Conservation Biology

Comment

Clarifying the role of fire in the deciduous forests of eastern North America: reply to Matlack

Michael C. Stambaugh,* ¶ J. Morgan Varner,† Reed F. Noss,‡ Daniel C. Dey,§ Norman L. Christensen,** Robert F. Baldwin,†† Richard P. Guyette,* Brice B. Hanberry,* Craig A. Harper,‡‡ Sam G. Lindblom,§§ and Thomas A. Waldrop***

*Department of Forestry, University of Missouri, 203 ABNR Building, Columbia, MO 65211, U.S.A.
†Department of Forest Resources & Environmental Conservation, Virginia Polytechnic Institute and State University, 324 Cheatham Hall, Blacksburg, VA 24061, U.S.A.
‡Department of Biology, University of Central Florida, Orlando, FL 32816, U.S.A.
§U.S. Department of Agriculture Forest Service Northern Research Station, University of Missouri, 202 ABNR Building, Columbia, MO 65211, U.S.A.
**Nicholas School of the Environment, Duke University, Box 90329, Durham, NC 27708, U.S.A.
††Department of Forestry and Environmental Conservation, Clemson University, 221 Lehotsky Hall, Clemson, SC 29634, U.S.A.
‡‡Department of Forestry, Wildlife, and Fisheries, University of Tennessee, 280 Ellington Plant Sciences, Knoxville, TN 37996, U.S.A.
§§The Nature Conservancy, Virginia Chapter, 490 Westfield Road, Charlottesville, VA 22901, U.S.A.
***U.S. Department of Agriculture Forest Service Southern Research Station, Clemson University, 233 Lehotsky Hall, Clemson, SC 29634, U.S.A.

Introduction

Fire is an important disturbance in ecosystems across the eastern deciduous forests of North America (Brose et al. 2014). Matlack (2013) provided an interpretation of historical and contemporary fire in this region. Although we applaud Matlack for correcting simplistic assumptions that fire was ubiquitous and all plant communities need to burn regularly to maintain biodiversity, we believe his interpretation of the role of fire is erroneous on several counts. Most problematic is his statement " . . . it seems prudent to limit the use of prescribed burning east of the prairie-woodland transition zone." Adherence to this overgeneralized advice would inevitably result in losses of native diversity across the eastern deciduous forest.

Fire History Evidence

Much more is known about fire history in the "mesic deciduous forest (MDF)" than Matlack asserts. Charcoal studies provide ample fire evidence over several millennia (e.g., Delcourt & Delcourt 1997; Foster et al. 2002), and substantial compilations of regional fire scar history data exist (Guyette et al. 2006, 2002 [$n > 40$]; Hart & Buchanan 2012 [$n > 70$]) (Fig. 1). Instead of considering these, Matlack " . . . selected 14 studies unsystematically based on citation frequency . . . ," disregarding the clear biases of this approach. Paleoecological studies associate fire with human activities from the Late Woodland Period to European contact (Hart et al. 2008; Fesenmyer & Christensen 2010). Anthropological studies and historical accounts suggest anthropogenic fire was historically widespread in the MDF (Stewart 2002). Matlack (2013) speculated that high fire frequency was common only to barrens and that human ignitions were historically rare because of low population density and concentration in villages. Contrary evidence to both of these points exists. In southern Appalachian deciduous forests (40 km from known Native American village sites), frequent fires occurred across a gradient from cove to oak-chestnut to oak-pine forest (Fesenmyer & Christensen 2010). In contrast to the "village-centered fire scenario," hunting, gathering, trade, and conflict required long-distance movement, including ignitions distant from villages (King 2007). Historically, frequent burning (<5 years) required

¶email stambaughm@missouri.edu
Paper submitted July 24, 2014; revised manuscript accepted September 30, 2014.

