Updating Models for Restoration and Management of Fiery Ecosystems

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14 **Abstract**

15 Scientific models that guide restoration/management protocols should be reviewed periodically
16 as new data become available. We examine ecological concepts used to guide restoration of pine
17 savannas and woodlands, historically prominent but now rare habitats in the southern North
18 American Coastal Plain. For many decades, pine savanna management has been guided
19 predominantly by a biome-centric succession model. Pine savannas have been considered early-
20 successional communities that, in the absence of fire, transition rapidly toward closed-canopy
21 hardwood forests. Recurrent fires have been viewed as exogenous disturbances that maintain
22 savanna ecosystems as a sub-climax, blocking succession to an equilibrium steady state (closed-
23 canopy forests). Over recent decades, a vegetation-fire feedback model has emerged in which
24 pine savannas are conceptualized as persistent, non-equilibrium communities maintained by
25 endogenous, co-evolutionary vegetation-fire feedbacks. Endemic plant species are resistant to
26 fires and specialized for post-fire conditions generated by frequent lightning fires, primarily
27 within a distinct fire season. These species produce pyrogenic fine fuels that are easily ignited.
28 The resulting fire regimes, entrained by these vegetation-fire feedbacks, are predicted to result in
29 persistent pine savannas. Local variation over space and time in evolutionary feedback
30 mechanisms between pyrogenic vegetation and fire regimes produces heterogeneous landscapes.
31 Disturbances of these feedbacks, such as human fire suppression, are postulated to result in rapid
32 transition to communities lacking feedback elements, such as closed-canopy forest and those
33 without pyrogenic species. Succession-based management focuses on reversing the transition to
34 forest, primarily by removing hardwoods and reintroducing fire as a disturbance. However, we
35 advocate restoration and management approaches that target reinstitution of functional
36 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.

Keywords: alternative state, disturbance, ecosystem model, savanna, succession, vegetation-fire feedbacks

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 & 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 Figure 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 C₄ grasses, such as *Aristida stricta*, *A. beyrichiana*, and *Schizachyrium scoparium* (Wahlenberg, 1946; Croker & 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 (Myers & 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.

We reassess guiding concepts used in pine savanna restoration and management of 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.

Figure 1 (single column). 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.

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 & 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).

The succession model has been assumed to apply to pine savannas (Fig. 2). Pine savanna physiognomy (low tree density and diversity, open-canopy structure, and low groundcover) has been assumed to indicate that pine savannas are an early seral or sub-climax state (e.g., Whittaker, 1953) or even a climax state (e.g., Chapman, 1932) maintained by exogenous fires that repeatedly reset transitions toward forest (see reviews in Menges & Hawkes, 1998; Platt, 1999; Noss et al., 2015). As a result, pine savannas have been repeatedly labeled as early-successional habitat (e.g., Kush et al., 1999; van Lear & Harlow, 2000; Hunter et al., 2001; Trani et al., 2001; Evans et al., 2013). The presence of woody species (e.g., oaks and hickories) has suggested that shade-tolerant, "late" successional species (*sensu* Connell, 1978) would invade communities dominated by "early" successional species (e.g., pines, grasses; Veno, 1976). In the absence of fire, shade-tolerant hardwoods are hypothesized to ultimately replace pine savannas with closed-canopy hardwood forests (e.g., Harper, 1911; Gano, 1917; Wells & Shunk,

113 1931; Heyward, 1939; Quarterman & Keever, 1962; Monk, 1965; Huston & Smith, 1987; Van
 114 Lear et al., 2005). The succession model has often invoked humans as the primary causative
 115 agent for pine savanna sub-climax ecosystems (i.e., as “cultural artifacts”; see Van Lear et al.,
 116 2005), despite abundant evidence that these systems have been associated with fire for millions
 117 of years (Noss et al., 2015).

SUCCESSION MODEL

118
 119 **Figure 2 (2-column).** Successional model for restoration and management of pine savannas and
 120 woodlands in the southeastern United States. Boxes indicate landscapes and arrows denote
 121 possible transitions related to fire/no fire. Increases/decreases in life forms are shown as they are
 122 expected to occur under within the succession theory framework.

