Part IV

Synthesis

19

Water Limitation, Fire, and Savanna Persistence

A Conceptual Model

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19.1 Introduction

Savannas are terrestrial biomes typically characterized by the coexistence of grasses and woody plants (Chapter 1). Two broad physiognomies can be distinguished in savannas on the basis of the presence or absence of a woody overstory. The savanna physiognomy (hereafter savanna) is broadly characterized by a continuous herbaceous ground layer, which we collectively refer to as "grass," and an incomplete overstory of woody plants (Sarmiento and Monasterio 1975; Sarmiento 1984; Huber 1987; Scholes and Archer 1997; van Auken 2000; Werner and Prior 2013). The grassland physiognomy (hereafter grassland) also has a continuous grass layer, but no obvious woody overstory. The grass layer in both physiognomies consists of predominantly C_4 species in warm temperate, and sub-tropical and tropical regions (Werner 1991; Edwards et al. 2010). The composition of the grass component is consistent across both physiognomies (e.g. Weaver 1960; Daubenmire 1978). The savanna woody cover can vary widely in density from scattered, large-statured individuals (i.e. trees) to nearly closed woody canopy, and often comprises species that do not occur in adjacent forests (Platt et al. 1988b; House et al. 2003; Ratnam et al. 2011; Staver et al. 2011). Savanna is thus intermediate, structurally and compositionally, between grassland and forest.

A central challenge in savanna ecology has been to identify the mechanisms that maintain savannas (e.g. Sarmiento 1984; Scholes and Archer 1997). A variety of savanna maintenance mechanisms (SMMs) have been postulated to drive the coexistence of grasses and woody plants. We do not review all proposed SMMs, as they have been reviewed elsewhere (e.g. Jeltsch et al. 2000; Sankaran et al. 2004; Murphy and Bowman 2012). While no single mechanism has emerged as a universal savanna determinant, precipitation has consistently been identified as an important driver of woody cover at

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broad geographic scales (Sankaran et al. 2005; Bucini and Hanan 2007; Sankaran et al. 2008). Phenomenological studies have found increasing woody cover (e.g. Sankaran et al. 2005; Bucini and Hanan 2007), and greater likelihoods of transition from savanna to forest states (Staver et al. 2011; Favier et al. 2012), as moisture increases.

We develop a conceptual framework that describes (i) how SMMs vary with water availability, and (ii) corresponding expectations for the functional characteristics of savanna and forest woody species. In our conceptual model, as precipitation increases, SMMs shift from water limitation to recurring fire disturbances and then to internal feedbacks on fire. Our model is based on the changing nature of resource limitation in savannas, from soil water in arid regions to understory light in mesic regions. While not explicitly considered in our framework, other mechanisms hypothesized to control coexistence of grasses and woody plants, such as herbivory and soil nutrients, can be incorporated into our conceptual model.

19.2 Conceptual Model

We organize SMMs into three general classes that align with precipitation, as illustrated in Figure 19.1: these are water limitations, fire disturbances, and internal vegetation–fire feedbacks. Water limitation in arid regions restricts tree populations, inhibiting the development of a closed overstory canopy and preventing the competitive exclusion of the grass understory through reduced understory light levels (e.g. Hennenberg et al. 2006). Recurring fire disturbances can limit woody populations through elevated mortality (usually acting most strongly on early demographic stages – see Chapter 12), inhibiting the formation of a closed canopy, and maintaining the community in an open savanna state (e.g. Bond et al. 2005). Both water limitations and fire disturbances can be considered part of a broadly defined "depressant effects" class of SMMs that are similar to each other in that they prevent formation of a closed woody canopy (i.e. Jeltsch et al. 2000). Our third class of SMMs is vegetation–fire feedbacks, where the strength of the depressant effect is dependent on the state of the system. These feedbacks, which are internal to the system, can potentially bound communities in a savanna state, for example, when the strength of the depressant effect on woody canopy cover declines as the system approaches a treeless state and increases as it approaches a forest (Beckage et al. 2009, 2011). SMMs have been organized in other frameworks, as well (e.g. Jeltsch et al. 2000; Hoffmann et al. 2012; Murphy and Bowman 2012; Werner and Prior 2013), and these alternate frameworks are not orthogonal to the classification presented here.

