The Demise of Fire and "Mesophication" of Forests in the Eastern United States

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A diverse array of fire-adapted plant communities once covered the eastern United States. European settlement greatly altered fire regimes, often increasing fire occurrence (e.g., in northern hardwoods) or substantially decreasing it (e.g., in tallgrass prairies). Notwithstanding these changes, fire suppression policies, beginning around the 1920s, greatly reduced fire throughout the East, with profound ecological consequences. Fire-maintained open lands converted to closed-canopy forests. As a result of shading, shade-tolerant, fire-sensitive plants began to replace heliophytic (sun-loving), fire-tolerant plants. A positive feedback cycle—which we term "mesophication"—ensued, whereby microenvironmental conditions (cool, damp, and shaded conditions; less flammable fuel beds) continually improve for shade-tolerant mesophytic species and deteriorate for shade-intolerant, fire-adapted species. Plant communities are undergoing rapid compositional and structural changes, some with no ecological antecedent. Stand-level species richness is declining, and will decline further, as numerous fire-adapted plants are replaced by a limited set of shade-tolerant, fire-sensitive species. As this process continues, the effort and cost required to restore fire-adapted ecosystems escalate rapidly.

Keywords: fire-adapted species, oak-pine, prescribed burning, forest floor, restoration

Fire was widespread and frequent throughout much of the eastern United States before European settlement (Pyne 1982, Abrams 1992). Widespread burning created a mismatch between the physiological limits set by climate and the actual expression of vegetation—a common phenomenon throughout the world (Bond et al. 2005). In the eastern United States, presettlement vegetation types were principally pyrogenic; that is, they formed systems assembling under and maintained by recurrent fire (Frost 1998, Wade et al. 2000). Prime examples include tallgrass prairies, aspen (*Populus*) parklands, oak (*Quercus*)-dominated central hardwoods, northern and southern "pineries," and boreal spruce-fir (*Picea–Abies*) forests (Wright and Bailey 1982). In turn, an extensive array of eastern animal and plant species have adapted to and depend on fire, either directly (e.g., jack pine [*Pinus banksiana* Lamb.]) or through the use of fire-maintained habitat (e.g., Kirtland's warbler [*Dendroica kirtlandii*]).

A diverse mix of vegetation and site conditions of the eastern United States supported a range of presettlement fire regimes, from intense stand-replacing burns on pine barrens to "asbestos-like" communities that rarely burned (e.g., northern hardwoods). However, most presettlement fire regimes produced low- to mixed-severity surface burns, which maintained the vast expanses of oak and pine forests that dominated much of the eastern United States, often in open "park-like" conditions (Wright and Bailey 1982, Frost 1998). Native Americans were the primary ignition source in many locations, given the moist and humid conditions of the East (Whitney 1994). Historical documents indicate that Native American ignitions far outnumbered natural causes (principally lightning) in most locations (Gleason 1913, DeVivo 1991). In this respect, humans were a "keystone species," actively managing the environment with fire over millennia (Sauer 1975, Guyette et al. 2006). Nonetheless, within the fire-maintained landscapes, variations in human population and land use, topography, and riparian areas (firebreaks) created a mosaic of burned and unburned vegetation types (Heinselman 1973, Anderson 1991, Whitney 1994).

Fire regimes changed in various ways with European settlement, often profoundly. In many instances, fire frequency and severity increased as forests were cut and burned, either intentionally (for agricultural land clearing) or unintentionally (e.g., sparked by wood- and coal-burning steam engines). This transition was most stark for mesic hardwood

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systems that seldom burned in presettlement times (e.g., northern hardwoods, mixed mesophytic forests). Most noteworthy were the postcutting conflagrations of the upper Great Lakes (Haines and Sando 1969), which led to unprecedented changes in vegetation composition and structure (Webb 1973, White and Mladenoff 1994, Cole et al. 1998). For instance, a sizeable proportion of northern hardwoods converted to aspen-birch (*Populus–Betula*) or oak through repeated cutting and burning (Palik and Pregitzer 1992, Schulte et al. 2007). Fire frequency remained the same or even increased where settlers adopted Native burning practices, such as in the central hardwood region (Cole and Taylor 1995). Here, frequent understory burning helped maintain the dominance of oak and of fire-adapted associates, especially grasses for pasturage.

On the most flammable landscapes (e.g., midwestern grasslands) where the danger to humans and improvements (e.g., buildings, fences) from fire was especially high, fire was effectively extinguished with European settlement (Gleason 1913, Abrams 1992, Wolf 2004). Here, fires declined for several reasons, including the loss of Native American ignitions, the rapid conversion of native vegetation to croplands and pasturage, landscape fragmentation (caused by roads and railroads), and active suppression efforts (Nuzzo 1986). In areas not dedicated to agriculture, the release of fire-suppressed sprouts (grubs) from centuries-old oak root systems turned native grasslands and oak savannas into closed-canopy forests at astonishing rates (Loomis and McComb 1944, Cottam 1949, Anderson 1991, 1998).

Regardless of the directional shifts of the early postsettlement era, fire regimes began to converge with the onset of fire-suppression policies in the 1920s. As a result of these policies, fire declined through effective wildfire detection and universal containment. This wholesale shift in fire regimes had unforeseen ecological consequences across the United States. A cascade of compositional and structural changes took place whereby open lands (grasslands, savannas, and woodlands) succeeded to closed-canopy forests, followed by the eventual replacement of fire-dependent plants by shade-tolerant, fire-sensitive vegetation. This trend continues today with ongoing fire suppression.

Many studies have individually documented fire regime change and subsequent shifts in vegetation over time (Heinselman 1973, Clark 1990, Abrams and Nowacki 1992, Wolf 2004). However, a broadscale synthesis, projection, and discussion of fire-regime change across the eastern United States is currently lacking. Similarly, discussions regarding the ecological consequences of long-term fire suppression have been largely restricted to local levels. Here, using geospatial analyses of past and current fire regimes, we estimate the extent and magnitude of fire regime change throughout the East. We focus on the vast oak-pine and tallgrass prairie-savanna formations in the eastern United States to illustrate and discuss the biotic and abiotic ramifications of fire regime change and, in the process, to document the near-universal "mesophication" of fire-dependent communities.

Estimating fire regime change

We evaluated the best available geospatial data layers covering the entire eastern United States to derive past and current fire regimes (figure 1). Fire regime groups were assigned to data layers according to Fire Regime Condition Class (FRCC) protocols (figure 1c; *http://frcc.gov*), based on known fire-vegetation relations, the autecology of principal plant species or functional groups, and expert opinion. All selected layers were uniformly converted to 1-kilometer pixels for this coarse-scale assessment.

Schmidt and colleagues' (2002) potential natural vegetation (PNV) groups and Frost's (1998) presettlement fire frequency regions were evaluated for portraying presettlement fire regimes. These two sets of geospatial data generated similar outputs of fire regime groups. Because the PNV-based output provided a slightly higher resolution and was supported by previously published documentation (Schmidt et al. 2002), it was ultimately selected to depict past fire regimes. Some of the best tangible data quantifying past fire regimes come from tree fire scars. Therefore, we used a fire-scar compilation, spanning the eastern United States (table 1; Guyette et al. 2006), to verify our map. Locational data obtained from Michael Stambaugh (Missouri Tree-Ring Laboratory, University of Missouri–Columbia, personal communication, 26 January 2007) were geospatially registered and merged with our past fire regime map for direct comparison. Twenty-seven sites were used in the comparative analysis after eliminating those (a) outside our study area (seven Ontario sites), (b) without pre-European fire data (six sites), and (c) misregistered or lacking locational data (two sites). All fire-scar sites were classified as belonging to fire regime group I, since they possessed trees that survived multiple (indicative of low- and mixed-severity burns) and frequent fires (< 35 years; see figure 1c classification). We found a high correspondence, as 74% of the sites were mapped correctly by our past fire regime map (20 sites), whereas the remaining 26% were misclassified as fire regime group II (1 site), III (5 sites), and IV (1 site).

Current fire regimes were based on a "hybrid" vegetation map that combined the classification strengths of two spatial data layers: Advanced Very High Resolution Radiometer (AVHRR) and the National Land Cover Dataset (NLCD). AVHRR data (with a superior number of forest types and cover classes) were used to classify forestlands, whereas NLCD data were applied to the remaining, primarily nonforested lands. Fire regime group assignments for the selected layers are listed in tables 1–3. We did not attempt to validate our current fire regime map using Guyette and colleagues' (2006) database, as most sites did not register any fire over the past 50 years or so, making it impossible to calculate a meaningful current fire-return interval (Michael Stambaugh, personal communication, 26 January 2007).

