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The Enemy of My Enemy Hypothesis: Why Coexisting with Grasses May Be an Adaptive Strategy for Savanna Trees

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ABSTRACT

Savannas are characterized by the coexistence of trees and flammable grasses. Yet, tree–grass coexistence has been labeled as paradoxical—how do these two functional groups coexist over such an extensive area, despite being generally predisposed to excluding each other? For instance, many trees develop dense canopies that limit grass growth, and many grasses facilitate frequent/intense fires, increasing tree mortality. This study revisits tree–grass coexistence with a model of hierarchical competition between pyrogenic grasses, ''forest trees'' adapted to closed-canopy competition, and ''savanna trees'' that are inferior competitors in closed-canopy communities, but more resistant to fire. The assumptions of this model are supported by empirical observations, including a systematic review of savanna and forest tree community composition reported here. In general, the model simulations show that when savanna trees exert weaker competitive effects on grasses, a self-reinforcing grass community is maintained, which limits forest tree expansion while still allowing savanna trees to persist (albeit as a subdominant to grasses). When savanna trees exert strong competitive effects on grasses, savanna trees cover increases initially, but as grasses decline their inhibitory effect on forest trees weakens, allowing forest trees to expand and exclude grasses and savanna trees. Rather than paradoxical, these results suggest that having weaker competitive effects on grasses may be advantageous for savanna trees, leading to greater long-term abundance and stability. We label this the ''enemy of my enemy hypothesis,'' which might apply to species coexistence in communities defined by hierarchical competition or with species capable of generating strong ecological feedbacks.

Key words: coexistence; facilitation; forest; invasion; Lotka–Volterra; niche; tree–grass coexistence; stability.

INTRODUCTION

Tropical and subtropical savannas are one of the most extensive terrestrial biomes, covering approximately 20% of the terrestrial landmass (Scholes and Archer 1997). A defining characteristic of tropical savannas is the coexistence of tree

and grass species, usually with a continuous grass layer and scattered individual trees or clumps of trees (Scholes and Archer 1997). Yet, the coexistence of trees and grasses in savannas is often considered to be paradoxical (Sarmiento 1984). Indeed, many tree species are capable of growing taller than grasses and developing a dense canopy, resulting in grass extirpation (Hoffmann and others 2012; Dohn and others 2013) and many grass species can facilitate fires that limit tree establishment (Scholes and Archer 1997; Bond 2008). Tree and grass species can also have resource-use overlap belowground, further complicating the potential for coexistence (Walter 1971; Sarmiento 1984). Therefore, it is unclear how trees and grasses coexist, or at least co-occur, over a large geographic range, even though they are generally predisposed to excluding each other. Known as ''the savanna question,'' this enigma has been major research focus in tropical ecology for at least 40 years, inspiring research that also contributes to general coexistence theory (Walter 1971; Sarmiento 1984; Sankaran and others 2004).

The understanding of savannas and other tropical vegetation types has expanded considerably since the savanna question was posed (Sankaran and others 2004). For instance, the potential mechanisms explaining tree–grass coexistence as a stable equilibrium have grown from a focus on root-niche partitioning and edaphic variation (Walter 1971) to include the countervailing influences of browser and grazer populations (Holdo and others 2013), resource niche partitioning in multiple dimensions of time and space (Weltzin and McPherson 1997; Kulmatiski and others 2010), hydraulic redistribution (Yu and D'Odorico 2015), and the ability of fires to offset factors that increase tree growth rates (Jeltsch and others 2000; Murphy and Bowman 2012). Proposed answers to the savanna question now include non-equilibrium dynamics as well (for example, Higgins and others 2000; Jeltsch and others 2000). For instance, Higgins and others (2000) argued that demographic asymmetries can interact with fluctuating resource availability and disturbance frequency to generate a metastable state comprised of grasses and trees. Thus, tree–grass coexistence can result from interannual rainfall fluctuations, random fire occurrences, and other periodic sources of mortality (Fernandez-Illescas and Rodriguez-Iturbe 2003; D'Odorico and others 2006). The rapid growth of multi-site studies and remotely sensed data has greatly increased the ability to address this growing portfolio of hypotheses (Bowman 1992; Sankaran and others 2005; Hirota and others 2011;

Staver and others 2011; Lehmann and others 2014).

Two particular advances in tropical ecology are at the core of this study. First, growing empirical and theoretical evidence supports the idea that savannas with a continuous, productive grass layer can constitute a self-reinforcing, alternative state (or attractor) to forests in tropical areas receiving approximately 800–2000 mm of annual precipitation (Van Langevelde and others 2003; D'Odorico and others 2006; Hirota and others 2011; Staver and others 2011; Staver and Levin 2012; Xu and others 2016; but see Hanan and others 2014). Flammable C_4 grasses maintain this state by quickly producing flammable fuels, which facilitates frequent ground fires that can kill tree seedlings or keep resprouting saplings in a ''fire trap'' (Higgins and others 2000; Gignoux and others 2009; Hoffmann and others 2012). Grass–fire feedbacks can be so strong that grasslands and savannas extend far into areas that could support closed forests in the tropics and elsewhere (Sankaran and others 2005; Hirota and others 2011; Staver and others 2011; Murphy and Bowman 2012), persisting for decades or longer near forested areas (Schwartz and others 1996; Wiedemeier and others 2012; Ratajczak and others 2014). Forests can also incite their own set of positive feedbacks once established, by increasing rainfall (Bonan 2008) and phosphorus deposition (Lawrence and others 2008), and creating microsite conditions that reduce the potential for frequent or intense fires (Trauernicht and others 2012; Ibanez and others 2013a). As an alternative attractor, grass dominance is resistant to transitions to a closed environment until a threshold in tree:grass ratios is crossed, at which point transitions to forest will be difficult and slow to reverse (D'Odorico and others 2006; Staver and Levin 2012; Staal and others 2015).

The second advance at the core of this study is that trees species found co-occurring with grasses tend to have very different traits than trees common in closed-canopy forests (Ratnam and others 2011; Hoffmann and others 2012). In this study, we use the term ''savanna trees'' to refer to tree species that are often found co-occurring with pyrogenic grasses and ''forest trees'' for tree species more commonly found in areas with closed tree canopies and a marginal to nonexistent grass layer (similar to Beckage and others 2009; Ratnam and others 2011; Hoffmann and others 2012; Staver and Levin 2012). Compared to forest trees, savanna trees usually allocate more resources to thicker bark tissues (providing insulation against fires) and

storage of resources belowground (promoting vigorous resprouting after fire-induced top-kill) (Lawes and others 2011; Ratnam and others 2011; Hoffmann and others 2012; Rosell and others 2014). Forest trees have faster vertical growth, larger maximum heights, greater leaf area index, and larger crowns, but thinner bark and less carbon reserves belowground (Lawes and others 2011; Ratnam and others 2011; Hoffmann and others 2012). Many forest tree species also have traits that allow them to establish in areas with lower light availability, whereas savanna tree seedlings tend to have low shade-tolerance (Bowman and Panton 1993; Hoffmann 1996).

