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silviculture

Missouri Ozark Forest Ecosystem Project: A Long-Term, Landscape-Scale, Collaborative Forest Management Research Project

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The Missouri Ozark Forest Ecosystem Project (MOFEP) is a long-term, landscape-scale study that exemplifies a model of forest research emphasizing interagency and multidiscipline collaboration. Established in 1989 in the Ozark Highlands of southeastern Missouri, MOFEP uses a randomized complete block design to test the effects of three forest management systems (even-aged management, uneven-aged management, and no-harvest management) on response variables across a range of disciplines. Within this overarching experimental design, other studies have been nested to address specific research questions across spatial and temporal scales. This project is driven by management needs and is designed to evaluate the effects of forest management systems practiced by a state agency, the Missouri Department of Conservation (MDC), on an operational scale. Treatments are applied with entries at 15-year intervals over the course of the project's planned 100-year rotation length. To date, MOFEP has produced over 65 publications in peer-reviewed journals from scientists at federal, state, academic, and nonprofit organizations. This project is unique in that it is supported and maintained by a state agency, with keys to success including long-term commitment of resources and personnel, communication of results to scientific and management communities, and collaboration among and within those communities.

Keywords: even-aged management, MOFEP, silviculture, uneven-aged management

The Missouri Ozark Forest Ecosystem Project (MOFEP) is a long-term, landscape-scale study that was designed to determine the effects of alternative forest management systems on a variety of ecosystem responses. Originally conceived to guide land managers concerned with the effects of timber harvest on bird populations on state lands in Missouri, MOFEP developed into a framework that supports scientific research across ecological disciplines. The dynamic character of forest ecosystems is fundamental; they are constantly changing in response to external forces and internal processes that include succession, cycling of resources, and disturbance (Connell and Sousa 1983, Attiwill and Adams 1993, Attiwill 1994). The complexity of ecosystems has led to an organizational structure for ecosystem research that is commonly demarcated by taxonomic discipline (O'neil et al. 1986, Christensen et al. 1996). This research model is well-suited for designing detailed investigations of specific questions but is often challenged to adequately study ecological processes that occur over long time scales or across spatial scales or disciplines (Franklin et al. 1990, Magnuson 1990).

The traditional model for field research in ecological sciences generally operates over short time frames and within relatively limited locations (Callahan 1984, Tilman 1989). The reasons for this structure are varied but are in many cases intuitive: Logistically, experimental studies are more feasible if conducted over limited spatial and temporal scales; there is uncertainty in the availability of long-term research funding; the common academic model is that of relatively short-term graduate student projects with an expectation of immediate deliverables; and challenges often exist in coordinating collaboration among researchers across locations or disciplines. Increased understanding of the complexity of forest ecosystems has resulted in recognition of the importance of conducting research across spatial scales, time scales, and ecological disciplines (Til-

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man 1989, Magnuson 1990, Christensen et al. 1996). Fields such as landscape ecology and metapopulation biology demonstrate that some ecological processes (e.g., landscape connectivity or source-sink dynamics) operate at broad spatial scales but may be undetectable at local scales (Franklin 1993, Hanski 1998). Long-term studies that provide information to understand the often nonlinear trajectories of ecosystem processes over time have become more common in recent decades. For example, the Long Term Ecological Research (LTER) program was established in 1980 and now includes 26 research sites that are located across several biomes (Callahan 1984, Franklin et al. 1990, Hobbie et al. 2003). These studies and others demonstrate the importance of biotic interactions across taxonomic groups in shaping ecosystem function (e.g., Jones et al. 1998).

MOFEP is unique not only in its temporal and spatial scope but also in that it was initiated and is maintained as an independent project by a state agency. In contrast to many other research projects of this scale, MOFEP originated from the need for science-based answers to management questions and has largely remained a management-driven project. Since its establishment, other experiments, such as the Hardwood Ecosystem Experiment in Indiana (Swihart et al. 2013), have been modeled after MOFEP to determine ecological responses to forest management in other regions. The primary objective of this paper is to describe MOFEP as a model for multidisciplinary, collaborative research in forest science that provides the framework for evaluating response variables across ecological scales. Specifically, we will describe the history and technical aspects of MOFEP, review the literature of studies published in peer-reviewed scientific journals that have thus far resulted from this project, and discuss challenges and lessons learned throughout the duration of the project to date.

History and Context of MOFEP

MOFEP is located in the Ozarks Highlands of southeastern Missouri, a predominately forested area at the western edge of the Central Hardwood Region. To fully understand the structure and composition of contemporary forests of MOFEP, one must consider the long history of human and natural disturbances that have impacted southeastern Missouri. Early explorers of the region noted the widespread occurrence of fire set by Native Americans and its influence on presettlement conditions (Guldin 2008). Frequent surface fires were a major force in the development of extensive shortleaf pine (*Pinus echinata* Mill.) and mixed shortleaf pine-hardwood forests and woodlands in the Missouri Ozarks prior to European settlement (Guyette et al. 2007, Stambaugh et al. 2007). The first wave of commercial logging in the Ozarks focused on harvesting the vast resource of virgin pine, with no consideration for forest regeneration. Exploitative harvesting of shortleaf pine started around 1880 in the Ozarks and drove Missouri's forest industry until the early 1900s. Many of the harvested pine sites regenerated to hardwood stands dominated by oaks (*Quercus* spp.) or oak-pine mixtures with a relatively minor pine component.

Today, the southeastern Missouri Ozarks, including MOFEP sites, are largely dominated by mature, second-growth, oak-dominated forests that commonly include black oak (*Quercus velutina* Lam.), scarlet oak (*Quercus coccinea* Muenchh.), white oak (*Quercus alba* L.), and post oak (*Quercus stellata* Wangehn.). Although commercially important to the forest products industry of the Ozarks, black and scarlet oaks are vulnerable to oak decline, a widespread disease complex that is particularly acute for these shorter-lived species (Shifley et al. 2006, Kabrick et al. 2008a, Voelker et al. 2008). Extensive oak mortality has been observed by forest managers of the Missouri Department of Conservation (MDC) over the past few decades. However, common even-aged regeneration methods of the late 20th century, such as clearcutting, were limited in their use due to public perception and uncertainties over the effects of increased fragmentation on bird populations (Richard Blatz, Missouri Department of Conservation, pers. comm., Mar. 20, 2014). Uneven-aged treatments offered an alternative for managing large areas of oak decline while reducing visual impacts and habitat fragmentation; however, it was not clear how these alternative forest management practices would subsequently affect Missouri forests (Clawson et al. 1997).