We focus on water as a limiting factor and describe changes in operating SMMs with increasing water availability (Figure 19.2). We expect a shift in the limiting resources from soil water to understory light with increasing precipitation. At low precipitation, water limitations will prevent trees from forming an overstory canopy (Figure 19.2, region i). Overstory individuals will increase in density with increasing water availability, leading to lowered understory light levels and reduced grass biomass (Figure 19.2, region ii). Fire disturbances will increase in importance for maintaining open savannas as water limitations ease. Closed forests will eventually become a potential ecosystem state as a water availability threshold is reached (Figure 19.2, region iii). Understory light, rather than soil water, will become the limiting resource, and competitive

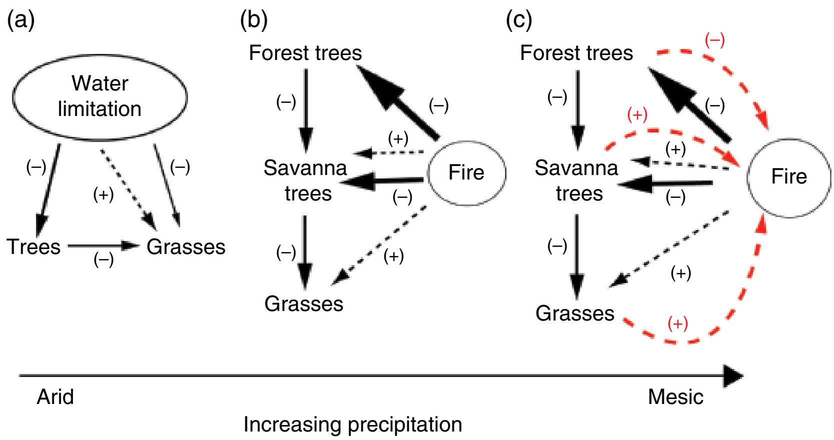

Figure 19.1 Three classes of savanna maintenance mechanisms (SMMs) in relation to precipitation. (a) Environmental constraints, such as a water limitation, can limit woody populations, maintaining an open canopy and preventing the competitive displacement of understory grasses through shading. Although water limitation may have a direct, negative effect on the grass layer, the net result is an indirect positive influence on grass persistence. (b) As precipitation increases, woody populations can form a more closed canopy so that competition shifts from soil moisture to understory light. The result will be a shift in canopy composition from savanna woody species to forest species in the absence of fire; forest species are shade-tolerant, but sensitive to fire, while savanna species are shade-intolerant, but resistant to fire. Recurrent fires that are frequent, relative to population growth rates of forest species, are needed to limit populations of forest species and prevent formation of a closed forest canopy that would exclude savanna species through shading. (c) As moisture availability continues to increase, recurrent fires will become difficult to maintain because of mesic conditions. Vegetation – fire feedbacks, where the frequency (or intensity) of fire is a function of ecosystem composition, can prevent conversion of savanna to forest; fire frequency increases with the abundance of pyrogenic vegetation, which, in turn, increases with increased fire frequency. Black arrows indicate effects on ecosystem components; solid arrows represent direct effects; while dashed arrows represent indirect effects. Red arrows indicate feedback effects on the frequency or intensity of fire. (*See color plate section for the color representation of this figure*.)

dominance will shift from species that are better competitors for soil water (e.g. grasses) in more arid regions to species that are better competitors for light (e.g. trees) in mesic regions. Grasses will be competitively excluded by low light levels beneath closed canopies, but frequent fires that limit woody populations can lead to persistent savannas in regions with sufficient precipitation to support forests.