The traits of savanna and forest trees predispose them to very different environmental conditions. Although many savanna trees suffer frequent mortality from fire, their reduced rates of top-kill and ability to resprout following fires often allow savanna trees to form sustainable populations in frequently burned areas (Hoffmann 1999; Murphy and others 2010; Gignoux and others 2009). Forest tree traits make them susceptible to fire (Bowman and Panton 1993; Hoffmann 1999; Gignoux and others 2009; Ibanez and others 2013a), but under low fire frequencies they are much more capable of reducing grass dominance and savanna tree growth through light limitation (Silva and others 2002; Banfai and Bowman 2007; Hoffmann and others 2012). Together, these different trait combinations set up a competitive hierarchy and the potential for indirect interactions: Grasses and forest trees can exert strong competitive effects on each other, where either functional group can create a self-sustaining state if they achieve sufficient dominance (cover, height, density, and so on) and external forces remain relatively constant (for example, rainfall, dry season length, ignition event frequency); savanna trees cannot effectively compete with forest trees, but are less negatively affected by competition with grasses and fire in particular (Figure 1).

The factors we consider malleable are the competitive effects of savanna trees on grasses and savanna tree resistance to grass competition and fire. First consider a tree species that is capable of surviving in a fire-prone environment and has a strong competitive effect on grasses. This species could establish in open grass-dominated environments, but would degrade the grass layer making it more likely that forest trees will colonize and dominate the patch. This might be a viable strategy if the savanna trees species could reproduce quickly and spread its propagules to new open patches. Such a species would be well adapted to
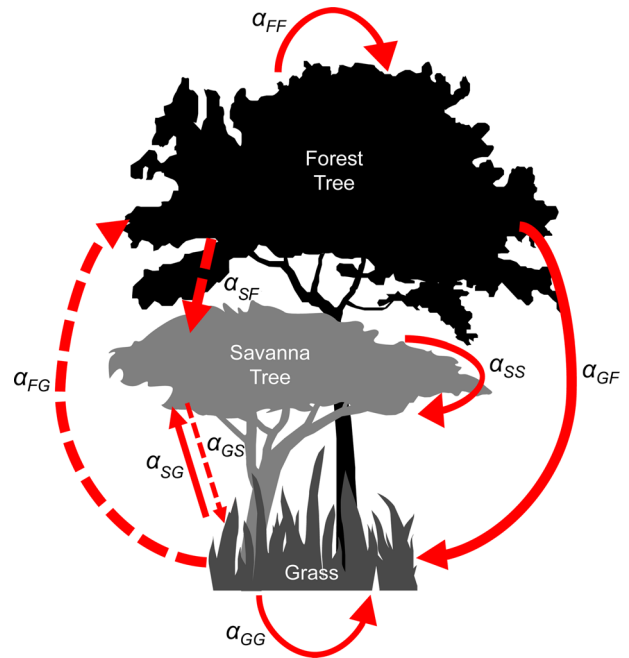

Figure 1. A pictorial representation of the model. *Thicker arrows* represent stronger limitation (larger competition coefficient values). The pathway of *different dashed arrows* represents a potential opportunity for savannas to facilitate their own growth via reduced limitation on grasses, which repels forest trees. For parameter definitions, see Table 1.

shifting savanna–forest ecotones, but unlikely to persist with grasses for long, and therefore, only qualifies as tree–grass coexistence in a transient sense. Yet many savannas can be stable for decades to centuries (Schwartz and others 1996; Wiedemeier and others 2012). An alternative functional type is to possess fire-adapted traits, but exert weaker competitive effects on grasses. This species would be able to colonize fire-prone environments, while maintaining a grass layer that is more likely to repel forest trees. For tree species that cannot effectively compete with forest trees in the absence of fire, this combination of traits could prove advantageous (Figure 1). The feasibility of this scenario increases after considering the trade-offs induced by developing fire-resistant traits. Given a finite pool of nutrients and assimilated carbon, it is impossible for a plant species to maximize all functions (Grime 2006). Therefore, increased allocation to fire-resistance traits necessarily leaves fewer resources for vertical growth and the development of the large, dense canopies associated with superior competition for light (Ratnam and others 2011; Hoffmann and others 2012), reducing the competitive effect of a tree species on grasses.

We forward the hypothesis that following the expansion of open-canopy communities approximately 15 million years ago (mya) and pyrogenic C_4 grasses approximately 8 mya (Edwards and others 2010; Stromberg 2011), some tree species have evolved traits to withstand fire, but exert weaker competitive effect on grasses, maintaining a fire-prone community where grasses and savanna trees coexist. Alternatively, some tree species might have already possessed this combination of traits and were favored when pyrogenic grassy biomes expanded. During this hypothetical course of evolution or species reordering, grass-dominated areas occupied by trees that were both fire-adapted and exerted weaker competitive effects on grasses would be more likely to persist, leading to greater fitness or dominance for these tree species. We address our hypotheses using simulation modeling, based on assumptions supported by empirical research in several savanna systems. We do not model evolution or species reordering directly, but assess the viability of different strategies spanning an array of savanna tree resistances to grass competition/fire and competitive effects of savanna trees on grasses. We also performed a systematic literature review to evaluate the assumption that forest trees are excluded from open vegetation and that savanna trees are excluded from closed-canopy forests.

METHODS

To address our hypotheses, we developed a model of vegetation dynamics accounting for the hierarchical competition among grasses, savanna trees, and forest trees, including their interaction with fires. The model aims to capture the main aspects of grass–savanna tree–forest tree competition, with as few assumptions and parameters as possible. We used the model to assess the feasibility of savanna trees taking advantage of the fire sensitivity of forest vegetation to prevent competitive exclusion by forest trees. To do so, the model would need to show that savanna trees benefit from lowering their competitive effect on grasses. Model simulation is an attractive option for hypothesis generation in savannas because these systems are generally slow moving, and therefore require long time periods for hypothesis testing. In contrast, there is a rich literature of empirical studies on biotic–abiotic interactions and species relationships in savannas and savanna–forest boundaries (Walter 1971; Sarmiento 1984; Scholes and Archer 1997; Bowman 1992; Sankaran and others 2005; Bond 2008; Lehmann and others 2014) that is available

to inform model development (for example, Van Langevelde and others 2003; Beckage and others 2009; Staver and Levin 2012; Holdo and others 2013; Staal and others 2015).

The model is a formulation of the classic Lotka–Volterra competition model, with notation following Chesson (2000). The model aims to capture the dynamics of vegetation in areas with annual precipitation ranging from about 800–2000 mm, where savanna and forest potentially constitute alternative self-reinforcing states maintained primarily through differences in fire dynamics (for example, Sankaran and others 2005; Staver and others 2011). The model has three functional groups: grasses (G), savanna trees (S), and forest trees (F), and their abundance is expressed in terms of vegetation cover per unit ground at the spatial resolution of an area that would fit one fully grown forest tree and multiple individual grasses. We assume that cover is proportional to the size of a single tree in this patch. Together, the three groups do not necessarily sum to 100%, because vegetation can have multiple, overlapping layers and systems with more species often achieve greater biomass/cover than monocultures, through complementary use of resources or other mechanisms (Tilman and others 2014).

The dynamics of these three functional groups are given by the following three equations:

$$dS/dt = r_S S(1 - \alpha_{SG}G - \alpha_{SF}F - \alpha_{SS}S) + \xi_1$$

$$dF/dt = r_F F(1 - \alpha_{FG}G - \alpha_{FF}F) + \xi_2$$

$$dG/dt = r_S G(1 - \alpha_{GS}S - \alpha_{GF}F - \alpha_{GG}G) + \xi_3$$

r_S, r_F, and r_G are maximum growth rates. α_{ij} are competition coefficients, representing the competitive effect of species j on species i, with larger values indicating that species j reduces species i's growth more. The α_{ii} coefficients, therefore, are self-limitation coefficients that can be interpreted as 1/carrying capacity. Each equation is also driven by independent additive Gaussian white noise $\xi_{1–3}$, accounting for sources of uncertainty associated with disease, herbivory, resource variability, and other stochastic factors (for example, Ridolfi and others 2011).

