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Local Facilitation May Cause Tipping Points on a Landscape Level Preceded by Early-Warning Indicators

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ABSTRACT: Positive biotic interactions play a significant role in shaping ecological communities. We used an individual-based model to demonstrate that plant facilitation on a microscale may cause ecosystem shifts on a landscape scale that can be announced by generic early-warning indicators. Recruitment of woody plants in harsh environments such as drylands often depends on nurse plants that ameliorate stressful conditions and facilitate the establishment of seedlings under their canopy. We found that these facilitative interactions may cause a treeless and a woodland state to be alternative stable states on a landscape scale if nurse plant effects are strong and if the environment is harsh enough to make facilitation necessary for seedling survival. A corollary is that under such conditions environmental change can bring drylands to tipping points for woody plant encroachment or woodland collapse. We show that the proximity of tipping points may be indicated by slowness of recovery of woody vegetation cover from small perturbations as well as by elevated temporal and spatial autocorrelation and variance. These signs are known to be indicators of critical slowing down. This is the first demonstration that the systemic phenomena of tipping points, announced by critical slowing down as a warning signal, may plausibly arise from microscale individual interactions, such as plant facilitation.

Keywords: alternative stable state, dryland, ecological transition, individual-based model, positive interaction, vegetation shift.

Introduction

Our understanding of how biotic interactions shape the composition and structure of ecological communities has been enriched during the past decades by the recognition that facilitative interactions are a widespread phenomenon in aquatic and terrestrial ecosystems. The inclusion of fa-

cilitation has altered our theoretical predictions about how populations and communities respond to environmental gradients (Bruno et al. 2003). Positive interactions are also involved in large-scale feedbacks between organisms and the environment. For instance, in some terrestrial ecosystems rainfall can be stimulated by the presence of vegetation, which further benefits plant growth (Scheffer et al. 2005), and in shallow lakes submerged aquatic plants may cause the water to become clear, thus promoting growth conditions for such plants (Scheffer et al. 1993). It has been well known that such large-scale positive feedbacks are essential in nonlinear ecosystem dynamics, especially for the emergence of tipping points between distinct ecosystem states. However, how facilitative interactions occurring between neighboring individuals can scale up to influence landscapes and ecosystem dynamics has rarely been explored (but see D'Odorico et al. 2007). Interestingly, the empirical and theoretical work on facilitative interactions has developed almost in parallel with the extensive work on ecosystem dynamics, tipping points, and early-warning signals. In this article, we aim to link these two active but to date largely unconnected research fields by exploring the implications of local facilitation for shifts between ecosystem alternative states and illustrating them through recent findings in tropical ecosystems.

Tree cover in tropical regions across all continents shows three distinct modes associated with forest, savanna, and treeless states (Hirota et al. 2011; Staver and Levin 2012). The distinct modes for savanna and closed forest have been explained by a feedback between tree cover and fire dynamics, as denser tree cover reduces fire ignition (Archibald et al. 2009; Staver et al. 2011), causing alternative tree cover states over a range of precipitation levels (Bond 2008; Hoffmann et al. 2012; Murphy and Bowman 2012). The treeless state has been speculated to be the result of an Allee

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effect due the fact that tree recruitment could be severely limited in the absence of existing trees (Van de Koppel et al. 1997; Hirota et al. 2011; Van Nes et al. 2014). Tree recruitment limitation under low tree cover often results from multiple mechanisms that constrain the availability of propagules (seed production or dispersion) and of suitable microsites for successful seedling establishment (Acácio et al. 2007).

