Fire Feedbacks with Vegetation and Alternative Stable States

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Positive feedbacks between vegetation and fire disturbance may lead to nonlinear ecosystem responses to variation in fire regime. We used a cellular automaton model of fire-vegetation dynamics based on pine savanna communities to explore the potential for fire-vegetation feedbacks to lead to ecological thresholds and abrupt transitions between alternate ecosystem states. We show that (*i*) ecosystems can rapidly move between grassland and forest states in response to gradual changes in fire regimes or initial landscape composition and that (*ii*) hurricane disturbances can mediate the frequency of fire that leads to ecological thresholds. Nonlinear ecosystem dynamics lead to sensitivity to initial conditions and bistable ecological communities that can exist in either a grassland or forest state under the same disturbance frequency. Our results indicate that gradual changes in global climate that influence disturbance frequency may result in the rapid transformation of landscapes through feedbacks between fire and vegetation.

1. Introduction

Positive feedbacks between disturbance and vegetation dynamics may result in rapid transformations of ecological systems to alternate stable states following small changes in disturbance frequency. Feedbacks can lead to nonlinearities and threshold responses to linear changes in external forcing, where a gradual change in a process causes a disproportionate response once a critical threshold is crossed [1, 2]. Negative feedbacks can stabilize systems, but positive feedbacks lead to accelerating changes and a rapid transformation to an alternate state [3]. Fire-frequented ecosystems might be characterized by nonlinearities and threshold responses because of positive feedbacks between fire frequency and vegetation [4-6]. The likelihood of fire is influenced by the composition of the vegetation, which provides the fuel for fire, and the composition of the vegetation is, in turn, affected by fire frequency [6, 7]. Plant species that are adapted to fire increase in abundance following fires, while species that are fire-intolerant decline [7, 8]. While fire-adapted plant species have life-history traits that protect them from damage in fires, they can also have characteristics that facilitate fire initiation and spread [9-11]. In contrast, fire-intolerant species that are susceptible to damage in fires can have characteristics that inhibit fire [10, 12]. The increasing abundance of fire-adapted species facilitates fire in pine savannas of the southeastern United States, while the relative inflammability of fire-intolerant species inhibits fire [9, 11].

Nonlinearities and ecological thresholds can complicate the prediction of ecosystem state in response to incremental climate change or anthropogenic management. At ecological thresholds, small shifts in fire regime can lead to disproportionate changes in ecosystems and ecological "surprises" or sudden changes in state [13]. The behavior of ecological systems may also be sensitive to initial conditions in the presence of ecological thresholds, and the location of these thresholds is likely to be dependent on the state of the ecosystem. This dependence of threshold locations on ecological state can lead to a hysteresis with multiple stable states depending on the direction of change (Figure 1). If climatic conditions decrease fire occurrence below a critical frequency, for example, fire-inhibiting plant communities will replace fire-facilitating communities, creating a positive feedback further decreasing fire frequency and pushing the ecosystem to a state in which fires are more rare than would be predicted by the change in climate alone. A return of climate to its prior state may not return the ecosystem to its initial state since the ecosystem now inhibits fire; instead, more extreme climatic conditions that favor fire may be needed [14]. The system dependence on initial state can lead to the existence of alternative ecological communities that could exist under the same environmental conditions depending on past direction of change.

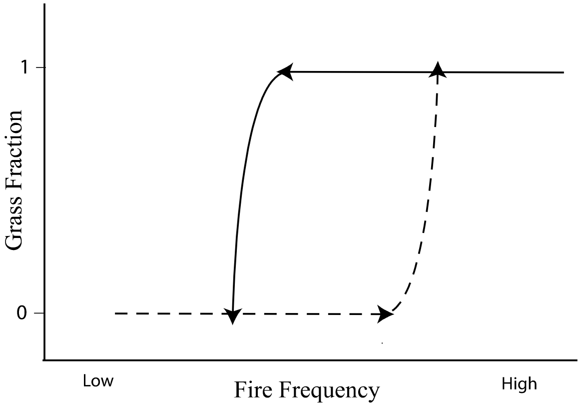


Figure 1. The location of ecological thresholds depends on the direction of change of the fire regime. When the community is in a grassland state (i.e., grass fraction near 1), fire frequency must be reduced to a low level before the community converts to a forest state without grass. This results from the high flammability and connectivity of grass fuels in the landscape. As fire frequency is increased from this forest state, the community does not transition back to a grassland state until high fire frequencies are reached. Forests are relatively inflammable and a high incidence of fire starts is needed to burn the

landscape, converting the forest to a grassland. Two different stable community states are possible between these two ecological thresholds, that is, grassland or forest, depending on initial conditions.

