

SPECIAL FEATURE

GRASS–WOODLAND TRANSITIONS

Fire, percolation thresholds and the savanna forest transition: a neutral model approach

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Summary

1. Recent empirical and theoretical analyses have suggested that biomes could correspond to alternative equilibrium states; one such example is the transition between forest, savanna and treeless states.
2. Fire supposes to be a key functional component of savanna ecosystems and is a powerful predictor of tree cover that can differentiate between forest and savanna ecosystems. Interestingly, empirical evidence suggests that fire occurrence drops at a threshold tree cover near 40%. Since savannas are ecosystems characterized by a discontinuous tree canopy cover immersed in a continuous grass layer a 40% of tree cover implies around 60% cover of grasses, which are the flammable component of this ecosystem.
3. In this article, we hypothesize that the observed common pattern of 40% tree cover versus 60% in grass cover often reported for savanna ecosystems is the outcome of a spatial phase transition associated with the existence of a critical percolation threshold for fire spread.
4. To test this hypothesis, we developed a spatially explicit neutral metacommunity model to explore the relationship between species cover and the emergence of percolation patterns. The model is intended to emulate savanna dynamics under neutrality assumptions.
5. Using a statistical mechanical approach, we show that a second-order phase transition behaviour is observed for the probability that a grass species develops a percolating cluster. Using a simple finite size scaling analysis, the percolation threshold p_c for our model was estimated to be in the range of 0.53–0.62.
6. *Synthesis.* Our results point out that the emergence of a spatial phase transition associated with percolation is a robust result of neutral metacommunity dynamics with a critical threshold of space occupancy close to $p_c \sim 0.6$, which supports our hypothesis that the empirically observed 40% tree cover (60% grass cover) is associated with a percolation threshold for C_4 grasses that in turn imply the existence of a spatially connected or spanning cluster of grass cover over which fire can spread.

Key-words: fire, neutral model, percolation, plant population and community dynamics, savanna forest transition, threshold

Introduction

The world is richly endowed with fascinating spatial asymmetries or patterns in plant species distribution, from local to planetary scales. One of the earlier examples of spatial

asymmetries was described by Humboldt & Bonpland (1807) in their famous essay on the geography of plants and the accompanying ‘Tableau physique’, which is among the first attempts to describe and understand the factors underlying large-scale pattern formation in vegetation, in their case, the arrangement of vegetation in bands or belts along an altitudinal gradient as a consequence of physical changes in the environment. In a similar way, Köppen’s (1931) world climate

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zone and later Holdridge's (1947) life-zone characterization provided a simple explanation for the arrangement of vegetation as restricted to particular combinations of temperature, precipitation and potential evapotranspiration, with different plant forms dominating across gradients in either variable. Recent empirical (Hirota *et al.* 2011; Staver, Archibald & Levin 2011a) and theoretical analyses (Staver, Archibald & Levin 2011b; Staver & Levin 2012; van Nes *et al.* 2013) have suggested that these different life-zones or biomes could correspond to alternative equilibrium states. In particular, these studies have interpreted the transition between forest, savanna and treeless states as a nonlinear response to precipitation of a system characterized by multiple stable states represented by peaks in tree cover distribution. In general, the idea of multiple alternative stable states in ecosystems is already well-established in ecology and has strong theoretical as well as empirical support (e.g. May 1977; Knowlton 1992; Scheffer *et al.* 2001; Dent, Cumming & Carpenter 2002; Scheffer & Carpenter 2003; Beisner, Haydon & Cuddington 2003; Schröder, Persson & De Roos 2005) and has been invoked several times to explain the forest-savanna transition (Walker *et al.* 1981; Sternberg 2001; Van Langevelde, Van Der Vijver & Kumar 2003; D'Odorico *et al.* 2007; Favier *et al.* 2012; Hoffmann *et al.* 2012).