Evidence that trees and shrubs can facilitate further tree recruitment has been reported in both wet and dry tropics (Holmgren et al. 1997; Zanini and Ganade 2005; Callaway 2007; Holmgren and Scheffer 2010). In the wet tropics, treeless conditions are found in abandoned pastures, where tree recruitment is primarily limited by low seed dispersal, high seed and seedling predation, competition with grasses, and lack of soil nutrients (Uhl et al. 1988; Aide and Cavelier 1994; Nepstad et al. 1996; Slocum 2001; Holl 2002). Trees and shrubs can ameliorate these constraints. Many studies have demonstrated higher animal seed dispersal below woody vegetation than grass (Vieira et al. 1994; Da Silva et al. 1996; Duncan and Chapman 1999; Toh et al. 1999). Trees and shrubs also provide more favorable growing conditions for young tree seedlings both directly (e.g., lower temperatures, higher water and nutrient availability) and indirectly (e.g., lower grass competition, lower herbivore damage; e.g., Aide and Cavelier 1994; Zanini and Ganade 2005). These facilitative effects may be especially important for the recruitment of drought-intolerant and shade-tolerant species (Vieira et al. 1994; Slocum 2001). In the dry tropics, treeless conditions become increasingly common as water limitation constrains tree growth and grass cover is replaced by a matrix of bare land with occasional grasses during wet seasons or years. There is much empirical work in these systems showing that recruitment, growth, and survival of tree seedlings can be strongly dependent on nurse plants that ameliorate thermal stress by shading, increase water and soil nutrient availability, or reduce herbivore damage (Holmgren et al. 1997; Tewksbury and Lloyd 2001; Aerts et al. 2006; Biaou et al. 2011; Encino-Ruiz et al. 2013).

Although the role played by facilitation has been widely documented in plant communities, very few studies have explored the link between this microscale plant-plant interaction and alternative vegetation states. D'Odorico et al. (2007) combined field and modeling approaches to show that amelioration of water stress by the canopy of established plants could facilitate the establishment of new individuals and explain the persistent differences between vegetated patches and the bare conditions in water-limited systems. Here, we expand this analysis to explore the role played by facilitation on larger spatial scales by evaluating whether a treeless ecosystem state could represent a "trap" in the sense that it could be persistent under the same rain-

fall conditions as a state with trees (Hirota et al. 2011; Staver et al. 2011; Van Nes et al. 2014). We assess under which conditions facilitative interactions between neighboring plants could explain the existence of alternative ecosystem states with and without woody vegetation on a landscape scale in water-limited systems. Depending on the type of dryland, these woody plants can be trees or shrubs.

We use a minimal model to mimic the facilitative effect in a spatially explicit way along environmental gradients. This allows evaluating the implications of facilitative interactions along stress gradients for spatial patterns of woody vegetation and relating those to early-warning indicators at the onset of critical transitions in woody cover. Earlier work exploring possible mechanisms of pattern formation in dryland vegetation has been based on differential equation models or cellular automata models (e.g., Rietkerk et al. 2002; Kéfi et al. 2007a; Scanlon et al. 2007) without evaluating the individual-plant-level effects on which facilitative interactions have been typically quantified in the field. Here we use an individual-based modeling approach where each woody plant has a unique position and size. This allows a straightforward analysis of the effects that existent woody plants have on the recruitment of new individuals and that the size distributions of individual plants have on the emerging landscape patterns of woody vegetation. We explore under which conditions alternative stable states can arise and whether the proximity of tipping points might be expected to result in specific (Rietkerk et al. 2004; Kéfi et al. 2007a) or more generic (Scheffer et al. 2009, 2012) indicators of resilience.

Methods

Model Description

In our model (see table 1), individual (woody) plants are represented as circles in a continuous two-dimensional space ($100 \times 100 \text{ m}^2$). Changes occur in discrete time steps (each time step represents 1 year), at which reproduction and adult mortality take place. To keep the model as simple as possible, growth of individual plants is not incorporated. Each plant has an equal fecundity, and all offspring individuals are dispersed at random over the area, with sizes (surface areas of the circles) drawn from a normal distribution (e.g., Mohler et al. 1978; we also tested for single-size and uniform distributions and found no difference in the results). Directly following the reproduction, offspring die with some probability. The probability of mortality of a given offspring individual i (M_i) is a function of environmental harshness (h_e) and of the distance (d_i) to the nearest neighboring adult (eq. [1]):

$$M_i = [1 - f(d_i)](c(d_i) + h_e). \quad (1)$$

Table 1: Description of model parameters and state variables

Symbol	Description	Value range/default value	Unit
M_i	Mortality probability of a given seedling i	0–1	%
f	Relative intensity of facilitation	0–1	...
c	Relative intensity of competition	0–1	...
h_e	Harshness of the environment	0–1	...
d_i	Distance of seedling i to its nearest adult plant	0–100	m
P_f	Exponent in the Hill function for facilitation	4	...
P_c	Exponent in the Hill function for competition	2	...
h_f	Distance of d_i where the facilitation is reduced by half of its maximum	1.5	m
h_c	Distance of d_i where the competition is reduced by half of its maximum	3.0	m