Based on FRCC classification axes (figure 1c), a fire regime gradient, from most to least frequent or severe, strikes diagonally from the lower right-hand to the upper left-hand corner. We selected color palettes to reflect this fire

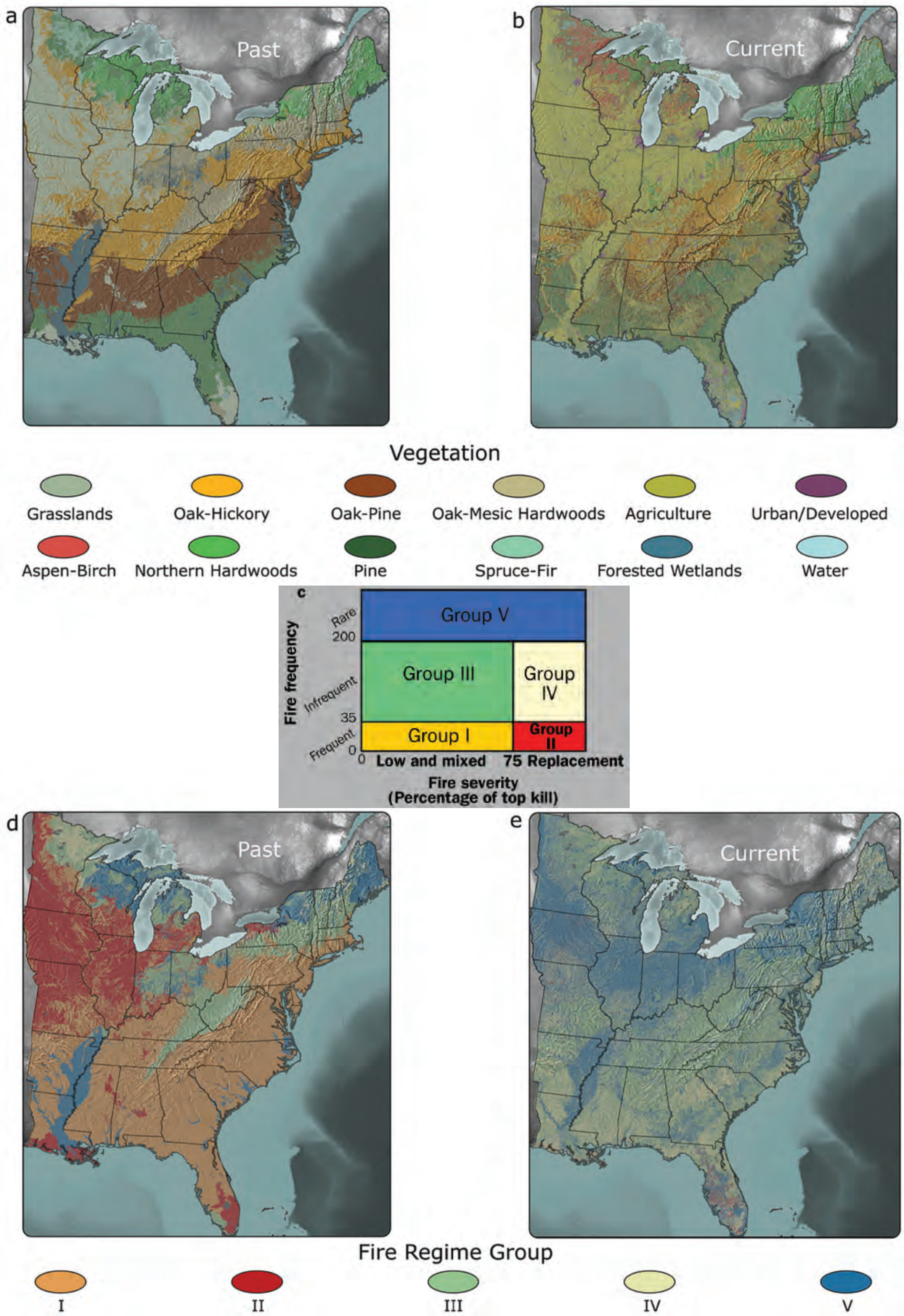

Figure 1. Composite chart of (a) past vegetation map, (b) current vegetation map, (c) fire regime group classification, (d) past fire regime map, and (e) current fire regime map. The past vegetation map (a) is based on potential natural vegetation (Schmidt et al. 2002). The current vegetation map (b) is based on the Advanced Very High Resolution Radiometer and the National Land Cover Dataset. Fire regime groups (c) are classified in two-dimensional space depicting fire severity and frequency and have been colored to reflect a fire gradient from extreme (red; group II) to rare (blue; group V). Past (d) and current (e) fire regime maps were derived by applying the classification (c) to the past and current vegetation maps (a and b, respectively).

Table 1. Potential natural vegetation codes, classes, and assigned fire regime groups.

Code	Class	Fire regime group
32	Plains grassland	II
33	Prairie	II
36	Wet grassland	II
38	Oak savanna (North Dakota)	I
39	Mosaic bluestem/oak-hickory	II
40	Cross timbers	I
41	Conifer bog (Minnesota)	IV
42	Great Lakes pine forest	III
43	Spruce-fir	IV
44	Maple-basswood	III
45	Oak-hickory	I
46	Elm-ash	V
47	Maple-beech-birch	V
48	Mixed mesophytic forest	III
49	Appalachian oak	I
50	Oak–northern hardwoods	III
51	Northern hardwoods	V
52	Northern hardwoods–fir	V
53	Northern hardwoods–spruce	V
54	Northeastern oak–pine	I
55	Oak-hickory-pine	I
56	Southern mixed forest	I
57	Loblolly–shortleaf pine	I
58	Blackbelt prairie	II
59	Oak-gum-cypress	III
60	Northern floodplain	III
61	Southern floodplain	V
62	Barren	II

Table 2. Advanced Very High Resolution Radiometer vegetation classes and assigned fire regime group, by tree cover class.

	Tree cover class (percentage)			
Vegetation class	0–9	10–24	25–59	60–100
White-red-jack pine	II	I	III	IV
Spruce-fir	II	I	III	IV
Longleaf–slash pine	II	I	III	IV
Loblolly-shortleaf pine	II	I	III	IV
Oak-pine	II	I	III	III
Oak-hickory	II	I	III	III
Oak-gum-cypress	II	I	III	III
Elm-ash-cottonwood	II	V	V	V
Maple-beech-birch	II	V	V	V
Aspen-birch	II	I	III	III
Ponderosa pine	II	I	III	IV
Lodgepole pine	II	I	IV	IV
Pinyon-juniper	II	I	IV	IV

Table 3. National Land Cover Dataset codes, classes, and assigned fire regime groups.

Code	Class	Fire regime group
21	Low-intensity residential	V
22	High-intensity residential	V
23	Commercial/industrial/transport	V
31	Bare rock/sand/clay	V
32	Quarries/strip mines/gravel pits	V
33	Transitional	V
41	Deciduous forest	V
42	Evergreen forest	IV
43	Mixed forest	III
51	Shrubland	I
61	Orchards/vineyards/other	V
71	Grasslands/herbaceous	II
81	Pasture/hay	IV
82	Row crops	V
83	Small grains	IV
84	Fallow	V
85	Urban/recreational grasses	IV
91	Woody wetlands	V
92	Emergent herbaceous wetlands	IV

regime gradient, from pyrogenic systems, with the most frequent and intense fires (fire regime group II, red), to "asbestos" systems that rarely burn (fire regime group V, blue). Note that the color spectrum (red hot to cool blue) deviates somewhat from fire regime group enumeration (fire regime groups I–V).

To calculate past-to-current fire regime change for geospatial display, we converted the numeration of fire regime groups to arabic numerals to capture the fire gradient from hottest (most frequent and severe) to coolest (less frequent and severe). Thus, the following values were applied: fire regime group I = 2, fire regime group II = 1, fire regime group III = 4, fire regime group IV = 3, and fire regime group V = 5. A fire regime change map was then generated on a pixel-by-pixel basis, using the following equation:

Fire regime change = past fire regime group – current fire regime group.