123

124 Sub-climax communities like pine savannas have been presumed to be maintained by
 125 exogenous disturbance regimes. Fire is viewed as a recurrent, external disturbance ignited by
 126 lightning or humans (Whittaker, 1953; White, 1979, Van Lear et al., 2005). Over time the

vegetation is predicted to evolve resistance to repeated disturbances (Van Lear et al., 2005), resulting in a distinct sub-climax state (Whittaker, 1953). This succession paradigm has pervaded scientific theory and practical fire management in the southeastern United States for almost a century.

2.2 Vegetation-fire feedback model. Challenges to the succession paradigm of pine savannas have emerged in recent decades. Research has suggested that old-growth populations of pine savanna trees (*sensu* Landers, 1991) are maintained as uneven-aged and sized stands by fire regimes generated by endogenous feedbacks involving shed pine needles as pyrogenic fuels (e.g., Platt et al., 1988b, 1991, 2015a; Beckage et al., 2006, 2009; Noss et al., 2015). More recent study has suggested that ground layer species, such as C₄ grasses and some indigenous savanna trees, also may be involved in vegetation-fire feedbacks (e.g., Kane et al., 2008; Beckage et al., 2011; Fill et al., 2012). The vegetation-fire feedbacks, depicted in the left side of Fig. 3, are hypothesized to produce characteristic landscape patterns (*sensu* Peterson, 2002) that do not change greatly in the intervals between fires, varying among states ranging from grasslands to savannas to woodlands depending on local fire regimes (Beckage et al., 2006) within landscapes (Noel et al., 1998; Hctor et al., 2006; Platt et al., 2015a). Persistence of local environments over evolutionary timescales is postulated to result in extensive endemism as plants, especially those in the ground layer, become specialized for local environmental conditions generated by vegetation-fire feedbacks (Platt, 1999; Noss et al., 2015; Platt et al., 2015a).

VEGETATION-FIRE FEEDBACK MODEL

Figure 3 (2-column). Vegetation-fire-feedback model for restoration and management of pine savannas and woodlands in the southeastern United States. Boxes indicate landscapes and arrows denote possible transitions related to fire/no fire. **Left:** various savanna landscapes, as for example, upland and lowland landscapes along an elevation gradient. Transitions among woodland, savanna, and grassland physiognomies are based on changes in pyrogenicity of vegetation and resulting vegetation-fire feedbacks. **Right:** Disturbance sequence involving removal of fire-feedbacks from savanna landscapes. The resulting transition is to a transient pine - hardwood forest. Prolonged loss of fire-feedbacks, as with fire suppression, results in no pine regeneration, forest tree recruitment, and loss of savanna species, and a consequent shift to hardwood forest. Restoration of evolutionary savanna landscapes involves removal of forest tree species, reintroduction of lost savanna species, and reinstitution of fire-feedbacks systems. Restoration programs might involve prescribed fire that shifts ecosystems to de novo fiery

ecosystems, but does not shift toward evolutionary savanna landscapes because evolutionarily-derived vegetation-fire feedbacks are no longer present.

Contemporary vegetation-fire feedback models postulate that pine savannas are maintained over time. Strong positive feedbacks (*sensu* Holling, 1973; Beckage et al., 2009; Hobbs & Suding, 2009) among key abiotic and/or biotic variables are hypothesized to maintain savanna landscapes and block transition to alternate states (*sensu* Scheffer et al., 2001; Suding et al., 2004; Odion et al., 2010). We envision the most important feedbacks as involving two state variables: fire regime and vegetation (e.g., Beckage et al., 2009; Lehmann et al., 2011; Murphy & Bowman, 2012). At small spatial scales and on short ecological time scales, individual fires in pine savannas produce non-catastrophic effects on species composition and dynamics (*sensu* Connell & Slatyer, 1977; Platt & Connell, 2003), resulting in short-term, localized changes (*sensu* Pickett & White, 1985; Poff, 1992) while maintaining ecosystem properties (*sensu* Peterson, 2002). At large spatial scales and long evolutionary time scales (Poff, 1992), individual fires become components of fire regimes that constitute integral aspects of the environment of landscapes rather than recurrent independent phenomena within landscapes. Such patterns inherent in fire regimes (historical range of variability, White, 1979; Resh et al., 1988; Richardson, 1998; Platt, 1999; Keane et al., 2009) can result in strong co-evolutionary relationships between fire and the vegetation (*sensu* Mutch, 1970; Gagnon et al., 2010; Platt et al., 2015a), maintaining persistent states (*sensu* Peterson, 2002; Beckage et al., 2009; Keeley et al., 2011). The resulting co-evolutionary history of fire and plants in savannas, which spans millions of years (Fig. 4), forms the basis for understanding vegetation dynamics and fire effects in pine savannas. We suggest that these co-evolutionary patterns involving vegetation and fire