We investigate the potential for fire-vegetation feedback loops to lead to rapid shifts in ecosystem state in response to changing fire frequency. We explore system behavior using a cellular automaton (CA) model of disturbance (fire + hurricanes) and vegetation dynamics in order to identify ecological thresholds. We use a CA because they have a relatively simple structure but are capable of capturing complex dynamics [15]. CAs model the state of a multidimensional grid of cells, typically one- or two-dimensional, where the state of an individual cell depends both on its own state as well as those of its neighbors. The spatial scale of neighborhoods can vary as can the nature of the interactions, for example, whether interactions are deterministic or stochastic. Our specific CA is based on vegetative dynamics observed in pinelands of the southeastern United States [11, 16]. We investigate (*i*) whether feedbacks between vegetation and fire frequency may lead to ecological thresholds and (*ii*) if the location of these thresholds is sensitive to initial conditions. Finally, we also examine (*iii*) whether disturbances that do not have feedbacks with vegetation, such as hurricanes, produce ecological thresholds.

2. Methods

2.1 Model System

We explore the potential for nonlinear dynamics using a CA model of pine savanna communities in the southeastern United States. Pine savannas are characterized by widely spaced pine trees that form a discontinuous overstory in a graminoid-dominated groundcover or "grassland" matrix [17], but can also transition to treeless grasslands or closed forests in response to disturbance [18]. The savanna overstory is usually comprised of longleaf pine (*Pinus palustris*), except in southern Florida where south Florida slash pine (*Pinus elliottii* var. *densa*) is the overstory dominant [8, 11, 19]. The ground-layer vegetation is comprised of herbaceous species, particularly grasses, along with sedges and forbs [7, 11]. Ground-layer fires typically burn pine savannas several times a decade, increasing the mortality of pine seedlings and juveniles, but only having modest effects on mortality of larger pines [11, 20]. In addition to these two community states (i.e., pine overstory and graminoid groundcover), a hardwood vegetation state is possible: the pine overstory and graminoid groundcover is displaced by fire-intolerant hardwood forests in the absence of frequent fire [21, 22]. Hurricanes are also frequent disturbance events in the southeastern United States: 35 tropical cyclones impacted south Florida, for instance, in the period from 1886 to 1992 [19]. Hurricanes produce elevated overstory mortality in pine savannas, but in contrast to fire, hurricanes increase the mortality of large overstory trees, while having only limited effects on mortality of small size classes [19, 23, 24].

2.2 Model

We simulate pine savanna dynamics using a cellular automata model operating on a grid of 50×50 cells. Each cell represents a discrete area (e.g., $10\,\text{m} \times 10\,\text{m}$) and could be in one of five states: grass, juvenile pine, adult pine, juvenile hardwood, or adult hardwood. In this model framework, a pine savanna consists of a mixture of interdispersed pine and grass cells (Figure 2). The landscape was first initialized into one of three states: grassland, a mixed state with all three vegetation types, or a hardwood forest (Figure 2). Then, the landscape was updated each time step (equated to one year) in response to three primary processes: vegetative succession, fire initiation and spread, and hurricane disturbance. A model run was completed when a maximum number of time steps (i.e., 500 years) was reached or when the landscape reached a stable composition, which we defined as no more than 1% change in landscape composition over 10 years. We explored ecosystem dynamics in response to variation in disturbance intensity by varying the number of lightning strikes in the landscape and the annual probability of a hurricane.