This formula projects fire regime change over nine ordinal classes, from –4 through 0 to +4. Positive values represent trends toward more fire than in the past, whereas negative values represent fire reductions. The more negative or positive the values are, the more substantial the trend.

The analysis indicates that there has been a general "cooling" of the eastern United States landscape (i.e., less fire) over time (figure 2). This trend is consistent with the historical record, which points toward wholesale fire reduction, both spatially and temporally, across the East (Pyne 1982, Wright and Bailey 1982, Abrams 1992, Anderson 1998, Frost 1998). The suppression of fire was due to a culmination of events, including the elimination of Native burning, the construction of road networks (serving as firebreaks and providing access for firefighting), the conversion of forest and prairie to croplands (resulting in fuel change and reduction), overgrazing, and aggressive 20th-century fire-suppression efforts.

The degree of change between past and current fire regimes varied geographically across the East (figure 2). The largest fire reductions (depicted in blue) were centered in the Midwest, where a topographically controlled mosaic of pyrogenic grasslands, savannas, and woodlands was replaced by an intensively managed agricultural landscape that seldom burns (Iverson and Risser 1987, Anderson 1998). Those areas not cultivated or pastured quickly succeeded to closed-canopy forests, often through the release of oak grubs (Gleason 1913, Loomis and McComb 1944). Fire suppression has continued for such a long time now that certain fire-sensitive tree species, such as red maple (Fei and Steiner 2007), have expanded their range into the Midwest and Central Plains. Land-use conversion and fire suppression have been so complete that midwestern tallgrass prairies and oak savannas are now some of the rarest ecosystems in the world. For instance, 11 to 13 million hectares (ha) of former oak savanna has now been reduced to 2607 ha—a mere 0.02% of its presettlement coverage (Nuzzo 1986). In Missouri, cultivation, overgrazing, and fire suppression have reduced native prairie land from 4.8 million ha to approximately 16,000 ha (Schroeder 1981).

Substantial reductions in fire (represented by shades of green) extended east and southward from the former Midwest grasslands, essentially enveloping the southern two-thirds of the eastern United States. Here too, the conversion of fire-dependent systems to an agriculture-dominated landscape is prominent. This conversion, coupled with compositional shifts of the remaining forestland to increasingly fire-sensitive species (e.g., from oaks to mixed mesophytic species in the central hardwoods; from pine to hardwoods in the South), indicates the reduction of broadscale fire. Fire reductions extended into the sub-boreal landscapes of northern Minnesota as well—a phenomenon well documented in the literature (Heinselman 1973, Clark 1990).

Landscapes with nonpyrogenic tendencies, in particular the Mississippi embayment and the northern hardwood region, displayed little change. In essence, landscapes that historically did not burn (because of prevailing moist to wet conditions) still do not burn. However, some exceptions exist within the northern hardwood region (upper Great Lakes states and New England). Most of these cases of increased fire are an artifact of higher present-day levels of aspen-birch, oak, and off-site pine (*Pinus*) plantations (fire-dependent forest types)—a legacy of past logging, subsequent fires, field abandonment, and Civilian Conservation Corps activities of the 19th and early 20th centuries (Palik and Pregitzer 1992, Cole et al. 1998, Schulte et al. 2007). Whether the signature of these pyrogenic forest types truly translates into more fire today is suspect, especially considering that these forest types are currently perpetuated by means other than fire (e.g., clear-cutting for aspen, artificial regeneration for pine). Consequently, this anomaly is probably more a reflection of these forests responding to a combination of disturbances than an indicator of actual elevated fire conditions. This illustrates the need for caution when interpreting fire regimes solely on the basis of vegetation characteristics.

Further shortcomings occur when using vegetation layers classified solely by overstory dominance. For instance, understory and shrub cover characteristics, which influence fire behavior and flammability, must be assumed on the basis of their ecological association with overstory components. In most instances, this does not necessarily pose a problem, as shrub cover has been substantially reduced because of livestock overgrazing, lack of rejuvenating fires (Anderson 1991), elevated deer density and browse pressure (Côté et al. 2004), and resource monopolization by youthful developing forests (stem exclusion stage; Oliver and Larson 1996), hence rendering them less susceptible to fire today (largely in concert with overstory-based fire regime change).

However, exceptions do occur. For instance, mountain laurel (*Kalmia latifolia* L.) and rhododendron (*Rhododendron maximum* L.)—two highly flammable, sclerophyllous evergreen shrubs—have become prominent along the Appalachian chain as a result of past canopy disturbance (logging and

Figure 2. Past-to-current fire regime change map based on spatial analysis of past and current fire regime maps. Negative values represent temporal shifts toward less fire, whereas positive values represent shifts toward more fire. The departure from zero relates to the extent of fire regime change.

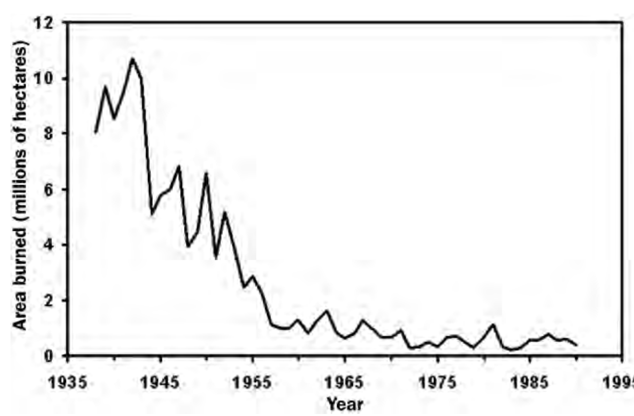

Figure 3. Area burned in the eastern United States (1938–1990) based on historic fire records held at the US Forest Service, Fire and Aviation Management, Washington Office, and compiled by Regina Winkler (R6 Information Technology Specialist). Area includes Minnesota, Iowa, Missouri, Arkansas, Lousiana, and all states eastward.

chestnut blight [*Cryphonectria parasitica*]), the cessation of fire and livestock grazing, and the shrubs' shade tolerance (Monk et al. 1985). Their presence could potentially result in more fire than is reflected in our maps (figures 1, 2; Moser et al. 1996; H. Grissino-Mayer, University of Tennessee––Knoxville, personal communication, 22 December 2006). Other forests along the northeastern coastal plain have experienced large increases in different native and invasive shrub species, particularly the flammable greenbriar (*Smilax*), following agricultural abandonment. While most oak and pine forests are currently less prone to severe fire as a result of fire suppression, certain forest understories are now more prone to severe fire because of dense shrub cover of unpalatable or invasive species.

Ecological ramifications of fire regime alteration

In the Americas, the antiquity of natural-origin fires (spanning millions of years), supplemented by human ignitions over thousands of years, has served as a strong evolutionary driver (Scott 2000, Bond et al. 2005). Where fire was common in a landscape, an abundant assortment of fire-tolerant species emerged over time. This explains the diverse array of fire-adapted species and plant communities existing in the eastern United States upon European contact (Wright and Bailey 1982, Abrams 1992, Whitney 1994, Wade et al. 2000, Lorimer 2001). Concurrently, presettlement burning maintained open, high-light environments, which favored sun-loving (heliophytic) plants (Cottam 1949, Anderson 1998).

In most locations, fire continued to be an important landscape disturbance during early European settlement, thus maintaining fire-adaptive communities. At times, fire-adapted species actually increased because of other disturbance factors acting as fire surrogates, such as increases in oak and aspen caused by the extensive cutting of northern hardwoods (Palik and Pregitzer 1992, Schulte et al. 2007) or the replacement of blight-killed American chestnut (*Castanea dentata* [Marsh.] Borkh) by oak (Abrams 1992). However, with time, fire suppression eventually prevailed (figure 3), with profound and unforeseen repercussions for fire-dependent environments (figure 4). Without the rejuvenating effects of recurrent fire, environmental conditions shifted incrementally to favor fire-sensitive, shade-tolerant competitors. Under this scenario, larger life forms (trees > shrubs > grasses or forbs) gain a distinct advantage by overtopping and shading their competitors. Over time, trees grew to form closed-canopy forests. Under reduced light conditions, fire-adapted species performed poorly in the understory and increasingly gave way to shade-tolerant species.