Savannas are dual life-form communities of coexisting trees and grasses (Scholes & Archer 1997; House *et al.* 2003; Bond 2008) with patches of grasslands, scattered trees or closed woodlands that vary in their proportions in different places and at different times (Hochberg, Menaut & Gignoux 1994; Scholes & Archer 1997; Gillson 2004; Wiegand, Ward & Saltz 2005). A quintessential feature of savannas, however, is the presence of C₄ grasses (e.g. Ratnam *et al.* 2011) characterized by high C:N ratios, low decomposition, high productivity and flammability (D'Antonio & Vitousek 1992; Ehleringer &

Monson 1993; Bond 2008) and more importantly tolerant to recurrent fire events the same as the trees with which they coexist (Ratnam *et al.* 2011).

Fire is a key functional component of savannas (Bond, Woodward & Midgley 2005; Staver & Levin 2012) and is a powerful predictor of tree cover that can differentiate between forest and savanna ecosystems (Cardoso *et al.* 2007; Scheiter & Higgins 2009). In fact, Staver, Archibald & Levin (2011a) recently showed that in areas with similar climate, the presence of savanna ecosystems was associated with fire otherwise forest dominated (see Fig. 1a for the African example). Fires rely on grass biomass as fuel load, which in turn, is inversely related to the proportion of the landscape occupied by woody vegetation. As tree cover increases grass cover will decrease due to competitive effects and will eventually lead to a reduction in fire recurrence time (Levick & Rogers 2011). Interestingly, as tree cover becomes $\geq 40\%$, the amount of burnt area abruptly decreases (Fig. 1b) (Favier *et al.* 2004; Archibald *et al.* 2009; Sankaran *et al.* 2005; Staver, Archibald & Levin 2011b). Since savannas are ecosystems characterized by a discontinuous tree canopy cover immersed in a continuous grass layer (Scholes & Archer 1997), a 40% of tree cover implies around 60% cover of grasses. Thus, although the importance of fire in controlling, the coexistence of trees and grasses is well-established (Hopkins 1992; Cochrane *et al.* 1999; Favier *et al.* 2004; Bond, Woodward & Midgley 2005; D'Odorico *et al.* 2007; Bond 2008; Staver & Levin 2012; van Nes *et al.* 2013), the mechanisms underlying the existence of a 40% of tree cover as a tipping point is not. Recently, a tree cover for fire spread has been included explicitly as a parameter to model the transition between forests and savannas, assuming that both represent alternative stable states (Staver & Levin 2012; van Nes *et al.* 2013). This threshold value has been linked to the percolation dynamics

