processes is the goal, questions persist about how well current prescribed fires emulate the ecological effects of pre-suppression era fires. One major area of concern is the extent to which current fuel loading exceeds pre-industrial levels. Many fire effects are closely tied to the amount of fuel consumed (Ryan 2002; Knapp et al. 2007, 2009), and initial restoration burns after long fire-free periods can therefore lead to undesirable effects (Ryan and Frandsen 1991), such as killing or stressing large remnant trees, including those of normally very fire-resistant species (Figure 3; Ryan and Reinhardt 1988; Varner et al. 2005; Hood 2010; Harrington 2012).

Variability in fuel distribution generated by periodic fire caused historical fires to burn in a patchy mosaic (e.g., Show and Kotok 1924). This created numerous unburned refugia where fire-sensitive plant species or small, non-mobile animals survived to recolonize burned areas. Increased forest density and accumulation of litter, duff, and wood debris has produced a more continuous, uniformly flammable fuelbed (Knapp and Keeley 2006). As a result, in long-unburned areas, prescribed fire or wildfire often leave few such refugia. Subsequent fires at shorter intervals can re-establish patchiness (Figure 4). However, prescribed fires are also often ignited in linear strips or at multiple points along regular grids (Figure 5a). Uniform ignition, driven by the operational need to maintain control, produces more uniform burns with fewer residual unburned patches. In contrast, wildfires typically ignite landscapes in large fingered fronts or via lofted embers (spotting), both of which lead to substantial heterogeneity in burn patterns. Our understanding of how refugia and heterogeneity affect organisms at different spatial scales remains incomplete (Knight and Holt 2005; Collins et al. 2009).

Many prescribed burns are conducted in different seasons and under higher moisture conditions than historical fires (Figure 1; Knapp et al. 2009). A common criticism is that such “cool season” burns fail to achieve fuel consumption and restoration goals. In the western US, the lack of fire crew availability frequently pushes prescribed burning to the cool spring or fall margins of the fire season, whereas the majority of the area historically burned in the summer, when conditions were warmer and drier (Figure 1). In the southeastern US, dormant-season burns are often preferred over late spring/summer (i.e., lightning-season) burns (Figure 1) to moderate effects, reduce the probability of fire escape, and avoid impacts on breeding birds. Such dormant-season burns are generally less effective for killing encroaching fire-sensitive hardwoods (Streng et al. 1993). In western woodlands and montane forests, fires historically maintained low tree density by thinning primarily susceptible juveniles (Cooper 1960; Kilgore 1973), but after prolonged fire exclusion many invading trees become large and thick-barked enough to resist stem injury from low-intensity fires (Schwilk et al. 2009; Engber et al. 2011). Prescribed fire alone, especially at the low end of the intensity spectrum, is therefore often inadequate for meeting forest restoration and management goals, and may require augmentation by mechanical means. In other situations, excess fuels, especially around the base of large pines (Figure 3), may lead to excessive stem and root injury and
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Figure 4. Unburned patch resulting from reduced flammability of prostrate ceanothus (Ceanothus prostratus) within a prescribed burn in heterogeneous fuels, 10 years after the first prescribed burn in Klamath National Forest, California. Such potential fire refugia may play an important role in the resilience of species to wildfire or prescribed fire, and are less common in long-unburned areas.

death of the remnant trees that managers most wish to protect (Varner et al. 2005; Hood 2010).

Variations in fire susceptibility among organisms as a result of differing phenology or life-history stage at the time of burning can lead to species shifts (Kauffman and Martin 1990; Howe 1994). However, the majority of studies show little or no influence of timing of burns, relative to other factors such as fire intensity, that also typically vary with season (Knapp et al. 2009). Over the long term, many plant and animal populations appear to be most strongly influenced by how fire alters their habitat, regardless of burning season (Knapp et al. 2009).