We expect savanna vegetation to develop positive feedbacks on fire (e.g. increased flammability), which maintain frequent fires in regions that otherwise would transition to forest (Figure 19.2, region iii). Forests and savannas will thus emerge as alternate states in mesic regions; savannas will be associated with frequent fires, while forests will be associated with the absence of fire. Overstory canopy-forming woody species will correspondingly differentiate into what we refer to as "savanna trees" and "forest trees" in response to conditions associated with these alternative ecosystem states. Savanna trees will have adaptations to frequent fire and high light environments, including traits that facilitate frequent fires, while forest trees will have traits adaptive to low light environments. The reduction of fire frequency, or the re-initiation of a regime of frequent fire, can drive transitions between these alterative "basins of attraction." Eventually

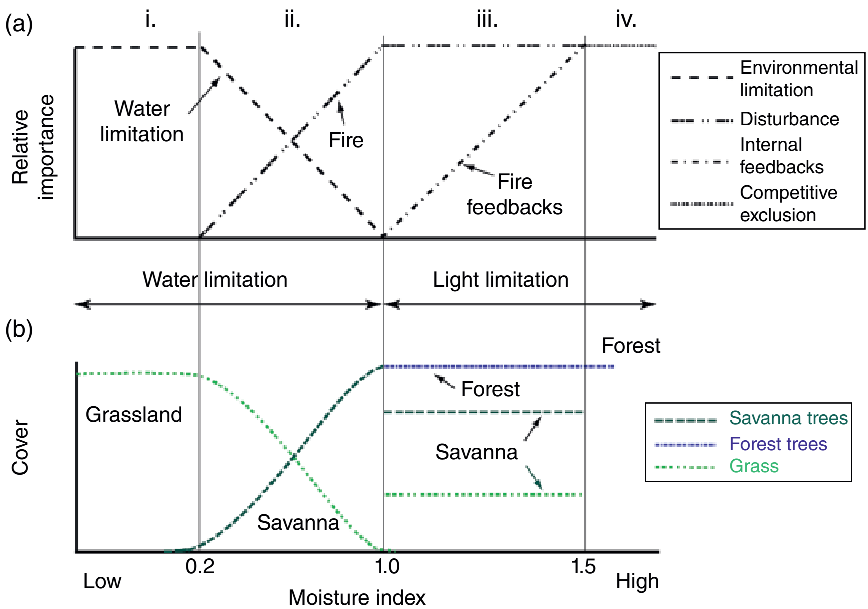

Figure 19.2 Hypothesized importance of savanna maintenance mechanisms (SMMs) (a) and the corresponding potential ecosystem states (b), relative to moisture availability. The moisture index is defined by the ratio of precipitation to potential evapotranspiration over the growing season; the shapes of the curves with respect to moisture index are illustrative rather than empirically based estimates. Four regions (i–iv) are delineated along the moisture gradient. Moisture limitations at the arid end of the gradient (i) are sufficient to exclude larger woody plants (trees), leading to dominance of grasses or smaller woody plants (shrubs). Increasing water availability (ii) leads to expanding woody populations until moisture conditions are sufficient to support a more closed overstory canopy; recurrent fires become increasingly important to limiting woody canopies and frequent fires are needed to exclude forest species. Increasingly moist conditions (iii) inhibit frequent fires and, thus, feedbacks of savanna vegetation on fire become an important savanna maintenance mechanism; forest and savanna emerge as alternative stable states depending on fire frequency. Forest becomes the dominant ecosystem state (iv) as increasingly mesic conditions prevent frequent fires, even in the presence of vegetation feedbacks on fire. (*See color plate section for the color representation of this figure.*)

moisture conditions will preclude frequent fires, even in the presence of vegetation–fire feedbacks, and forests will be the only potential ecosystem state (Figure 19.2, region iv).

Below, we discuss in more detail each of the SMMs presented in Figure 19.1, i.e. water limitations, fire disturbances, and internal vegetation–fire feedbacks.