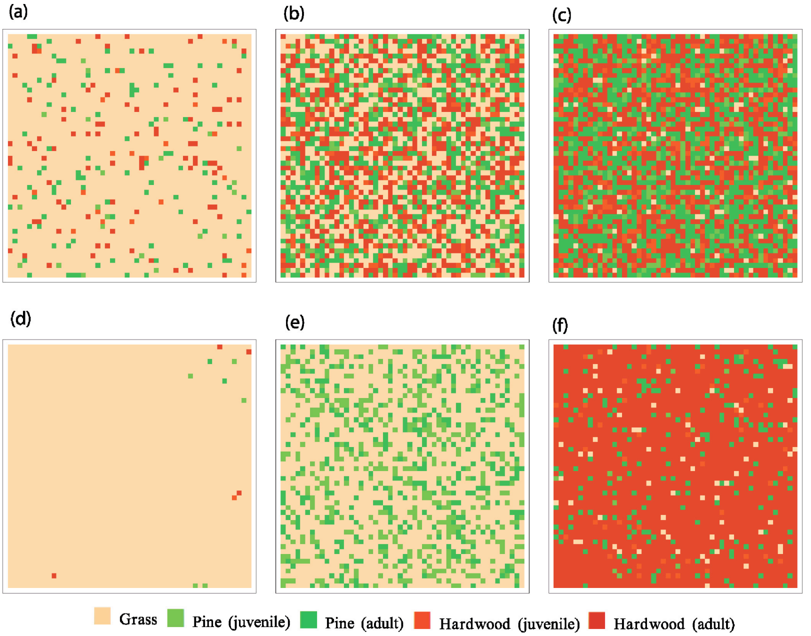


Figure 2. Representative initial and final states are shown for model landscapes. The top row (a) through (c) shows examples of initial landscape states

used in simulations. The bottom row (d) through (f) shows examples of final landscape states produced by simulations. The various states are (a) grassland initial state, (b) mixed initial state, (c) forest initial state, (d) grassland final state, (e) pine savanna final state, and (f) hardwood forest final state. Vegetative states of individual cells are given in the color key.

2.2.1 Succession

Vegetative succession was defined by transition probabilities between cell vegetative states, by the dispersal distance for each vegetation type, and by survival in fires and hurricanes (Figure 3). Survival probabilities were dependent on vegetation type, disturbance type, and age class, reflecting observed patterns in pine savannas [11, 20, 21], and are given in Table 1.

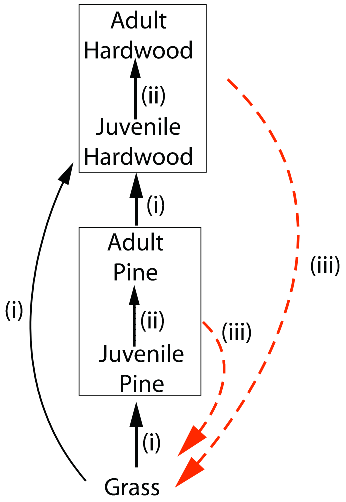


Figure 3. Cell transitions between vegetative states are shown. (i) Cell transitions between vegetative states take place stochastically with a fixed probability. If the transition does not occur, then the cell remains in its current state. (ii) Deterministic transitions occur within vegetation types. Juvenile pines transition to adult pines after 10 time steps (e.g., 10 years). Juvenile hardwoods also transition to adult hardwoods after 10 time steps. (iii) Disturbances that result in mortality of pine or hardwoods cause the cell to transition to a grass state.

		Pine		Hardwood	
	Grass	**Juvenile**	**Adult**	**Juvenile**	**Adult**
Burn probability	0.4	0.1	0.1	0.05	0.05
Survival in fire	1.0	0.3	0.8	0.1	0.2
Survival in hurricanes	1.0	0.99	0.8	0.99	0.8
Dispersal distance	1	NA	4	NA	1
Reproductive maturity	1	10	—	10	—
Transition Probability without Fire or Hurricane Mortality					
	From				
		Pine		**Hardwood**	
To	**Grass**	**Juvenile**	**Adult**	**Juvenile**	**Adult**
Juvenile pine	0.03	0.98	—	—	—
Adult pine	—	1^{*}	0.98	—	—
Juvenile hardwood	0.01	0.02	0.02	—	—
Adult hardwood	—	—	—	1^{*}	1
Transition Probability after Fire or Hurricane Mortality					
	From				
		Pine		**Hardwood**	
To	**Grass**	**Juvenile**	**Adult**	**Juvenile**	**Adult**
Grass	1	1	1	1	1

*After 10 time steps.