185 have become widespread across the southern North American Coastal Plain as C₄ grass
 186 expansion resulted in savannas becoming a dominant habitat in the late Miocene (Fig. 4).
 187

EVOLUTIONARY HISTORY OF FIRE-FEEDBACKS

188
 189 **Figure 4 (single column).** Key points in evolutionary time illustrating the temporal history of
 190 vegetation-fire feedbacks relative to anthropogenic influences in the history of pine savannas.
 191 Numbers indicate events on a time scale of 550 million years. Geological scale (eras and
 192 subdivisions) indicate a 440 my history of fire in vegetation, a 100 my history of fire-adapted
 193 traits in pines, a 50 my history of savannas in the southeast, and an 8 my history of C₄ grasses
 194 dominating ground layers in savannas. All predate human history in the region. (^aPausas and
 195 Keeley, 2009; ^bHe et al., 2012; ^cGraham, 1999; ^dEdwards et al., 2010; ^eRichardson, 1998)

196

197 **3. Evolutionary processes in the models.**

3.1. *Succession model.* In both the succession and vegetation-fire feedback models, fire is an important driver of vegetation change. Accordingly, in the first stage, vegetation traits evolve that enable plants to inhabit areas subject to repeated fires (see discussion of regeneration traits related to fire in Wahlenberg, 1946; Croker and Boyer, 1975; Rowe, 1983; Pausas et al., 2004; Keeley et al., 2011). The initial evolutionary result of repeated fires is likely to be reflected in traits that affect survival (Platt, 1999). For example, characteristics of fire regimes influence distributions and relative abundances of species with reseeding vs. resprouting recovery strategies in pine savannas and similar habitats worldwide (e.g., Menges & Kohfeldt, 1995; Keeley & Zedler, 1998; Bond & Midgley 2003; Menges 2007, Crandall & Platt, 2012). Some pine savanna species have been shown to produce seed banks that allow them to evade fire (e.g., Maliakal et al., 2000; Cohen et al., 2004). The most common overstory species, *Pinus palustris*, is a non-resprouter well-known for the ability of juvenile and adult trees to survive fires, beginning at an early age (see Platt et al., 1988b; Platt, 1999 and references therein). Many indigenous species survive fires as below-ground organs such as roots or growth buds at ground level (Platt, 1999). Indeed, underground storage organs appear to be a common, independently evolved trait of many savanna plant species (e.g., Drewa et al., 2006; Simon & Pennington, 2012; Maurin et al. 2014).

Species that survive/evade fires are subjected to natural selection on traits important in post-fire environments. These fire-regulated traits include heat-stimulated germination (Wiggers, 2011) and fire-stimulated flowering (e.g., Lemon, 1949; Clewell, 1989; Brewer & Platt, 1994; Fill et al., 2012). The succession model postulates that fire regimes maintain transitional communities. Therefore, under the succession model these fire-regulated traits are viewed as advantageous insofar as the disturbance regime persists and thus such traits confer an advantage.

If fires do not occur, these early successional species are presumed to be suppressed or eliminated by forest hardwoods via shading during the transition to forest.