Model Parameterization

We relied on empirical observations to set the relative parameter values of the model, which are further explained in Table 1 (see Appendix 1 for sensitivity analyses). For simplicity, we give all

Table 1. Parameter Values and Their Justification

Parameter (meaning)	Value	Justification
r_G, r_S, r_F (maximum growth rate)	0.4	Tuned so that transitions to forest take $\sim$50–100 time steps, matching observed transition rates (for example, Hoffmann and others 2012)
α_{GG}, α_{SS}, α_{FF} (self-limitation)	0.01 (1/100)	Results in a 100% cover carrying capacity for each group
α_{GS} (grass limitation by savanna trees)	Variable but $< \alpha_{GF}$	Many savanna trees are not especially strong competitors for light, and therefore, their competition coefficients are less than the effects of forest trees on grasses
α_{SG}, α_{FG} (competitive limitation by grasses)	Variable but $\leq \alpha_{FG}$, 0.0125 (=1/80)	Grasses generate fires and compete for water and nutrients, which can limit the growth of trees species. α_{FG} is set to equal α_{GF} so that the dominance of forest trees depends on past events and initial conditions. α_{SG} is less than α_{FG} due to fire-resistant traits in savanna trees
α_{GF}, α_{SF} (competitive limitation by forest trees)	0.0125 (1/80)	Forest trees can usually exclude savanna trees and grasses once established (for the range of precipitation we consider). Therefore, forest trees limit grasses and savanna trees growth more than their own
ξ (Gaussian white noise)	1	White noise strength

species the same intrinsic growth rates and self-limitation coefficients, such that $\alpha_{SS} = \alpha_{FF} = \alpha_{GG} = 1/100$, setting the maximum equilibrium cover of each species to 100%. Savanna trees are considered to not limit the growth of forest trees, because forest trees are primarily excluded by fire, which savanna trees do not usually facilitate directly (Ratnam and others 2011; Hoffmann and others 2012; but see Beckage and others 2009). Forest trees, in contrast, are capable of exerting strong per capita competitive effects on grasses (α_{GF}) and savanna trees (α_{SF}), and we assume the strength of these effects to be the same ($\alpha_{SF} = \alpha_{GF}$) (Ratnam and others 2011; Hoffmann and others 2012; Table 2). We treat these two parameters as constants, because forest trees are generally adapted to maximize competitive ability in late succession, closed environments. Grasses can exclude forest trees if they have high biomass and coverage, and frequent ignition events occur (Hoffmann 1999; Gignoux and others 2009; Ratajczak and others 2014). To allow grasses and forest trees to exclude each other, we have grasses and forest trees limit each other's growth more than their own growth (that is, $\alpha_{GG} < \alpha_{FG}$ and $\alpha_{FF} < \alpha_{GF}$). For simplicity, our default parameterization is $\alpha_{GF} =$

α_{FG}, which makes the asymptotic state depend on initial grass and tree cover and/or parameters related to the competitive interactions of savanna trees and grasses (α_{SG} and α_{GS}). The competitive effect of grasses on savanna trees (α_{SG}) and competitive effect of savanna trees on grasses (α_{GS}) are considered flexible parameters that roughly correspond to differences in savanna tree traits. We stress that dominant C_4 grasses probably evolve toward having traits that increase flammability, fire survival, and competition for belowground resources, similar to results from models (Schieter and others 2012) and the paleo-record (Stromberg 2011). Therefore, any change in α_{SG} would be driven by savanna trees adaptations that reduce the effects of fire on savanna trees and reduce resource competition with grasses (for example, thicker bark, protected meristems, greater belowground carbon storage, development of deep roots). Changes in α_{GS} are also determined by variation in savanna tree traits such as canopy size, canopy density, canopy shape, vertical growth rates, and root system characteristics.

To summarize the competitive hierarchy, we have that $\alpha_{GF} = \alpha_{FG} = \alpha_{SF} > \alpha_{SS} = \alpha_{FF} = \alpha_{GG}$; α_{GS} is variable, but smaller than $\alpha_{GF} = \alpha_{FG} = \alpha_{SF}$; likewise,

α_{SG} is variable but less than α_{FG}, reflecting savanna tree resistance to fire (Figure 1; Table 1).

Simulations

All simulations were run in R (R core team 2015) and solved numerically (code available upon request). We ran the model through simulations over a large span of savanna tree competitive effects on grasses (α_{GS}) and competitive effect of grasses on savanna trees (α_{SG}). For α_{GS}, we considered a range of values, from less than α_{FG} but greater than α_{SS} (savanna trees limit grass growth more than their own) to $\alpha_{SG} < \alpha_{SS}$ (savanna trees limit their own growth more than they limit grass growth). We considered a similar range for α_{SG}, including instances where grasses limit savanna tree growth more than their own growth ($\alpha_{SG} > \alpha_{GG}$) or grasses limit their own growth more than savanna tree growth ($\alpha_{SG} < \alpha_{GG}$). For this large factorial combination of α_{GS} and α_{SG} values, we determined the attracting states numerically by starting with different initial conditions of each functional group, ranging from 1 to 100% cover (in intervals of 10% cover and factorial combinations of initial conditions).

The second set of simulations was expansion trials. These have the same mechanics as invasion trials, where the system starts in a (native) grass-dominated state with savanna trees and forest trees (the invaders) attempting to expand simultaneously from low initial cover. Expansion trials provided an assessment of how savanna tree functional types affect the resistance to forest tree incursion and the ability of savanna trees to become established in grasslands. We ran two separate sets of expansion trials, one with all three functional groups and a second without forest trees and their corresponding parameters. The purpose of the expansion trials without forest trees was to determine whether the results of the 3-species model are dependent on the presence of forest trees. The initial conditions for the first set of expansion trails were 100% grass cover, and 3% savanna and forest tree cover. For the second set of expansion trails, the initial conditions are 100% grass cover and 3% savanna cover. We also performed a set of sensitivity analyses for the expansion trials to determine whether variations in the competition coefficients affected our results. In Appendix, we discuss how these parameter variations are potentially related to several types of environmental variation (for example, precipitation, grazers, fire frequency; see Appendix 1, 2).