19.2.1 Water Limitation

Mean annual precipitation or, more generally, metrics of water balance that integrate temperature, associates low woody cover with water limitations globally (Figure 19.3), which is consistent with studies that have examined woody cover only in tropical regions (Sankaran et al. 2005; Bucini and Hanan 2007). Water limitations shift the competitive balance between trees and grasses toward grasses because of the greater water demands of higher leaf area index (e.g. Baldocchi 2012), and lowered water use efficiency of larger-statured woody plants, particularly compared

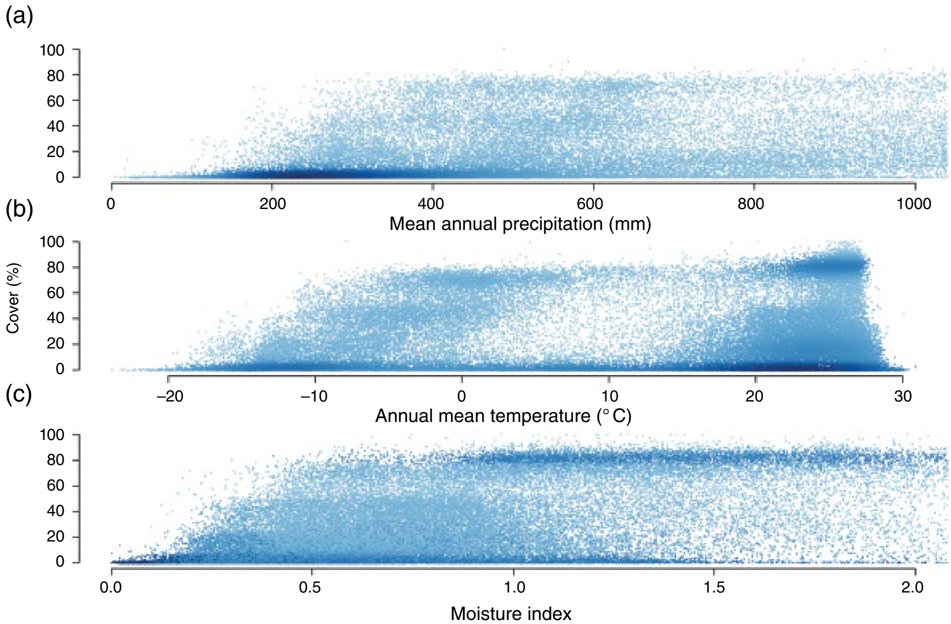

Figure 19.3 Woody cover in relation to precipitation, temperature, and a moisture index that integrates both precipitation and temperature (average of monthly precipitation: potential evapotranspiration ratio over the growing season). (a) Potential canopy cover is constrained by mean annual precipitation. (b) Other environmental factors, such as annual mean temperature, are associated with depressant effects of dry conditions on woody cover. (c) Integration of precipitation and temperature produces bimodal woody cover across a wide range of conditions. Canopy cover data (Hansen et al. 2003) were randomly sampled from MODIS points between approximately 80° N and 55° S, which includes most terrestrial surfaces, while the corresponding precipitation and temperature data were derived from global climate databases (Hijmans et al. 2005; www.worldclim.org). (*See color plate section for the color representation of this figure.*)

with C_4 grasses. The greater negative impact of water limitations on trees, relative to grasses, results in an indirect positive effect of water limitations on grasses (Figure 19.1) (e.g. Sankaran et al. 2004). Water addition in a semi-arid savanna, for example, can increase competitiveness of grasses, which, in turn, suppresses trees (February et al. 2013). Water limitations that inhibit development of a closed woody canopy allow for sufficient understory light to support understory grasses, thus maintaining savannas.

The severity of water limitation also depends on the seasonal distribution of precipitation, as well as other environmental conditions (e.g. Scholes and Archer 1997; Sankaran et al. 2004; Bucini et al. 2017). Sandy soils, for example, allow rapid percolation of water to deeper soil layers, potentially facilitating tree–grass niche partitioning; trees may have exclusive access to deep soil water through tap roots, while grasses are better competitors for shallow soil water because of their extensive systems of surface roots (Walter 1971; Walker et al. 1981; Walker and Noy-Meir 1982; Casper and Jackson 1997). Intense precipitation may result in more water penetrating into deep soil layers, favoring trees (Kulmatiski and Beard 2013).