The facilitation and competition strengths are modeled as sigmoidal functions of distance to the nearest adult (eqq. [2] and [3]):

$$f(d_i) = \frac{h_f^{p_f}}{h_f^{p_f} + d_i^{p_f}}, \quad (2)$$

$$c(d_i) = \frac{d_i^{p_c}}{h_c^{p_c} + d_i^{p_c}}, \quad (3)$$

where the exponents p_f and p_c determine the steepness of the sigmoids and h_c and h_f are the half-saturation constants. In dryland ecosystems, facilitative effects mostly operate at short distances from the benefactor plants due to canopy shading, while plant competition for water or other soil resources occurs on a larger scale because of lateral extension of roots (Lejeune et al. 1999; Coutron and Lejeune 2001; Casper et al. 2003; Caylor et al. 2006; Barbier et al. 2008). Such short-range facilitation and long-range competition are modeled by setting the default h_c twice as large as h_f . In addition, p_f is set twice as large as p_c to mimic the fact that facilitation vanishes quickly if beyond the canopy zone.

In addition to the offspring mortality, a fraction of the adult plants is killed at each time step. The fate of each adult plant is determined through a stochastic process that compares a random number between 0 and 1 to the environmental harshness h_e . The expected mortality rate of all adult plants is thus equal to h_e . If all plants are eliminated in a harsh environment, a single offspring is generated (to allow recolonization).

In what follows, the results are presented in the case where plant-plant interactions are assumed to occur only between the nearest neighbors (hereafter, the nearest-neighbor model). To test the robustness of our results to this assumption, we also considered a scenario where the facilitative/competitive effects are exerted from all neighbors (hereafter, the all-neighbor model; app. B; apps. A and B are available

online). The nearest-neighbor and all-neighbor models show very similar results (app. B, figs. B1–B5).

Model Analysis

Alternative Stable States of Woody Cover. We studied the response of woody cover to changing environmental conditions (h_e) in the presence and absence of facilitation. We studied hysteresis due to gradual environmental change by running the model with increasing/decreasing harshness by a small value of 0.002 at each time step. Apart from this, we detected the (approximate) equilibria of woody cover along the same harshness gradient by running the model for 20,000 time steps at different fixed values of harshness and calculating the mean woody cover.

Early-Warning Indicators. We examined whether the distance of the environmental harshness to the critical value at a tipping point was related to published indicators of resilience (for recent reviews, see Dakos et al. 2012, 2015; Kéfi et al. 2014), including the shape of regular Turing patterns (Rietkerk et al. 2004), the distribution of patch sizes (Kéfi et al. 2007a), spatial/temporal autocorrelation (Dakos et al. 2008, 2010), spatial/temporal variance (Carpenter and Brock 2006; Guttal and Jayaprakash 2009), and recovery rate after perturbations (Van Nes and Scheffer 2007).

At a range of fixed values of environmental harshness, we first used 100 time steps to stabilize the dynamics and then calculated the indicators. Lag-1 temporal autocorrelation (AR1) and temporal variance (standard deviation) were calculated on the basis of fluctuations in total plant cover over a 500 time-step simulation. To quantify the spatial indicators, the $100 \times 100\text{-m}^2$ space was divided into $4 \times 4\text{-m}^2$ quadrats, and woody cover was calculated by quadrat at each time step. Spatial autocorrelation at 1-quadrat distance was measured using Moran's I coefficient, and spatial variance was calculated as the standard deviation of within-quadrat woody cover. A perturbation experiment was conducted to

measure recovery rate. We did this by decreasing or increasing woody cover by about 10% through random elimination or addition of some individuals. The recovery rate was then measured using the coefficient of exponential fit (Van Nes and Scheffer 2007). Each simulation was repeated 200 times to calculate the 95% confidence intervals of the indicators. All simulations and analyses were done in MATLAB (ver. R2011b).