Literature Review

A primary assumption of our model is that trees associated with open-canopy communities are rarely found in closed-canopy communities, due to the low shade tolerance and maximum canopy height of savanna trees (Figure 2). Conversely, we expect trees that usually dominate closed-canopy forests will be absent from open grass-dominated areas, reflecting their sensitivity to fire. If these assumptions are supported, we predict that the tree community composition will be distinct in open- and closed-canopy communities, except in areas transitioning from one community type to another. We also expect a relatively abrupt turnover in community composition at the savanna–forest
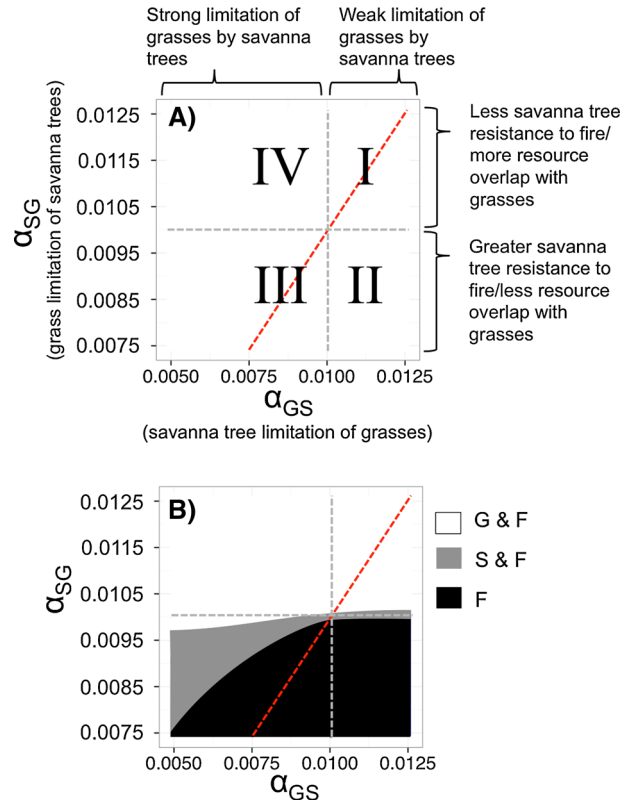

Figure 2. A *Four different zones* of parameter space, described in detail at the beginning of results. The *red line* is the 1:1 line for the effect of grasses and savanna trees on each other (**A**) ($\alpha_{SG} = \alpha_{GS}$). **B** Long-term stable states for different parameter values, with *white fill marking* where the system is bistable, supporting grassland or forest, *gray* is bistable supporting savanna or forest, and *black parameter values* that only have forest as a stable state. The results for a given combination of α_{SG} and α_{GS} reflect the range of final cover found for each functional group and all combinations of initial conditions, after 800 time steps.

Table 2. Summary of Results from Studies in Literature Review

Location/study #[a]	Multivariate[b]	Clustering[c]	Jaccard distance[d]	Other results[e]
1				Forest spp. were restricted to closed canopies and large groves, whereas savanna ("woodland") spp. were found in open-canopy communities and smaller groves. Woodland spp. appeared to frequently destabilize grass dominance, leading to their eventual replacement by forest trees
2				Tree community composition exhibited an abrupt change at ~0.57 canopy closure (on a canopy closure index ranging from 0 to 1)
3				Spp. with high importance values in closed forest were rare or absent in savanna patches. The most dominant woody spp. in savanna were rare in closed forest
4a			0.95	
4b	MV+		0.89	Savanna spp. (especially juveniles and seedlings) comprised <1% of stems in forest. Several spp. were only abundant at the forest edge and in unburned savanna
4c				Shifts in forest/savanna spp. dominance occurred abruptly at the savanna–forest boundary. Forest spp. made up <20% of trees in savanna and savanna spp. made up ~0% of trees in forests
5	MV+		0.76	
6	MV+	C+	0.98	
7	MV+		0.68	Community composition changed abruptly at the savanna-forest boundary
8			0.93	
9			0.54, 0.73	Fire suppression led to greater a greater number of forest spp. in savanna
10	MV+		0.51	
11	MV–	C–	0.95	
12				Some spp. usually indicative of savanna were found at the near-forest edge, and vice versa
13a				Forest spp. were absent beyond the boundary marking frequent fires and savanna trees were absent from forest
13b	MV+		0.83	Community composition changed abruptly at the savanna-forest boundary
14	MV+			The composition of a third intermediate vegetation type, referred to as "thicket," was distinct from savanna and forest
15a			1.00	Areas in the early stages of grass-layer decline were colonized by intermediate tree spp., not forest spp.
15b			1.00	Only ~50% of intermediate spp. were also found in mature forest
16a	MV+			~70% of "common spp." were found exclusively in savanna or forest
16b	MV–		0.25, 0.32	
17a				An abrupt shift community composition occurred at the savanna–forest boundary. Several intermediate tree spp. (not core forest spp.) specialized in colonizing savanna. These intermediate spp. were rare further into forest patches

Table 2. continued

Location/study #[a]	Multivariate[b]	Clustering[c]	Jaccard distance[d]	Other results[e]
17b		C+	0.71	
18			0.90	
19				In the one purely forested plot, forest spp. made up 76% of stems. Forest spp. made up 3% of trees in open communities
20	MV−		0.87	Some spp. that dominated the most flammable community (Chipya) were also dominant in the least flammable community (Mateshi)
21	MV+	C+	0.68	Abrupt change in composition occurred at the savanna–forest boundary
22			0.83	A few large savanna trees were found in forest patches, but savanna juveniles were not present in forests
23	MV+/MV−		0.81	While many spp. were cosmopolitan, most tended to reach peak abundance at a specific distance into savanna or forest
24			1.00	Abundance-based similarity values were also low
25		C+	0.80, 0.89	Some spp. were dominant in open and closed community types
26	MV+	C+		
27a				Adult rainforest spp. were absent from stable savannas. In stable forests, savanna spp. made up ~40% of adult tree basal area and ~30% of basal area of smaller size classes. Savannas that were infrequently burned were more likely to transition to forest and had significantly fewer savanna spp. recruits and more forest spp
27b				Forest spp. made up ~50% of basal area in stable savannas, but ~90–100% in forest patches
27c				Half of common species were found in both savanna and forest communities. However, 96 out of 100 species had significantly different abundance in forest, ecotone, or savanna communities
28		C+		Forest was expanding, resulting in some large savanna trees in forested areas, but no savanna juveniles were found at the ecotone or under closed canopies. Juvenile forest trees were only found within 20 m of the forest edge. Juvenile "ecotone" spp. were absent from forests
29a				Spp. that dominated forest were absent from savanna and vice versa. Rare spp. were often found in both communities
29b	MV−			The tree that dominates groves, *Callitris intratropica*, sometimes formed more open-canopy stands
30				The dominant savanna sp. was only found up to 40 m into forests, whereas forest trees were only found up to 10 m into savannas
31				No adult rainforest spp. were found in savanna, and no savanna spp. of any size were found in forest

Table 2. continued

Location/study #[a]	Multivariate[b]	Clustering[c]	Jaccard distance[d]	Other results[e]
32a			0.89	Two Eucalyptus spp. dominated the open-forest/rainforest ecotone, but were rare in savanna and forest
32b				Community composition changed abruptly at the savanna–forest boundary

[a]Numbers in this column correspond to the same numbered locations in Figure 5. References are: 1) Brener and Silva 1995; 2) Dantas and others 2013; 3) Dezzeo and others 2004; 4a) Felfi and Da Silva 1992; 4b) Geiger and others 2011; 4c) Hoffmann and others 2009; 5) Loschi and others 2013; 6) Marimon and others 2006; 7) Müller and others 2012a; 8) Pérez-García and others 2010; 9) Rodrigues-Souza and others 2015; 10) Ruggiero and others 2002; 11) Adejuwon and Adesina 1992; 12) Attua and Pabi 2013; 13a) Azihou and others 2013; 13b) Müller and others2012b; 14) Charles-Dominique and others 2015; 15a) Cuni-Sanchez and others 2016; 15b) White and others 1996; 16a) Frederiksen and Lawesson 1992; 16b) Wolf 1998; 17a) Hennenberg and others 2005; 17b) Hovestadt and others 1999; 18) Jensen and Friis 2001; 19) Kikula 1986; 20) Lawton 1978; 21) Mapure 1997; 2012; 22) Mitchard 2009; 23) Nangendo 2006; 24) Pennec and others 2016; 25) Smith and Fisher 2001; 26) Walpole and others 2004; 27a) Banfai and Bowman 2005; 27b) Banfai and Bowman 2006; 27c) Bowman 1992; 28) Bowman and others 1990; 29a) Bowman and Fensham 1991; 29b) Trauernicht and others 2012; 30) Ibanez and others 2013b; 31) Macdermott and others, in press; 32a) Turton and Duff 1992; 32b) Unwin 1989.
[b]"MV+" indicates that plots from savanna and forest communities did not overlap in multivariate space; "MV−" indicates that some forest and savanna communities did not overlap in multivariate space. "MV+/MV−" indicates that some forest and savanna communities overlapped in multivariate space.
[c]"C+" indicates that all savanna plots were placed in a different cluster than forest plots. "C−" indicates that some savanna and forest plots were placed in the same cluster.
[d]Reporting of multiple Jaccard distances for a single study indicates comparisons between different savanna and forest sub-communities.
[e]"sp." and "spp." refer only to singular and plural tree species, unless otherwise noted.