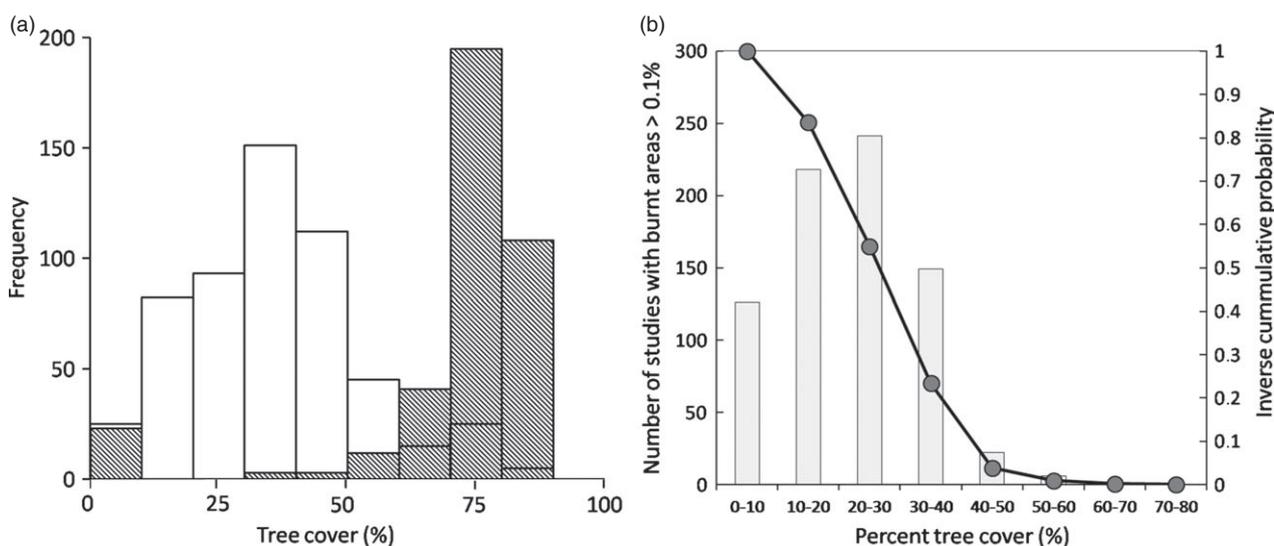


Fig. 1. (a) Frequency distributions of tree cover in areas of intermediate rainfall (1000- to 2500-mm MAR) and mild seasonality (dry season < 7 months) in Africa, with fire present (white bars) and with fire absent pattern bars (after Staver, Archibald & Levin 2011a). (b) Number of studies reporting burned areas bigger than 0.1% (of 100 × 100 km windows) for categories of percent tree cover (bars). Line shows the inverse cumulative probability or the probability of having a fire event above a given tree cover (after Archibald *et al.* 2009).

formalism often considered appropriate to model the phenomena of fire spread (Staver & Levin 2012; Schertzer, Staver & Levin 2014), but the conditions that will lead to its existence as well as its consequences have not yet been assessed.

In this article, we hypothesize that the observed common pattern of 40% tree cover versus 60% grass cover often reported for savanna ecosystems may be the outcome of a spatial phase transition associated with the existence of a critical percolation threshold (Stauffer 1979; Grassberger 1983; Milne 1992; Stauffer & Aharony 1992). The implications of this conjecture are severalfold: (i) percolation models are devoid of any mechanism, representing a null model for an stochastic spatial process, and thus can help us to understand the emergence of patterns in vegetation; (ii) a percolation threshold entail a transition in connectedness, a condition required for fire to spread and potentially reach out anywhere; and (iii) percolation theory predicts an asymptotic value for the transition point at $p_c = 0.59$, a value in close agreement with empirical observations of grass cover needed to maintain a savanna ecosystem. Accordingly, we believe it is important to assess the existence of percolation-like phenomena in models for savanna ecosystems to rule out whether the 60% grass cover is a threshold expected from spatial stochasticity, before invoking more complex mechanistic explanations. To test our hypothesis, we developed a simple spatially explicit neutral metacommunity model that shows that a percolation threshold naturally arises under neutrality, suggesting that a spatial phase transition underlies the shift between the alternative savanna and forest equilibrium.

Materials and methods

To test our hypothesis, we developed a simple spatially explicit neutral metacommunity model. In this metacommunity, species share a common geographic space represented by a square lattice with N cells along each side and changes in their abundance obey neutral dynamics. We consider that neutrality is an important starting point or null model to assess the emergence of spatial patterns in ecological systems (see Marquet *et al.* 2014) and in particular for testing the emergence of spatial patterns typical of percolation phenomena (see Appendix S1 in Supporting Information for a brief review of the main quantities used to characterize percolation).

In our spatially explicit model represented by a square lattice, each out of the $N \times N$ cells corresponds to a local community connected by fluxes of individuals to its immediate neighbours. Each local community is occupied by several species of a similar kind (e.g. C_4 grass species or alternatively woody species) whose abundances fluctuate in time in response to random deaths of individuals, and the influx of immigrants and newly born individuals. Although each species can show temporal dynamics in abundance, the total community abundance in each site was kept fixed, defining a zero-sum model, where losses are balanced by new arrivals. On each site, the total number of species simulated were $S = 100$. The maximum number of individuals allowed was set at $J = 2500$. Preliminary runs of the model showed that results were robust against changes in S and J , which only affected the computational time needed to reach the steady state in abundance. Each model run consisted of $t \times N^2$ Monte Carlo updates, where $t = 500$ and N^2 corresponds to the number of cells in the lattice. No significant changes occurred in more than 5% of species'