Results

Alternative Stable States

Facilitation has a strong effect on the system's behavior along gradients of environmental harshness. If nurse plant effects are absent, woody cover decreases gradually as environmental harshness increases (fig. 1A). By contrast, when facilitation is included in the model, alternative stable states can arise under a range of environmental conditions, leading to the possibility of sharp transitions between stable states as a result of stress amelioration (fig. 1B, blue lines). With sufficiently strong facilitation, woody vegetation per-

sists at relatively high cover under a broad range of environmental conditions until a threshold (e.g., a harshness of 0.7 in fig. 1B) is reached at which woody cover drops to zero (roughly treeless). Conversely, when environmental harshness decreases gradually, the system remains treeless until another threshold (at a harshness around 0.55), at which the facilitative effect of nurse plants on seedling establishment propels an abrupt transition from a treeless to a woodland state (fig. 1B). We checked that the hysteresis in these simulations is indeed the result of alternative stable states in the model by performing long simulation runs (20,000 time steps), making sure that a steady state is reached at a given harshness level. Overall, these results demonstrate that simple nurse plant effects, as widely observed and experimentally studied, may indeed explain the emergence of treeless and woody vegetation conditions as alternative stable states.

Spatial Patterns

Our nearest-neighbor model produces irregular patterns (fig. 2). If nurse plant effects are included, the size distribution of the resulting woody vegetation patches is characterized by a hump with a distinct tail of large patches (app. A, fig. A1, panel 1). This pattern is indeed common in many drylands around the world. As conditions become harsher and overall woody cover declines, the patch size distribution becomes dominantly characterized by the occasional few individuals that are found. The right tail representing larger clusters disappears (app. A, fig. A1, panel 2). A similar loss of larger patches is observed with declining woody cover in the model without facilitation and without tipping points, although the tail of the patch size distribution representing clusters of plants is always much less pronounced in this situation without facilitation (app. A, fig. A2). Our model can also produce regular Turing-like patterns, but this happens only in the all-neighbor model if we amplify the effect of long-range competition (app. B, fig. B6).

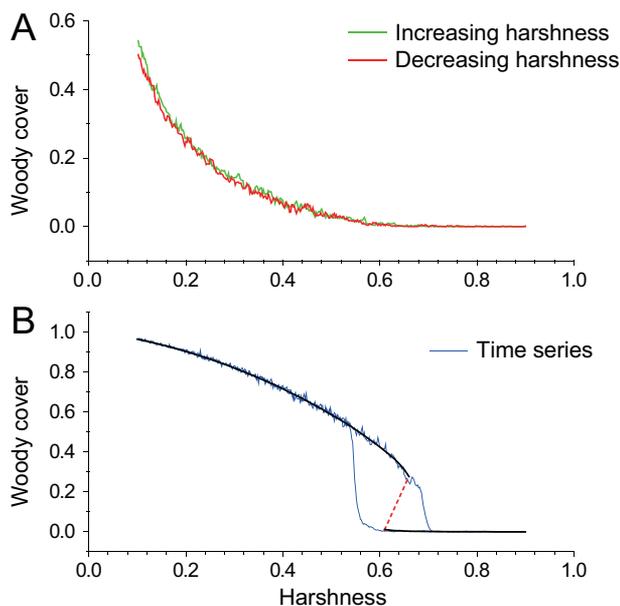


Figure 1: Simulated dynamics of woody cover in response to a slow increase and subsequent decline in environmental harshness based on the nearest-neighbor model. In the absence of facilitation, the model predicts no hysteresis (A). If facilitation is strong enough, the model has alternative stable states over a range of harshness conditions (B). The blue line represents the change in woody cover for gradually increasing and subsequently decreasing harshness. The black lines represent equilibria detected by allowing the model to stabilize for 20,000 generations at fixed harshness levels. The dashed line represents the approximate border between the alternative basins of attraction.

Critical Slowing Down and Its Indicators

To explore whether the generic phenomenon of critical slowing down occurs in the vicinity of the tipping points, we conducted perturbation experiments and also analyzed temporal and spatial autocorrelation and variance as indirect indicators of slowing down. Indeed, recovery time after perturbations increases systematically toward both tipping points (app. A, figs. A3, A4). In the woody state, recovery after removal of a fraction of the plants is slower, as the system is closer to the tipping point for a shift to the treeless state. Similarly, in the treeless state decline after a small addition of plants becomes slower, as the system is closer to