Table 1. Parameter values used in our pine savanna simulation model.

2.2.2 Reproduction and Dispersal

Tree cells were initially in a juvenile state following transitions from other states, and were therefore unable to influence succession in adjacent cells through reproduction. Tree cells transition to an adult stage after 10 time steps (i.e., 10 years) as an approximation to the time to reach reproductive maturity (e.g., "Slash Pine" in [25]). Dispersal distance was one cell for grasses, up to four cells for pines, and one cell for hardwoods (Table 1), reflecting the potential long-distance dispersal of pines by wind [26], compared to the ground-layer vegetation and hardwoods [27].

2.2.3 Disturbance

Fires were initiated by lightning strikes and subsequently could spread to adjacent cells. Fire initiation was dependent on the state of the struck cell. The number of lightning strikes in the landscape at each time step was modeled as a Poisson process with the mean or lambda parameter equal to lightning strike intensity multiplied by the number of cells in the landscape. Lightning strike intensity was varied from 0 to 0.4, which corresponded to an expectation of 0 to 1000 lightning strikes in a 50 × 50 cell landscape. After a successful fire start, fire could potentially spread across the landscape in a probabilistic manner dependent on the state of surrounding cells. Burn probability and subsequent survival of vegetation types reflect the fire tolerance of pines and ground-layer vegetation and the sensitivity of hardwoods to fire (Table 1) [11, 16, 17].

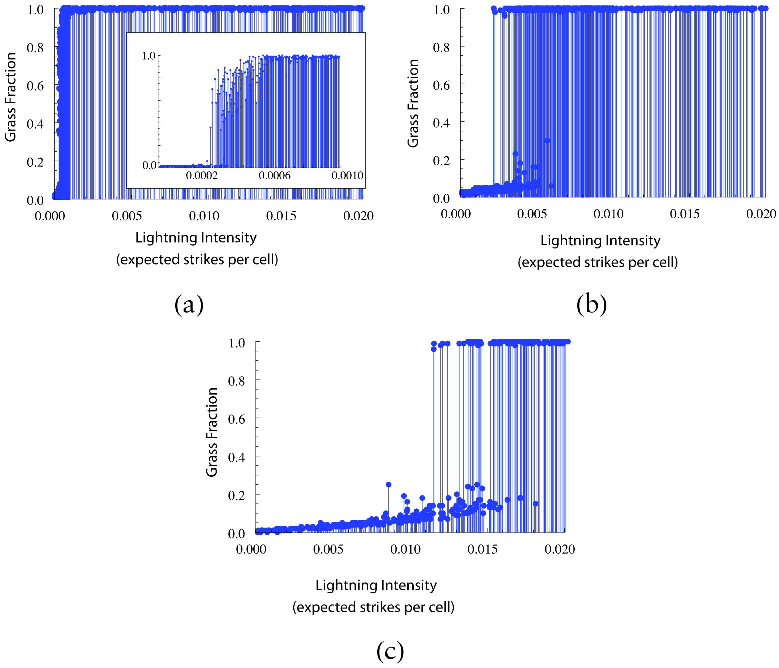
Hurricane disturbance, in contrast, was a global event that could occur annually with a given probability. We varied the annual probability of a hurricane over the range 0 to 1, corresponding to the absence of hurricanes in the landscape to annual hurricanes. Survival of vegetation types and demographic stages within size classes in hurricanes are based on observations in the southeastern United States (e.g., [17, 24]) (Table 1).

2.2.4 Code

We coded our pine savanna model in the Java programming language for portability, developmental efficiency, and computation speed, but called the program from within *Mathematica* to take advantage of its graphical and analytical features. The Java program contained 11 classes that implemented landscape behavior, cell behavior, statistical analysis, GUI display/interaction, and file I/O. We used CERN's Colt library to generate random distributions. Though run times were dependent upon specific parameterization, a sample 500-year model run consumed about 10 seconds.