3.2. Vegetation-fire feedback model. The vegetation-fire feedback model is predicated on fire regimes maintaining persistent, non-transient communities. Thus, although the evolution of resistance to recurrent fires and survival in post-fire environments (*sensu* Platt 1999) is shared with the succession model, the evolution of traits that modify fire regimes in ways that favor pyrogenic species is postulated to occur in the vegetation-fire feedback model (Platt 1999). Further, the fire regimes become modified by the vegetation-fire feedbacks in ways that maintain the savannas. Invasion by less fire-tolerant species is suppressed by recurrent fires that favor pyrogenic species. Thus, less fire-tolerant species are likely never to be present as established plants, except in local edaphic settings (e.g., solution holes in limestone outcroppings in the Florida Rocklands in the Everglades; Schmidt et al., 2002). We also suggest that pyrogenic and non-pyrogenic communities can be maintained within local landscapes if mechanisms exist that 1) ignite fires within the pyrogenic communities, and 2) block entry of fires into non-pyrogenic communities.

Over long temporal scales, a predictable fire regime can emerge from the evolution of strong feedbacks between vegetation and fire. Natural selection for traits that influence flammability potentially can result in assemblages of specialized species (Mutch, 1970; Gagnon et al., 2010) that determine fire regimes. Such fire regimes should be entrained by aspects of climate, such as seasonal times of natural lightning ignition (Platt, 1999; Platt et al., 2015a). This feedback provides a selective filter for vegetation attributes (Myers & Harms, 2011; Richardson, 1998; Platt, 1999; Ackerly, 2003; Cavender-Bares et al., 2004; He et al., 2012; Veldman et al., 2013),

by means of which fire becomes an endogenous part of the system (Mutch, 1970; White, 1979; Odling-Smee, 1996; Platt, 1999, Platt et al., 2015a). Plant life history characteristics, in turn influence fire regime attributes (Odling-Smee et al., 1996; Platt, 1999; Erwin, 2008; Bond & Scott, 2010). The natural fire regime is therefore not simply an exogenous, climate-initiated disturbance to pine savannas, but is modified by biotic components that are intrinsic, and often endemic, to these communities, thereby maintaining community persistence and ensuring fire occurrence (Mutch, 1970; Platt, 1999; Erwin, 2008; Ursino, 2014). On evolutionary time-scales (Fig. 4), therefore, feedbacks between system variables can link fire and vegetation functionally, freeing the ecosystem from directionality imposed under the succession paradigm (Erwin 2008; Beckage et al., 2009; Whitlock et al., 2010). Moreover, as the nature of vegetation-fire feedbacks changes over time, so should the characteristics of fires, resulting in the evolution of fire regimes that vary locally depending on the feedbacks involved (also see Hctor et al., 2006).

4. Concepts of disturbance in the models.

4.1. Succession model. In the succession model, disturbances are considered to result in “blank slates” on which community organization and assembly occurs (White, 1979; Platt & Connell, 2003). If recurrent disturbances are similar in their effects, then species with traits that result in survival of the disturbances should persist as sub-climax communities. In this context individual fires can be considered part of a disturbance regime that becomes part of the environment (e.g., Rykiel, 1985). This view considers fires to be an important driving force in species evolution when they occur repeatedly over time.

4.2. *Vegetation-fire feedback model.* In the vegetation-fire feedback model, the presence of positive feedbacks is predicted to enhance the persistence of landscapes with the species that produce the feedbacks. Rather than requiring recurrent exogenous disturbances, the flammable vegetation increases the likelihood of that subsequent ignitions will result in fires that spread across the landscape. Individuals that facilitate fire spread are postulated to benefit (Gagnon et al. 2010), and as a result the savanna landscape is maintained. This modification of the environment (*sensu* Platt 1999) in a way that benefits the flammable species allows evolution to occur in a number of different ways. For example, different species may influence characteristics of fires differently, and so different landscapes may result (Fig. 3). Species also may respond to characteristics of the physical environment (e.g., soil characteristics, moisture regimes) expressed in post-fire environments, resulting in endemic species responding to landscape differences not directly produced by recurrent fires, but made possible by such fire regimes.