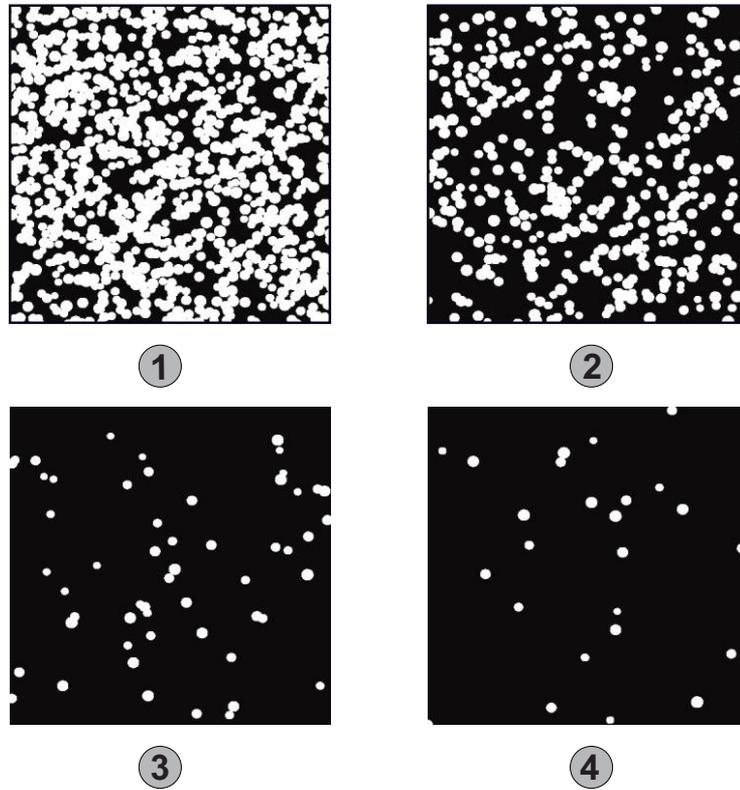
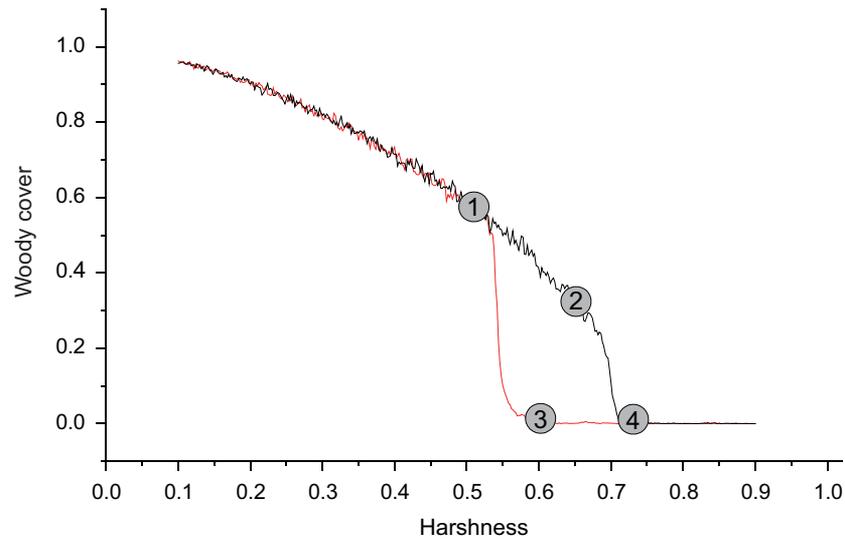


Figure 2: Distribution patterns of plants (white patches) in the woody (1, 2) and nonwoody (3, 4) states generated by the nearest-neighbor model.

the tipping point for woody plant encroachment. As expected from theory on indicators of slowing down, there is also a marked increase in temporal (fig. 3) and spatial (fig. 4) autocorrelation as well as variance toward both tipping points.

Discussion

Our results show that enhanced survival of woody plants close to other existing individuals may explain treeless and woody states as alternative stable states on a landscape scale.

