Forest Ecology and Management 481 (2021) 118681

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Editorial

Processes underlying restoration of temperate savanna and woodland ecosystems: Emerging themes and challenges

ARTICLE INFO

Keywords
Biodiversity
Ecosystem services
Mesophication
Open forests
Pinus
Prescribed fire
Quercus
Silviculture

ABSTRACT

Open forests of savanna and woodlands span the spectrum between closed canopy forests and treeless grasslands, and therefore contain structure, composition, and function distinctive from either endpoint. In this special issue, researchers provide examples from different open forest ecosystems to examine the underlying ecological principles and specific management challenges affecting successful restoration of these systems. Emergent themes include the role of open forest systems for biodiversity, fire as an underlying process, and the similarities and differences in ecosystem restoration goals under different ecological and social contexts. Consistent challenges include effective application of fire, the commonly observed pattern of "mesophication" that occurs in the absence of fire (including woody densification and changes to belowground processes) and the distinction between structural restoration and compositional restoration – where the former is necessary but not sufficient to restore the latter. Given the uncertainty of ecosystems increasingly stressed by human activity, the restoration of open forests should be among the suite of options considered given both their historic prevalence and current benefits to ecosystem services and biodiversity.

1. Introduction

Open forests of savannas and woodlands (hereafter open forests), comprised of a bilayer of overstory trees and an herbaceous ground flora, occur globally and present unique restoration challenges (Griffith et al., 2017; Hanberry et al., 2018). Open forests supply the indeterminate continuum between closed canopy forests and treeless grasslands, and therefore contain distinguishing structure, composition, and function, but have not been recognized as ecosystems (Hanberry et al., 2018; Ratnam et al., 2011). These distinctive ecosystems also experience challenges related to their unique attributes across their global distribution, some of which have arisen due to management practices and alterations to environmental conditions. For instance, a consistent trend in the degradation of semi-open systems is the systematic loss of fire and sun-adapted understory species yielding to encroachment by fire-intolerant woody species (Griffith et al., 2017; Hanberry et al., 2018; Nowacki and Abrams, 2008). These losses have important consequences for regional biodiversity and can affect ecosystem resilience to threats such as invasive species (Hanberry et al., 2020 this issue).

In this special issue, researchers provide examples from different open forest ecosystems to examine the underlying ecological principles and specific management challenges affecting successful restoration of these systems. Key processes underlying the emergence of open forest ecosystems include fire, herbivory, competitive interactions among life forms, water balance, and nutrient cycling (Bragg et al., 2020 this issue; Hanberry et al., 2020 this issue; Meunier and Shea, 2020 this issue; Rother et al., 2020 this issue). Restoration to reduce woody vegetation will support herbaceous and graminoid plants, fungi, and animals, including large mammals (Hanberry et al., 2020 this issue; Nghikembua et al., 2020 this issue) and pollinators (Grundel et al., 2020). We anticipate that the combination of literature review of the processes underlying the open canopy condition, a set of restoration case studies spanning multiple biomes and exploring different challenges underlying the restoration of such systems, and concluding with a management synthesis, will inform the development of effective management to maintain and restore open forest systems as self-reinforcing ecosystem states (Bassett et al., 2020 this issue; Bragg et al., 2020 this issue; Ladwig et al., 2020 this issue; Quigley et al., 2020 this issue).

2. Content summary

2.1. Biodiversity

The eastern United States historically contained great herbaceous species richness, which is not supported in current closed forests (Hanberry et al., 2020 this issue). In turn, plant resources are critical to insects, many species of which provide essential ecosystem services, such as pollinators, and insect biodiversity (including pollinators) are experiencing global decline (Grundel et al., 2020). Indeed, open forest loss throughout most of the eastern United States has affected multiple conditions and ecological functions, leading to associated declines in the abundance and richness of many life forms (Hanberry et al., 2020 this issue). Historically, frequent surface fires supported more complete plant and fungal diversity (Semenova-Nelsen et al., 2019) and the

https://doi.org/10.1016/j.foreco.2020.118681

0378-1127/Published by Elsevier B.V.

diminishment (or loss) of this process-driving perturbation has caused managers to see its replacement (in part) through the creation of superficially similar early successional forests. However, this approach has not worked well for disturbance-dependent birds, as many types of avifauna continue to decline (Hanberry and Thompson, 2019). Likewise, pollinator declines remain a global problem, and one that does not seem to be adequately addressed solely through early successional forests (Hanberry et al., 2020 this issue).