boundary. To assess these assumptions, we identified studies that compare savanna and forest tree communities, using transects that cross from savanna into forest or plots/inventories from proximate patches of open- and closed-canopy vegetation. For details on how we performed the literature search and inclusion criteria, see Appendix 3.

In evaluating the studies, we prioritized reporting objective results such as: Measurement 1 were species categorized as having savanna or forest affinities only restricted to their respective communities?; Measurement 2 how many species were found in both communities?; Measurement 3 were savanna and forest plots completely separate, based on a multivariate analysis such as a principal components analysis or similar methods?; and Measurement 4 did a clustering analysis put any savanna and forest plots in the same cluster? Most studies that were ultimately included in the review reported at least one of these measurements directly or had tables that allowed us to calculate measurement two (presence/absence compositional overlap). To standardize our reporting for measurement two, we calculated species overlap using the inverse of the Jaccard index (Jaccard distance), because it is easy to interpret, requires only presence/absence data, and some studies that did not report tables of species occurrence did report Jaccard distance values. Jaccard distances were calculated as $(A + B)/(A + B + C)$, where A is the number of species found only in savanna and B is the number of species found only in forest, and C is the number of species found in both communities. This measurement ranges from 0 to 1, with higher values indicating that a greater proportion of species are found only in one of the two community types.

RESULTS

To organize the simulation results, we have separated the bivariate parameter space of α_{GS} and α_{SG} values into four zones (Figure 2a): in zone I both grasses and savanna trees limit each other's growth more than their own ($\alpha_{GS} > \alpha_{SS}$, $\alpha_{SG} > \alpha_{GG}$); in zone II savanna trees limit grass growth more than their own growth ($\alpha_{GS} > \alpha_{SS}$), but grasses limit their own growth more than savanna tree growth ($\alpha_{SG} < \alpha_{GG}$); in zone III both savanna trees and grasses limit each other's growth less than their own growth ($\alpha_{GS} < \alpha_{SS}$, $\alpha_{SG} < \alpha_{GG}$); and in zone IV savanna trees limit grass growth less than their own ($\alpha_{GS} < \alpha_{SS}$) and grasses limit savanna tree growth

more than they limit their own growth ($\alpha_{SG} > \alpha_{GG}$). The gray dotted lines divide the plot into these four zones in Figures 2, 3 and 4. The red dotted line demarks another important set of parameter space: above this line, grasses limit savanna tree growth more than savanna trees limit grass growth ($\alpha_{G-S} < \alpha_{SG}$), and below this line, savanna trees limit grass growth more than grasses limit savanna tree growth ($\alpha_{GS} > \alpha_{SG}$).

Attractors

In the vast majority of simulations with different initial conditions and combinations of α_{GS} and α_{SG}, the system tends to converge on two potential states of grass and forest tree cover: (1) a state of 80–100% grass cover and less than 4% forest cover; or (2) a state of less than 4% grass cover and approximately 100% forest cover. Final savanna tree cover ranges from 0 to 40% and only tends to exceed 4% when forest tree cover is less than 4%. Therefore, we focus on three attractors, which are classified as: grassland (grass cover ∼80–100%, savanna tree cover <4%, forest tree cover <4%), savanna (grass cover >80%, savanna tree cover >4%, forest tree cover <4%), and forest (grass and savanna tree cover <4%, forest tree cover ∼100%).

Figure 2b depicts when the system exhibits only forests as a stable equilibrium (black), bistability of grassland and forests (white), or bistability of savannas and forests (gray). If savanna trees strongly limit grass growth and grasses have a weak effect on savanna trees, the forest state is the only long-term stable state (zone II and part of zone III). The bistable zone of grasslands and forests is generally restricted to where grasses have a greater effect on savanna trees than on themselves (zone I and IV), effectively reducing the system to only grasses and forest trees. In zone IV, grasses directly exclude savanna trees and for most of zone I, even when savanna trees increase in cover, it is at the expense of grasses, resulting in transitions to forest. The largest portion of parameter space where savanna is a potentially stable state is when grasses and savanna trees limit each other's growth less than their own growth. The savanna state is also stable for a small area where grasses and savanna trees limit each other's growth the same or slightly more than their own (Figure 2b).

Expansion Trails

We start with the expansion trials including all three species (Figure 3b–d). In most of zone I and all of zone IV, the system remains in grass-dominated state with about 0% savanna and forest tree cover. The system remains grassland in these zones because grasses limit savanna tree more than their own growth and grasses start as the dominant species, which does not allow savanna or forest tree growth to expand from low abundance. In zone II, savanna trees increase in biomass initially because grasses limit their own growth more than savanna trees and savanna trees strongly limit grass growth. However, this reduction in grass cover allows forest trees to expand and eventually exclude both savanna trees and grasses, resulting in transitions to forest for this entire parameter space (similar to Figure 4e).

The expansion trial results are not consistent across all of zone III (Figure 3a–c). Within this zone, there is a triangular area of α_{GS} and α_{SG} values where savanna trees reduce grass cover enough for forest trees to invade and achieve dominance (similar to the dynamics of all points in zone II). Time series of these scenarios in Figure 4f, g illustrate the cascading set of events that unfold when savanna trees exert a strong competitive effect on grasses. For the rest of parameter space in zone III, savanna trees have enough resistance to competition with grasses to expand above 4% cover, but a weak enough effect on grass growth that forest trees cannot expand, resulting in long-term coexistence (Figure 4c, d). This portion of parameter space illustrates where coexisting with grasses leads to greater long-term savanna tree cover and stability.

In the absence of forest trees, the expansion trial results change considerably (Figure 3d, e). In zone II, where the competitive effect of grasses is weak and savanna trees limit grass growth more than their own growth, savanna trees are able to expand and exclude grasses. With no forest trees present to suppress savanna trees, the savanna trees remain dominant through the end of the simulations. In zone III, savanna trees exclude grasses for very high values of grass limitation by savanna trees (α_{GS}). For the rest of this zone, the two species coexist, with savanna tree cover increasing as α_{GS} increases and α_{SG} decreases. Critically, in the absence of forest trees there is no point at which savanna trees benefit from decreasing their competitive effect on grasses, unlike the model with forest trees present. As before, grasses are dominant for most of zone I and all of zone IV, because in this parameter space grasses limit savanna tree growth more than their own growth and grasses start as the dominant species.