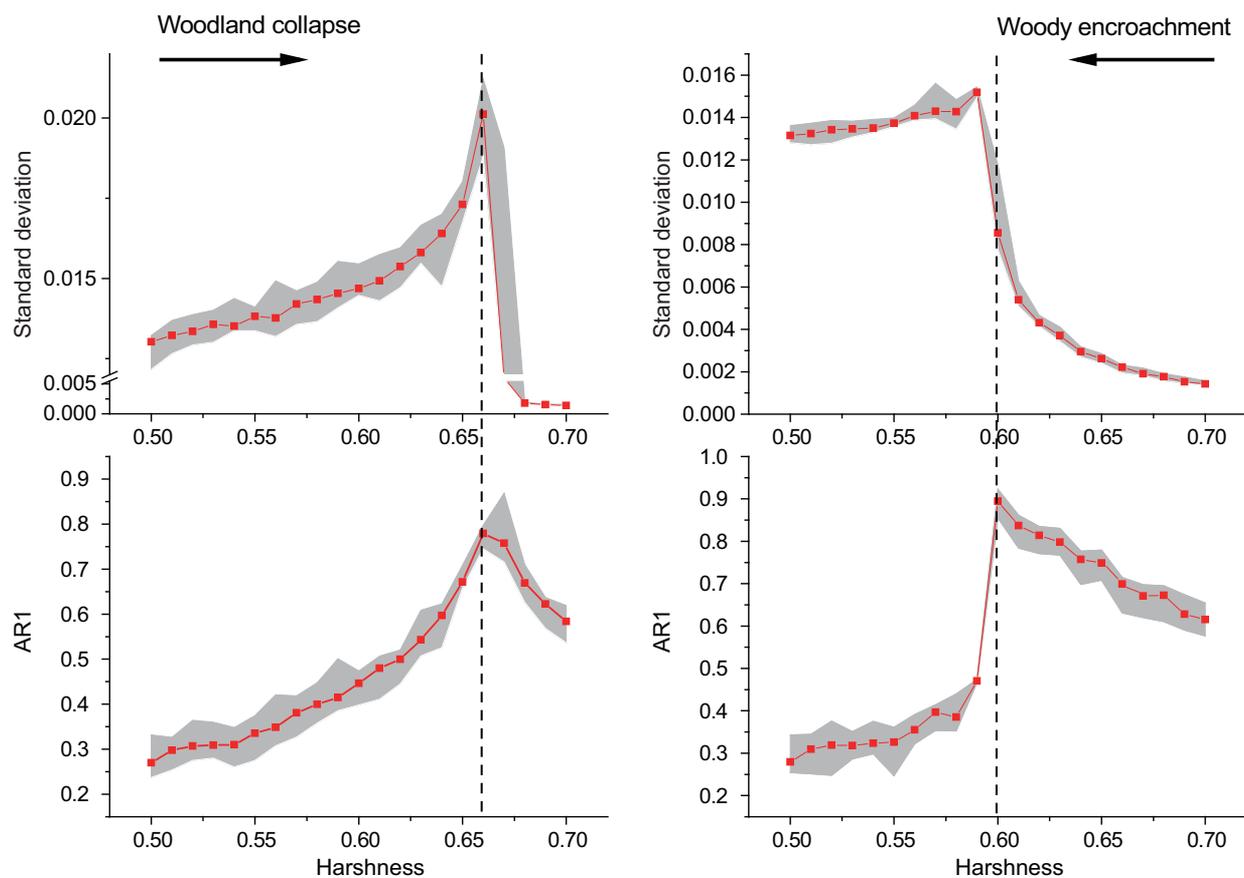


Figure 3: Temporal indicators of critical slowing down based on the nearest-neighbor model. Variance (standard deviation; *top*) and temporal correlation (lag-1 autoregressive coefficient [AR1]; *bottom*) in simulated time series rise toward tipping points (dashed lines) for a shift from high to low woody cover (woodland collapse) as well as for a shift from low to high woody cover (woody encroachment).

The proximity of tipping points for transitions between these alternative ecosystem states may be detected from indicators of critical slowing down, such as elevated autocorrelation and variance in space and time. While these early-warning signals are thought to be rather generic across systems with underlying zero-eigenvalue bifurcations (roughly tipping points; Scheffer et al. 2009, 2012), our results are the first to illustrate that the systemic phenomena of tipping points and critical slowing down may plausibly arise from micro-scale ecological interactions, such as the well-studied nurse plant facilitation. Our modeling results show how ecological interactions could help us understand the transitions between treeless and savanna states. Detecting these states on large scales is not easy since there are potential caveats in the use of remotely sensed data for detecting low-tree-cover conditions in tropical vegetation (Hanan et al. 2014; Staver and Hansen 2015).