occupancy patterns after the $t = 500$ time horizon. In each iteration, we perturbed local communities by removing a random proportion μ of J taken from a uniform distribution $U [0, 1]$. These mortality losses were balanced out by an influx of $K = J - (J \times \mu)$ new individuals using a multinomial sampling scheme where the probability of a species to be included in each of the K independent trials was proportional to its relative abundance in the neighbourhood, including the focal community, in which case, it corresponds to a local birth event (Volkov *et al.* 2007). We used eight nearest neighbours to define neighbourhood (i.e. Moore neighbourhood).

Species abundance was used as a criterion to assess if a particular species was present in a given community. A given species was assigned to a given community only if its abundance showed a positive or no trend in it through time (using only the last 250 time steps). The rationale of this labelling scheme was to exclude from calculations any site that did not contain a self-sustaining local population and thus may represent transient occupancy and relaxing this procedure did not impacted our results. All simulations were done in R (see code in Appendix S2).

To analyse our results in the context of percolation theory, we define a *tuning* and an *order* parameter to be collected from each species in the metacommunity. We defined our *tuning* parameter as the proportion of occupied cells showing either zero or positive temporal trend, $p = p^+ / N^2$, where p^+ is the number of positive or zero trend cells occupied by a given species in the lattice, and N^2 is the total number of cells in the lattice. While simulations were run, we collected maps on a species by species basis, and quantified whether or not a spanning cluster was observed. For every species' map, we calculated p to serve as a control or *tuning* parameter representing site occupancy. Temporal trends in abundance were checked by fitting Poisson regression on the time series for each cell in the lattice (Link & Sauer 1998). If regression fits showed positive or non-significant fits, we coded the cell as positive (because both are conditions of persistence).

We labelled p^+ clusters using the Hoshen–Kopelman cluster labelling algorithm (Hoshen & Kopelman 1976). The *order* parameter was then estimated using cluster size statistics derived from the classified maps. There are many *order* parameters of interest that can be calculated, but we focused our attention on the spanning cluster probability $SC(p)$ (see Appendix S1 for other patch metrics that could be explored) which implies a connected pattern of occupancy. Percolation theory predicts that there must be a critical threshold p_c below which the spatial distribution disconnects (Sornette 2000; Stauffer 1985). Recall that in the context of the savanna forest, a transition to a connected pattern of occupancy by grass species would enhance the chances that fire spreads across space, thus the importance of detecting the existence of such a percolation threshold. It is well known that the size of the lattice affects the value p_c at which the transition occurs, because in small lattices, it is easier to form patches that connect the entire map. Therefore, in order to obtain an asymptotic estimate for this threshold, we performed a finite size scaling analysis. For this, we run simulations for different lattice sizes ($N = 20, 40, 60, 100$) and obtained p_c values from them. By regressing p_c against $1/N$, the intercept becomes an estimate for a lattice of infinite size (Stauffer 1979, 1985; Sornette 2000; Oborny, Meszena & Szabo 2005). We used quantile regression to assess the upper (95%), mid (50%) and lower (5%) quantile limits of this relationship.

Results

We have implemented a simple spatial model with the aim of detecting whether or not percolation may emerge in an

assemblage of species sharing a common space under neutrality. Note that, for our present purposes, it is not truly important to distinguish between grass and woody species, because one is the complement of the other in terms of space occupancy in savanna ecosystems. We believe that simply calculating vegetation cover does not provide a demonstration of the existence of percolation. Rather, we propose that other features of the phenomena must be deployed, such as the emergence of spanning connectivity above a threshold of vegetation coverage.