In response to concerns over the uncertainties of forest management on bird communities, scientists from MDC and University of Missouri-Columbia proposed a project in 1989 to evaluate the effects of forest management on migratory songbirds that nest and breed in the Missouri Ozarks (Brookshire et al. 1997). During an initial review of this project, it was realized that uncertainties existed regarding more than just migratory songbird responses to forest management, which led to expansion of the original project to include other ecological responses. Consequently, the objectives of this effort were broadened to evaluate forest management impacts on multiple ecosystem attributes. Out of this collaboration, MOFEP was born as an MDC-supported research project that has since fostered collaborations among federal, state, academic, and private organizations. The role of MDC in maintaining a project of this scale is unique among state agencies but is critical to the success of MOFEP. Annual expenditures have varied depending on the project phase and sampling needs, with nearly $1,000,000/year spent in the years of project establishment and pretreatment measurements, $750,000/year in subse-

Management and Policy Implications

Forest managers and ecosystem scientists require information that is representative of relevant ecological scales to understand the effects of forest management on ecosystem responses. There is accumulating evidence that many important ecological processes operate across large spatial extents and over long time frames. Consequently, short-term or isolated studies may be unable to detect patterns or responses that are critical to the outcomes of forest management practices. To understand the effects of contemporary management practices on an operational scale, the Missouri Department of Conservation (MDC) established the Missouri Ozark Forest Ecosystem Project (MOFEP) in 1989 on close to 10,000 acres in southeastern Missouri. This overarching project has encompassed numerous, specific studies, the results of which have been incorporated directly back into state land management practice and policy. Through commitment of MDC to support this project for its 100-year duration, MOFEP provides the opportunity for extensive research across disciplines and over spatial and temporal scales that are rare in forest science. Moreover, the collaboration among agencies and between the scientific and management communities bridges basic and applied science to provide meaningful information to forest managers.

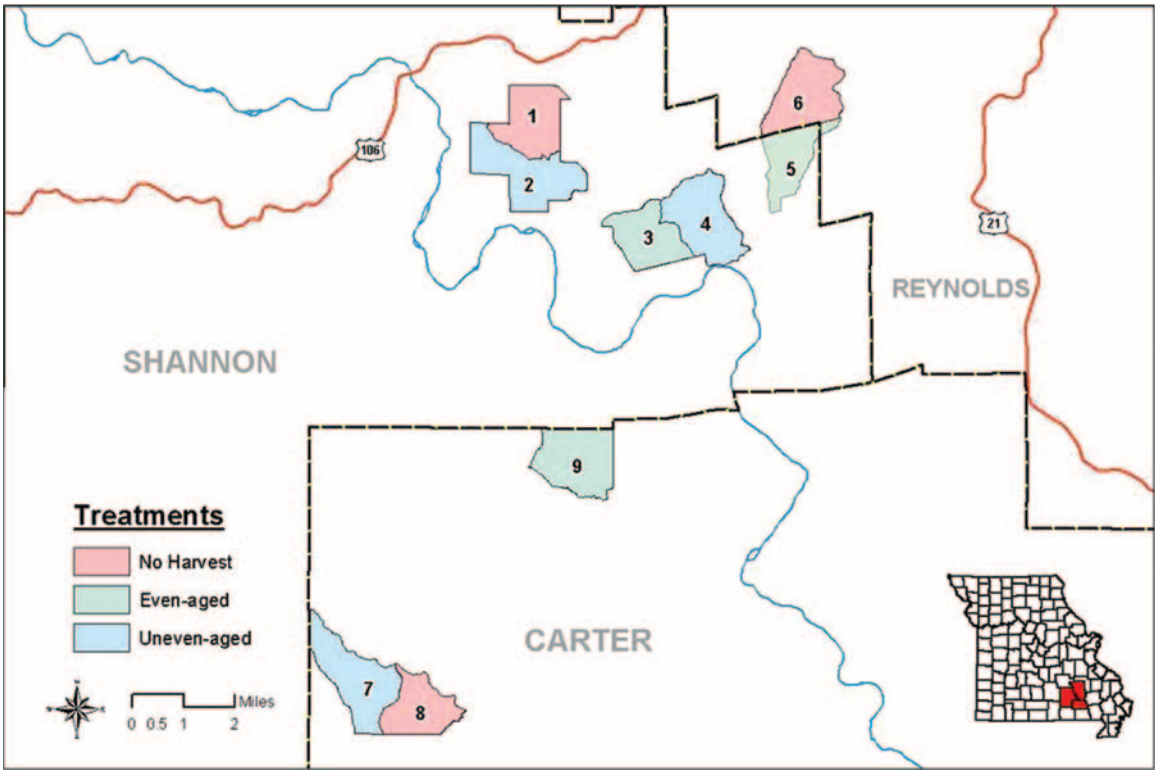

Figure 1. Map of study sites and management treatments of the Missouri Ozark Forest Ecosystem Project in southeastern Missouri, USA.

quent years of intensive sampling, and $150,000/year in "down" years between intensive measurement periods. In part, this effort is supported by the allocation of 0.125% of state sales tax to MDC, which provides an important source of funding for this work and other conservation work in the state.

Technical Aspects of MOFEP

The MOFEP experiment is laid out in a randomized complete block design. Treatments are three forest management systems applied at the scale of the compartment, a multistand management unit of MDC, and include even-aged management (EAM), uneven-aged management (UAM), and no-harvest management (NHM). Each treatment is replicated three times as part of three complete blocks. Treatments are applied to nine management compartments (herein referred to as *sites*) on public lands managed by MDC in Carter, Reynolds, and Shannon Counties of Missouri. As management compartments, MOFEP sites are multistand management units ranging in size from 770 to 1,240 acres each; collectively, the nine MOFEP sites cover roughly 9,400 acres (Figure 1).