Thus began the cycle of "mesophication," a term coined here to describe the escalation of mesic microenvironmental conditions, accompanied by ever-diminishing prospects for fire and fire-dependent heliophytic species. By altering environmental conditions, shade-tolerant species deter fire through (a) dense shading that promotes moist, cool microclimates and (b) the production of fuels that are not conducive to burning (flaccid, moisture-holding leaf drop; moist, rapidly decaying woody debris). This phenomenon is reinforced and amplified by feedback loops, whereby conditions continually improve for shade-tolerant mesophytic species and further deteriorate for shade-intolerant, fire-adapted species. This phenomenon is not confined to this region but is happening worldwide as a result of fire exclusion (Bond et al. 2005).

Fire suppression and mesophication in oak-pine ecosystems

In presettlement times, recurrent surface burns maintained oak-pine ecosystems in a variety of open states, allowing high-light conditions to sustain an abundance of grasses, forbs, and shrubs (Abrams 1992, Whitney 1994, Anderson 1998, Lorimer 2001). Witness-tree studies bear this out, with open-canopy, low-density conditions prevailing (22 to 155 trees per ha; table 4). Presettlement tree density was largely a function of fire frequency and severity. The resulting variation was richly displayed on the presettlement landscape, wherein annually burned prairies were bounded by a continuum of savannas, open woodlands, and closed-canopy forests with increasing distance (Nuzzo 1986, Anderson 1998), although abrupt prairie-forest transitions did exist along natural firebreaks (e.g., rivers). Similar structural and compositional gradients, from fire-dependent oak savanna to fire-intolerant mesophytic forests, often ringed Native villages or travel corridors from which broadcast burning emanated (Dorney and Dorney 1989). Even though presettlement trees tended to be large on average (quadratic mean diameter of 30 to 42 centimeters [cm]), stand basal areas were low to moderate, as a result of tree sparseness (9 to 22 square meters [m^2] per ha; Fralish et al. 1991).

The cumulative effects of logging, grazing, and the eventual suppression of surface fires have radically changed oak-pine systems. Compared with their predecessors, modern communities are substantially denser (133 to 650 trees per ha), representing increases of up to tenfold (table 4). Much of this increase is in small size classes, as illustrated by structural shifts toward inverse J-shaped diameter distributions. Although average tree diameters are smaller (quadratic mean diameter of 17 to 35 cm), tree densities have compensated, permitting higher stand basal areas to prevail (15 to 30 m^2 per ha; Fralish et al. 1991). A compositional shift from fire-dependent xerophytic species (oak, pine, chestnut) to fire-sensitive mesophytic species (maple [*Acer*], cherry [*Prunus*], hemlock [*Tsuga*]) is readily apparent (table 5, figure 5a). Accordingly, stand-level tree richness has also increased (table 4) as a new suite of previously fire-restricted species has recruited into tree size classes. However, this is probably only a temporary phenomenon that will reverse itself in time, as oak, pine, and other fire-adaptive species give way to shade-tolerant species through gap-phase replacement. Where limited pools of replacement species exist (e.g., on highly fragmented landscapes or where past fire regimes greatly inhibited late-successional trees; Cottam 1949, Auclair and Cottam 1971), tree richness could fall well below historic levels.

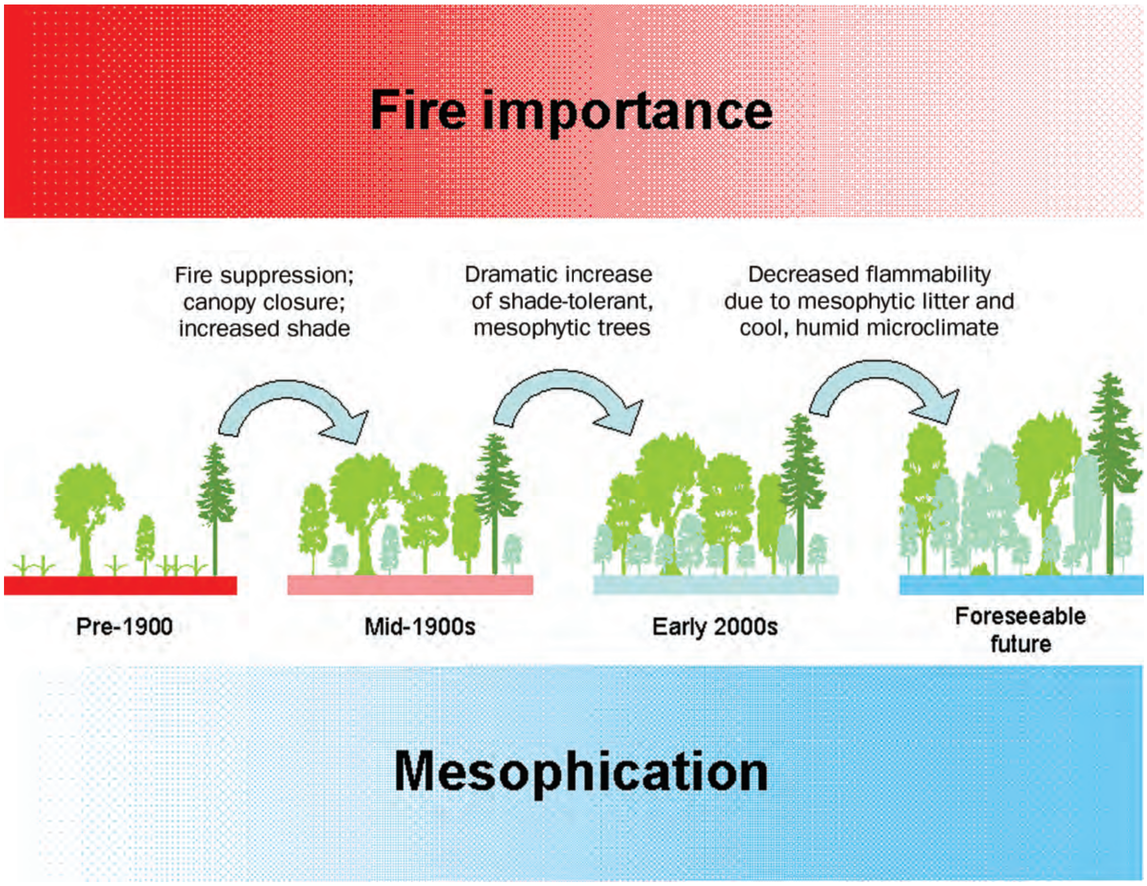

Figure 4. Temporal changes in fire importance (fire frequency and severity) and mesophication (development of cool, moist understory conditions) for oak-pine ecosystems in the eastern United States. Olive green trees represent oaks, dark green trees represent pines, and aquamarine trees represent mesophytic species (e.g., sugar maple).

The dramatic decline in oak and pine recruitment over the last 50-plus years on all but the most xeric and nutrient-poor sites dates directly to the 1940s and 1950s, when broadcast burning plummeted in the East (figure 3). In the absence of fire, a variety of highly competitive, later-successional, gap-opportunistic, mesophytic hardwoods now regenerate, including red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), beech (*Fagus grandifolia* Ehrh.), birch, cherry, tulip poplar (*Liriodendron tulipifera* L.), and blackgum (*Nyssa sylvatica* Marsh.) (table 5, figure 5a; Abrams 1992). The high leaf area of shade-tolerant species casts heavy shade and limits air movement, effectively altering understory microclimate. Increased relative humidity and decreased radiation and wind speeds result in a cooler and moister understory and forest floor (Nauertz et al. 2004). These microclimatic conditions decrease understory flammability both directly (through dampness) and indirectly (through moisture-accelerated decomposition and fuel load reduction), and produce a seedbed more conducive for mesophytic species, thus promoting the mesophication cycle. Documented current and projected future increases in atmospheric humidity might further augment the mesophication process (Willett et al. 2007).