5. Evidence for an evolutionary vegetation-fire feedback model. Recent studies of fire regimes in the North American Coastal Plain support an evolutionary feedback-centric model for pine savanna dynamics. Although moisture levels in the region (mean annual precipitation 1040-1750 mm; Brockway et al., 2005) can support closed canopy forests, pine savannas have been present in the southeast prior to human burning practices (Noss et al., 2015). Historically, lightning was a dominant ignition source. The southeast has the highest lightning strike frequency in the United States, with high rates of wildfire ignitions (Komarek, 1964; Robbins & Myers, 1992; Genton et al., 2006; Outcalt, 2008), especially in pine savannas (Chapman, 1950; Duncan et al., 2010; Platt et al., 2015a). Historical average fire return intervals, predicted to be the shortest in the United States (Guyette et al., 2012), are commonly noted to be as frequent as

1-2-3 years in the southeastern U.S. based on tree ring data from as early as the late 16th century (Henderson, 2006; Huffman, 2006; Harley et al., 2011; Stambaugh et al., 2011). Further, these same studies suggest that fires historically occurred predominately in the transition from dry springs to wet summers, at the times that lightning storms first occurred during the year and when fine fuels were most likely to be dry (Beckage et al., 2003; Slocum et al., 2010b; Fill et al., 2012; Platt et al., 2015a). These fires could burn considerable areas under favorable climatic and fuel conditions (Slocum et al., 2003, 2010a; Platt et al., 2015a). These studies indicate that natural variation within fire regimes is likely much less than is often hypothesized using succession models based on fire as a disturbance.

Research has also demonstrated fire-dependent characteristics of endemic ground layer flora and their influence on fire regimes. Life history strategies and phenologies of many taxa are tied to fire regime characteristics, including frequency and seasonality (Streng et al., 1993; Platt, 1999; Schmitz et al., 2002; Platt et al., 1988a; Myers & Harms, 2009; Fill et al., 2012). In turn, local variation in fine fuel flammability (e.g., of pine needles, grasses, hardwood leaves; Hiers et al., 2007; Kane et al., 2008; Reid et al., 2012; Ellair & Platt, 2013; Hiers et al., 2014) and spatial distribution within landscapes feeds back to fire regime characteristics such as frequency, intensity, and extent (Platt et al., 1991; Platt, 1999; Thaxton & Platt, 2006; Ellair & Platt, 2013; Robertson & Hmielowski 2014). As a result, evolutionary fire regimes should deviate from those expected if fires were strictly exogenous disturbances based on climate (Platt 1999) or human ignitions (Van Lear et al., 2005; Platt et al., 2015a).

The vegetation-fire feedback links pyrogenic vegetation with likelihoods and characteristics of fires. These feedbacks vary among vegetation types within local landscapes. For example, spatial and temporal variation in ground layer fuels influence both fire intensity and juvenile tree

mortality (Thaxton & Platt, 2006; Ellair & Platt, 2013), thereby regulating recruitment success of both juvenile hardwoods and pines into the overstory (Platt et al., 1988b; Grace & Platt, 1995) and in turn, fine fuel accumulation (Veldman et al., 2013). Low-intensity prescribed fires and those applied when hardwoods are physiologically dormant are less likely than growing season fires to cause complete hardwood mortality (Olson & Platt, 1995; Glitzenstein et al., 1995; Drewa et al., 2002, Van Lear et al. 2005). However, some species (e.g., oaks) may produce flammable litter (Kane et al., 2008) or provide fire refugia (e.g., creating patchiness) in frequently-burned uplands. Some pines and hardwoods smolder, and thus may later ignite areas that may not have burned initially, diversifying local fire return intervals and effects on vegetation. Some species, like *Serenoa repens*, may result in increased fire intensity above ground level by erect, highly flammable evergreen leaves. Timing also influences reproduction and persistence in endemic understory species (e.g., Platt et al., 1988a; Clewell, 1989; Fill et al., 2012), whose composition influences fuel structure (e.g., fuel loads and bulk density; Reid et al., 2012). These examples indicate that fire characteristics can develop over time as species with differences in pyrogenicity are added and lost from communities (also see Gagnon et al., 2010).