Figure 2 shows the pattern of spatial occupation and p for six different species and notice the existence of a spanning cluster for larger p values (bottom row). This pattern was consistent between simulations, and suggests the existence of a second-order phase transition in accordance with the percolation phenomenon and manifested in a sharp increase in the

probability of observing a spanning cluster above a threshold p value (Fig. 3). The finite size scaling analysis (Fig. 4) predicts an estimate of p_c for very large lattices in the range of 0.53–0.62, depending on the chosen quantile regression. For a fit in the lower range of variability, the intercept was estimated at a value 0.532 with confidence interval [0.514 and 0.535]. In the upper range of variability, the quantile fit estimates p_c at 0.624 [0.612 and 0.626]. The median estimate was at 0.554 [0.545 and 0.566]. All these alternative estimates are in close agreement with our test of hypothesis for grass species cover around 60%. Also, this value is close to the proposed 0.59 for site percolation models (Stauffer & Aharony 1992).

Our results show that, a simple non-interactive model with a small set of constraints is capable to display a threshold in vegetation cover rather close to the empirical values reported

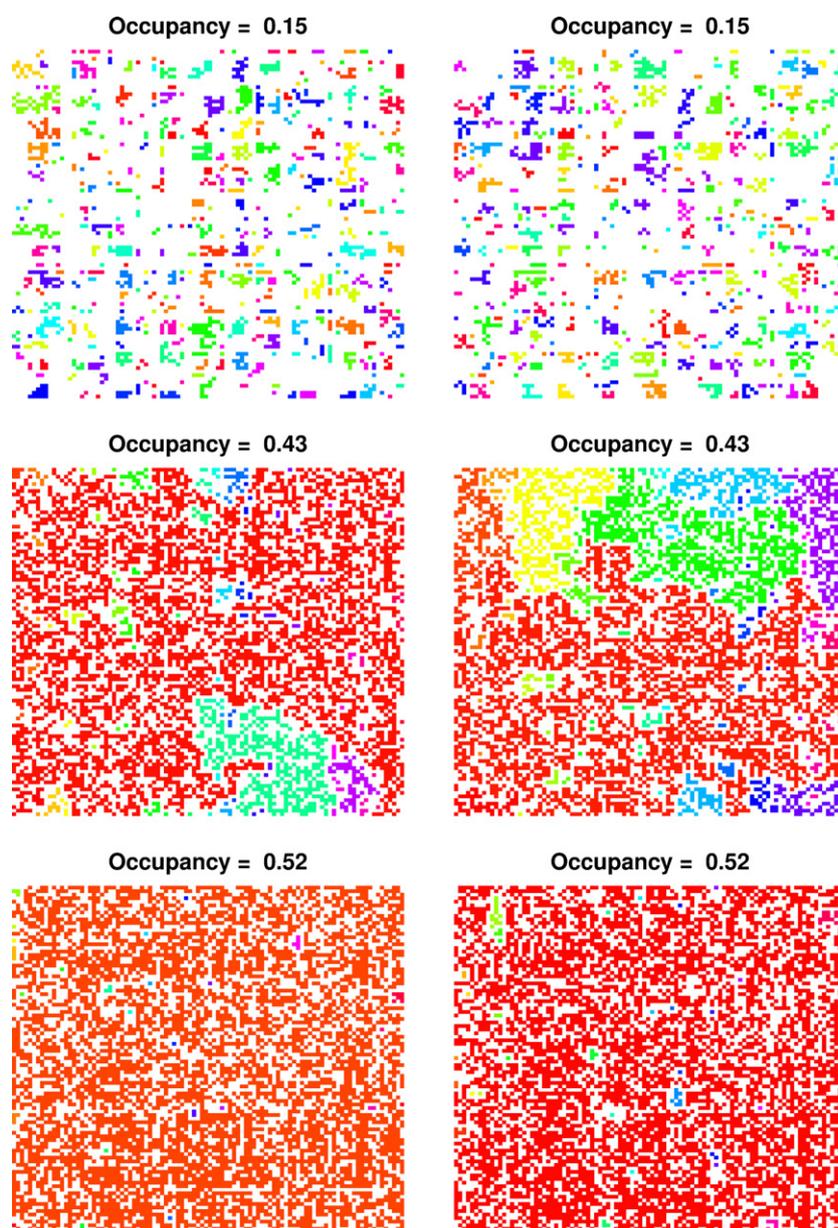


Fig. 2. Simulation snapshots. Each map illustrates patch occupancy patterns for one species. Colours are labels for individual patches. Upper row are species for which occupancy were below p_c , showing no spanning clusters. Middle and lower row are species whose occupancy was close or above p_c respectively.