The expansion trial sensitivity analyses suggest that the model was robust to a 15% increase/decrease in most competition parameters (Appendix
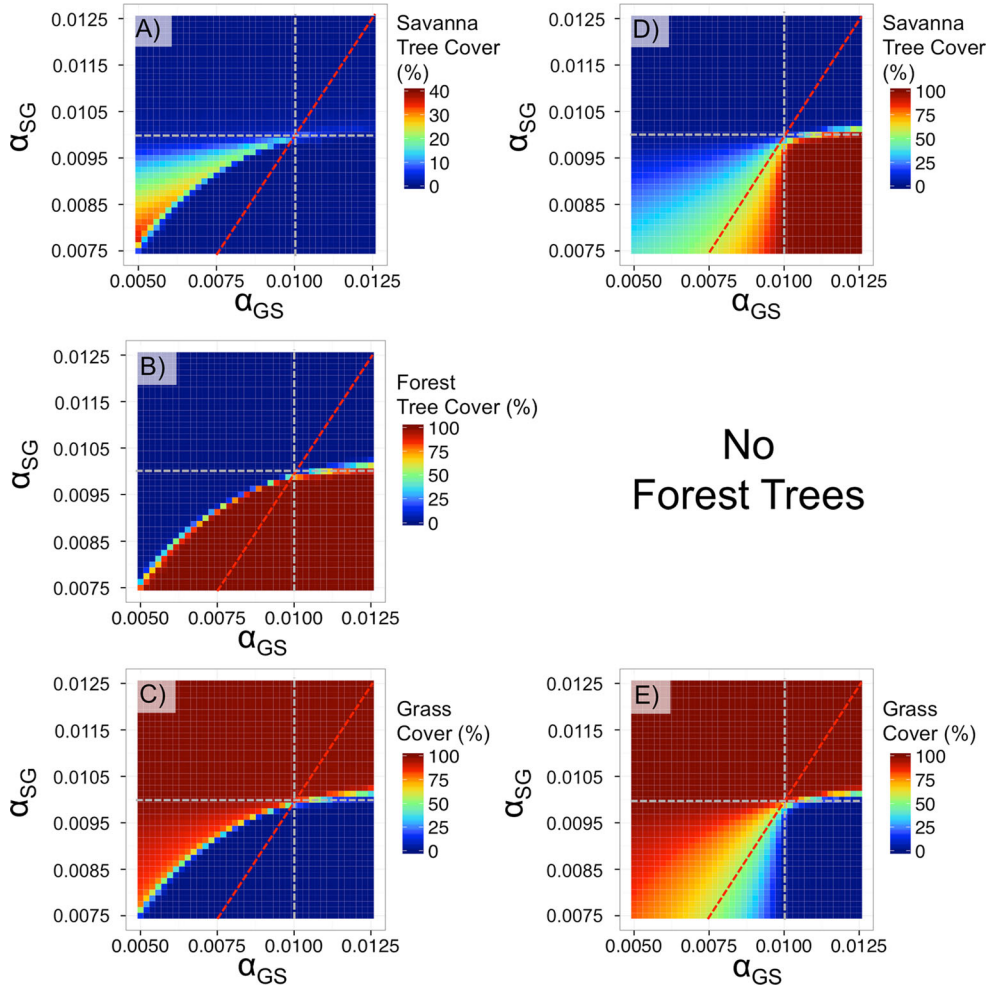
Figure 3. A–C Outcome of tree expansion trials with both savanna and forest trees present and with respect to different grass limitation by savanna trees (α_{GS}, *x*-axis) and savanna tree limitation by grasses (α_{SG}, *y*-axis). Initial conditions were grasses at 100% cover, savanna trees at 3% cover, and forest trees at 3% cover. **D, E** Tree expansion trials without forest trees present. For all panels, ''warmer'' colors correspond to greater final cover of savanna trees (**A, D**), forest trees (**B**), and grasses (**C, D**). *Each pixel* (small colored square) represents the average final cover of 100 iterations of the model, after 600 time steps. Note that the *color scales* for savanna tree cover vary in (**A**) and (**D**).

1). The effect of grass-facilitated fires on forest trees (α_{FG}) had one of the highest sensitivities. Therefore, we performed a second sensitivity analysis of a wider range of α_{FG} values. Changes in α_{FG} are related to environmental factors. Namely, as precipitation increases and/or dry season length decreases, α_{FG} will eventually decrease because grass fuels become less flammable (Hirota and others 2010). Mirroring empirical assessments (Hirota and others 2011; Staver and others 2011), forest is the only stable state beyond a threshold in α_{FG} and therefore a precipitation threshold (Appendix 2). However, the threshold is at lower values of α_{FG} (higher precipitation) when savanna tree traits favor grass–savanna tree coexistence (Appendix 2).