Occasional years with high rainfall may also allow for the establishment and persistence of trees during intervening years of low rainfall. Thus, a temporal partitioning of rainfall can lead to long-term coexistence of trees and grasses through a "storage effect," where positive population growth rates during infrequent "wet" years are sufficient to maintain trees in the landscape (Chesson 2000). Higher atmospheric CO_2 concentrations favor growth rates of C_3 woody plants relative to C_4 graminoids (Ehleringer et al. 1997; Edwards et al. 2010), ameliorating water limitations through reduced transpiration rates, and shifting the competitive balance between trees and grasses toward trees (Drake et al. 1997; Polley et al. 1997; Bond and Midgley 2000, 2012).

19.2.2 Fire

Fire will become the dominant SMM as water limitations ease. Woody cover will increase with water availability, lowering understory light levels, and shifting resource limitations from soil water to understory light. Higgins et al. (2010), for example, identified a threshold on a rainfall gradient, above which fire is necessary for tree–grass coexistence. The competitive relationship between grasses and trees will shift from comparatively symmetric competition for soil water in arid savannas to asymmetric competition for light that favors taller growth forms, such as trees, in mesic savannas. Recurrent fires reduce woody cover below environmentally determined upper limits, promoting the occurrence of savannas in regions that could otherwise support forests (Sankaran et al. 2004; Bucini and Hanan 2007; Bucini et al. 2017). Dynamic global vegetation models have been used to estimate that forests, for example, would double in global coverage in the absence of fire (Bond et al. 2005). This illustrates the potential for alternative ecosystem states to emerge where soil moisture is adequate to support forests but frequent fires lead to savannas (Moncrieff et al. 2013). Other processes beside fire, of course, can contribute to alternative states, for example, between shrubland and grassland physiognomies (D'Odorico et al. 2012, 2013).

The efficacy of fire in maintaining mesic savannas will be sensitive to long-term variation in fire frequency. Savannas will be persistent only if the frequency of fire remains within a specified range of frequencies to maintain savannas – frequent enough to prevent canopy closure, but not so frequent as to exclude trees (Beckage et al. 2006). Long-term reductions in fire frequency will shift mesic savannas toward forests, while increases in fire frequency will shift savannas toward grassland physiognomies (Jeltsch et al. 2000; Beckage et al. 2006; Beckage and Ellingwood 2008). The required fire regime will depend on environmental conditions that influence the rate of woody canopy closure and subsequent competitive exclusion of shade-intolerant savanna species (e.g. Huston 1979). Low-nutrient soils, for example, are associated with reduced rates of woody canopy closure and thus should require less frequent fire to maintain an ecosystem in a savanna state (Cruz Ruggiero et al. 2002). Fire disturbances could thus be relatively infrequent, but still important in maintaining savannas with slower rates of woody canopy closure (Scheintaub et al. 2009; Nano and Clarke 2010). Conversely, higher concentrations of atmospheric CO_2 could enhance woody growth rates, thus necessitating more frequent fire to maintain savannas (Bond and Midgley 2012; Hoffmann et al. 2012).

19.2.3 Fire Feedbacks

Fire frequency is influenced by precipitation (e.g. Archibald et al. 2009). Sufficient precipitation is required to produce fine fuels (e.g. grass), but too much precipitation can inhibit wildfire ignition and spread. Increasing precipitation and declining water limitations, however, eventually makes fire ignition and spread difficult, decreasing the expected frequency of fire. Climate is unlikely to keep precipitation within the range needed to maintain fire frequencies that are conducive to savannas over long time periods (i.e. millennia), because climate normals fluctuate for a given region (Rahmstorf 2002; Pierce et al. 2004; Schoennagel et al. 2007). As precipitation increases, alternating wet and dry periods can facilitate recurrent fires; plant biomass accumulates during the wet season and fine fuels dry out during the dry season, enhancing spread of lightning-ignited fires at the transition to the next wet season (Beckage and Platt 2003; Slocum et al. 2010).