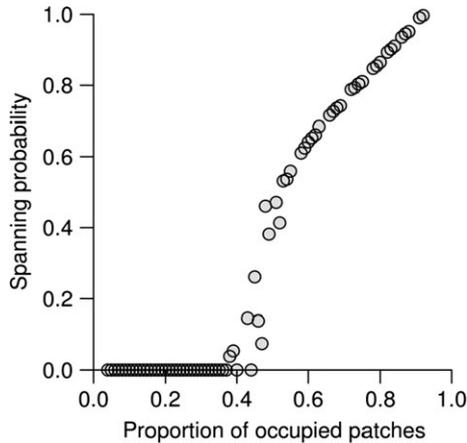


Fig. 3. Percolation pattern associated with the neutral metacommunity model. Spanning probability corresponds to the frequency of species at a given coverage that showed at least one patch that connected the entire landscape.

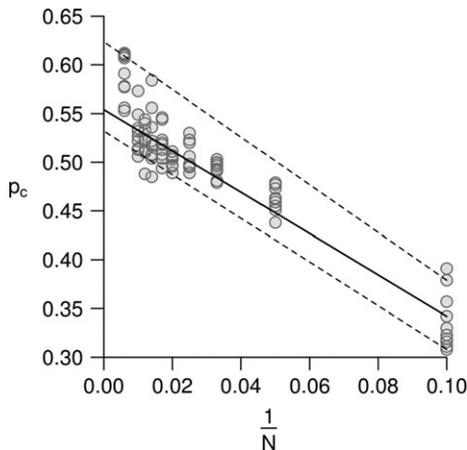


Fig. 4. Finite size scaling analysis. Estimated values of p_c obtained after simulations on different lattice sizes. The upper, middle and lower fitted regressions are 95%, 50% and 5% quantile regressions.

in the study of savanna ecosystems. However, it is worth mentioning that p_c can take other values depending on the local rule used to define a neighbourhood (see Appendix S3). Thus, caution must be taken to establish the appropriate ratio between extent and grain of the landscape whenever these kinds of analyses are performed on real data bases.

The existence of a percolation at $p_c \sim 0.6$ suggests that the empirically observed 40% tree cover could be associated with a percolation threshold for C_4 grasses that would imply the existence of a spatially connected or spanning cluster of grass cover for fire spread.

Discussion

In this contribution, we tested the idea that the empirically observed 60% grass cover (i.e. 40% tree cover) in savannas reflects a critical percolation threshold that provides substrate for fire spread. The existence of this threshold has been assumed in theoretical models of fire spread (Grassberger

1983; MacKay & Jan 1984), and here, we show that the existence of such a threshold must be expected even in a simple neutral model. Therefore, percolation phenomena can be responsible for creating the connectivity needed to provide the spatial flammable substrate over which fire can spread, and as a result reinforce the presence of this highly connected spatial structure.

NEUTRAL MODEL

To test for the existence of thresholds as the outcome of our model, we have relied almost entirely on the statistical phenomenology provided by percolation theory to quantify order. However, for this study, we defined a *tuning* parameter in a slightly different manner than in classical statistical physics to distinguish truly persisting cells to attain a more functional description of occupancy patterns of grass or tree species. This parameter relates to the probability that any given site within the spatial distribution of a species is a site where the species will be found in the long term. The consideration was that highly persistent cells would be likely to produce immigrants into nearby cells, acting as source populations (e.g. Pulliam 1988; Eriksson 1996) and thus creating spatially connected clusters. In practice, one can compute occupancy in this manner employing temporal data bases of satellite images.