Our proposed paradigm shift requires reconsideration of what constitute disturbances in pine savannas. As illustrated in the right side of Figure 3, disturbances involve disruptions of evolved vegetation-fire feedbacks: changes in the fire regime or loss of pyrogenic species. Changes in the frequency, seasonality, severity, or extent of the fire regime that deviate from the historical range of variability tend to cause loss of pyrogenic vegetation and hence fire-feedbacks. In this context, we contrast the often highly specific context of natural lightning-ignited fire regimes with those that are possible given human control of ignitions (e.g., Platt et al., 2015a). Attempts to introduce variation in characteristics of prescribed fire regimes (e.g., Robbins and Myers,

1992) may actually be incorporating disturbance into prescribed fire regimes (Platt et al., 2015a). Thus, if vegetation-fire feedbacks are removed by such disturbances, pine savannas can shift to a variety of other systems, only one of which would be hardwood forest. De novo ecosystems might be more likely (Fig. 3). The loss of pyrogenic species responsible for the vegetation-fire feedbacks impedes the transition back from forest to savanna (with reinstitution of fires; a hysteresis). If savanna species have not survived in suppressed states or do not re-colonize, such reversal will not be possible. Thus ecological processes hypothesized to transition pine savannas toward forest under the succession model become one type of disturbance under the fire-feedback model.

Human activities in pine savannas often introduce disturbances to pine savanna vegetation-fire feedbacks. Common disturbances include fire exclusion (Beckage et al., 2006; Beckage & Ellingwood, 2008; Slocum et al., 2010b). In addition, human-induced changes in fire regimes that affect fine fuel properties (Platt et al., 2015a) and produce changes in vegetation structure and composition alter subsequent vegetation-fire feedbacks and thus fire regimes (e.g., Waldrop et al., 1992; Brockway & Lewis, 1997; Glitzenstein et al., 2003; Platt et al., 2015a). Alterations of fire regime characteristics can cause structural and functional change at the community level, including increased shrub and tree density, declines in endemic herbaceous flora and fauna, formation of a closed canopy, and changes in functional species assemblages and nutrient fluxes (Huffman & Blanchard, 1991; Glitzenstein et al., 1995; Menges & Hawkes, 1998; Gilliam & Platt, 1999; Carter & Foster, 2004). As indicated in Figure 3, prolonged disturbances potentially result in landscapes characterized by fire regimes and vegetation-fire feedbacks outside the historical range of variability; such de novo landscapes potentially could have their own self-organizing feedbacks (e.g., Hobbs et al., 2006; Keith et al., 2013). Such landscapes include not

only closed-canopy hardwood forest, but also de novo savanna-type landscapes without evolutionarily-derived feedback mechanisms. Reintroduction of fire alone is insufficient for restoration of evolutionarily-derived landscapes if the evolutionary feedback mechanisms have disappeared (e.g., Huffman & Blanchard, 1991; Huffman & Werner, 2000; Varner et al., 2005).

5. Restoration and management of pine savannas based on the models.

5.1 Succession Model. Changes in disturbance regimes are considered the primary cause of pine savanna vegetation change. Frequent fires are viewed as maintaining plant communities that readily burn because of the abundance of fine fuels produced by grasses and pines, the “early-successional” species (Van Lear et al., 2005). Extending fire return intervals, and especially fire exclusion, is predicted to facilitate invasion by woody plants (“late successional” species). As the ground layer becomes more shaded and fires become less likely to burn, forest hardwoods that are less fire tolerant are predicted to invade and increase in abundance and size, eventually forming a closed canopy forest, while those herbaceous species typical of pine savannas are predicted to become shaded and eventually lost (Veno, 1976). Pine savannas are thus considered as almost always in some stage of transition toward forest (see references cited in Platt, (1999); Van Lear et al., (2005)).

Pine savanna restoration and management using the succession model have relied primarily on reinstitution of fire regimes (using prescribed fires). Prescribed fires, if reintroduced and repeated over time, are hypothesized to generate conditions favorable for pine savanna species and block succession to closed-canopy forest (Van Lear et al., 2005). Reinstitution of some historical fire regime, often predicated to be of human origin (Van Lear et al., 2005) is suggested as optimal for reformation of the early successional pine savannas containing indigenous species

(Van Lear et al., 2005). The central thesis for restoration has been to reintroduce fires as recurrent disturbances, with the proviso that frequent disturbances are necessary to generate conditions needed by early successional pine savanna species (e.g., McGuire et al., 2001) and to avoid stand-replacing high intensity fires that might result with longer fire return intervals (Van Lear et al., 2005). Indigenous species are assumed to recolonize once conditions have been restored (the “Field of Dreams” hypothesis; Palmer, 1997).

