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Review and synthesis

Updating models for restoration and management of fiery ecosystems

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ABSTRACT

Scientific models that guide restoration/management protocols should be reviewed periodically as new data become available. We examine ecological concepts used to guide restoration of pine savannas and woodlands, historically prominent but now rare habitats in the southern North American Coastal Plain. For many decades, pine savanna management has been guided predominantly by a biome-centric succession model. Pine savannas have been considered early-successional communities that, in the absence of fire, transition rapidly toward closed-canopy hardwood forests. Recurrent fires have been viewed as exogenous disturbances that maintain savanna ecosystems as a sub-climax, blocking succession to an equilibrium steady state (closed-canopy forests). Over recent decades, a vegetation-fire feedback model has emerged in which pine savannas are conceptualized as persistent, non-equilibrium communities maintained by endogenous, co-evolutionary vegetation-fire feedbacks. Endemic plant species are resistant to fires and specialized for post-fire conditions generated by frequent lightning fires, primarily within a distinct fire season. These species produce pyrogenic fine fuels that are easily ignited. The resulting fire regimes, entrained by these vegetation-fire feedbacks, are predicted to result in persistent pine savannas. Local variation over space and time in evolutionary feedback mechanisms between pyrogenic vegetation and fire regimes produces heterogeneous landscapes. Disturbances of these feedbacks, such as human fire suppression, are postulated to result in rapid transition to communities lacking feedback elements, such as closed-canopy forest and those without pyrogenic species. Succession-based management focuses on reversing the transition to forest, primarily by removing hardwoods and reintroducing fire as a disturbance. However, we advocate restoration and management approaches that target reinstitution of functional vegetation-fire feedbacks. Such approaches should favor native pyrogenic plant species and reinstitute fire regimes that mimic historical, evolutionarily derived fire regimes. Vegetation-fire feedback concepts should be useful in addressing resistance and resilience of fiery ecosystems worldwide to inherent changes in feedback mechanisms, constituting a framework useful in addressing global management challenges.

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1. Introduction

Ecosystem restoration and management practices should be guided by informed conceptual models of ecosystem dynamics. Because protocols based on different models can have different outcomes, restoration and management practitioners should benefit from keeping pace with advances in ecological theory through periodic re-evaluation of system-specific models. Periodic review also is vital for keeping activities in a global context. This inclusive perspective is essential for developing management approaches that can benefit from research in systems guided by similar models (Falk et al., 2006; Hobbs and Suding, 2009; Shackleford et al., 2013).

In this paper we review ecological concepts used to guide restoration and management of an exemplary set of intensively managed pyrogenic habitats. We focus on warm temperate & subtropical pine savannas and woodlands (hereafter pine savannas) in the southern region of the North American Coastal Plain (Noss et al., 2015). These ecosystems resemble humid grasslands, savannas and woodlands with high biodiversity in other parts of the world (e.g., Ratnam et al., 2011; Parr et al., 2014; Veldman et al., 2015). Historically, these pine savannas contained a two-layered physiognomy (Gilliam et al., 2006). As illustrated in Fig. 1, the non-contiguous overstory was dominated by variable densities of trees (typically pines, such as longleaf pine, *Pinus palustris*) and the diverse ground layer was dominated by warm-season C_4 grasses, such as *Aristida stricta*, *A. beyrichiana*, and *Schizachyrium scoparium* (Wahlenberg, 1946; Croker and Boyer, 1975; Harcombe et al., 1993; Platt, 1999; Van Lear et al., 2005; Peet, 2006; Noss et al., 2015). These savannas and associated inclusions (e.g., patches of hardwood trees or edaphic wetland communities) contain about 85% of the 1816 endemic vascular plants in the North American Coastal Plain biodiversity and endemism hotspot (Noss et al., 2015). Geographically, they extended from southeastern Virginia to eastern Texas, and the northern Georgia mountains to the Florida Keys; similar systems extended into the Caribbean and coastal Central America (Frost, 2006; Myers and Rodriguez-Trejo, 2009). Locally they varied along elevation gradients from xeric uplands to seasonally flooded lowlands (Platt, 1999; Peet, 2006). Following European settlement, pine savannas underwent extensive fragmentation and habitat alteration and now occur in less than 4% of their former range (Noss et al., 2015). All remaining pine savanna landscapes are managed using prescribed fire. Up-to-date ecosystem models based in current scientific research are crucial to restoration and management of these unique ecosystems.