MOFEP treatments are representative of the primary forest management systems used by MDC for managing state lands (Table 1). Under the EAM system, sites are managed on a 100-year rotation by treating individual stands with even-aged silvicultural methods for tending and regeneration, modified from Roach and Gingrich (1968). The primary EAM regeneration method used on MOFEP sites has been clearcutting with reserves (residual basal area < 10 ft^2/ac), which is applied to roughly 10–15% of the site area in each entry. During each entry, intermediate thinning treatments have been applied as needed according to MDC stand inventories, with the method of thinning applied dependent on stand-specific considerations. Under the UAM system, the primary regeneration method used has been single-tree selection, with or without group openings. The 1996 entry was primarily based on the guidelines of Law and Lorimer (1989), but the 2011 entry did not include regulated group openings. Roughly 10% of the area for both EAM and UAM sites have been reserved as old-growth or designated as extended rotation areas. Harvest entries in both systems occur on a 15-year cycle; to date, there have been two harvest entries at MOFEP sites, occurring in 1996 and 2011. The areas treated during each entry are summarized in Table 2, and several publications are available with more detailed information on the technical aspects of MOFEP (Brookshire and Shifley 1997, Shifley and Brookshire 2000, Shifley and Kabrick 2002).

Research at MOFEP may be supported through external funding or through MDC resources, which are prioritized to areas of high informational value for MDC. The MOFEP experiment has five ongoing, core research areas that are considered fundamental to the project: woody vegetation, ground flora, neotropical songbirds, herpetofauna, and small mammals. These core projects receive the highest priority for continued funding from MDC, and their data collection is conducted by MDC personnel to ensure continuity and consistency. Other projects are supported through external funding or competitive funding awarded by MDC to researchers from MDC or collaborators from other institutions. As a result, there has been a wide variety of concurrent research projects conducted across MOFEP during its duration to date (Figure 2). Finally, the large data sets generated from MOFEP provide opportunities for integrating previously collected data into new research directions or supplemental projects. Thus, MOFEP provides the framework for

Table 1. Summary of the silvicultural methods used in the application of forest management treatments at MOFEP.

Forest management system	Silvicultural method	Description	Notes
Even-aged management (EAM)	Clearcut with reserves	A regeneration or harvest practice that removes essentially all trees in the stand, with the exception of reserve trees left for other purposes	The basal area of reserve trees in MOFEP did not exceed 10 ft^2/acre and reserve trees were commonly shortleaf pines. Reserve trees were left for aesthetics, wildlife habitat, and as a potential seed source for shortleaf pine natural regeneration
	Shelterwood	A regeneration or harvest practice that removes most trees, leaving those needed to produce sufficient shade to produce a new age class in a moderated microenvironment	Shelterwood methods were not used in 1996 and were only used for Site 9 in 2011, demonstrating the adaptability of MOFEP to contemporary MDC management practice
	Intermediate thinning	Thinning treatment designed to enhance the growth, quality, vigor, and composition of the stand after regeneration and prior to harvest	Specific thinning methods were determined by stand inventories, in accordance with standard MDC practice. As an example, crown thinning may have been applied to remove low-vigor red oaks expressing decline, whereas thinning from below may also have been used to remove suppressed trees
Uneven-aged management (UAM)	Single-tree selection	Individual trees of all size classes are removed more or less uniformly throughout the stand, to promote growth of remaining trees and to provide space for regeneration	A basal area-maximum diameter-q (BDq) method was used to guide single-tree selection application but was modified according to stand inventory data to maintain desirable species composition following harvest
	Group selection	Trees are removed and new age classes are established in small groups	Three group sizes were used in MOFEP: (1) on south-facing slopes, group openings were ~1x tree height (70 ft diameter); (2) on ridges, group openings were ~1.5x tree height (105 ft diameter); (3) on north-facing slopes, group openings were ~2x tree height (140 ft)

Descriptions follow those of Helms (1998), and "Notes" refer to considerations specific to MOFEP.

Table 2. Area treated and method of treatment by site, management system, and year in MOFEP.

	Total		Clearcut with reserves				Shelterwood				Intermediate thinning				Uneven-aged[a]			
			1996		2011		1996		2011		1996		2011		1996		2011	
	Site	Acres	Acres	(%)	Acres	(%)	Acres	(%)	Acres	(%)	Acres	(%)	Acres	(%)	Acres	(%)	Acres	(%)
EAM	3	889	93	(10)	132	(15)	0	(0)	0	(0)	211	(24)	21	(2)	-	-	-	-
	5	772	114	(15)	89	(12)	0	(0)	0	(0)	142	(18)	176	(22)	-	-	-	-
	9	1,141	113	(10)	144	(13)	0	(0)	123	(11)	58	(5)	263	(23)	-	-	-	-
	TOTAL	*2,802*	*320*	*(11)*	*361*	*(13)*	*0*	*(0)*	*123*	*(4)*	*411*	*(15)*	*460*	*(16)*	-	-	-	-
UAM	2	1,271	-	-	-	-	-	-	-	-	-	-	-	-	876	(69)	575	(45)
	4	1,183	-	-	-	-	-	-	-	-	-	-	-	-	735	(62)	166	(14)
	7	1,240	-	-	-	-	-	-	-	-	-	-	-	-	513	(41)	724	(58)
	TOTAL	*3,694*	-	-	-	-	-	-	-	-	-	-	-	-	*2,124*	*(57)*	*1,465*	*(40)*

[a] Uneven-aged management was applied as single-tree selection interspersed with group selection in 1996, but only single-tree selection was applied in 2011.

No-harvest management, used in Site 1 (960 acres), Site 6 (1,086 acres), and Site 8 (839 acres), is not included.

research to be conducted across spatial and temporal scales and the necessary support for numerous studies nested within its overarching design. These studies have generated information on the responses of individuals, populations, or communities at local (e.g., stand-level responses to specific silvicultural practices) and landscape (e.g., responses to forest management systems) scales, as well as information on ecological processes occurring independently of the MOFEP treatments.