DOI: 10.1111/cobi.12473

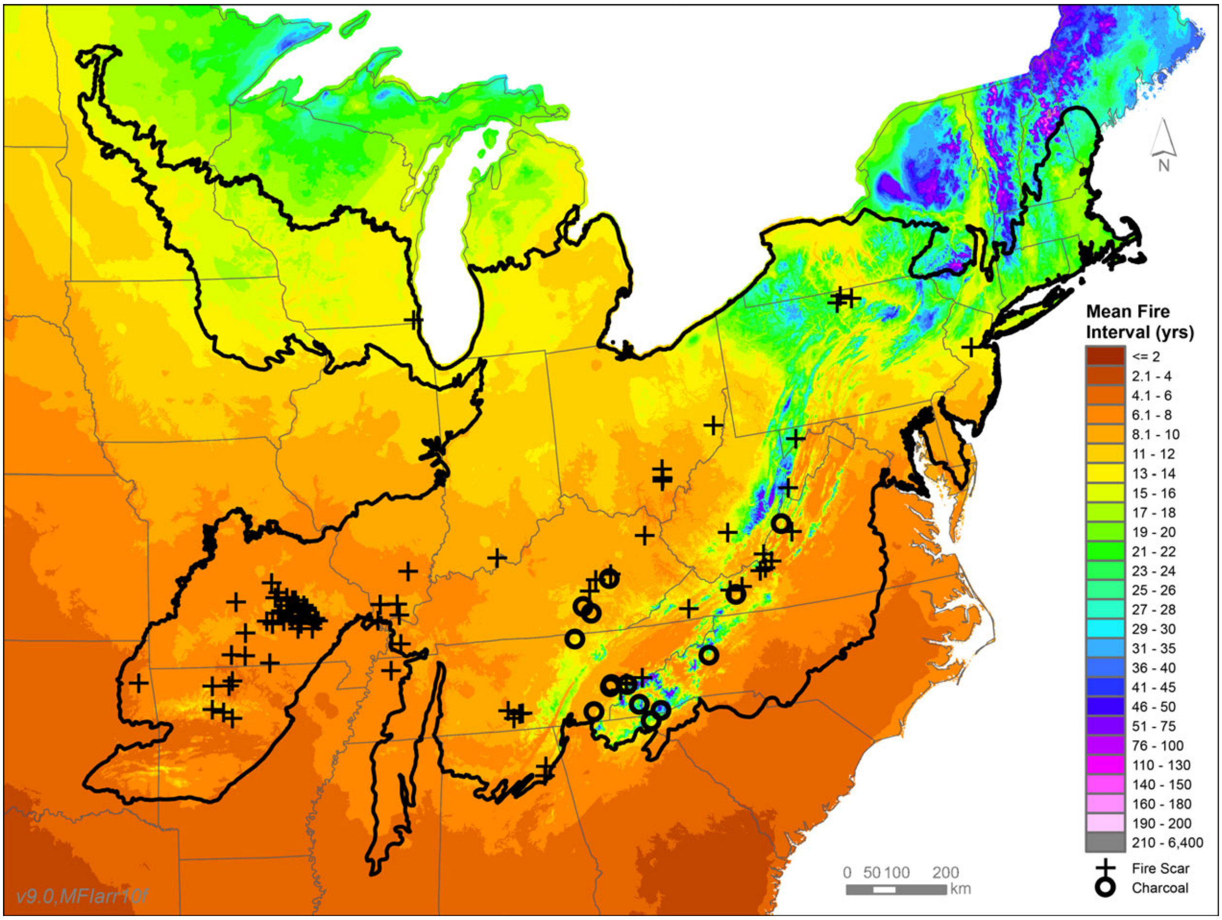

Figure 1. Area of mesic deciduous forest (MDF) (black line) as described by Matlack (2013), including locations of fire scar and charcoal fire history research sites within the region (adapted from Hart and Buchanan [2012]). Estimated mean fire intervals are from 1650 to 1850 CE based on the Physical Chemistry Fire Frequency Model (PC2FM) (Guyette et al. 2012). The PC2FM estimates are coarse-scale, based on a historic climate-fire frequency parameterization, and do not consider variability caused by humans, topography, vegetation, or other localized influences.

<1 human/km^2 in dissected landscapes and, in regions with little human occupation, can occur at least every 10 years (Guyette et al. 2002).

By igniting and managing fire, humans were a keystone species (Delcourt & Delcourt 2004) with profound effects on mesic environments. Although anthropogenic ignitions were likely more common than lightning ignitions in the MDF over the past 2 millennia, lightning ignitions contributed significantly to fire frequency. Matlack's MDF encompasses areas with coincident lightning and rain-free periods and climate-fire conditions capable of supporting frequent fire (Petersen & Drewa 2006; Cohen et al. 2007; Guyette et al. 2012) (Fig. 1).

Landscape Fire

Matlack suggested sites with frequent fire are not representative of the greater MDF, claiming fire histories from " . . . a small subset of possible landscape positions, including dry ridgetops, . . . barrens, steep slopes . . . " defy "generalization of frequent fire to all landscape positions." Fires did not occur across landscape positions equally (e.g., Batek et al. 1999), but the assertion that fire occurred only on isolated sites with "microclimatic and edaphic peculiarities" or that extensive fires did not occur historically (Cohen et al. 2007; McMurry et al. 2007) ignores that fire was a landscape phenomenon whether ignited by lightning or humans.