Further “fireproofing” occurs as fuel-bed inputs (leaf litter, woody debris) shift from oak and pine to mesophytic trees (cf. figure 5b and 5c; Washburn and Arthur 2003). The change in the composition and quality of litter greatly alters decomposition rates and flammability. The heat content of litter is a function of many factors, including specific leaf mass, carbon content (e.g., cellulose and lignin), leaf chemistry (volatiles), and packing ratio (White 1987, Scarff and Westoby 2006). A lower packing ratio creates a more open, better-aerated litter layer, which increases flammability (Scarff and Westoby 2006). The lignin content of leaf litter affects its decomposition rate, with high lignin litter decomposing less rapidly (Cromack and Monk 1975). For example, in a study of five eastern US tree species, leaf lignin content decreased as follows: pine > oak > maple > tulip poplar > basswood (*Tilia americana* L.; White 1987). The percentage of lignin and the sclerophyll index were typically higher in chestnut oak (*Quercus prinus* L.), scarlet oak (*Quercus coccinea* Muenchh.), white oak (*Quercus alba* L.), hickory (*Carya*), American

Table 4. Structural changes from presettlement oak-pine to modern forest types, determined by comparing witness tree data with modern vegetation surveys.

Reference	State (site)	Data	Years of comparison	Presettlement structure	Modern structure	Change
Fralish et al. 1991	Illinois (high north slope)	GLO and modern field surveys	1806–1807 and 1970s	Richness = 10 Density = 144 trees per hectare (ha) BA = 14 m^2 per ha QMD = 36 cm CI = 564	Richness = 15, 15 Density = 425 trees per ha, 377 trees per ha BA = 20 m^2 per ha, 26 m^2 per ha QMD = 25 cm, 30 cm CI = 597, 737	▲ Tree richness, density, BA, and CI ▼ QMD
Fralish et al. 1991	Illinois (low north slope)	GLO and modern field surveys	1806–1807 and 1970s	Richness = 16 Density = 146 trees per ha BA = 15 m^2 per ha QMD = 36 cm CI = 656	Richness = 23, 18 Density = 438 trees per ha, 345 trees per ha BA = 24 m^2 per ha, 28 m^2 per ha QMD = 26 cm, 32 cm CI = 712, 911	▲ Tree richness, density, BA, and CI ▼ QMD
Fralish et al. 1991	Illinois (ridgetop)	GLO and modern field surveys	1806–1807 and 1970s	Richness = 9 Density = 127 trees per ha BA = 14 m^2 per ha QMD = 38 cm CI = 561	Richness = 9, 15 Density = 487 trees per ha, NG BA = 24 m^2 per ha, 20 m^2 per ha QMD = 25 cm, NG CI = 543, 528	▲ Tree richness, density, and BA ▼ QMD and CI
Fralish et al. 1991	Illinois (rocky south slope)	GLO and modern field surveys	1806–1807 and 1970s	Richness = 7 Density = 125 trees per ha BA = 9 m^2 per ha QMD = 30 cm CI = 365	Richness = 12, 12 Density = 650 trees per ha, 393 trees per ha BA = 15 m^2 per ha, 15 m^2 per ha QMD = 17 cm, 22 cm CI = 349, 377	▲ Tree richness, density, and BA ▼ QMD
Fralish et al. 1991	Illinois (south slope)	GLO and modern field surveys	1806–1807 and 1970s	Richness = 7 Density = 144 trees per ha BA = 16 m^2 per ha QMD = 36 cm CI = 543	Richness = 17, 15 Density = 506 trees per ha, 415 trees per ha BA = 16 m^2 per ha, 21 m^2 per ha QMD = 22 cm, 25 cm CI = 501, 508	▲ Tree richness, density, and BA ▼QMD and CI
Fralish et al. 1991	Illinois (terrace)	GLO and modern field surveys	1806–1807 and 1970s	Richness = 24 Density = 155 trees per ha BA = 22 m^2 per ha QMD = 42 cm CI = 813	Richness = 23, 19 Density = 457 trees per ha, 311 trees per ha BA = 20 m^2 per ha, 30 m^2 per ha QMD = 23 cm, 35 cm CI = 906, 956	▲ Tree density and CI ▼ Tree richness and QMD
Cole and Taylor 1995	Indiana	GLO and modern vegetation surveys	1834 and 1985	*Quercus velutina* = 31 trees per ha, *Pinus* = 31 trees per ha, *Quercus alba* = 3 trees per ha, *Populus tremuloides* = 3 trees per ha Stand density = 68 trees per ha	*Q. velutina* = 107 trees per ha, *Pinus* = 3 trees per ha, *Q. alba* = 15 trees per ha, *P. tremuloides* = 1 tree per ha, *Acer rubrum* = 3 trees per ha Stand density = 133 trees per ha	▲ *Q. velutina, Q. alba, A. rubrum,* and total stand density ▼ *Pinus* and *P. tremuloides* density
Dyer 2001	Ohio	Witness trees and FIA	1788–1802 and 1991	Shannon-Wiener diversity index = 2.19 A quasi-even distribution of size classes	Shannon-Wiener diversity index = 3.07 Inverse J-shaped distribution of size classes	Shift from quasi-even to inverse J-shaped diameter distribution ▲ Tree diversity primarily due to greater evenness ▼ Tree sizes
DeSelm 1994	Tennessee	Witness trees and USFS forest survey	1807 and 1989	A quasi-even distribution of diameter classes Median tree diameter = 30 cm	Inverse J-shaped distribution of diameter classes Median tree diameter = 20 cm	Shift from quasi-even to inverse J-shaped diameter distribution ▲ Tree density in the smallest diameter class ▼ Tree density in larger diameter classes; median tree diameter (by 10 cm)

Table 4. (continued)

Reference	State (site)	Data	Years of comparison	Presettlement structure	Modern structure	Change
Dorney and Dorney 1989	Wisconsin	GLO and remnant woodlot	1834 and 1981	Density = 22 trees per ha	Density = 190 trees per ha	▲ Tree density
Cottam 1949	Wisconsin	GLO and modern vegetation survey	1833–1834 and 1946	Density = 35 trees per ha BA = 2.9 m^2 per ha Average BA per tree = 0.085 m^2	Density = 353 trees per ha BA = 24.2 m^2 per ha Average BA per tree = 0.077 m^2	▲ Tree density (10x) and BA (8x) ▼ Tree size

▼ = decreased; ▲ = increased; BA = basal area, CI = composition index, FIA, Forest Inventory and Analysis; GLO, General Land Office; NG, not given; QMD, quadratic mean diameter; USFS, United States Forest Service.

Note: For the information from Fralish and colleagues (1991), the first and second sequential modern values represent second-growth and old-growth stands, respectively.

chestnut, and white pine (*Pinus strobus* L.) than in red maple, tulip poplar, and dogwood (*Cornus florida* L.; Cromack and Monk 1975). Red maple, in particular, has a very low lignin concentration (Washburn and Arthur 2003). Litter decomposition is also affected by levels of leaf nutrients and of secondary defensive compounds. For these reasons, the resistance to decay and the flammability of oak and pine litter are higher than that of the later-successional, mesophytic hardwoods.

The leaves of oak species typically have greater thickness, specific mass, nitrogen content, and levels of phenolics (a defensive compound) when compared with many other mesophytic tree species in the eastern United States (Abrams 1990, Carreiro et al. 2000). Their rigid and irregular structure (lower packing ratio) allows oak leaves to dry more effectively and remain dry over a longer time than other hardwoods, whose thinner leaves lie flat and adhere to the forest floor, thus trapping moisture, minimizing air pockets (creating a higher packing ratio), and enhancing decomposition (Lorimer 1985, Van Lear 2004). Oak leaves often maintain their characteristic "curl" even under the weight of winter snows, thus sustaining satisfactory fuel beds for spring burns (figure 5b). Thicker and denser oak leaves with high phenolic content should lower their decomposition rate as described above. Pines have high levels of volatile leaf chemicals, lignin, and leaf phenolics (White 1987). These factors also result in the low decomposition rate and high heat content of pine needles.

Downed woody debris (DWD) of various sizes and structures comprises an appreciable amount of the forest floor (Chojnacky et al. 2004). Thus, as with leaf litter, compositional changes that affect the quality and quantity of DWD are equally important. In theory, fire should be enhanced by species that stockpile fuels by producing dry, long-lasting DWD, and vice versa. Decay rates prove critical in this regard. Not surprisingly, DWD decomposition mirrors that of leaf litter, with oak and hickory having the lowest decay rates, followed by beech, then maple (MacMillan 1988). The greatest differences in cellulose decay rates were between maple (high) and oak (low), whereas the greatest differences in lignin decay were between beech (high) and oak (low). Beech logs, in particular, experienced very rapid fragmentation. A compilation of studies by Tyrrell and Crow (1994) showed that oak logs were most resistant to decay (half-life = 40 years) compared with pines (13 to 16 years) and mixed mesophytic species (maple and others; 6 to 15 years).