Maintaining open forest conditions is not the only challenge facing managers today. The concept of "mesophication" (*sensu* Nowacki and Abrams, 2008) nicely captures the interrelated processes that, in the absence of disturbance such as fire, systematically push the system toward a closed canopy condition. These processes include woody densification and loss of light to the understory that exclude sun-loving forbs and grasses and result in gradual accumulation of litter biomass into a more developed forest floor, a gradual decline in fuel quality necessary to carry fires, and (ultimately) a compositional shift toward mesic forest conditions and fire-sensitive forest composition that may be more resistant to fire.

Restoration of open forests offers considerable promise for reversing some of these trends. Unlike the ephemeral nature of early successional forests, open forests are comparatively stable through time, providing the needed structure and herbaceous communities to support invertebrate and vertebrate species throughout their lifetimes. The intermediate tree canopy cover found in restored open forests appears to be particularly effective for butterfly conservation (Grundel et al., 2020). Similarly, Nghikembua et al. (2020 this issue) found that removal of woody encroachment in thornbush savanna of Namibian farmlands overall increased abundance of large mammals (i.e., predators and ungulates) and thinning can be applied to restore wildlife habitats.

2.2. Fire as a key process

Fire regimes vary in severity and frequency by region and vegetation. To create an open forest structure, with limited tree presence in the under- and midstory, fire needs to be frequent enough to effectively control tree regeneration (Bassett et al., 2020 this issue). In some regions society has embraced this concept and put frequent fire into established management practice (Rother et al., 2020 this issue), while other regions have a long way to go before burn programs are applied extensively enough to enable open forest management at a sufficiently broad scale (Meunier and Shea, 2020 this issue). Studies from some regions suggest that prescribed fire alone may not bring back the full range of habitats to meet conservation goals (Roberts et al., 2020 this issue). This kind of cross-system comparison underscores not only the central role of fire in the emergence and maintenance of open forest systems, but also the need for customization of approaches based on the local ecology; customization can be informed in part by historic context (Ladwig et al., 2020 this issue; Meunier and Shea, 2020 this issue; Rother et al., 2020 this issue).

Past history of low to moderate severity fires may be difficult to detect using methods such as charcoal or historical notes of recent fires, but fire scar (dendrochronology) records are beginning to highlight the role of lower-severity fires (Roos et al., 2019; Tanner et al., 2018). Meunier and Shea (2020 this issue) reconstructed the fire regimes for historically pine (*Pinus* sp.) dominated ecoregions of Wisconsin using dendrochronology and contrasted those results with records of fire from proximate historical tree survey locations. They estimated fire rotations ranging between 12 and 34 years for historic pine sites, which is more frequent than that estimated by historical tree surveys, but consistent with less extensive tree-ring studies and expert accounts of fire history based on evidence (e.g., Guyette et al., 2016; Landfire, 2020). The notion that the region was affected by frequent but low severity burns also corresponds with the regeneration requirements of pines in the region, particularly red (*P. resinosa*) and white (*P. strobus*) pine species (Meunier et al., 2019). Likewise, Rother et al. (2020 this issue) reconstructed uninterrupted fire regimes for longleaf pine (*P. palustris*) of northern Florida and southwestern Georgia using dendrochronology. Mean fire return interval was about 2 years since about 1900, and was dominated by dormant to early growing season (January to mid-April) burns. Such patterns are consistent with the modern burn practices of the southeastern United States that, unlike areas further north (Meunier and Shea, 2020 this issue), reflect a long tradition of widespread application of prescribed burns.