Our model can be seen as a simplified variant of classical Hubbellian models (Hubbell 2001; Etienne & Alonso 2006; Volkov *et al.* 2007), where dynamics is driven by the stochastic interplay between random mortalities in sites and local births and migrations that varies stochastically across space, depending on the composition and relative abundance of species in local and adjacent communities. We have found that neutrality can have important consequences in shaping the spatial pattern of the species that compose the metacommunity. Those sites that by chance are perturbed with high levels of mortality tend to favour a few species to achieve robust spatial patterns characterized by spots of high dominance in abundance, while sites subjected to lower mortality levels diminish dominance and favour more even communities. This result suggest that many distributions observed in nature may not necessarily reflect optimal niche conditions; rather they can be the historical outcomes of community dynamics that shifted and pinned species' ranges stochastically (e.g. Fortin *et al.* 2005; Holt *et al.* 2005).

It has long been recognized that the spread of fire is akin to the spread of an epidemic and then suitable to be modelled using percolation theory (e.g. Grassberger 1983; MacKay & Jan 1984; Caldarelli *et al.* 2001). This has led to the establishment of critical thresholds for spread as relevant parameters to look at (e.g. MacKay & Jan 1984), since in the vicinity of thresholds order parameters such as the correlation length diverge. A corollary of the latter statement is that no typical length scale will dominate the system, and accordingly, scaling laws are better candidates to describe the emergent spatial structure (Stauffer 1979; Marquet *et al.* 2005). In fact, available empirical evidence has detected power law distributions in vegetation cluster size in Mediterranean

(Kéfi *et al.* 2007), as well as African woodlands and savanna ecosystems (Scanlon *et al.* 2007). It is well known that around percolation critical points power law behaviour exists. Thus, our results indicate that percolation phenomenon may play an overlooked role in shaping the spatial structure of ecosystems like savannas. In fact, previous studies have tried to make the link between the concept of tipping points and phase transitions to evaluate whether communities display alternative stable states (Rietkerk *et al.* 2004; van Nes *et al.* 2013). Our study shows that this could be the case for the structure of savanna ecosystems.

THRESHOLDS IN SAVANNA FOREST TRANSITION

Savanna ecosystems are found in areas supporting tree cover in a wide range of values, some of them well above the threshold for fire spread (Williams *et al.* 1996; Sankaran *et al.* 2005). This can be the result of different processes. In the first place, it could be misidentification of a forest by a savanna, as is usually the case in areas where fire has been suppressed and/or the forest has been opened by logging or other disturbances (Ratnam *et al.* 2011). Thus, although there can be mesic savannas at higher tree covers, this may not comply with Ratnam *et al.* (2011) definition of savanna that requires an active fire regime. Previous studies have found that fire spread, frequency or size becomes significant in shaping savannas or tree–grass communities, only when tree cover is below the 40% tree cover (Sankaran *et al.* 2005; Hennenberg *et al.* 2006; Archibald *et al.* 2009; Pueyo *et al.* 2010; Staver, Archibald & Levin 2011a,b; Archibald, Staver & Levin 2012; Schertzer, Staver & Levin 2014). Therefore, we suggest that this tree cover threshold is associated with a threshold grass cover (i.e. 60% grass cover Fig. 1) and seems to be robust at large scales. Indeed, out of the 854 savanna sites studies across Africa in Sankaran *et al.* (2005), 196 had woody cover below 1%, hence, were mainly dominated by grasses. Out of the rest, 96% had a tree cover below ca. 40% despite having enough rainfall to achieve higher woody cover.

Finally, the connectivity rule (i.e., number of neighbours) employed (Albinet, Searby & Stauffer 1986; Stauffer & Aharony 1992, See Appendix S3) as well as exogenous factors, not considered in the model, can affect the position of the threshold, which could also differ if fire can propagate beyond nearest neighbours due to flame radiation (Zekri *et al.* 2005; Adou *et al.* 2010) or due to other ‘exogenous’ factors that are known to affect the spread of fire (such as wind velocity and/or topography e.g. McKenzie & Kennedy 2011). In general, the net effect of considering exogenous factors is that fire will have a higher probability of moving along a particular direction transforming the isotropic random site percolation problem in an anisotropic directed site percolation one, with the consequence that the percolation threshold will be located at a lower value (von Niessen & Blumen 1986) in the range 0.4–0.6. Similar results have been reported in experimental settings (Téphany, Nahmias & Duarte 1997) and in the numerical simulation of reaction diffusion models of fire spread in heterogeneous media, composed of different types

of fuel and non-combustible parts (Simeoni, Salinesi & Morandini 2011).