To summarize, the compositional shifts from oak and pine to mesophytic hardwoods as a result of 20-century fire suppression are causing forest floors to be less flammable throughout much of the East. This is in sharp contrast to the coniferous-dominated West, where fire suppression has led to increases in live and dead fuel, stand density, and changes in species composition, making forests more, rather than less, prone to fire (Parsons 1976, Brown et al. 2000). This explains, at least in part, why recent fire is so much more pronounced in the western United States than in the East (table 6).

Table 5. Compositional changes from presettlement oak-pine to modern forest types, determined by comparing witness tree data with modern vegetation surveys.

Citation	State (site)	Years of comparison	Presettlement dominants (percentage)	Modern dominants (percentage)	Taxa showing decreases	Taxa showing increases
Foster et al. 1998	Connecticut (central uplands)	1700–1800 and 1993–1996	*Pinus* (22), *Quercus* (21), *Tsuga* (14), *Acer* (10), *Fagus* (10)	*Acer* (24), *Quercus* (24), *Pinus* (16), *Betula* (13), *Tsuga* (12)	*Fagus, Pinus*	*Acer, Betula*
Foster et al. 1998	Connecticut (Connecticut Valley)	1700–1800 and 1993–1996	*Quercus* (45), *Pinus* (17), *Castanea* (8)	*Acer* (30), *Quercus* (22), *Tsuga* (15), *Pinus* (11), *Betula* (11)	*Quercus, Castanea, Pinus*	*Acer, Tsuga, Betula*
Foster et al. 1998	Connecticut (eastern lowlands)	1700–1800 and 1993–1996	*Quercus* (59), *Pinus* (17), *Castanea* (6)	*Quercus* (35), *Acer* (23), *Pinus* (21), *Betula* (8)	*Quercus, Castanea*	*Acer, Pinus, Betula*
Foster et al. 1998	Connecticut (Pelham Hills)	1700–1800 and 1993–1996	*Quercus* (38), *Pinus* (18), *Castanea* (14), *Fagus* (6)	*Acer* (27), *Quercus* (21), *Tsuga* (15), *Betula* (15), *Pinus* (11)	*Fagus, Quercus, Castanea, Pinus*	*Acer, Tsuga, Betula*
Foster et al. 1998	Connecticut (whole region)	1700–1800 and 1993–1996	*Quercus* (33), *Pinus* (20), *Tsuga* (10), *Castanea* (8), *Fagus* (7)	*Acer* (25), *Quercus* (24), *Pinus* (15), *Betula* (12), *Tsuga* (11)	*Fagus, Quercus, Castanea, Pinus*	*Acer, Tsuga, Betula*
Fralish et al. 1991[a]	Illinois (high north slope)	1806–1807 and 1970s	*Quercus alba* (IV = 65), *Quercus velutina* (19), *Carya ovata* (4)	*Q. alba* (48, 9), *Quercus rubra* (6, 31), *Carya glabra* (14, 17), *Q. velutina* (17, 6)	*Q. alba, Q. velutina*	*Q. rubra, Carya*
Fralish et al. 1991[a]	Illinois (low north slope)	1806–1807 and 1970s	*Q. alba* (IV = 39), *Q. velutina* (26), *Liriodendron tulipifera* (9)	*Acer saccharum* (14, 44), *Q. rubra* (22, 8), *Q. alba* (21, 1), *Q. velutina* (13, 1)	*Q. alba, Q. velutina, L. tulipifera*	*A. saccharum, Q. rubra*
Fralish et al. 1991[a]	Illinois (ridgetop)	1806–1807 and 1970s	*Q. alba* (IV = 45), *Q. velutina* (33), *C. glabra* (6)	*Q. alba* (53, 54), *Q. velutina* (17, 12), *C. glabra* (14, 8), *Quercus stellata* (7, 11)	*Q. velutina*	*Q. alba, C. glabra, Q. stellata*
Fralish et al. 1991[a]	Illinois (rocky south slope)	1806–1807 and 1970s	*Q. stellata* (IV = 76), *C. glabra* (9), *Quercus marilandica* (6)	*Q. stellata* (59, 40), *Q. marilandica* (13, 16), *Carya texana* (14, 12), *Q. alba* (6, 13)	*Q. stellata*	*Carya, Q. marilandica, Q. alba*
Fralish et al. 1991[a]	Illinois (south slope)	1806–1807 and 1970s	*Q. alba* (IV = 81), *Q. velutina* (5), *Q. stellata* (5), *C. glabra* (4)	*Q. alba* (30, 57), *Q. velutina* (22, 10), *Q. stellata* (18, 12), *C. glabra* (13, 9)	*Q. alba*	*Q. velutina, Q. stellata, Carya*
Fralish et al. 1991[a]	Illinois (terrace)	1806–1807 and 1970s	*Q. alba* (IV = 27), *Q. rubra* (12), *Liquidambar styraciflua* (11), *L. tulipifera* (11)	*A. saccharum* (32, 51), *L. tulipifera* (17, 6), *Fagus grandifolia* (5, 13), *Carya cordiformis* (2, 9)	*Q. alba, Q. rubra, Liq. styraciflua*	*A. saccharum, F. grandifolia, Carya*
Glitzenstein et al. 1990	New York	Before 1760 and 1984	*Q. alba* (47), *Q. velutina* (16), *Quercus* (unspecified) (16), *Carya* (12)	*Acer* (30), *Quercus prinus* (14), *Q. rubra* (10), *Pinus* (9), *Carya* (9), *Tsuga* (7)	*Q. alba, Q. velutina*	*Acer, Q. rubra, Q. prinus, Tsuga, Pinus*
Dyer 2001	Ohio	1788–1802 and 1991	*Q. alba* (40), *Carya* (14), *Q. velutina* (12), *Fagus* (8)	*Q. alba* (15), *Q. velutina* (14), *Liriodendron* (11), *Carya* (8), *A. saccharum* (8)	*Q. alba, Carya, Fagus*	*Acer, Liriodendron, Pinus, Populus, Prunus, Fraxinus*
Abrams and Ruffner 1995	Pennsylvania (Allegheny Front)	1765–1798 and 1988–1990	*Q. alba* (30), *Q. prinus* (14), *Pinus strobus* (11), *Pinus rigida* (10), *Carya* (8), *Q. velutina* (7), *Castanea dentata* (7)	*Q. alba* (18), *Pinus virginiana* (16), *Q. prinus* (13), *Q. rubra* (12), *A. rubrum* 12), *P. strobus* (9)	*Cas. dentata, Q. alba, Carya, P. strobus, P. rigida*	*Q. rubra, P. virginiana, A. rubrum*
Abrams and Ruffner 1995	Pennsylvania (Allegheny Mountains)	1765–1798 and 1988–1990	*Q. alba* (19), *Acer* (15), *C. dentata* (15), *P. strobus* (11), *P. rigida* (10)	*A. rubrum* (35), *Q. alba* (19), *Q. rubra* (11), *Q. prinus* (9), *Populus grandidentata* (5)	*Cas. dentata, Q. velutina, P. strobus, P. rigida*	*Q. prinus, Q. rubra, A. rubrum, Po. grandidentata*

Table 5. (continued)

Citation	State (site)	Years of comparison	Presettlement dominants (percentage)	Modern dominants (percentage)	Taxa showing decreases	Taxa showing increases
Abrams and Ruffner 1995	Pennsylvania (ridge and valley)	1765–1798 and 1988–1990	*Q. alba* (21), *Pinus* (19), *Carya* (11), *Q. velutina* (9), *Q. prinus* (8), *Cas. dentata* (7), *P. strobus* (7)	*Q. prinus* (28), *A. rubrum* (15), *Q. rubra* (14), *Q. alba* (13), *Q. velutina* (8)	*Cas. dentata, Q. alba, Carya, P. strobus*	*Q. prinus, Q. rubra, A. rubrum*
DeSelm 1994	Tennessee	1807 and 1960–1961	*Q. stellata* (11), *Quercus coccinea/Quercus shumardii* (10), *Q. alba* (10), *Carya* (8), *Fagus* (8),	*Carya* (23, 16), *Q. alba* (7, 20), *Q. velutina/rubra/falcata* (8, 11)	*Fagus*	*Carya*
Cottam 1949	Wisconsin	1833–1834 and 1946	*Quercus macrocarpa* (IV = 183), *Q. alba* (98), *Q. rubra/Q. velutina* (46)	*Q. alba* (207), *Q. rubra/Q. velutina* (116), *Prunus serotina* (20), *Q. macrocarpa* (13)	*Q. macrocarpa*	*Q. alba, Q. rubra/Q. velutina, Pr. serotina*

IV, importance value.