Summary of MOFEP Findings

In the nearly 25 years since its inception, data from MOFEP have contributed to over 65 peer-reviewed journal publications and hundreds of conference proceedings, reports, and technical papers. Several proceedings publications are available to summarize the establishment and initial findings of the project (Brookshire and Shifley 1997, Shifley and Brookshire 2000, Shifley and Kabrick 2002). This body of work represents the efforts of hundreds of researchers, foresters, and biologists and covers a broad range of scientific disciplines. Figure 3 summarizes the number of peer-reviewed journal publications generated from common ecological disciplines, with publications that cover multiple disciplines being tallied multiple times. A strength of MOFEP is that the overall study design provides a framework for addressing a range of ecological questions (Larsen et al. 1997). Specific questions of interest can be investigated using designs that are nested within the overarching study, resulting in a large volume of scientific output. In the proceeding section, we describe findings from the MOFEP project for the major discipline areas shown in Figure 3.

Microclimate and Biogeochemistry

Climatic conditions measured within a localized area (i.e., microclimate) provide critical control over ecosystem function and associated processes (Geiger 1965, Chen et al. 1999). Variability in site characteristics, forest structure, and their interactions can greatly affect the microclimate of sites across spatial and temporal scales (Chen et al. 1999). For example, soil temperature, air temperature, and soil moisture varied significantly both within and among stands within the Missouri Ozarks, with the varia-

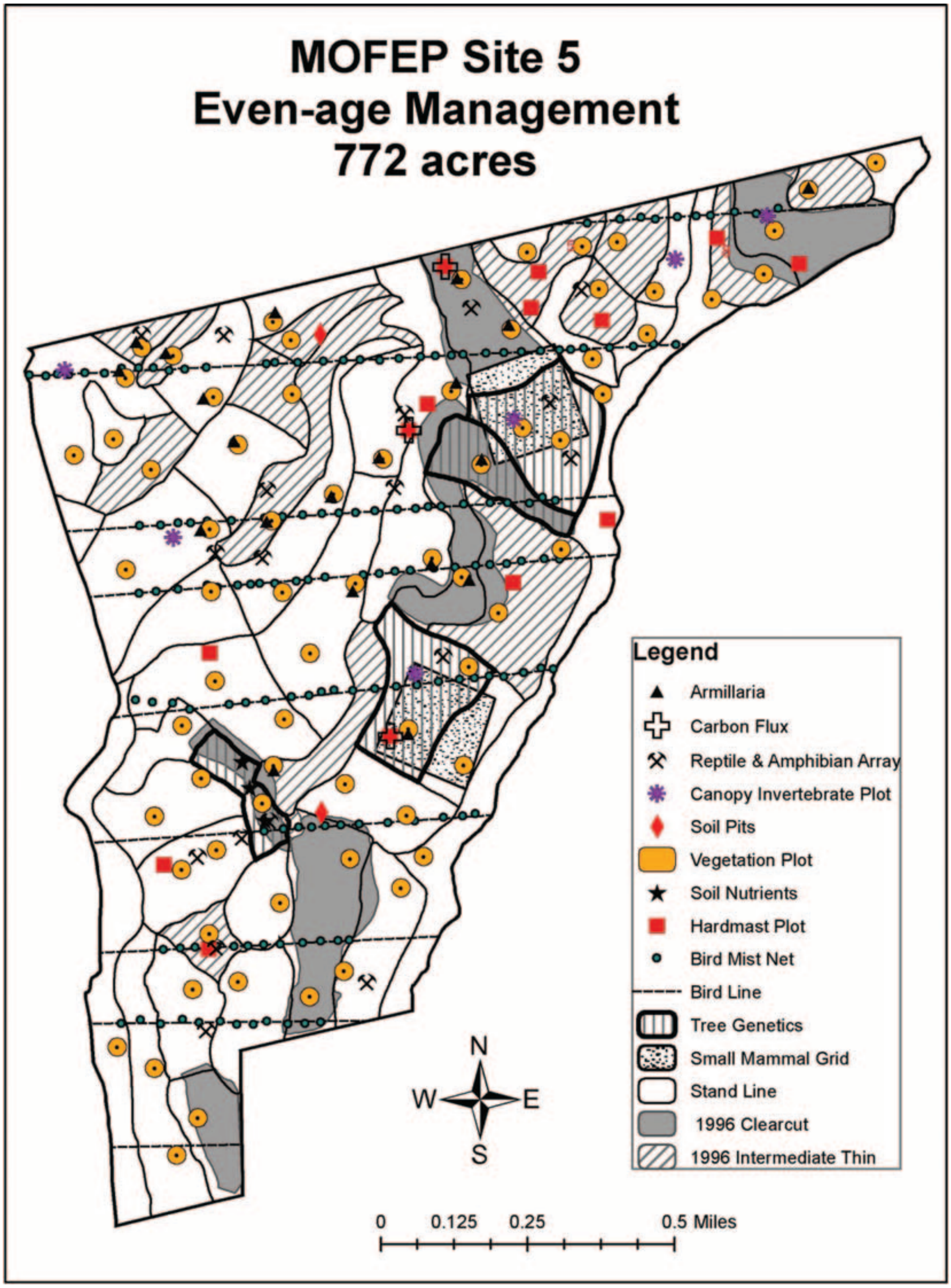

Figure 2. Example of the variety of research projects and sampling designs implemented at MOFEP Site 5, an even-aged management treatment unit.

tion in temperature and moisture increasing with the spatial scale of observation (Xu et al. 1997, Xu et al. 2000). As expected, temperatures (air and soil) were found to be higher on south-facing slopes and ridge tops than on north-facing slopes, but the variation in temperatures was also highest on south-facing slopes (Xu et al. 1997). The management systems used in MOFEP had temporally variable effects on mean soil moisture and mean soil temperature, with evidence of interactions of the management treatments with annual weather conditions (Xu et al. 2011). For example, Xu et al. (2011) reported that site-level soil moisture was higher on UAM and EAM sites than on NHM sites in wetter years but lower on UAM and EAM sites in drier years, with no difference in mean soil moisture over their 5-year study period. Other studies from MOFEP report that EAM treatments resulted in lower soil temperatures than UAM treatments at the stand level in the 6th year after treatment (Concilio et al. 2005) and in the 8th year after treatment (Li et al. 2007). The importance of evaluating variation in microclimate conditions in addition to