A plethora of studies have attempted to account for the tree–grass coexistence in savanna ecosystems, with most explanations invoking either competition mediated coexistence, or coexistence mediated by demographic bottlenecks for tree establishment, or a mixture of both (e.g. Walter 1971; Scholes & Archer 1997; Scholes 2003; Sankaran, Ratnam & Hanan 2004). Competition-based models have for long invoked differences in resource use and acquisition between trees and grasses (Walter 1971; Walker *et al.* 1981; Walker & Noy-Meir 1982; Fernandez-Illescas & Rodriguez-Iturbe 2003; Van Langevelde, Van Der Vijver & Kumar 2003; Scholes 2003). However, an elegant and simple study by Rodríguez-Iturbe *et al.* (1999) is particularly important in the context of our paper, because the authors made a simple spatially explicit model of tree–grass competition for soil moisture considering grass and tree physiological characteristics and parameterized it using empirical data from the Nylsvley savanna in Africa. The authors found that local plant competition promotes a stable coexistence between trees and grasses when tree cover is ~40% a value that minimises hydric stress of the vegetation, nonetheless, this value could change depending on weather fluctuations. In terms of our model, stable coexistence between species implies equal fitness and hence neutrality, thus if water stress promotes coexistence and thus neutrality at 40% tree cover, it would be compatible with our model results. However, further investigations on the model described by Rodríguez-Iturbe *et al.* (1999) from a percolation perspective may help to better understand how both models are related.

WOODY PLANT ENCROACHMENT AND PERCOLATION

From the perspective of our percolation theory approach, the world-wide encroachment of savanna ecosystems would be related to changes that alter the probability of grass percolation or the amount of fuel stored in the grass layers. In either case, the result will be fire suppression and a progressive increase in its recurrence time. The processes that could affect grass percolation are associated with increases in the cover of savanna trees followed by colonization of forest trees. Reduction in fire intensity or fire frequency could increase the presence of seedlings or saplings of forest species that can grow and cast shade to C₄ grasses, which are shade intolerant (e.g. Veenendaal, Shushu & Scurlock 1993). Similarly, microclimatic conditions promoted by shade (e.g. higher soil humidity) create positive feedbacks that exclude fire and promote the establishment of shade-tolerant no-fire resistant species (Trauernicht *et al.* 2012). However, fire suppression will usually act in tandem with other disturbances such as herbivory, which could promote the establishment of no-palatable species (Van Langevelde, Van Der Vijver & Kumar 2003; Holdo *et al.* 2009). Accordingly, encroachment in South African savannas has been associated with the presence of unpalatable macrophyllus species with high concentrations of toxic chemicals or mechanical defences such as spines (Balfour & Midgley 2006; Wakeling & Bond 2007; Gordijn, Rice & Ward

2012). Finally, increases in average rainfall may provide tree species opportunities for recruitment, therefore promoting encroachment of trees into savannas (Knoop & Walker 1985). A recent study showed that, increases in woody vegetation in northern South Africa was caused by increases in large rainfall events (Gordijn, Rice & Ward 2012). Although many factors can promote increases in tree cover, acting alone or in tandem (Bond 2008; Midgley, Lawes & Chamailé-Jammes 2010), the 40% tree cover threshold is likely to be the tipping point for encroachment through disrupting grass percolation and thus suppressing fire spread.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Basics of percolation theory.

Appendix S2. R code for the neutral model simulation.

Appendix S3. The effect of neighbourhood size on the percolation threshold.