Earlier work on tipping points and early-warning signals in dryland vegetation used grid-based models (Kéfi et al.

2007b) or differential equation models (Lejeune et al. 1999; Von Hardenberg et al. 2001; Rietkerk et al. 2002; Meron et al. 2004). Some of these models predict regular Turing patterns because of scale-dependent feedbacks between vegetation and local water availability in the soil (e.g., Rietkerk et al. 2004). Such patterns are found in some drylands (Deblauwe et al. 2011). In an adapted version of our all-neighbor model, such regular patterns can also arise, but only if a very strong long-range negative effect is included (app. B, fig. B6). This confirms the view that the interplay of small-scale facilitation with such larger-scale “repellent effects” of competition are needed to generate Turing patterns in dryland vegetation (Manor and Shnerb 2008; Von Hardenberg et al. 2010). By contrast, our nearest-neighbor model, dominated by random mortality and local nurse plant facilitation, generates irregular patterns. Indeed, in most drylands woody plants form irregular patches rather than periodic ones. Earlier work used cellular automata or differential equation models to produce such irregular patchy patterns (Kéfi et al.

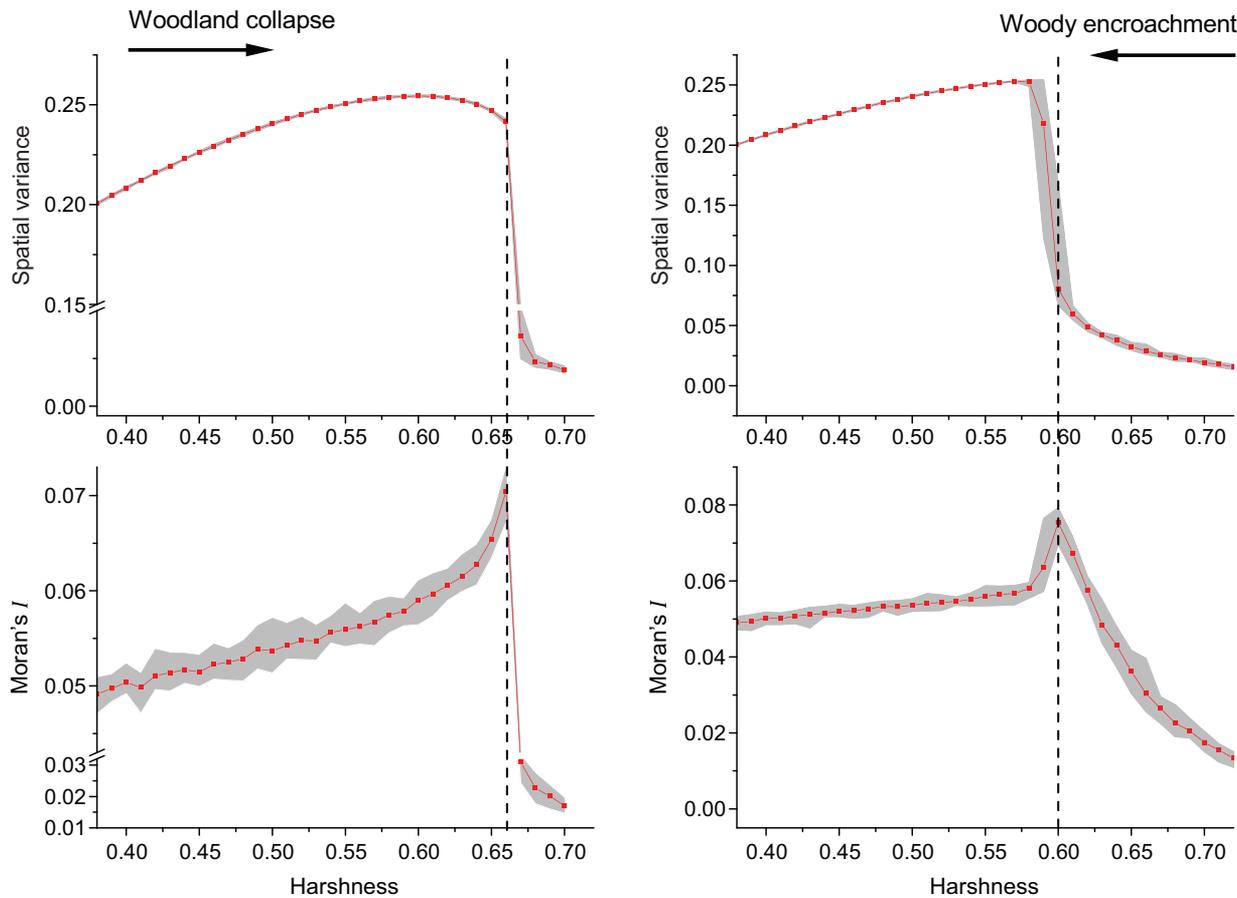


Figure 4: Spatial indicators of critical slowing down based on the nearest-neighbor model. Spatial variance (*top*) and spatial correlation (Moran's I index at lag-1 distance; *bottom*) in simulated time series rise toward tipping points (dashed lines) for a shift from high to low woody cover (woodland collapse) as well as for a shift from low to high woody cover (woody encroachment).

2007a; Scanlon et al. 2007; Manor and Shnerb 2008; Von Hardenberg et al. 2010). A specific prediction of these models is that the shape of the patch size distribution will change when approaching a systemic tipping point for vegetation collapse (Kéfi et al. 2011). Cellular automata and differential equation models mostly generate patch size distributions with a heavy tail that can be described by a power law. However, as the system is closer to the tipping point for collapse, larger patches fragment into smaller ones, causing the distributions to increasingly deviate from pure power laws (Kéfi et al. 2011). Field studies in various systems are in line with these predictions (e.g., Kéfi et al. 2007a; Lin et al. 2010; Moreno-de las Heras et al. 2011).

The loss of the heavy tail toward the tipping point for woodland collapse detected in our model (app. A, fig. A1) is consistent with these results on the changes of patch size distributions. However, the spatial patterns predicted from our individual-based model differ from those produced by cellular automata. Indeed, the cellular automata models pre-