The restoration goals using the succession model have been primarily to reverse hardwood encroachment into savannas. Prescribed fire, often in conjunction with other human disturbances (i.e., mechanical and chemical treatments; Menges & Gordon, 2010), have focused on reducing size and numbers of woody plants, while benefitting native herbaceous species, especially when combined with ecologically-oriented timber management (e.g., Masters et al., 2003). However, the emphasis primarily on reinstituting frequent fires (rather than all aspects of a fire regime) and removal of especially larger hardwoods, irrespective of species’ flammability (e.g., Kane et al., 2008; Ellair & Platt, 2013), not only impedes re-establishment of the vegetation-fire feedback but may even eliminate it entirely. Endemic, fire-facilitating ground-layer vegetation may not recolonize after mechanical treatments such as plowing. Such approaches to restoration, especially combinations of prescribed fires and herbicides, may not be synergistic and thus may not result in restoration of original pine savannas, but instead may shift communities to new states (e.g., Platt et al., 2015b) if feedback elements are lacking.

5.2. Vegetation-fire feedback model. The feedback-centric model predicts that there may be multiple vegetation-fire feedbacks that operate within the range of characteristics of historical fire regimes. These feedbacks should likely operate on different spatial and temporal scales, resulting in variation in fire regimes. This paradigm places emphasis understanding what

feedbacks are disrupted by disturbances in fire-frequented systems, so that actions can be effective at restoring and managing for evolutionarily-generated feedbacks. Restoration should involve reinstitution of components of fine fuels in disturbed landscapes to produce fire regimes whose characteristics lie within those expected under natural conditions. Thus, in contrast to succession models, the reinstitution of fire regimes needs to be coupled with reinstitution of vegetation that produces the vegetation-fire feedbacks present historically. Thus, forming a flammable mixture of fine fuels using species such as warm season C₄ grasses, pines such as longleaf pine that produce pyrogenic shed needles, and flammable shrubs and herbs are crucial for restoring vegetation–fire feedbacks that can operate across landscapes (Platt, 1999; Ellair & Platt, 2013; Hiers et al., 2014; Platt et al., 2015a,b).

Fire prescriptions that vary appropriately within historical fire regimes should produce different savanna mosaics by encouraging diverse feedback mechanisms with native vegetation. Some of these feedbacks might be especially useful in managing for wildlife populations or endangered/threatened species that interact with multiple landscape components. For example, the flatwoods salamander (*Ambystoma cingulatum*) is one species that depends on frequently-burned wetlands (Gorman et al., 2009), and possibly even on wiregrass (*Aristida stricta*, *A. beyrichiana*) structure in wetland ecotones (Jones et al., 2012). A highly flammable species, wiregrass burns under a variety of conditions, but responds to “fire season” fires (*sensu* Platt et al. 2015) with increased flowering (Fill et al., 2012), increasing the likelihood of fire spread from uplands into wetland ecotones and producing vegetation structure conducive for the flatwoods salamander following such fires. Such fine-tuned relationships indicate the importance of prescribed fire management plans based on vegetation-fire feedback models that include climatic

drivers similar to those that historically operated within the North American Coastal Plain (e.g., Guyette et al., 2012; Platt et al., 2015a).

Efforts to practice management based on reinstitution of vegetation-fire feedbacks have not been widespread. Nonetheless, some attempts have been ongoing for more than a decade (e.g., Platt et al., 2006a; Hiers et al., 2012; Clewell & Aronson, 2013; Platt et al., 2015a). In the context of restoring fire regimes that facilitate vegetation-fire feedbacks, developing recurrent fires that mimic those occurring naturally (i.e., lightning-ignited “fire season” fires) have been demonstrated to result in increases in warm season grasses, especially in lower, often wetter habitats that connect uplands in the landscape (Slocum et al., 2010a,b; Platt et al., 2015a). As a result, larger fires occur that spread across landscapes, generating a range of vegetation-fire feedbacks that result in maintenance of a range of local pyrogenic habitats (ecosystems, *sensu* Hoctor et al., 2006).