Vegetation feedbacks on fire frequency can facilitate the persistence of savannas in mesic regions (Beckage et al. 2009, 2011). Precipitation and fire frequency are stochastic in nature, but internal vegetation–fire feedbacks can mediate the frequency of fire (Figure 19.1) and maintain fire regimes within a range conducive to savannas. Vegetation–fire feedbacks result from the influence of vegetation composition on fire frequency and intensity, and the reciprocal influence of fire regimes on vegetation composition and structure (Mutch 1970; Williamson and Black 1981; Zedler 1995; Platt 1999; Schwilk 2003; Behm et al. 2004; Mermoz et al. 2005). Fire-adapted plants have life history traits that protect them from damage in fires, allowing them to survive and increase in abundance, relative to plants that lack such adaptations, as fire frequency increases (Platt et al. 1988a; Brewer and Platt 1994; Beckage and Stout 2000). Fire-adapted plants can also have characteristics that increase the likelihood and intensity of fire, compared with fire-intolerant plants (Williamson and Black 1981; Streng and Harcombe 1982; Stevens and Beckage 2009; Gagnon et al. 2010; Beckage et al. 2011; Ellair and Platt 2013). For example, high concentrations of volatile organic compounds in leaves can increase pyrogenicity of plants, or lower leaf area index of trees in savannas can support grasses and other fine fuels that facilitate fire (Breshears et al. 1997; Ratnam et al. 2011).

Savanna trees should have traits that facilitate frequent fire in mesic savannas (Hoffmann et al. 2012; Platt et al. 2016). Positive feedbacks of savanna vegetation on fire, which increase in strength with increasing water availability, can maintain savannas in mesic regions that would otherwise support closed canopy forests (Swaine et al. 1992; Beckage and Ellingwood 2008). Forest trees that are fire-sensitive, but shade-tolerant, will invade mesic savannas in the absence of fire, replacing savanna with closed forest where understory light is the limiting resource. A positive feedback of grasses, savanna trees, or both, on fire can maintain frequent fires, preventing the competitive exclusion of savanna trees by forest trees, while also maintaining understory light levels that can support grasses (e.g. Beckage et al. 2011). The resultant open savanna physiognomy itself supports the production of fine fuels that sustain frequent, low-intensity ground fires that disproportionately impact (fire-sensitive) forest trees, thus maintaining an open savanna. A reduction in fire frequency leads to increased woody cover, a decrease in understory fuels, and less frequent fires, in a feedback loop that can convert a savanna to forest. Forests and savannas thus emerge as alternative states associated with either frequent or infrequent fire, respectively, in mesic regions (Swaine et al. 1992;

Beckage and Stout 2000; Bucini et al. 2017). Other disturbances that reduce woody cover (e.g. hurricanes) can potentially re-initiate a regime of frequent, low-intensity ground fires (Platt et al. 2000, 2002) and a shift from a forest to a savanna state, although often with a hysteresis (Beckage and Ellingwood 2008, Beckage et al. 2009). Empirical data provide evidence in support of the flammability of savannas (Peterson and Reich 2001; Platt et al. 2016).

We expect woody plants to differentiate into two functional groups associated with forest and savanna alternative states. Mesic savannas will be characterized by frequent fire and high understory light compared with low levels of understory light and infrequent fire in forests. Therefore, trees in mesic savannas will be expected to have acquired a set of functional traits for fire tolerance, rather than shade tolerance, and will be associated with characteristics such as thick, fire-resistant bark, or large underground carbohydrate reserves for post-fire recovery (e.g. Hoffmann et al. 2012; Pellegrini et al. 2016). Savanna trees will also be expected to have comparatively low leaf area index and limited shade tolerance, compared with forest trees, because of the high light environment in savannas (Hoffmann and Franco 2003; Ratnam et al. 2011). Forest trees, in contrast, will broadly be characterized by shade tolerance traits that are adaptive to low light levels found in forest understories or, conversely, traits for rapid growth in transient canopy gaps (e.g. Platt and Strong 1989; Hoffmann and Franco 2003), but with little investment in fire tolerance traits. Forest trees will thus be better competitors for light than savanna trees, but will be more vulnerable to fire (Hoffman et al. 2003, 2004; Mayer and Khalyani 2011; Ratnam et al. 2011).