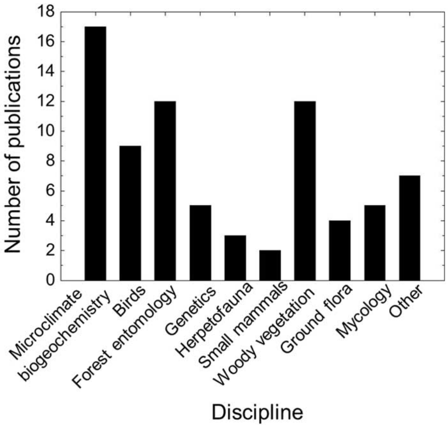

Figure 3. Number of papers that use MOFEP data and have been published in peer-review journals, organized by discipline or taxonomic group. This summary is based on 67 total publications; those that included multiple disciplines in the study objectives were tallied more than once.

mean values was demonstrated by Xu et al. (2002), who reported that seasonal means in air and soil temperatures and soil moisture were similar at the landscape and stand levels, but the variation in microclimate differed by the scale of observation (Xu et al. 2004). Moreover, Zheng et al. (2000) found that the within-site variability in soil moisture and soil temperature was higher in EAM treatments than in UAM treatments in the first 2 years after harvest.

Microclimate is a major driver of ecosystem processes such as decomposition, respiration, and nutrient dynamics. Generally, soil moisture and soil temperature are positively related to decomposition, although the relationship with temperature has been reported to be linear and that with moisture nonlinear (Chen et al. 1999). However, Li et al. (2009) reported that increased rates of decomposition 8 years after harvesting at MOFEP were related to changes in the chemistry of the litter rather than changes in soil moisture or temperature. Rates of decomposition also differed among litter types, suggesting that forest composition and management treatments can interact to affect decomposition rates (Li et al. 2009). Soil respiration is an important source of ecosystem respiration, contributing 70% of ecosystem respiration at the MOFEP sites (Li et al. 2012). Harvesting treatments, especially single-tree selection used in the UAM treatments, increased soil respiration rates 6 years (Concilio et al. 2005) and 8 years (Li et al. 2012) after treatment at the stand level. However, the factors affecting respiration were found to be complex; despite increases in soil moisture and soil temperature associated with harvesting at year 6, these variables were found to be poor predictors of soil respiration without additional information on litter depth, forest composition, and the specific harvest treatment (Concilio et al. 2005).

Biogeochemical cycles are critical to ecosystem function, and the factors affecting nutrient pools and fluxes are complex. Kabrick et al. (2011) used the MOFEP framework to determine relationships between geomorphic and soil properties and exchangeable Ca and Mg, both of which are important base cations that affect soil acidity and nutrient availability. Their results determined that both depth to bedrock and lithology were important factors affecting exchangeable Ca and Mg concentrations, with weathering of the dolomite bedrock common in the Ozark Highlands likely the source of the nutrients (Kabrick et al. 2011). Such patterns may contribute to the distribution of forest tree species on the landscape, with black oak and scarlet oak found to be associated with sites low in Ca concentration but species such as chinkapin oak (*Quercus muehlenbergii* Engelm.) and Shumard oak (*Quercus shumardii* Buckl.) associated with sites with high exchangeable Ca and Mg concentrations (Kabrick et al. 2011). Likewise, vegetation dynamics affect nutrient cycling; for example, Spratt (1998) found that litter inputs were critical for maintaining surface soil organic S, K, and Mg. Harvesting treatments have both direct and indirect effects on nutrient dynamics through the removal of biomass as well as the alteration of the microclimate (Spratt 1998, Chen et al. 1999, Li et al. 2007). The silvicultural treatments used in EAM and UAM at MOFEP reduced the stand-level live tree C pool but increased the coarse woody debris C pool relative to the NHM treatment, with the magnitude of the effect greater in EAM than in UAM (Li et al. 2007). The coarse woody debris and soil C pools were also positively related to soil N, suggesting the interdependence of multiple nutrients affected by management treatments (Li et al. 2007).

Birds

The MOFEP study was originally designed to address questions related to the effects of forest management on bird populations, and several publications have reported impacts on bird abundance. Densities of several bird species decreased on the NHM sites in the posttreatment period, potentially confounding the interpretation of results but also demonstrating the importance of a manipulative experiment of this scale that includes untreated controls and pretreatment data to account for external factors (Thompson et al. 2000, Gram et al. 2003). Generally, densities of forest interior bird species decreased following harvesting treatments and densities of edge/early successional species increased, with the magnitude of response greater on EAM than on UAM treatments (Gram et al. 2001). At the landscape scale, ovenbirds (*Seiurus aurocapillus*), a forest interior species, significantly declined in density on even-aged treatments relative to controls within the first 3 years following treatment, but other forest interior birds (Kentucky warbler (*Oporornis formosus*) and worm-eating warbler (*Helmitheros vermivorus*)) increased on sites with harvesting treatments (Gram et al. 2003). Wallendorf et al. (2007) evaluated the response of the same species at the stand level and reported similar results, with the exception of the opposite effect of harvesting on worm-eating warblers. Moreover, Wallendorf et al. (2007) found that intermediate thinning treatments decreased densities of ovenbirds and Acadian flycatchers (*Empidonax virescens*). At both landscape and stand-level scales, densities of the edge/early succession species indigo bunting (*Passerina cyanea*), prairie warbler (*Dendroica discolor*), and yellow-breasted chat (*Icteria virens*) increased following harvesting treatments (Gram et al. 2003, Wallendorf et al. 2007). Over time, patterns in density were variable among species; for example, initial increases in the densities of indigo bunting, prairie warbler, and yellow-breasted chat were no longer evident 14 years following harvest but those for white-eyed vireo (*Vireo griseus*) and hooded warbler (*Setophaga citrina*) remained (Morris et al. 2013). These results suggest that even-aged reentry intervals of less than 14 years may be appropriate for maintaining habitat for early successional species on the landscape, but evaluating effects on multiple species requires consideration of landscape features such as habitat extent, patch size, and edge density (Howell et al. 2000).