The restoration of structural complexity that was historically generated by frequent low- to mixed-severity wildfire is a key goal of current federal forest land management. When prescribed fire is used, restoration benefits from a variable fire regime – burning at different times of the year, under different weather and fuel moisture conditions, and employing variable ignition patterns (Knapp et al. 2009), all factors that complicate fire management operations. With prescribed burning, maintaining control of the fire is a primary concern, thereby encouraging the use of low-intensity fire. In addition, common ignition patterns, such as strip head fires (linear strips of fire ignited evenly and in close succession at right angles to the slope and/or wind direction; Figure 5a), are designed to homogenize fire behavior, which in turn also tends to homogenize fire effects. Greater randomness in ignition, including variable, ground-based firing patterns (Figure 5b) or aerial ignition, may increase heterogeneity and better emulate the complexity that historical burning once produced. Since forest management has embraced stand- to landscape-scale structural complexity as a tenet, prescribed fire objectives should ideally seek to incorporate these same outcomes (Noss et al. 2006).

Strategic management of wildfires is an especially promising means of generating heterogeneity, due to the inherent variation in fire intensity and severity within wildfire boundaries (Collins et al. 2009). In addition, strategic management of wildfires may allow larger land areas to be burned than can be realistically treated with prescribed fire.

Legal, political, and operational challenges in a risky world

Research has improved our understanding of the ecology associated with prescribed burning and will continue to play an important role in successful fire management. However, ecological concerns typically pale in comparison to legal, political, and operational challenges. In the US, tension exists between fire and a variety of socioenvironmental values. Prescribed fire treatments must be conducted within the framework of a suite of environmental laws, including the National Environmental Policy Act, the Clean Air Act, the Clean Water Act, and the Endangered Species Act, and the resulting analysis and review processes that accompany land management often lead to conflicts. For example, while the Clean Air Act had the beneficial effect of reducing hazardous particulates from industry and automobiles, it has also made the use of prescribed fire or allowing wildfires to burn much more difficult. Smoke was likely an ever-present reality of fire seasons in the pre-Euro–American landscape (Leenhouts 1998; Stephens et al. 2007), but decades of increasingly effective fire suppression and urbanization has resulted in a public that is out of touch with landscape burning. Recent transmigrations have fragmented the land with subdivisions (Gude et al. 2013; Peters et al. 2013) and many people are unaware of the past prevalence of fire and smoke. Prescribed fire is a point pollution source and therefore easy to regulate. In times of poor air quality, it is often politically less challenging to limit land managers’ fire use than to constrain other sources of pollution (eg emissions from automobiles or industry).

While some environmental laws have bolstered the case for managers to use fire (eg the federally listed fire-obligate red-cockaded woodpecker and many others; Means 2006), in other situations, environmental laws can actually impede prescribed burning (Quinn-Davidson and Varner 2012). The Endangered Species Act requires managers to analyze the immediate short-term risks associated with actions such as prescribed burning, but not the long-term risks associated with inaction. Thus, the law creates a disincentive to treat lands inhabited by endangered species. Short-term risks to a species (eg displacement, injury, direct mortality) should ideally
prescribed burning legislation (e.g., Wade and Brenner 1992), and is emulated by other southeastern states (Sun and Tolver 2012). Further testament to the importance of prescribed burning in the Southeast are the long-standing Prescribed Fire Councils that originated in Florida and that have since expanded to other fire-prone southeastern states. These “communities of practice” (Wenger 2000) have been influential in the legislative process and in the training and education of managers and land owners. In contrast, fledgling Prescribed Fire Councils in the western US have yet to petition for protective legislation for burners.