Note: For the information from Fralish and colleagues (1991), presettlement and modern dominants are reported in terms of importance value rather than percentage composition. The first and second sequential modern values represent second-growth and old-growth stands, respectively. Cottam (1949) also reports presettlement and modern dominants in terms of importance value.

Table 6. Total area burned (in hectares) in the western and eastern United States (2001–2006).

Year	West	East
2001	1,088,353	269,145
2002	1,772,458	250,224
2003	1,162,438	214,074
2004	359,292	228,327
2005	1,450,800	268,914
2006	2,762,011	1,126,082

Note: West includes data from the Northwest, northern California, southern California, northern Rockies, eastern Great Basin, western Great Basin, Southwest, and Rocky Mountains geographic areas (excludes Alaska). East includes data from the eastern and southern geographic areas.

Data converted from lightning and human-caused acres from the National Interagency Fire Center (16 January 2008; *www.nifc.gov/fire_info/lightning_human_fires.html*).

Alternative stable states

Mesophication meshes well with the theory of alternative stable states, according to which a community may exist in a number of different equilibrium points or states that are locally stable (Beisner et al. 2003). A community will stay in a certain state until a substantial shift in biotic (e.g., nonnative invasion) or abiotic factors (e.g., climate change) triggers a switch to a new stable state. Although perturbation is normally the force or thrust that causes state shifts in classical terms (Scheffer et al. 2001), the opposite is true for fire-adapted landscapes, wherein the lack of perturbation initiates this change. We apply this theory to help illustrate and explain fire and mesophication relations on two very different landscapes (mesic versus xeric; figure 6).

Fire-adapted species assemble and form various communities on mesic landscapes with a long history of recurrent fire (figure 6a). However, the resilience of these communities is tenuous because of their high dependence on fire (as illustrated by shallow, nonconfining basins on the upper plane; figure 6a). Without fire (figure 6b), fire-tolerant, shade-intolerant species are progressively replaced by fire-intolerant, shade-tolerant species, and mesophication ensues. Species shifts are most rapid on mesic landscapes that have favorable growing conditions (e.g., fertile, deep soils with high water capacity). Even a short period of fire suppression allows fire-adaptive communities to convert readily to mesophytic hardwoods (figure 6b). This state switch (represented by the folded slope and deep basin in figure 6b) is accompanied by hysteresis: the failure of an ecosystem that has been changed to return to its original state when the cause of the change is removed (Beisner et al. 2003). In other words, ecosystems can easily fall in, but prove difficult to be pulled out (i.e., restored). Even though communities experience a forward shift at the bifurcation point (F_1), much more energy (in this case, fire) is needed to reverse conditions far enough to reach the backward shift point (B_1), thus allowing a return to the upper plane (Scheffer et al. 2001). In essence, the horizontal distance between these two points represents the extra energy and resources needed (in terms reestablishing a burning regime in a system not prone to burn) to restore fire-based systems on the landscape after it becomes mesophytic.

On xeric landscapes, fire-based communities are more entrenched and resilient (note deeper basins on the upper plane in figure 6c). As a result, shifts toward mesophytic

*Figure 5. Photo collage of oak-dominated forests: (a) Large, veteran white oak trees with a dense understory of red maple at Savage Mountain, Maryland. (b) A northern pin oak (*Quercus ellipsoidalis *E. J. Hill) stand at Stevens Point, Wisconsin. The flammable characteristics of oak litter and woody debris encourage fire. (c) An oak stand with a dense understory of red maple. The maples' rapidly decomposing, moisture-retaining leaf drop greatly deters surface burns. (d) An untreated, overstocked oak stand with a low-light, leaf-dominated, species-poor understory adjacent to (e) a treated (thinned and burned five times over the past 15 years) oak stand with a high-light, mineral-based, species-robust understory at Western Star Flatwoods, Mark Twain National Forest, Missouri. Photographs: (a–c) Marc D. Abrams, (d and e) Paul W. Nelson.*

hardwoods are more gradual when fire is suppressed (note the higher berm before the forward-shift point). This is consistent with ecological theory, according to which oak and other fire-adapted, drought-tolerant species compete better against nutrient- and moisture-demanding, late-successional species on infertile, drought-prone landscapes (Abrams 1990). On the most environmentally severe sites (extremely sandy or shallow-to-bedrock soils), these communities may continue to exist even in the absence of fire (as represented by shaded balls on the upper plane; figure 6d). State changes on xeric landscapes are not as abrupt, and not necessarily as enduring, as those on mesic landscapes, as illustrated by the reduced bifurcation fold and basin depth of mesophytic hardwoods.

These illustrations of alternative stable states (figure 6) have practical implications for managing fire-adaptive landscapes, especially those with altered fire regimes. The rate at which fire-adaptive communities undergo mesophication and convert to mesophytic hardwoods is dictated by landscape conditions. Generally, the more mesic and fertile a system is, the more rapid and steadfast the conversion will be. However, overstory disturbance (cutting, windstorms) can accelerate this transition on any landscape where a mesophytic understory is present (Abrams and Nowacki 1992). Once communities turn mesophytic, the prospects of returning fire and fire-adapted communities to the landscape are limited because of mesophication barriers, the loss of fire-adapted species pools, the establishment of nonnative invasives, and prohibitive management costs associated with prescribed burning. Millions of hectares are in this situation (Abrams 2005). If land managers do not act soon, they will face increasingly expensive and difficult restoration efforts in the future. Furthermore, far more energy is required to restore burning regimes and fire-adapted species on mesic landscapes than on xeric landscapes. Because of this, prevention through prescribed burning is most urgently needed on mesic landscapes. However, once communities have converted to mesophytic hardwoods, efforts are probably best spent on retaining fire-adaptive communities on xeric systems.

The magnitude of change and the need for restoration

Although humans have a long history (about 12,000 years) on the North American continent, the magnitude of change wrought by European settlement has no parallel since the last glaciation (Whitney 1994, Cole et al. 1998). In New England, rates of landscape change have been far greater in the past 300 years than in the previous 1000 years as a result of forest cutting, agricultural conversion, urban development, altered fire regimes and herbivore populations, nonnative species introductions, and atmospheric pollution (Fuller et al. 1998). Concurrently, there has been a homogenization of regional vegetation and a dissociation of past vegetation-climate relations (also see Glitzenstein et al. 1990). There has been no return to presettlement conditions because of continuing low-level disturbance and perhaps insufficient recovery time. McIntosh (1972) drew the same conclusion from research in the Catskill Mountains, noting that nothing suggests that the presettlement dominance of beech or extensive hemlock forest will reemerge anytime soon, if ever.

In the upper Great Lakes states, changes during the last 150 years were found to be 2.4 times greater than the changes recorded over the preceding 1000 years (Cole et al. 1998). Here, forestland declined by 40%, and much of the remaining forest was converted to early successional forest types as a result of extensive logging. Pine forests, boreal forests and conifer swamps, and northern mesic forests all decreased (by 78%, 62%, and 61%, respectively), whereas aspen-birch forest increased (by 83%; Cole et al. 1998). Likewise, the presettlement pattern of hemlock forest may have been irretrievably lost because of logging and fire (White and Mladenoff 1994). Climate-driven changes during this period are probably inconsequential compared with the effects wrought by Europeans (Webb 1973). The severity of late 19th- and early 20th-century disturbance, coupled with present-day overbrowsing by white-tailed deer (*Odocoileus virginianus*), has greatly homogenized regional vegetation, in terms of the composition and structure of both overstory (Schulte et al. 2007) and understory strata (Rooney et al. 2004).

In the central hardwoods, pollen data indicate that rates of vegetation change over the last 150 years are at least an order of magnitude higher than during the previous 4000 years (Cole and Taylor 1995). This extreme shift in rate change is attributed to intensive logging and burning during the late 19th century, exotic species invasion, atmospheric nitrogen deposition (resulting in accelerated succession), and recent fire exclusion.