The material legacies of open forests also have important ramifications for subsequent informational legacies (i.e., species adaptations to disturbance regimes) in the form of wildlife habitat (Roberts et al., 2020 this issue). For example, ponderosa pine (*P. ponderosa*) forests of the western United States historically had a mixed severity fire regime, resulting in a wide range of structural attributes, such as tree density, standing dead trees, and downed woody debris. Roberts et al. (2020 this issue) examined these structural characteristics from the perspective of diverse wildlife communities as a function of fire severity and time since fire in remnant ponderosa pine savannas of western Nebraska, USA, that had a recent history of wildfire. They found that the full fire severity gradient (low, moderate, and high-severity classes) generated sufficient patch-level structural heterogeneity to provide for all species, such as black-backed woodpeckers (*Picoides arcticus*) that forage on beetle outbreaks after fires. Therefore, for these ecosystems, application of low severity prescribed fires alone or minimization of fire severity in wildlands will not fully meet all restoration goals.

2.3. Restoration and management

Several papers in this special issue addressed different dimensions of ecosystem restoration across a broad spectrum of ecosystem types under active restoration. Bassett et al. (2020 this issue) demonstrated a common theme in open system restoration – that structural restoration often precedes compositional restoration. The authors investigated the effects of prescribed burning and burning plus mechanical thinning treatments vs unmanaged controls in terms of canopy structure (openness) and understory composition (coverage, diversity, and indicator species) within an oak (*Quercus* sp.) savanna restoration operation in central Michigan, USA. They found that the burning plus thinning treatment had consistently stronger effects on both structure and composition related to restoration goals over the 8-year period. Understory herbaceous cover lagged, but was contingent on, the opening of the canopy in either treatment, requiring multiple burns when not accompanied by mechanical thinning. Likewise, canopy openness regressed by the end of the study, demonstrating the importance of repeated treatments before the structural and compositional changes can reach a less intensive maintenance phase.

Related to compositional restoration of open savannas, a common practice is the supplementation of herbaceous and graminoid species via commercially-available native seed mixes. Yet little is known about how such mixes compare with the composition of remnant and historic savanna ecosystems. Ladwig et al. (2020 this issue) compared and contrasted the understory composition of oak savannas of the 1950s (Bray, 1960) with contemporary field measurements 60 years later as well as the composition of regional commercial seed mixtures from both phylogenetic and functional trait perspectives. They found strong separation in the phylogenetic composition of all three groups. From a functional trait perspective, they found areas of important overlap, such as seed size, as well important differences including specific leaf area and especially plant height. Such analyses can help guide future priorities in the acquisition of seed sources and inform the use of commercial native seed mixes in the context of savanna restoration more generally.

Quigley et al. (2020 this issue) investigated belowground processes related to soil fertility relative to restoration stage where the goal is to create more self-sustaining (i.e., low fertility) open ecosystems overlaying sandy soils in Wisconsin, USA. They found that not only did current vegetation affect soil fertility patterns, but vegetation and

disturbance history had persistent legacies within the upper soil layers. Specifically, deciduous forest and transitional hardwood brush states tended to have greater cation stocks than open barrens, while conifer forests tended toward deeper forest floor. These soil characteristics persisted within restored barrens from each respective vegetation history. Meanwhile, fire frequency influenced soil properties such as pH, presumably due to ash deposition through time (Quigley et al., 2019).

Bragg et al. (2020 this issue) reviewed management practices in the open oak and pine forests of the eastern United States. While open forest management objectives are very different from those of closed-canopy forests, the silvicultural tools (such as some mechanical and chemical treatments and plantings) available can be very similar to those used in more conventional production forestry contexts. Other practices such as the application of frequent prescribed fire and limitation of tree regeneration at present are more unique to open forest management. Rather than attempting to increase tree stocking and maximize wood production, open forest management focuses on maintaining an herbaceous ground layer, retaining of overstory trees, and controlling tree regeneration. Ultimately, open forest management focuses much less on the commercial harvest of timber and replacement of closed canopies, which results in reduced economic gains but increased ecosystem services.