3. Results

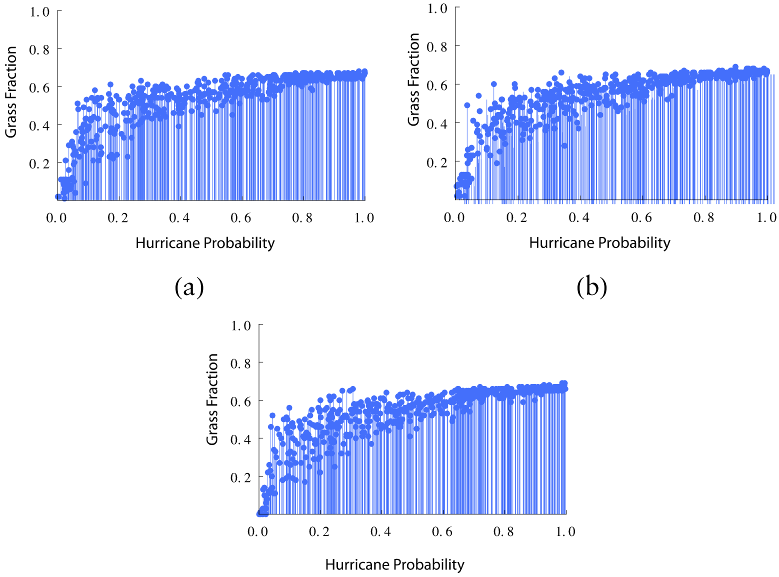
Positive feedbacks between fire frequency and grass vegetation lead to rapid transitions between a forested and grassland landscape with changing lightning intensity (Figure 4). The positive feedback results from increased fuel continuity and fire spread as the portion of grass cells increases. Frequent fire maintains the landscape in a predominately grassland state with scattered trees (Figure 2(d)); for example, grass fraction is near 1 when lightning intensity is above some threshold value. The landscape transitions to a closed hardwood forest (Figure 2(f)) as lightning intensity declines. The location of the ecological threshold is dependent on the initial landscape state and direction of change (e.g., Figure 1): the ecological threshold is located at lower lightning intensities when the community is initially in a grassland state compared to a forested initial condition (Figure 4(a) vs. 4(c)). Hurricane disturbances, in contrast, do not result in an abrupt threshold between grassland and forest states, but rather a gradual transition, and the location of the transition between community states is not related to initial conditions (Figure 5). The absence of nonlinearities in vegetation response to hurricane disturbance results from the lack of feedbacks between hurricane frequency and vegetation. Hurricanes do interact with lightning intensity, however, to influence the location of the fire-induced ecological threshold (Figure 6). In the absence of hurricanes, the transition between forests and grasslands occurs at a much higher lightning intensity than with hurricanes present in the landscape. Periodic hurricanes remove trees from the landscape, creating areas of grass that provide fuels for subsequent fire initiation and spread, such that hurricanes can facilitate the conversion of forests to grasslands. An increasing frequency of hurricanes limits the potential density of trees, bounding the community away from a forest state and facilitating the development of savannas at lower lightning intensities (Figure 6).



(a) (b)

(c)

Figure 4. Fire disturbance leads to ecological thresholds and abrupt transitions between grassland and forest states. The location of the threshold depends on the initial state of the landscape: the threshold occurs at increasing values of lightning intensity as the initial condition moves from a grassland (a) to a mixed state (b), and finally to a forest state (c). The result is a hysteresis as illustrated in Figure 1: a low lightning intensity is required to transition a grassland to a forest, but a much higher lightning intensity would be required to move the ecosystem back to a grassland from a forest state.



(a)

(b)

(c)

Figure 5. Hurricane disturbances lead to relatively smooth transitions between forested and savanna states. Hurricane disturbances alone are not able to drive the system to a grassland state without a decrease in the survival probability of trees in hurricanes (see Table 1), but instead result in a savanna state. The location of the transition region is independent of the initial state of the landscape, occurring at approximately the same annual probability of hurricane disturbance, whether the initial landscape state was grassland (a), mixed (b), or forest (c).