The demise of fire across the East documented here (figures 2, 3) is consistent with the dramatic and unprecedented rate shifts of vegetation change expressed above. Restoration opportunities are rapidly waning as (a) fire-adaptive floras are progressively lost to shading, competition, and preferential herbivory; (b) older seed-bearing individuals succumb to old age and existing seed banks lose viability over time; and (c) understory and forest floor conditions become increasingly mesophytic (Abrams 2005). In some cases, fire suppression has allowed for successional changes that have no ecological analogue or antecedent (Auclair and Cottam 1971). Unprecedented levels of deer herbivory further complicate things, directing succession toward less palatable species, including exotics (Côté et al. 2004, Rooney et al. 2004).

Fire suppression–induced shifts to closed-canopy forests are most serious on formerly open pyrogenic landscapes where fire-based evolutionary filters have constrained the distribution and availability of fire-sensitive, shade-tolerant species. Here, tree diversity, which is cresting because of the intermingling of fire-adaptive, shade-intolerant species with fire-sensitive, shade-tolerant species, might eventually sink to historic lows because of the scant number of shade-tolerant replacements coupled with ongoing deer herbivory (Côté et al. 2004). Indeed, diversity reductions and extirpations have already happened among ground flora associates in the

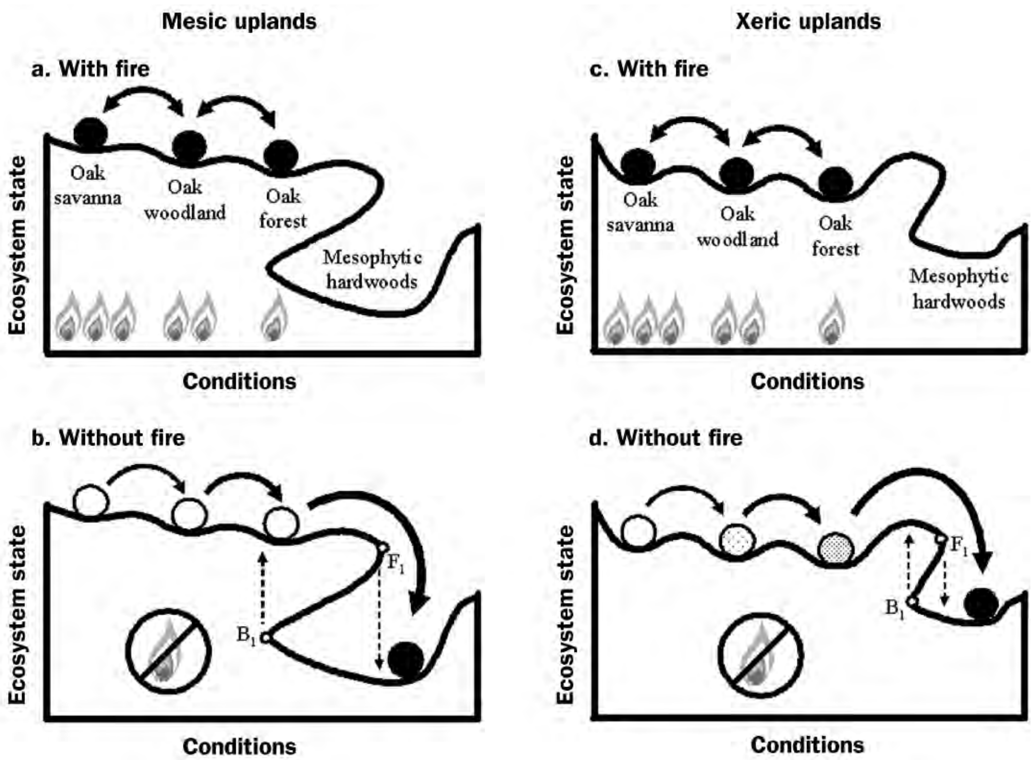

Figure 6. Ball-in-cup diagrams showing conceptual alternative stable states for two contrasting landscapes with abiotic factors held constant. Balls represent community states under the prevailing disturbance regime (with and without fire). Basins in the surface represent domains of attraction; their size and configuration (depth; surrounding slopes) govern the degree of attraction and thus of community stability. Forward (F_1) and backward (B_1) shifts occur at inflection points along the bifurcated fold; their horizontal distance corresponding to the degree of hysteresis (state entrenchment). (a) A number of fire-adaptive community states exist along a fire continuum on mesic uplands. Shallow basins permit communities to shift in accordance with fire frequency and severity. (b) Without fire, fire-adaptive communities progressively destabilize (hollow balls), eventually shifting wholesale to a mesophytic hardwood-dominated state. Hysteresis is invoked once in this state, making it difficult and costly for fire-adaptive communities to be restored. (c) On xeric uplands with fire, fire-adaptive communities are moderately resilient, represented by deeper basins along the upper plane. (d) Without fire, state shifts proceed slowly because of edaphic controls (infertility; drought) on the mesophication process, with some states partially maintained even in the absence of fire (shaded balls). Hysteresis is not as severe in the mesophytic state as on mesic landscapes.

absence of fire (figure 5d; Anderson and Schwegman 1991). This alarming harbinger of things to come can be avoided through the reintroduction of fire onto eastern landscapes (figure 5e). But time is running out, as systems may be approaching critical ecological thresholds and near-irreversible state shifts.

Setting restoration priorities using prescribed burning can be difficult, as all fire-based communities are important. Burning regimes should be established according to the relations between fire and vegetation, with prairies burned most frequently (annually or biennially) and with progressively longer fire return times for savannas, woodlands, and forests (Anderson 1991, 1998). Site conditions (mesic versus xeric) should be considered along this fire-community gradient (prairie to forest), as they dictate the rapidity of vegetation change without fire. Priority should be placed on prescribing fire on mesic sites, as once these sites undergo mesophication, it is difficult to reestablish burning regimes. From a landscape perspective, restoration opportunities are probably greatest on oak and pine woodlands and forests, since lands formerly harboring tallgrass prairie-savanna systems have been largely converted to agriculture, with little land-use change in sight (Iverson and Risser 1987). By focusing on large, contiguous ownerships, especially on federal and state lands where restoration is a priority, larger landscapes could be burned, thereby maximizing benefit-to-cost ratios (spreading relatively fixed costs over a larger area) and allowing variation in fire behavior to form a more "natural" mosaic of burn severities, vegetation patches, and niches for a greater array of species. Considering the scale of fire-suppression effects across the eastern United States, burning larger landscapes is the only feasible approach to make any real headway.

Conclusions

Before European settlement, vast areas of the eastern deciduous biome were dominated by fire-adapted ecosystems, most notably tallgrass prairies and oak-pine savannas, woodlands, and forests. Although surface burns were most prevalent, presettlement fire regimes varied according to climate, topography, and Native American populations (primary igniters), creating a mosaic of vegetation types within each of the major formations. European settlement dramatically altered eastern disturbance regimes through land clearing, extensive timber harvesting, severe fires, and the introduction of nonnative pathogens (e.g., chestnut blight) and invasive plants. In most cases, fire-dependent species maintained themselves during this period either directly through fire or indirectly through other surrogate disturbance agents (e.g., cutting).

Euro-American ties with the land began to change in the early 1900s as a result of technology (with increased farm productivity leading to field abandonment) and continued to change as a result of conservation measures (with fire suppression policies affecting succession and game laws leading to deer overabundance). This time, however, the changes in disturbance regimes worked against fire-adapted species. Without fire or fire surrogates, the competitive balance quickly shifted from heliophytic, fire-adapted species to shade-tolerant, fire-sensitive species. This change is apparent in oak-pine systems, wherein oak and pine recruitment has waned on all but the most xeric sites. Oak and pine are aggressively replaced by mesophytic and later-successional hardwood species, such as red maple, sugar maple, beech, blackgum, and black cherry (*Prunus serotina* Ehrh.). Forest microenvironments, in turn, become shadier, cooler, and moister. The leaf litter of these replacement species is less flammable and more rapidly mineralized than that of oaks and pines, reinforcing the lack of fire and the mesophication of eastern forests. Vegetation changes associated with fire suppression and mesophication are swifter and more enduring on mesic than on xeric sites. The trend toward mesophytic hardwoods will continue on landscapes where fire is actively suppressed, rendering them less combustible and creating further difficulties for land managers and conservationists who wish to restore past fires regimes and fire-based communities.

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