Among the objectives of open forest restoration is to promote the ecosystem feedbacks that facilitate more self-sustaining systems that, presumably, require less energy to maintain (Bragg et al., 2020 this issue). Woody densification was a central theme of several case studies in this special issue (e.g., Bassett et al., 2020 this issue; Nghikembua et al., 2020 this issue; Quigley et al., 2020 this issue). Fire is one method to control tree regeneration, but certainly other management options exist (Bragg et al., 2020 this issue; Nghikembua et al., 2020 this issue). As Quigley et al. (2020 this issue) demonstrated, some of the essential feedbacks (i.e., soil fertility, forest floor development, etc.) that underlie competitive interactions related to tree regeneration occur belowground. Despite the central role of belowground processes underlying mesophication, studies of soil feedbacks with respect to fire and restoration practices remain an understudied dimension of open forest restoration and management.

3. Conclusions

Historically, open forests were ubiquitous across the eastern United States (Hanberry et al., 2020 this issue) and characteristic of systems dominated by ponderosa pine in the western United States (Noss et al., 2006). Ecosystems with both an herbaceous and tree layer occur elsewhere, under different names such as tropical and subtropical savannas, and can be found in regions with low to moderate precipitation levels and fire regimes (e.g., Nghikembua et al., 2020 this issue). Like their analogs in the United States, these open forest ecosystems are consistently declining (Stevens et al., 2017). Given their unique contribution to biodiversity worldwide (e.g., Hanberry et al., 2020 this issue; Nghikembua et al., 2020 this issue; Roberts et al., 2020 this issue), such declines have fundamental ramifications for the global biodiversity crises, underscoring the urgent need for ecosystem restoration.

A specific emergent scientific theme from this special issue was the importance of, and challenges to, the compositional restoration of open forests. Diverse composition of herbaceous plants is a critical component of open forests. Bassett et al. (2020 this issue) showed how compositional restoration is fundamentally interrelated with the application of fire and its effects on tree and shrub regeneration, while Ladwig et al. (2020 this issue) underscored the challenges of restoring the compositional and functional diversity of open forest understories, even with the benefit of commercial native seed sources. After all, open forest structure affects environmental conditions and ecological functioning (e.g., light, wind, rainfall, exposure, biogeochemical cycles), ecological processes (fire, herbivory), and light levels to understory plants, all of which combined help sustain the open forest condition. Management of open forests is therefore about fostering continuity in the overstory and understory by sustaining and emulating the supporting processes, bolstering the native biodiversity where necessary.

The diversity of studies within this special issue make an important contribution toward the effective restoration of open forests across a broad spectrum of ecological contexts. While this restoration entails the reestablishment of open forest structure, composition, function, and processes, the decision to restore ecosystems is ultimately a choice based on human needs and values. Among the greatest ironies in human ecology is that the very ecosystem (open forest) and disturbance (fire) that helped shape the emergence of the human species (Parker et al., 2016) are now among the most impacted by human actions. It is therefore fitting that Bragg et al. (2020 this issue) concluded with the many socio-economic challenges facing the restoration of open ecosystems at broad scales. Balancing the investment in restoration and the opportunity costs of lower timber production against the ecosystem services of biodiversity, wildlife habitat, recreation, and pollinator reservoirs (to name a few) that open forest ecosystems provide is a management decision that must be faced. Further, the coexistence of human societies with fire ecology is a critical issue of our time (Bowman et al., 2011) such that the persistence of open ecosystems dependent at least in part by fire face significant challenges (Bowman et al., 2013). Finally, restoration of open-forests, just like that of any other system of interest, remains a moving target as global climate change scales down to emergent change in regions that used to support open forest ecosystems, and it is plausible those regions favoring such systems will shift to new areas (e.g., Frelich and Reich, 2010). Contributions within this special issue highlight the need to keep restoration of open forests at the forefront of options to address this uncertainty, given both their historic prevalence and current benefits to ecosystem services and biodiversity.

CRediT authorship contribution statement

Brian R. Sturtevant: Project administration, Writing - original draft.
Brice B. Hanberry: Project administration, Writing - original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This special issue emerged from a special session of the of the same name for the North American Forest Ecology Workshop in held in Flagstaff, Arizona (USA) in June 2019, organized by Brian Sturtevant and Kathleen Quigley. We wish to thank all of the participants of that special session for their stimulating presentations and discussion, the majority of whom contributed to this special issue. We also wish to thank Don Bragg for his thorough critique of an earlier version of this manuscript, and the other contributors for their individual feedback.

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