Prescribed burning can be negatively affected by those rare mistakes or unexpected events that can overwhelm understanding of their ecological and economic benefits. Over 99% of prescribed fires are successfully held within planned perimeters (Dether and Black 2006). When prescribed burns go well, the immediate effects are often little noticed and landscape changes are gradual. But when burns escape, the consequences for future burning can be enormous. For example, high winds caused the May 2000 Cerro Grande prescribed fire in New Mexico’s Bandelier National Monument to breach control lines and burn about 19,000 ha and over 250 homes. In Colorado, during the spring of 2012, embers from a seemingly extinguished 4-day-old prescribed burn reignited in high winds, resulting in the Little North Fork Fire that killed three people and destroyed 27 homes. Such high-profile events have the immediate effect of halting prescribed burning until fact-finding concludes; more importantly, they fuel public fear and increase skepticism regarding prescribed burning.

Managers often receive public praise for suppressing wildfires but receive little recognition when conducting successful prescribed burns or allowing wildfires to burn for resource benefits. Disincentives for using fire, as well as societal intolerance of risk and a tendency toward short-term planning, lead to a focus on minimizing short-term risks (i.e., injury to species from heat or smoke, fire

Figure 5. Prescribed fire ignition patterns in Klamath National Forest, California. Ignition patterns can influence fire effects. Some common patterns include: (a) strip head fire, with evenly spaced strips placed sequentially from higher to lower elevations within the unit; and (b) tree-centered spot firing, with the objective of minimizing flame lengths under desired trees and producing variable flame lengths elsewhere.
escape). Long-term risks (and ecological consequences) posed by fire exclusion attract less discussion and decision-making attention than they probably should.

The risk of escape is greater when weather and fuel moisture conditions approximate historical burning conditions. Prescriptions are therefore often conservative, requiring fuel moisture, relative humidity, and wind speeds that minimize the chance of fire escape. Unfortunately, such conditions are uncommon, resulting in narrow burn windows of only a few days per year in many western landscapes (Quinn-Davidson and Varner 2012). Infrequent favorable conditions increase competition for resources and air quality permits, which are often major hindrances to burning. Thus, sociopolitical factors rather than ecological rationales often drive decisions regarding when and where treatments occur.

## Conclusions

Anthropogenic and lightning fires shaped North American landscapes for millennia, so that many ecosystems are dependent on periodic fire to maintain important components (Abrams 1992; McClain and Elzinga 1994; Delcourt and Delcourt 1997; Pausas and Keeley 2009; Nowacki et al. 2012). There is, however, still much to be learned, particularly with respect to how fire regimes (ie the frequency, timing, and severity of fire) affect stand-level processes, and how fire relationships change at increasing temporal and spatial scales. Most studies are relatively short term and often use data collected from small plots, whereas fire management planning occurs across decades and over large landscapes (Keeley et al. 2009).

Technology has greatly expanded our ability to modify fire regimes through fire suppression, prescribed burning, and mechanical manipulation. The ecological legacy of past practices has altered systems, in some cases irrevocably. Future climate conditions will further confound our understanding, and the magnitude and scale of accompanying changes to vegetation and fuels may limit our capacity to respond. These uncertainties constrain our ability to reintroduce fire to accomplish a suite of societal benefits, including protecting lives and property, enhancing ecosystem services, ecological restoration, and biological conservation. Experience indicates that neither laissez faire fire management nor full suppression will accomplish these goals. With current limits to prescribed burning, many managers have turned to mechanical surrogates (eg thinning and pile burning). Allowing lightning-ignited wildfires to burn for resource benefits where consistent with local management plans offers promise for restoring large, relatively roadless landscapes (Noss et al. 2006; Collins et al. 2009) but may be impractical in more developed areas.

Humans have been, and will continue to be, a dominant force in shaping the landscape (Denevan 1992; Nowacki et al. 2012; Ryan and Opperman 2013). Prescribed burning and managed wildfire have been, and should continue to be, major tools for affecting that process. The challenge for all natural resource management centers around not only conserving the species but also preserving and/or restoring biophysical processes. Given the current lack of public awareness and social acceptance (McCaffrey et al. 2013), subdivided and fragmented landscapes (Gude et al. 2013; Peters et al. 2013), and limited funding, expansion of prescribed fire programs will entail a redoubled effort to integrate fire and ecological sciences into management and policy.

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