Breeding behavior and success rates contribute to population viability, and reduced nest success and increased brood parasitism of ovenbirds in fragmented habitats compared to unfragmented habitats generally suggest that harvesting may contribute to reduced nesting success by increasing edge (Porneluzi and Faaborg 1999). However, there was little evidence of reduced nest success or increased parasitism associated with the management treatments within the first 14 years following harvest at MOFEP (Gram et al. 2003, Morris et al. 2013). Compared to highly fragmented habitats interspersed with agricultural land use, the forested Ozarks are less likely to support nest parasites such as the brown-headed cowbird, potentially reducing the impact of harvesting treatments on nest success. Research from MOFEP also demonstrates how complex interactions of landscape features, physical factors, and bird behavior can affect nesting success. Cox et al. (2013) found that temperature was positively correlated with predator activity, and higher temperatures resulted in increased nest predation of the Acadian flycatcher, a forest interior species, but had no effect on the northern cardinal (*Cardinalis cardinalis*), a habitat generalist. In an earlier study, Porneluzi (2003) found that ovenbirds returned to breeding sites in subsequent years based on prior reproductive success, suggesting that bird abundance is based on dispersal decisions as well as the physical environment.

Forest Entomology

Several MOFEP studies have investigated the complex patterns and interactions of forest insect communities in association with plant communities, physical site characteristics, and harvest disturbance. By evaluating the richness, density, and diversity of forest herbivore communities across a chronosequence of white oak stands, Jeffries et al. (2006) identified that insect communities were affected by forest age, forest structure, site factors such as aspect and temperature, and the plant community. Generally, insect species richness increased with forest age, with unique communities associated with old-growth stands. Structural complexity of forest vegetation contributed to diversity in insect communities, and differences in relative abundances of insect taxa and functional groups were found between the understory and canopy of white oak and black oak trees (Le Corff and Marquis 1999, Forkner et al. 2004). However, Weaver (1995) used data from MOFEP to stress the importance of considering the spatial scale of sampling when interpreting results from insect species abundance, as heterogeneity in the distribution of insect populations may affect their detection during sampling.

The effects of timber harvest on forest insects were dependent on the taxa and varied across spatial and temporal scales. At the landscape scale, leaf-chewing Lepidoptera herbivores were generally found to decrease following harvesting, and communities differed between cut and uncut areas within harvested sites (Forkner et al. 2006). In contrast, effects of harvesting on dung beetle communities varied at the stand level, with higher expected species richness reported in canopy openings than within the intact canopy (Masís and Marquis 2009) but lower abundance and species richness reported in clearcut areas (Masís and Marquis 2007).

Insect communities may be highly sensitive to shifts in ecological conditions due to interactions among parasites, pathogens, and vegetation characteristics. The concentrations of foliar phenolics and concentrated tannins in *Quercus* species provide a defense against herbivory (Forkner and Marquis 2004, Forkner et al. 2004). Following harvesting of the MOFEP plots, Forkner and Marquis (2004) reported variable effects of the management treatments on foliar phenolics and concentrated tannins of white oak and black oak in the understory and canopy. However, concentrations were consistently higher on south- and west-facing slopes than on north- and east-facing slopes. Leaf pubescence provides an additional form of defense against herbivory for forest trees, and the work of Lill et al. (2006) demonstrates that pubescence varies among tree species and among forest canopy strata. Results from MOFEP have further contributed to our understanding of parasitoid communities, an important form of control over forest insect herbivores. From census data collected from 1993–1995, parasitism was generally highest in the early period of the growing season and decreased through September, but rates differed among the feeding guilds observed (Le Corff et al. 2000). The impacts of forest management on parasitoid communities and resulting effects across trophic levels are not clear, but Stireman et al. (2005) discuss the importance of such interactions on ecosystem function in relation to climate change.

Genetics

The distribution and flow of genetic material within and among populations are critical considerations for species conservation and sustainable forest management (Gram and Sork 2001, Smouse et al. 2001). Pollen flow contributes to genetic variation (Smouse et al. 2001), and Dyer and Sork (2001) reported that forest vegetation structure and isolation by distance limited pollen movement of shortleaf pine on MOFEP sites. The genetic variability among common forest tree species in the Ozarks was found to be related to environmental heterogeneity at broad scales but also to vegetation structure at local scales (Gram and Sork 2001). However, population density was found to be a poor predictor of genetic variation for common Ozark tree species (white oak, mockernut hickory (*Carya tomentosa* (Poir.) Nutt), and sassafras (*Sassafras albidum* (Nutt.) Nees)) but was correlated with genotypic composition (Gram and Sork 1999). These findings suggest that conserving populations across a range of densities may be effective for conserving genetic variation. Although forest management may affect genetic diversity and pollen flow, data suggest that the initial harvesting treatments of MOFEP did not reduce genetic diversity of flowering dogwood (*Cornus florida* L.) (Sork et al. 2005).

Herpetofauna

At the landscape scale, the EAM treatments were found to reduce the population density of toads (*Bufo americanus* and *Bufo woodhousii*) 2 years following harvest (Gram et al. 2001), with a similar pattern extending into the 4th year following treatment (Renken et al. 2004). Local effects of harvesting within EAM treatments were examined by determining population densities relative to distance from the clearcut areas for 13 herpetofauna species. Of these, *Ambystoma maculatum*, *Rana clamitans*, and *Scincella lateralis* displayed patterns in which densities were lower within clearcuts than within the surrounding forest, whereas *Sceloporus undulatus* densities were highest within clearcut areas (Renken et al. 2004). In a different study, Herbeck and Larsen (1999) found that local densities of plethodontid salamanders were greatly reduced following timber harvest, with the highest densities in old-growth stands as compared to regenerating stands and mature, second-growth stands. For terrestrial salamanders with small territories, heterogeneous microhabitats provided by the coarse woody debris of old-growth forests are critical habitat features, suggesting that maintaining mature forests across the landscape will be important for maintaining high densities of plethodontid salamanders (Herbeck and Larsen 1999).