Distribution of Fire-Adapted Species

Matlack claims the majority of MDF flora do " . . . not display adaptations to fire . . . ," citing their lack of "insulating bark, serotinous cones, epicormic sprouting, resprouting from rhizome buds and root suckers, germination cued by combustion products, nonlinear seedling

Table 1. Forest regions that correspond to Matlack's (2013) mesic deciduous forest region.

Region	*States*	*Historical oak characteristics (reference)**
Oak-hickory	AR, IA, IL, IN MI, MN, MO, OK WS	75% oak (1)
Oak-chestnut	GA, MD, NC, PA, TN, SC, VA, PA, southern New England	Oak dominated (2, 3)
Maple-basswood	IA, MN, WS	>50% Oak (4)
Northeastern United States		
Beech-maple	IN, MI, NY, OH, PA, WS	Combination of mesic old-growth forests and open oak-dominated forests or woodlands; oaks may have comprised 30–55% of tree species composition (5, 6)
Mixed mesophytic	AL, GA, KY, MD, NC, OH, PA, SC, TN, VA, WV	
Western mesophytic	AL, IL, IN, KY, MS, OH, TN	

**Given to demonstrate the dominance of the generally more pyrophytic genus Quercus. Oaks occurred primarily in lower density woodlands and forests (Hanberry et al. 2014), and their widespread decline has been primarily attributed to altered fire regimes (Nowacki & Abrams 2008). References: 1, Hanberry et al. (2014); 2, Cogbill et al. (2002); 3, Thompson et al. (2013); 4, Hanberry et al. (2013); 5, Leitner & Jackson (1981); 6, Dyer (2001).*

growth, a germination requirement for brightly lit mineral soil, and basal sprouting." Plant fire-adaptive traits are diverse (Bond & van Wilgen 1996), and 2 dominant genera (Table 1), oaks (*Quercus*) and hickories (*Carya*), are overwhelmingly epicormic and basal sprouters (Burns & Honkala 1990). Many eastern oaks accrue thick and fire-protective bark (Jackson et al. 1999), compartmentalize fire injuries (Smith & Sutherland 1999), and have highly flammable litter (Kreye et al. 2013). Fire and acorn germination relationships are more complex than serotiny (a condition in at least 3 *Pinus* spp. embedded within or along the margins of the MDF), but fire's role in diminishing acorn predators and providing safe sites for germination and survival is well known (Dey 2002). In restored fire regimes, oak-sprout growth can equal or exceed competitors via increased carbon allocation to root development. Clearly there is more to learn about species traits and fire; to propose that MDF flora lack traits that enable persistence in fire-prone environments is inaccurate.

Plant and Animal Species of Concern

Without fire or other disturbances, canopy closure often diminishes understory plant species cover and richness (McCord et al. 2014). Frequently burned MDF environments support a diversity of native insects (Wood et al. 2011), birds (Reidy et al. 2014), and mammals (McShea et al. 2007). Biotic homogenization and loss of biodiversity associated with fire-dependent ecosystems is a worldwide problem (e.g., Bond et al. 2005).

Matlack stated, "[i]n removing aboveground stems fire is similar to herbivory" and provides an example of white-tailed deer (*Odocoileus virginianus*) shifting forest vegetation to grasses and ferns. Decreased plant and animal diversity following chronic overbrowsing by deer is well documented (e.g., Tilghman 1989; Webster et al. 2005), but effects of fire sharply contrast with conditions created by overbrowsing. Prescribed fire can create a more open structure through top killing of woody understory plants and midstory trees. Nevertheless, top-killed woody species may resprout, usually with an increase in herbaceous cover (McCord et al. 2014). Further, prescribed fire stimulates additional plant growth, enhancing habitat for many other species (Lashley et al. 2011; Barrioz et al. 2013).

Potential Effects of Burning

Results of research on MDF plant community response to fire differ because of differences in study sites (e.g., soils) and treatment conditions (e.g., fire frequency, intensity, seasonality). Matlack used this variability to argue against prescribed fire. Direct fire impacts on populations and movements of invertebrates, herpetofauna, birds, and mammals are temporary and subtle (McIver et al. 2013). Prescribed fires in long fire-excluded areas struggle to overcome residual effects and positive feedbacks on fuels and, with continued reintroduction of fire, the structure, composition, and ecological processes of communities will change, perhaps reversing the effects of 20th-century fire exclusion (Nowacki & Abrams 2008; Ryan et al. 2013).