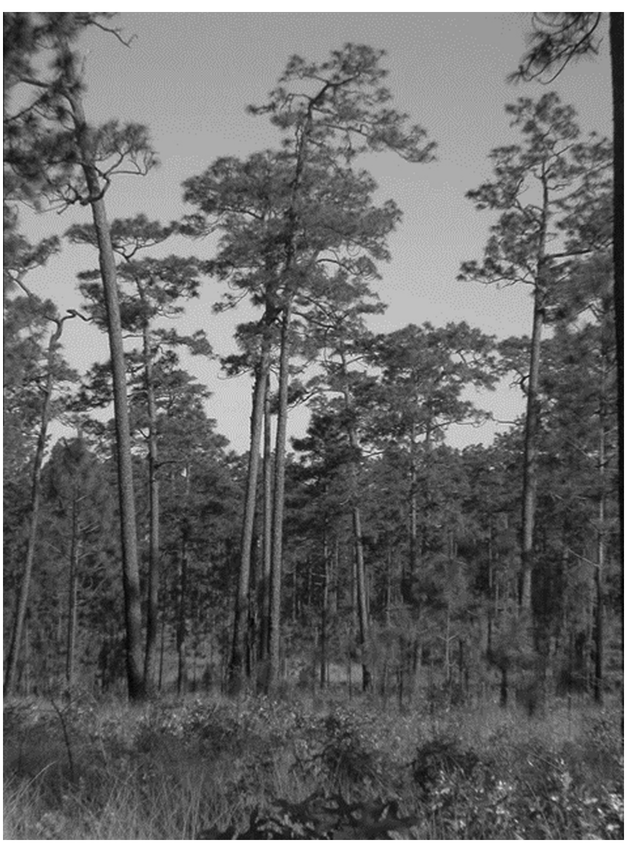

Fig. 1. Old-growth longleaf pine (*Pinus palustris*) savanna at the Wade Tract (Thomas County, GA). Longleaf pine in overstory; wiregrass (*Aristida beyrichiana*), turkey oak (*Quercus laevis*), runner oak (*Quercus pumila*), and herbaceous species in ground cover in foreground. Prescription fires, conducted most often in the spring (April–June) occur on a 1.5 year rotation on average. Photo: WJP, November 11, 2008.

We reassess guiding concepts used in pine savanna restoration and management by comparing two models and their applications. We first summarize the succession and the vegetation-fire feedback models, focusing on the proposed driving mechanisms for vegetation change over time. We then compare concepts of evolutionary change and disturbance inherent in the different models, and summarize the evidence for a vegetation-fire feedback model. Lastly, we consider restoration and management based in the two paradigms. Based on this review, we propose a shift to paradigms that involve vegetation-fire feedbacks as fundamental ecological and evolutionary processes in pine savanna ecosystems. We then project how application of the vegetation-fire feedback paradigm could affect restoration and management of savanna and grassland ecosystems worldwide.

2. The two models

2.1. Succession model

Concepts that currently underlie most pine savanna restoration and management practices originate from Clements' (1916) classic theory of succession. This model postulates that following disturbance, a directional progression of communities occurs toward an equilibrium climax state via autogenic changes in vegetation composition and structure (Whittaker, 1953; Walker et al., 2007; Hobbs and Suding, 2009). Climax states are defined by the physiognomy of dominant vegetation, constrained by climate (temperature and precipitation), and modified by edaphic conditions such as soil and topography (Tansley, 1935).