Literature Review

The literature review identified 47 suitable studies from 20 different countries (Figure 5; Table 2, see Appendix 3 for meta-data). Jaccard distances could be measured for 22 studies and typically focused on trees with a diameter at breast height of at least 5 cm. Jaccard distances ranged from 0.28 to 1, with an average of 0.81 and standard deviation of 0.18. All but one study had a Jaccard distance greater than 0.5, indicating that at least half of tree species tend to be restricted to only savanna or forest (which could depend on methods). A majority of Jaccard distances were greater than 0.80 (15/22), suggesting that it was common for only one in five tree species to be found in both savanna and forest (*inset* Figure 5). Of the studies employing multivariate methods, 10 out of 15 studies found no overlap between forest and savanna plots on the multivariate axes that explained most of the variation in composition (Table 2). In the five remaining studies, compositional overlap was marginal, with savanna and forest plots forming distinct, but slightly overlapping zones (Table 2). In 5 out of 6 studies that used a cluster analysis, all savanna and forest plots were placed in separate clusters (Table 2). All studies with a design that
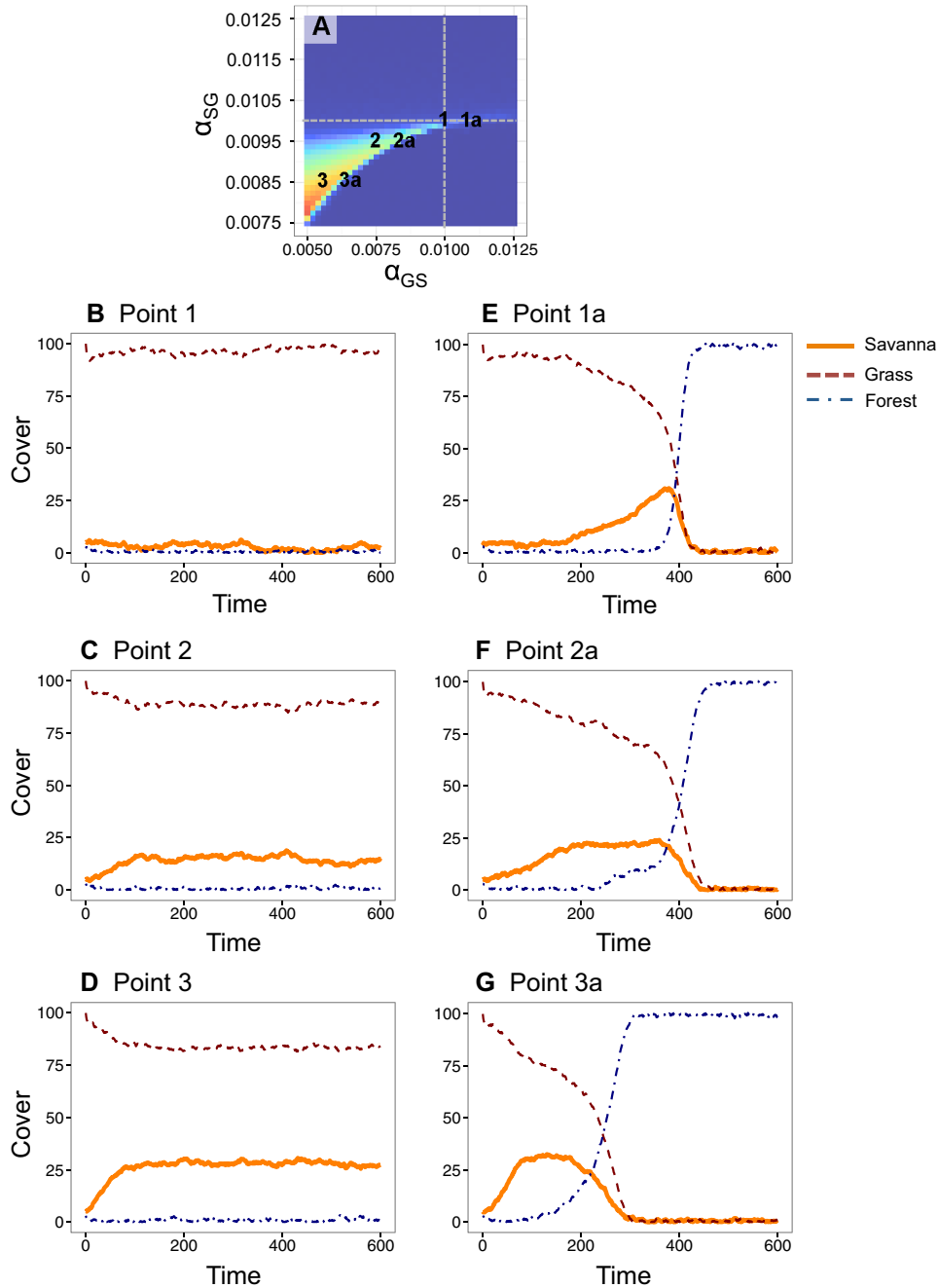
Figure 4. Examples of expansion trails for different values of savanna tree effects on grasses and grass effect on savanna trees (**B–D**), using parameter values shown in panel (**A**). Points 1 through 3 are parameter space where the savanna–grass competitive balance makes forest tree expansion unlikely (**B–D**). Points 1a through 3a are expansion trails with α_{GS} increased by 0.001 (relative to points 1 through 3) (**E–G**). The *solid orange line* is savanna trees, the *dashed red line* is grasses, and *blue dot-dashed line* is forest trees. The exact parameters values are: Point 1 ($\alpha_{SG} = 0.01$; $\alpha_{GS} = 0.01$), Point 2 ($\alpha_{SG} = 0.0095$; $\alpha_{GS} = 0.0075$), and Point 3 ($\alpha_{SG} = 0.0085$; $\alpha_{GS} = 0.0055$). Note panel (**a**) is a modified version of Figure 3a.

crossed savanna–forest boundaries at regular intervals or captured a continuous range of tree cover ($n = 11$) reported ''abrupt'' changes in composition at the boundary between savanna and forest (Bowman and Fensham 1991; Dantas and others 2013; Geiger and others 2011; Hennenburg and others 2005; Hoffmann and others 2009; Mapure 1997, 2012; Müller and others 2012a, b; Unwin 1989).

Several studies found forest and savanna composition to be similar. In vegetation mosaics of Zambian and Tanzanian highlands, the least

(''Mateshi'') and most flammable vegetation types (''Chipya'') share some dominant tree species, but few tree species with intermediately flammable Miombo woodlands (Lawton 1978; Kikula 1986; Mapure 2012). Nonetheless, the three community types had different composition, based on abundance-weighted multivariate methods. The greatest degrees of savanna–forest compositional overlap occurred in Senegal, with a Jaccard distance of 0.29 in one study (Wolf 1998). Another counter-example is in the plains of Venezuela, where the tree species typical of open environments frequently

excluded grasses, leading to eventual replacement by forest tree species (Brener and Silva 1995). For other results, see Table 2.

DISCUSSION

Our model demonstrates that in the presence of hierarchical competition, one viable strategy for a species that is a less effective competitor for a key resource (savanna trees competing for light) is to have a weaker competitive effect on a species (grasses) that can repel the other potentially dominant species (forest trees). In this particular case, certain combinations of resistance to grass competition and fire (α_{SG}) and exerting weaker competitive effects on grasses (α_{GS}) result in higher savanna tree cover and less potential for competitive exclusion by forest trees (Figure 3). This result depends on the presence of forest trees; otherwise, savanna trees do not benefit from coexisting with grasses. Therefore, in areas with historically little threat of forest tree expansion, such as more semi-arid locations (Sankaran and others 2005) or where evolutionary bottlenecks have reduced the abundance of forest trees (Bowman 1992), we would expect that having traits that increase tree–grass coexistence ceases to be an advantage, requiring other mechanisms for coexistence (for example, Walter 1971). Overall, our results suggest that tree–grass coexistence is not necessarily paradoxical in many savannas (Sarmiento 1984). Instead, coexisting with grasses can be beneficial for tree species that are inferior direct competitors with forest trees.

Much of our results depend on the feasibility of savanna trees to reduce their competitive effect on grasses and resist fire. This is not to say that savanna trees have no negative effect on the growth of flammable grasses, or vice versa, only that both of these competitive effects could be greater if savanna trees allocated resources differently. Indeed, it is unlikely that savanna trees have no negative effects on grasses and growth limitation of savanna trees by grasses is well-documented (Scholes and Archer 1997; Bond 2008; Dohn and others 2013). Reductions in competitive effects by savanna trees could be achieved by developing a less dense canopy and niche partitioning with grasses above and belowground. Many of these traits have been observed in savanna trees throughout the world (Weltzin and McPherson 1997; Kulmatiski and others 2010; Ratnam and others 2011; Hoffmann and others 2012). Moreover, process-based models have shown that grasses and trees can have substantial root profile overlap and still coexist (Holdo 2013). Savanna trees and grasses could also have minimal fitness differences in their ability to obtain belowground resources, which would allow for coexistence despite large niche overlap (Chesson 2000). It is also worth noting that the presence of savanna trees can sometimes boost grass productivity through hydraulic lift, N-fixation (Scholes and Archer 1997; Yu and D'Odorico 2015), and by creating a physical environment that deters grazing (that is, a landscape of fear; Riginos and Grace 2008). Traits to reduce fire sensitivity are also common in savanna trees, generally including a greater relative bark thickness and belowground carbon storage (Bond and Keeley 2005; Ratnam and others 2011; Hoffmann and others 2012).