Research and Management Needs

Studies of fire history, fire ecology, and fire treatment effects support fire's regional historic prevalence and provide critical information needed to understand the dynamic environment to which species adapted. We agree with Matlack's call for additional research, particularly to describe fine-scale fire and plant community gradients across landscapes. Fire history data may not be obtainable for all locations. Thus, research to develop proxies for historic fire regimes is needed (seed banks, plant-fire dependence, fire modeling) as is research on how prescribed fire influences species composition and ecosystem function, especially considering disassembly and reassembly of communities in response to fire exclusion and climate change. Fire is not a panacea for all MDF conservation issues, and its appropriate use should satisfy restoration and conservation objectives.

Sufficient knowledge of MDF ecology exists to develop reasonable management systems that include prescribed fire to achieve desired future conditions (e.g., Brose et al. 2014). Where we lack knowledge to restore fire-adapted communities, thoughtful ecosystem monitoring designs can support adaptive management. We view how the literature and management experience support the role of prescribed fire in eastern forests differently from Matlack. Diminishing fire use in the diverse deciduous forests of eastern North America would further imperil fire-dependent species and hamper maintenance of diversity.

Acknowledgments

We thank J. Hart for sharing coordinates of fire history research sites. Our work benefited from the comments of 3 anonymous reviewers.

Literature Cited

Barrioz SA, Keyser PD, Buckley DS, Buehler DA, Harper CA. 2013. Vegetation and avian response to oak savanna restoration in the Mid-South USA. American Midland Naturalist **169:**194–213.

Batek MJ, Rebertus AJ, Schroeder WA, Haithcoat TL, Compas E, Guyette RP. 1999. Reconstruction of early nineteenth century vegetation and fire regimes in the Missouri Ozarks. Journal of Biogeography **26:**397–412.

Bond WJ, van Wilgen BW. 1996. Fire and plants. Springer, Netherlands.

Bond WJ, Woodward FI, Midgley GF. 2005. The global distribution of ecosystems in a world without fire. New Phytologist **165:**525–538.

Brose PH, Dey DC, Waldrop TA. 2014. The fire-oak literature of eastern North America: synthesis and guidelines. General Technical Report NRS-135. US Forest Service, Northern Research Station, Newtown Square, Pennsylvania.

Burns RM, Honkala BH. 1990. Silvics of North America. Volume **2**. Hardwoods. USDA Forest Service, Agriculture Handbook 654, Washington, D.C.

Cogbill CV, Burk J, Motzkin G. 2002. The forests of presettlement New England, USA: spatial and compositional patterns based on town proprietor surveys. Journal of Biogeography **29:**1279–1304.

Cohen D, Dellinger B, Klein R, Buchanan B. 2007. Patterns in lightning-caused fires at Great Smoky Mountains National Park. Fire Ecology **3:**68–82.

Delcourt HR, Delcourt PA. 1997. Pre-Columbian Native American use of fire on southern Appalachian landscapes. Conservation Biology **11:**1010–1014.

Delcourt PA, Delcourt HR. 2004. Prehistoric Native Americans and ecological change, human ecosystems in eastern North America since the Pleistocene. Cambridge University Press, Cambridge.

Dey D. 2002. The ecological basis for oak silviculture in eastern North America. Pages 60–79 in Oak forest ecosystems. John Hopkins University Press, Baltimore, Maryland.

Dyer JM. 2001. Using witness trees to assess forest change in southeastern Ohio. Canadian Journal of Forest Research **31:**1708–1718.

Fesenmyer KA, Christensen NL. 2010. Reconstructing Holocene fire history in a southern Appalachian forest using soil charcoal. Ecology **31:**662–670.

Foster DR, Clayden S, Orwig DA, Hall B., Barry S. 2002. Oak, chestnut and fire: climatic and cultural controls of long-term forest dynamics in New England, USA. Journal of Biogeography **29:**1359–1379.

Guyette RP, Dey DC, Stambaugh MC, Muzika RM. 2006. Fire scars reveal variability and dynamics of eastern fire regimes. Pages 20–39 in MB Dickinson, editor. Fire in eastern oak forests: delivering science to land managers. General technical report NRS-P-1. US Forest Service, Northern Research Station, Newtown Square, Pennsylvania.

Guyette RP, Muzika RM, Dey DC. 2002. Dynamics of an anthropogenic fire regime. Ecosystems **5:**472–486.

Guyette RP, Stambaugh MC, Dey DC, Muzika RM. 2012. Predicting fire frequency with chemistry and climate. Ecosystems **15:**322–335.

Hanberry BB, Kabrick JM, He HS. 2014. Densification and state transition across the Missouri Ozarks Landscape. Ecosystems **17:**66–81.