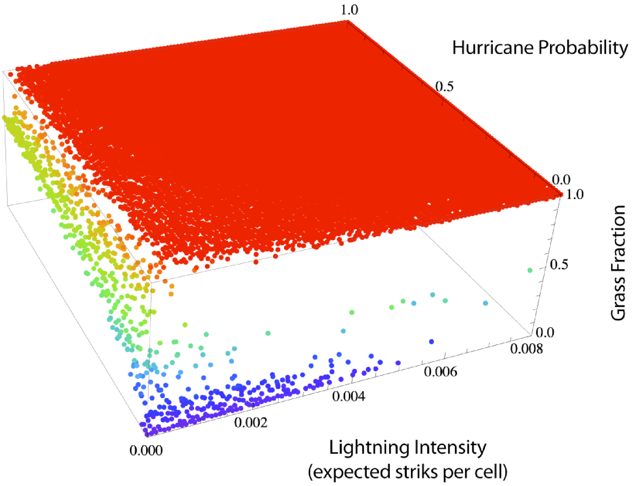


Figure 6. The combined effect of fire and hurricane disturbance on landscape composition is shown as the fraction of cells in a grass state. Hurricane probability interacts with lightning intensity to promote the formation of grasslands by removing overstory trees, thus increasing the connectivity of fuels and the spread of fires. Higher lightning strike frequencies are required to convert the landscape from forest to grassland in the absence of hurricanes (i.e., hurricane probability of 0) than when hurricanes occur periodically. High hurricane frequencies prevent the community from approaching a closed forest state, limiting tree density to a savanna state at low lightning intensities. Each point represents the results of a single simulation with a unique lightning intensity and hurricane probability. The initial landscape state was an equal mix of grasses, pines, and hardwoods (e.g., Figure 2(b)) for all simulations.

Fire-vegetation feedbacks produce a bimodal distribution of equilibrial ecosystem states in our model, with the final community either a forest or grassland (Figure 7). This bimodality occurs in simulations that begin from the same initial landscape with identical lightning strike intensity that is in the range of parameter space near the transition between forested and grassland states (Figures 7(a) and 7(b)). Changes in either lightning strike intensity or initial landscape composition can lead to nonlinear transformations from a forest to grassland state. The result is a bimodal distribution of ecosystem states near these ecological thresholds, with the landscape in either a forest or grassland state, without a corresponding abundance of landscapes between these two extreme states (Figures 7(a) and 7(c)). This behavior results from the stochastic initiation and spread of fire coupled with the strong positive feedback of vegetation type on fire, and does not occur with hurricane disturbance. The absence of a feedback between hurricanes and vegetation facilitates the potential for hurricanes to result in savanna communities with trees coexisting with grasses when coupled with low lightning intensities (e.g., Figures 2(e), 5, and 6).