Even though we did not directly parameterize our model from field studies, we used empirical observations to set the assumptions that this is a system with hierarchical competition (Ratnam and
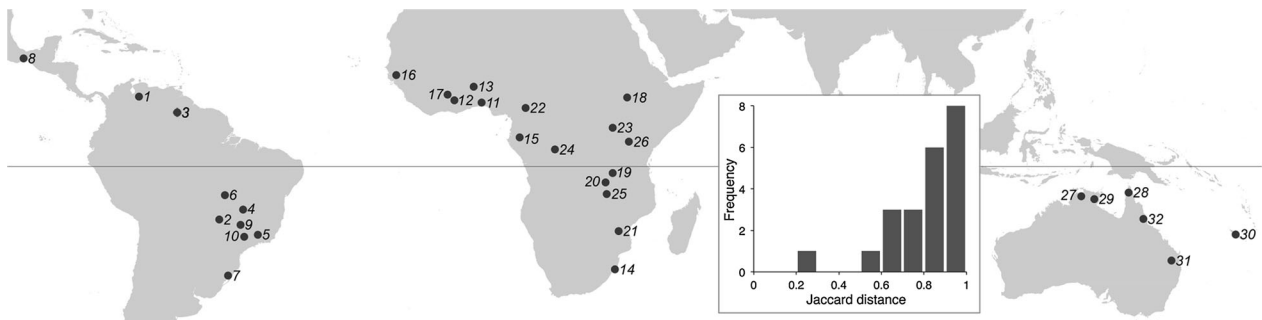

Figure 5. A map of where studies in the literature review were located. Numbered locations correspond to the studies in Table 2. Note that attribution of multiple sites to the same point in space does not mean that each study occurred in the exact same location, only the same general area. The *inset graph* is a histogram of Jaccard distances. When multiple Jaccard distances were calculated in a study (due to the existence of multiple sub-community types), we used the average of all Jaccard distances.

others 2011; Hoffmann and others 2012; Macdermott and others in press). This results in the key differences in the relative parameter values for each species. Moreover, our results are fairly robust to many large parameter changes (see Appendix 1). For example, if α_{GG} increases, then the competitive effect of savanna trees on grasses needs to decrease even more to prevent colonization by forest trees but the same general results still hold (Appendix 1). The sensitivity analyses also suggest that when savanna trees have traits that facilitate coexistence, it will probably take larger increases in precipitation to force a shift to a forest state (see Appendix 2).

Other Evidence

In our systematic literature review, the majority of the studies found that species that are abundant in closed-canopy communities are absent or rare far into open grassy patches. On average, 81% of tree species were found only in forest or savanna and community composition seldom overlapped between the two communities, based on abundance-based multivariate analyses (Table 2; Figure 5). The primary exceptions were areas with recent fire suppression, where forest trees were more abundant and had often begun displacing grasses and savanna trees (Table 2). To an even greater extent, trees typical of open environments were absent from forested patches, as juvenile savanna trees were seldom found in forest communities. This strong compositional separation suggests that it was rare for a tree species to have traits that allow it to establish in both open- and closed-canopy tree communities.

A reoccurring observation in many of the studies was the existence of a third distinct functional group, often found in a 20–200-m boundary zone between savanna and forest or as small patches in a savanna matrix. Prominent examples were the *Uapaca* genus in Central Africa (Lawton 1978), the *Callitris* genus in Northern Australia (Trauernicht and others 2016), and species associated with ''thickets'' in South Africa (Charles-Dominique and others 2015). These woody species were better at colonizing open grass-dominated areas than forest trees, but were rare to nonexistent far from the boundary between forests and savannas (for example, Lawton 1978; Trauernicht and others 2016; Table 2). Such trees are probably best referred to as ecotone, intermediate, or pioneer forest species and match the hypothetical set of parameter values of a tree that can survive fires (lower α_{iG}), but eventually shades grasses (high α_{Gi}), allowing forest trees to dominated the patch (parameter values marked 1a, 2a, and 3a in Figure 4).

Another implicit prediction of our model is that the expansion of open habitats approximately 15 mya followed by the expansion of C_4 grass biomes approximately 8 mya might have driven some forest trees to evolve to have traits like those of savanna trees in the model or led to switches in tropical tree abundance in favor of tree species with higher fire resistance and weaker competitive effects on grasses. Specifically, we would expect the evolution and/or expansion of ''savanna trees'' to be more common starting 15–8 mya. It is already established that many savanna trees in South America are related to tree species found in closed environments, but estimates of when related savanna and forest trees diverged from each other are still being refined (Simon and Pennington 2012). However, current best estimates suggest that many contemporary savanna trees did not diverge from closed-canopy relatives before 10 mya with many species divergences after 4 mya (Simon and Pennington 2012), which is in line with arguments that the expansion of flammable C_4 grasses has affected the evolution of tropical and subtropical trees (Bond and Keeley 2005). Similarly, the estimated emergence of *Acacia* trees adapted to open habitats in Africa, the Americas, and Australia occurred primarily from 15 to 5 mya (Bouchenak-Khelladi and others 2010).

Resource allocation trade-offs make this proposed course of evolution or species reordering more likely. Investment in fire-resistant tissues leaves fewer carbohydrates and nutrients for developing a large canopy and other tissues that might enhance light capture. Therefore, there is probably some trade-off where developing resistance to grass fire (reductions in α_{SG}) decreases the ability of savanna trees to compete for light and belowground resources (values of α_{GS}). Such a trade-off would largely restrict α_{GS} and α_{SG} to values that result in long-term coexistence of grasses and savanna trees (Figure 6). This trade-off also raises the possibility that the evolution of reduced competitive ability in savanna trees could stem from the selection for fire-resistant traits.

CONCLUSIONS

Our results suggest that evolution and/or filtering of existing tree species could be a mechanism favoring savanna trees that coexist with grasses over long timescales. To summarize these results, we invoke the phrase ''the enemy of my enemy is
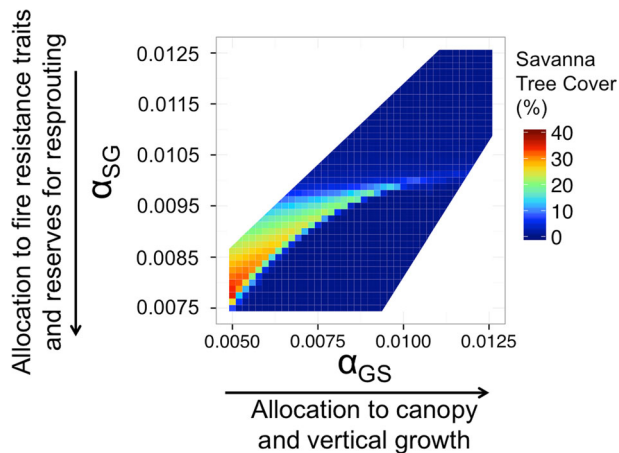
Figure 6. Due to morphological constraints, α_{SG} and α_{GS} are probably correlated because increases in allocation to resist fire damage and/or resprout after fire leaves fewer resources to invest in competing for light and other resources. This figure depicts how such morphological trade-offs would restrict the possible parameter values to a subset of those we considered in previous analyses. *White areas* in the bivariate space denote unrealistic combinations of α_{SG} and α_{GS} due to this trade-off.

my friend.'' Although grasses do limit savanna tree growth, limitation by grasses typically pales in comparison with the growth limitation forest trees can exert on savanna trees. Indeed, savanna trees can form viable populations in C_4 grass environments, but are often absent from areas with closed tree canopies (Table 2). In this case, the fitness of savanna trees is potentially higher if their competitive effect on grasses is lower, because it allows grasses to repel colonization by forest trees—making grasses the enemy of the greater enemy, forest trees. In the context of the savanna question, our results do not address the exact mechanisms of how grasses and savanna trees coexist. However, they do provide an explanation for why savanna trees might be driven toward traits favoring coexistence. The counter-intuitive result that reductions in competitive effects can sometimes lead to greater abundance for a species might apply to other systems with hierarchical competition (for example, Kerr and others 2002), especially when one or more species are capable of generating strong positive feedbacks that can alter the environment.

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