Hanberry BB, Palik BJ, He HS. 2013. Winning and losing tree species of reassembly in Minnesota's mixed and broadleaf forests. PLOS One **8:**(e61709) DOI: 10.1371/journal.pone.0061709.

Hart JL, Buchanan ML. 2012. History of fire in Eastern Oak forests and implications for restoration. Pages 34–51 in DC Dey, MC Stambaugh, SL Clark, CJ Schweitzer, editors. Proceedings of the 4th Fire in eastern oak forests conference. General technical report NRS-P-102. USDA Forest Service, Northern Research Station, Newtown Square, Pennsylvania.

Hart JL, Horn SP, Grissino-Mayer HD. 2008. Fire history from soil charcoal in a mixed hardwood forest on the Cumberland Plateau, Tennessee, USA. Journal of the Torrey Botanical Society **135:**401–410.

King DH. 2007. The Memoirs of Lt. Henry Timberlake: the story of a soldier, adventurer, emissary to the Cherokees, 1756–1765. Museum of the Cherokee Indian, Cherokee, NC.

Kreye JK, Varner JM, Hiers JK, Mola J. 2013. Toward a mechanism for eastern North American forest mesophication: the role of litter drying. Ecological Applications **23:**1976–1986.

Jackson JF, Adams DC, Jackson UB. 1999. Allometry of constitutive defense: a model and a comparative test with tree bark and fire regime. The American Naturalist **153:**614–632.

Lashley MA, Harper CA, Bates GE, Keyser PD. 2011. Forage availability for white-tailed deer following silvicultural treatments. Journal of Wildlife Management **75:**1467–1476.

Leitner LA, Jackson MT. 1981. Presettlement forests of the unglaciated portion of southern Illinois. American Midland Naturalist **105:**290–304.

Matlack GR. 2013. Reassessment of the use of fire as a management tool in deciduous forests of eastern North America. Conservation Biology **27:**916–926.

McCord JM, Harper CA, Greenberg CH. 2014. Brood cover and food resources for wild turkeys following silvicultural treatments in mature upland hardwoods. Wildlife Society Bulletin **38:**265–272.

McIver JD, et al. 2013. Ecological effects of alternative fuel-reduction treatments: highlights of the National Fire and Fire Surrogates Study (FFS). International Journal of Wildland Fire **22:**63–82.

McMurry ER, Stambaugh MC, Guyette RP, Dey DC. 2007. Fire scars reveal source of New England's 1780 Dark Day. International Journal of Wildland Fire **16:**266–270.

McShea WJ, Healy WM, Devers P, Fearer T, Koch FH, Stauffer D, Waldon J. 2007. Forestry matters: decline of oaks will impact wildlife in hardwood forests. Journal of Wildlife Management **71:**1717–1728.

Nowacki GJ, Abrams MD. 2008. The demise of fire and "mesophication" of forests in the eastern United States. BioScience **58:**123–138.

Petersen SM, Drewa PB. 2006. Did lightning-initiated growing season fires characterize oak-dominated ecosystems of southern Ohio? Journal of the Torrey Botanical Society **133:**217–224.

Reidy JL, Thompson FR, Kendrick SW. 2014. Breeding bird response to habitat and landscape factors across a gradient of savanna, woodland, and forest in the Missouri Ozarks. Forest Ecology and Management **313:**34–46.

Ryan KC, Knapp EE, Varner JM. 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. Frontiers in Ecology & the Environment **11:**e15-e24.

Smith KT, Sutherland EK. 1999. Fire-scar formation and compartmentalization in oak. Canadian Journal of Forest Research **29:**166–171.

Stewart OC. 2002. Forgotten fires: Native Americans and the transient wilderness. University of Oklahoma Press, Norman.

Thompson JR, Carpenter DN, Cogbill CV, Foster DR. 2013. Four centuries of change in northeastern United States forests. PLOS ONE **8:**(e72540) DOI: 10.1371/journal.pone.0072540.

Tilghman NG. 1989. Impacts of white-tailed deer on forests regeneration in northwestern Pennsylvania. Journal of Wildlife Management **53:**524–532.

Webster CR, Jenkins MA, Rock JH. 2005. Long-term response of spring flora to chronic herbivory and deer exclusion in Great Smoky Mountains National Park, USA. Biological Conservation **125:**297–307.

Wood EM, Pidgeon AM, Gratton C, Wilder TT. 2011. Effects of oak barrens habitat management for Karner blue butterfly (*Lycaeides samuelis*) on the avian community. Biological Conservation **144:**3117–3126.