Small Mammals

Population densities of *Peromyscus* spp. mice were determined prior to harvesting and during the first 2–5 years following timber removal (Gram et al. 2001, Fantz and Renken 2005). Regardless of the management treatment, including NHM, population densities were reduced through 2 years following the harvesting treatment, complicating the interpretation of treatment effects (Gram et al. 2001). However, Fantz and Renken (2005) reported that the EAM treatment maintained population density at pretreatment levels 6 years following harvest, whereas population declines were observed on the NHM treatment. These results suggest that the heterogeneity in habitats at the landscape scale provided by forest management may contribute to increased *Peromyscus* spp. population densities.

Woody Vegetation

Woody vegetation in forested ecosystems provides the foundational habitat for higher trophic levels and is therefore critical to the population dynamics of faunal communities. Recent recognition of the importance of snags and downed woody debris for wildlife habitat, as well as their roles in ecosystem processes such as nutrient cycling and forest hydrology, have resulted in increased research on the distribution and dynamics of dead trees in forested ecosystems. In Missouri and surrounding states, remnant, old-growth forests supported higher densities of standing snags and more downed woody debris than did nearby mature, second-growth stands (Shifley et al. 1997, Spetich et al. 1999). The volume of downed woody debris increased after stand age 80 and was largely associated with greater additions of large woody debris (Shifley et al. 1997, Spetich et al. 1999). Because of the time required for the development of snags or downed woody debris, management planning for such habitat features must be conducted on appropriate timescales. Data from the overstory plots at MOFEP were used to inform LANDIS, a spatially explicit landscape-scale forest disturbance model (Mladenoff et al. 1996) capable of predicting cavity tree density following alternative forest management scenarios (Fan et al. 2004). Over a 100-year simulation period, clearcutting on a 100-year rotation resulted in stable densities of cavity trees, and group selection, clearcutting on a 200-year rotation, and no-harvest treatments resulted in increased cavity tree density across the landscape.

Successional dynamics associated with forest management practices will ultimately shape the long-term development of the forested landscape. Although MOFEP is still early in its implementation (i.e., two of eight harvest entries completed), model simulations have been used to predict forest composition and age structure over time using different management practices (Gustafson et al. 2000, Shifley et al. 2000). Using the LANDIS model, Gustafson et al. (2000) predicted that across the landscape the proportion of black-scarlet oak and oak-pine types would increase while mixed oak and shortleaf pine stands would decrease with EAM and UAM treatments, with the magnitude of change greatest for EAM in all cases. Data on regeneration dynamics through 10 years after the initial harvesting entry on MOFEP showed that there were greater densities of red oak group species in the regeneration layer on the clearcut areas than on areas treated with single-tree selection, the combination of single-tree and group selection, or no cutting (Kabrick et al. 2008b). In contrast, species in the white oak group were regenerating in clearcuts as well as in areas treated with single-tree selection and group openings, suggesting that UAM will likely favor primarily white oak regeneration while EAM will favor a mixture of white and red oak species.

The oak decline issue in the Ozarks of Missouri and northern Arkansas has received considerable attention and has the potential to greatly affect the composition and development of forests in this region. MOFEP has provided an excellent source of data for describing oak decline and its contributing factors. Generally, species in the red oak group are more vulnerable to decline than those in the white oak group, with mortality rates reported to be three to six times higher for red oak species (Fan et al. 2006, Shifley et al. 2006, Fan et al. 2011). Individual tree characteristics also contribute to mortality rates, with higher rates of mortality observed for trees in lower crown classes (Fan et al. 2006, Shifley et al. 2006, Fan et al. 2011) and with lower annual diameter growth increments (Shifley et al. 2006). Moreover, specific levels of stand density have been recommended for minimizing red oak mortality or for prescribing management actions for at-risk stands. Although oak decline has been observed to be greater on droughty, nutrient-poor sites than on better quality sites, Kabrick et al. (2008a) determined that this pattern was due to the high abundance of red oaks species rather than a greater red oak mortality rate on poor-quality sites. Oak decline will continue to play an important role in the development of Ozark forests, and understanding the effects of forest management and additional factors contributing to mortality dynamics will be critical to management at both stand and landscape scales (Dwyer et al. 2004, Voelker et al. 2006).

Ground Flora

Ground flora provides critical habitat for forest insect and wildlife species and contributes greatly to the biodiversity of forest ecosystems. As a result, there is much interest in understanding patterns of ground flora richness and diversity and their responses to forest management. Across the landscape of MOFEP, Xu et al. (2000) determined that species richness was strongly correlated with heterogeneity of microclimate, suggesting the importance of physical factors in controlling plant communities. Generally, harvesting intensity was found to be positively related to short-term increases in total cover and species richness of ground flora at the stand level (Zenner et al. 2006). All methods of harvest (single-tree selection, group selection, thinning, and clearcutting) increased graminoid cover but reduced the cover of legumes, demonstrating short-term shifts in ground flora communities associated with alternative silvicultural practices used within MOFEP (Zenner et al. 2006).

Mycology

Red oak decline in Ozark forests has been associated with the presence of the fungi *Armillaria*, and MOFEP has greatly furthered our knowledge of the ecology of *Armillaria* species. Bruhn et al. (1998) developed a new methodology for identifying *Armillaria* field isolates using mycelial growth characteristics and patterns of isozyme production and evaluated the distribution of *Armillaria* species in relation to site characteristics and oak decline (Bruhn et al. 2000). Of the three common *Armillaria* species evaluated, *A. mellea* and *A. tabescens* were most associated with red oak mortality, while *A. gallica* was essentially nonpathogenic. Moreover, *A. mellea* commonly occurred on sites in which decline was observed (Bruhn et al. 2000). Although overlap in the species occurrence was observed in the field, *Armillaria* species expressed differential growth patterns and resource requirements that affected their dominance across site types (Bruhn et al. 2000, Mihail et al. 2002, Mihail and Bruhn 2005). More saprotrophic species, including *A. gallica*, developed large rhizomorph systems but may be outcompeted by the higher production of foraging tips in the rhizomorph systems of more parasitic species such as *A. mellea* and *A. tabescens* (Mihail and Bruhn 2005). Moreover, similar expression of bioluminescence was observed in parasitic *A. mellea* and *A. tabescens* but contrasted with that of *A. gallica*, although the ecological role of this phenomenon is not well-understood.