The growth forms of grasses should similarly vary with respect to the operating SMM. In arid regions, grasses should have water-conserving adaptations, such as a caespitose growth form (densely packed, small tillers, and ramets close to the ground surface), thus remaining in the boundary air layer near the surface (Fowler 1995; Burke et al. 1998). As available moisture increases, shifts from short, compact growth forms to more erect, looser growth forms have been documented (e.g. Stubbendieck et al. 1992); such shifts in morphology should contribute to increased flammability in mesic regions (Gagnon et al. 2010). In mesic savannas, grasses not shaded by trees also rapidly produce new above-ground biomass after fires, providing rapidly drying, flammable, and continuous fine fuels that should facilitate frequent fires (e.g. Sankaran et al. 2004; Accatino et al. 2010; Beckage et al. 2011; Accatino and de Michele 2013). Furthermore, these grasses have suites of traits (e.g. flowering stimulated by fires during certain seasons) that indicate adaptation to specific historical fire regimes (e.g. Streng et al. 1993; Platt 1999; Fill et al. 2012).

19.2.4 Other Processes

Savanna dynamics are also influenced by processes other than fire and water availability. While our framework does not explicitly consider other processes, they can be incorporated into our model. For example, increasing concentrations of atmospheric CO_2 associated with anthropogenic carbon emissions are likely to reduce plant transpiration rates, reducing plant moisture requirements, thus potentially moving ecological communities toward closed forest (e.g. Beckage et al. 2006; Bond and Midgley

2012; Higgins and Scheiter 2012). Community shifts are also likely to depend on corresponding increases in atmospheric temperature, seasonality of precipitation, and resulting patterns of wildfire (e.g. Bucini et al. 2017). The interactive effects of temperature change, amount and seasonality of precipitation, and physiological effects of CO_2 on savanna–forest transitions, are important areas for continued research. We also expect edaphic conditions to interact with precipitation to mediate moisture availability, and soil heterogeneity has been associated with heterogeneity in woody cover (Sankaran et al. 2005; Sankaran et al. 2008; Levick et al. 2010; van der Waal et al. 2011), particularly at finer spatial scales (Favier et al. 2012). Soils with a coarse texture, for example, would have lower moisture availability than finer textured soils at a given level of precipitation. Soil nutrients would similarly influence population growth rates, the rapidity of competitive exclusion and, thus, the required fire frequency needed to maintain savannas (Huston 1979). Herbivores can also alter savanna structure directly by reducing grass or woody biomass, mediating the competitive relationship between them, and indirectly by influencing fuel loads and fire frequency or intensity (Scholes and Archer 1997; Bardgett and Wardle 2003; van Langevelde et al. 2003; Holdo et al. 2007; Asner et al. 2009; Midgley et al. 2010). Thus, the framework presented here can accommodate other processes that can influence savanna dynamics.

19.3 Summary

We present a conceptual framework that emphasizes the changing nature of SMMs with water availability. These mechanisms are expected to shift from water limitation to fire, and then to vegetation–fire feedbacks, with increasing water availability (Figure 19.2). In arid conditions, water limitations exclude larger-statured woody individuals, leading to vegetation with low woody cover, such as grassland physiognomies. Canopy trees increase in density with water availability, leading to lowered understory light levels and reduced grass biomass. As water availability exceeds the threshold for supporting a complete overstory canopy, forests will become a potential ecosystem state (Figure 19.2). Understory light, rather than soil water, will become the limiting resource in mesic regions, and competitive dominance will shift to forest trees that are better competitors for light. Frequent fire will then become the dominant savanna maintenance mechanism, limiting woody populations through elevated stem mortality. We expect differentiation between "savanna trees" and "forest trees," where savanna trees have adaptations to frequent fire and high light environments, and forest trees have traits adaptive to low light environments, but lack traits for fire tolerance. Savanna vegetation in mesic regions should have positive feedbacks on fire (e.g. increased flammability) to maintain frequent fires in regions that otherwise would transition to forest. Forests and savannas will thus emerge as alternate states in mesic regions; savannas will be associated with frequent fires and forests with the absence of fire. The reduction of fire frequency, or the re-initiation of a regime of frequent fire, will drive transitions between these alterative basins of attraction. Increasingly moist conditions will eventually preclude frequent fires, and forests will be the only potential ecosystem state (Figure 19.2).

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