6. Toward a global savanna vegetation-fire feedback model.

Based on our review, we propose that restoration and management shift the conceptual foundation of protocols from a succession model to a vegetation-fire feedback model. The vegetation-fire feedback model shares ideas with the succession model. Nonetheless, instead of a linear model of change interrupted by fire as a disturbance, feedbacks are postulated to change over ecological and evolutionary time as species composition changes and as species evolve. We consider our contemporary framework useful for restoration and management of North American Coastal Plain pine savannas based on concepts involving distinct landscapes maintained by differences in vegetation-fire feedbacks. Our updated vegetation-fire feedback model should facilitate pine savanna management and restoration, but it should also serve to place these

activities in a global context. Vegetation-fire feedback concepts have been postulated for savannas elsewhere around the world (e.g., Staver et al., 2011; Hirota et al., 2011; Hoffmann et al., 2009). Thus, this global perspective should allow practitioners to benefit from research on savannas worldwide.

State-and-transition models are useful for describing ecosystem dynamics for management. They have been used extensively to model rangeland vegetation dynamics under various management scenarios, particularly for cases in which linear succession concepts were inadequate to explain ecosystem changes (e.g., Westoby et al., 1989; Laycock, 1991; Fuhlendorf & Smiens, 1997; Allen-Diaz & Bartolome, 1998). Similar conceptual models have been described for some pine savanna communities, such as isolated depression wetlands (Kirkman et al., 2000; De Steven & Toner, 2004), upland Florida scrub (Menges & Hawkes, 1998), and Florida pine flatwoods and dry prairie (Huffman & Werner, 2000). We urge that these models serve as a starting point for development of evolutionarily-based state-and-transition models that emphasize feedbacks between key vegetation species and fire regime characteristics at scales relevant to management (e.g., Odion et al., 2010; Fig. 4). An evolutionary perspective could thus be incorporated into spatially-explicit, context-specific models and planning scenarios. Current models and decision frameworks for pine savannas have advanced as far as incorporating fire effects on plants based on their life history characteristics (e.g., Pyke et al., 2010), but there is a paucity of models incorporating how plants involved in specific feedbacks might modify fire regimes.

The ecological and evolutionary perspective should be applicable to natural fire-dominated mesic and humid savannas and grasslands worldwide (Sage, 2004; Woinarski et al., 2004; Bond et al., 2005; Bowman, 2005; Beerling & Osborne, 2006; Staver et al., 2011). For example,

Australian eucalypt savannas (Staver et al., 2011; Werner & Prior, 2013), the Brazilian cerrado (Hoffmann et al., 2009), and mopane savannas of southern Africa (Kennedy & Potgeiter, 2003) all contain savanna trees that produce flammable fuels and all have flammable C4 grasses. Brazilian Campos grasslands (Fidelis et al., 2014) are also maintained by grazing and fire in a climate favorable to forest (Overbeck et al., 2007). This conceptual framework also has relevance to fire-prone shrublands (e.g., Burger & Bond, 2015). A global model thus could be based on the contemporary framework we propose for pine savannas, but modified so as to be general for natural savannas with an evolutionary time frame dating at least to the Miocene (Beerling & Osbourne, 2006).

We propose a global paradigm shift for the fire dynamics of pine savannas. We suggest replacing concepts of fires as exogenous disturbances (climatic or human in origin) with ones in which fires are evolutionary selection pressures on plant populations and ecosystems. For those natural savannas with a long evolutionary history, we further suggest that restoration and management focus on reinstitution of evolutionarily derived vegetation-fire feedbacks. Worldwide, the biodiversity of fire-coevolved savanna ecosystems is likely to survive only if concepts of fires as external disturbances are replaced by evolutionary concepts involving fire regimes and vegetation-fire feedbacks as the basis for restoration and management.

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