Integration

The broad scope of ecological research conducted in association with MOFEP demonstrates the utility of a landscape-scale experimental study to address questions across disciplines in natural resources as well as across spatial and temporal scales. In addition to that described above, data from MOFEP have been used to develop new statistical tools (Larsen and Speckman 2004) and to apply novel analytical methods for determining patterns in species distribution or site quality (Hooten et al. 2003, Sun et al. 2008). Several studies have determined relationships between physical factors of the environment and biological responses (Xu et al. 2000, Mihail et al. 2002, Peck et al. 2004, Kabrick et al. 2008a, Cox et al. 2013). Integrating ecological responses across taxa has been an underlying objective of MOFEP from its beginning. Gram et al. (2001) used a meta-analysis approach to determine the effects of forest management treatments on several faunal taxa and reported that EAM treatments had a greater effect on animal community density than UAM did at the landscape scale. This work also discusses the challenges of integration across different sampling designs and difficulties with interpretation of results following only one harvest entry of a long-term study. Ongoing efforts continue to evaluate responses across ecological levels and scales as more data become available.

Challenges, Lessons Learned, and the Future of MOFEP

Challenges

The broad spatial and temporal scales of MOFEP provide the project with unique scientific opportunities but also create challenges in controlling factors that may affect experimental outcomes. As common with ecological field research across disciplines, external factors such as climate, land-use legacies, stochastic disturbance events, and forest health issues act on response variables in ways that are often difficult to quantify or isolate. The heterogeneity of these factors increases over time and across space, suggesting that their cumulative effects over the duration of the project may affect the interpretability of study results. Such factors have been observed in the responses of several animal populations, with decreases in population densities of many species from the period prior to harvest to the period following harvest for all management treatments, including the NHM treatment (Gram et al. 2001, Gram et al. 2003, Renken et al. 2004, Fantz and Renken 2005). Although the cause of the decrease in densities was not clear, the experimental design allowed for comparison of the relative decrease in postharvest densities among treatments. Future disturbance events could further confound treatment effects. For example, oak decline affects stand composition and structure through the mortality of red oak species, and oak decline events produce an ecological shift that is additional to the study treatments. Other external factors, such as changing climate patterns or the introduction of invasive species, may interact with oak decline or other events to accelerate such processes.

Managing a project of the scope of MOFEP is also logistically complex. The overall experimental design provides a framework for the extensive research conducted under MOFEP, but individual studies often implement uniquely developed sampling designs to address specific questions (Figure 2). As a result, data from individual studies may not be directly compatible for cross-discipline analyses or may be best integrated with meta-analytical approaches (e.g., Gram et al. 2001). Given the long time frame of MOFEP, reentry for harvesting treatments may also occur in periods of shifting management emphasis for MDC. Because MOFEP is designed to represent the current management operations of MDC, the specific harvesting practices of the EAM or UAM treatments may also shift through time. For example, the 1996 entry used only clearcutting with reserves as the regeneration treatment in EAM sites, but the 2011 entry used both shelterwood and clearcutting methods (Table 1). As additional changes in MDC operations occur through time, retaining the integrity of the original experimental design will require effort and planning of MDC researchers and managers. Because the time frame for the project extends beyond the tenure of individuals associated with it, data management and information transfer among personnel are critical components of the long-term success of the project.

Lessons Learned and the Future of MOFEP

The MOFEP project serves as a model for long-term, landscape-scale ecological research, with several factors allowing the project to persist and continue to productively inform the scientific and management communities (Larsen et al. 1997). Key factors are commitment, communication, and collaboration. The continued support of MDC funding and personnel have allowed for the design, establishment, and maintenance of MOFEP and are essential for its continuation into the future. Funding derived from a state sales tax in Missouri provides MDC with the means to support a project of this scale, but prioritizing state resources to the project each year is also essential. The research scientists and field biologists associated with MOFEP have demonstrated a commitment to the project that is needed for maintaining it over long time periods. Effective communication of the importance and benefits of MOFEP is critical to fostering personal commitment to the project. Information derived from the project is transferred from scientists to managers through periodic symposia, conferences, and field trips, providing a feedback mechanism for maintaining relevancy of the science to the mission of MDC. Likewise, the operational needs of the agency are incorporated into new research projects that address emerging challenges and issues. As such, fostering good relationships among scientists, managers, and MDC administrators is critical to ensuring that the practical findings from MOFEP are communicated effectively so that the study remains a high priority of the MDC. Finally, this level of communication makes successful collaboration possible. From its inception, MOFEP has been a collaborative project that has operated across agencies and disciplines. To the credit of the hard work of those involved with the project, these efforts have created a research framework that is invaluable for ecological research.

Despite its initiation nearly 25 years ago, MOFEP is still in the initial stages of its design. As such, the study treatments have not yet been fully applied; with a 15-year harvesting reentry period, the entire area of each EAM site will not receive the designed treatments until one complete rotation has been achieved, while the UAM sites will require a minimum of three entries. Results from the project to date therefore represent only a proportional effect of the treatments across the landscape rather than the landscape-scale effects of the different management systems. Although this currently presents limitations to interpretation of landscape-scale effects, the accumulation of data that capture the temporal development of response variables will be critical for understanding the effects of implementing management systems on operational scales.

Conclusion

The MOFEP is an example of a long-term, landscape-scale study that creates the opportunity for ecological research across disciplines and agencies. Commitment to the project by the MDC provides the foundations of funding and personnel for supporting the project. As our understanding of ecosystem function increases, it is clear that multidisciplinary research that operates on appropriate spatial and temporal scales will be critical to furthering forest ecosystem science. Over the past 25 years, MOFEP has contributed to a diverse array of new scientific knowledge that has been applied by MDC land managers in the Missouri Ozarks. With a broad research framework that includes a strong statistical design within which other, more focused study designs may be nested, MOFEP is well-suited to individual studies or to the integration of research efforts across disciplines. Despite challenges inherent to maintaining an experimental study of such scale, the future looks promising for MOFEP; with continued commitment, collaboration, and communication, research from this project will inform forest managers and ecosystem science for generations to come.

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