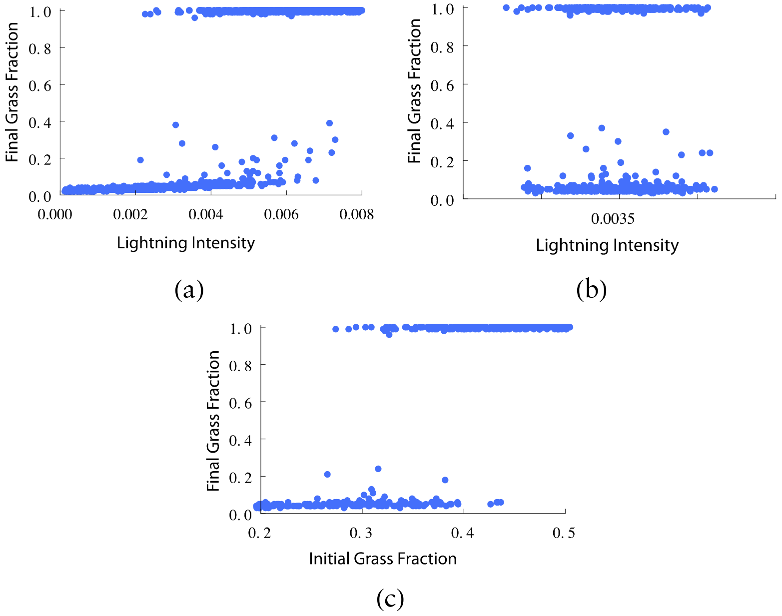


Figure 7. Bistability of ecosystem state is shown in response to lightning intensity and initial community state. (a) Two community states are possible across a range of lightning intensity values. The final community state is a forest at the lowest lightning intensities, but increasing lightning intensity moves the system first into a region of bistability where either a grassland or forest state is possible, and then finally to a region dominated by grassland at higher lightning intensities. Note that all simulations began from the same initial state with a probability of hurricanes equal to 0. (b) Bistability can also be achieved in repeated simulations that begin from the same initial landscape and the same lightning intensity (e.g., 0.0035 expected strikes per cell). The final landscape is predominately in either a grassland or forest state depending on the stochastic spread of fire. Note that white noise has been added to the x coordinates to separate the points, and the probability of hurricanes was 0 in all simulations. (c) Variation in initial conditions can also lead to alternate final community states and bistability. At low initial grass fractions, the final system state is forest, but an increasing initial fraction of grass cells moves the system into a range where the system can either be in a grassland or forest state. Continued increases in initial grass fraction results in a final grassland state. Lightning intensity was 0.0035 expected strikes per cell, and the probability of hurricanes was 0 in all simulations.

4. Discussion

Vegetation-fire feedbacks can result in abrupt shifts in ecosystem state once an ecological threshold is crossed. Strong feedbacks between grass and fire mean that the ecosystem can exist in either a grassland or forest state, but that intermediate savanna states are difficult to achieve. Disturbances that do not have feedbacks with vegetation, such as hurricanes or some nonspatial fire models, in contrast, can lead to savanna states [28]. While hurricanes do not produce ecological thresholds, they are important mediators of vegetation-fire feedbacks in our model: hurricanes remove canopy trees, promoting grass fuels, and subsequent fires. The result is a shift in the location of the ecological threshold to lower lightning intensities in the presence of hurricane disturbance (Figure 6) that could expand the potential range of environmental conditions (e.g., lightning intensities) that support grasslands. The potential for fire following hurricanes to drive ecological transitions between closed forests and open canopied savannas has also been suggested by other studies [29, 30].

We suggest that climate change may result in abrupt changes in the composition and distribution of ecological communities through nonlinear community responses to changing disturbance regimes. Forests in low latitude regions of the world, such as forests of the southeastern United States, are likely to be most influenced by the effects of climate change on disturbance regimes rather than directly by warming temperatures [31]. The frequency of hurricane and fire disturbances in the southeastern United States, for example, is expected to change in response to global warming [28]. Increased hurricane frequency and intensity have already been linked to warming global temperatures: the number of category 4 and 5 hurricanes has approximately doubled globally over the last 35 years, and the total number of hurricanes in the Atlantic basin has increased in conjunction with warming sea surface temperatures [32]. The total energy dissipated by hurricanes has more than doubled in the north Atlantic basin over the last 30 years [33]. Fire regimes are closely linked to global warming through its influence on the periodicity and amplitude of the El Niño Southern Oscillation (ENSO) [34, 35]. ENSO cycles exert a strong influence on winter rainfall and lightning frequency in the southeastern United States: fires are much more prevalent during La Niña phases and are reduced during El Niño phases of ENSO [35-37]. The El Niño phase of ENSO is expected to become increasingly frequent with global warming, with La Niña events decreasing in frequency [38, 39], creating conditions that should favor less frequent fires. Lowered fire frequency would be expected to drive ecological communities toward a forested state, but the transformation could occur rapidly once an ecological threshold is crossed. Decreased fire frequency might be offset by increased hurricane activity, however, because of the potential for hurricanes to shift the ecological threshold between grassland and forested states to lowered fire frequencies. Our simulations emphasize the difficulty of predicting the effects of global climate change on ecological communities because of nonlinear ecological responses that are sensitive to initial landscape state, disturbance, and their interactions [2, 40-42].

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