dict the smallest patch sizes to be the most abundant. By contrast, we predict unimodal patch size distributions that are dominated by an intermediate patch size. This pattern arises from the combination of the size distribution of the individual woody plants forming the hump (not present in cellular automata models, where all cells have, by construction, the same size) and the plant clusters causing the tail of the distribution. Detailed analyses of Google Earth images show that such patch size distributions are ubiquitous for woody plants in drylands across continents (Xu et al. 2015), suggesting that the well-studied nurse plant effect we assume here may indeed capture the essence of what drives the dynamics of many of these systems on a microscale.

The role played by facilitative interactions along environmental gradients is an active field of research. Although many studies have shown that neighboring plants can ameliorate moderate and very harsh abiotic and biotic conditions, there is at present no consensus on the general shape of these relationships (Bertness and Callaway 1994; Holm-

gren and Scheffer 2010). For example, the facilitative effect via increasing soil moisture in the vicinity of existing canopies is more pronounced in drier than in wetter regions but is lost under extreme dry conditions (D'Odorico et al. 2007). Such a changing role of facilitation along the stress gradient was not explored in our model, but we can expect that the enhanced positive feedback due to stronger facilitation will cause the system in more stressful environments to have a larger range of conditions with alternative stable states (and thus larger hysteresis; D'Odorico et al. 2007; Scheffer 2009).

Clearly, the individual-based nurse plant model that we use is not meant to be a realistic description of encroaching vegetation. Instead, it is a minimal representation of the facilitative effects of nurse adult plants on seedling recruitment. One simplification is that we assumed facilitation and competition to take place only during the establishment of seedlings and not at later life stages. Simulations showed that the results are similar if we assume that these mechanisms (also) occur at the adult stage (not shown). In addition, we did not simulate growth of individual plants. Again, this simplification had little effect on the qualitative results, as size actually has little effect in the model. Furthermore, we are unsure how many neighbors need to be taken into account for the facilitative effects. Considering only the nearest neighbors would mean that the positive effects are very local. These local positive effects may include temperature amelioration by shading, higher soil water availability (e.g., through hydraulic lift, condensation, or lower evapotranspiration), nutrient accumulation, and herbivore protection. Considering all neighbors with weak downweighting of the neighbors that are farther away would mean that, in addition to the positive effect of the closest individuals (potential pathways above), the overall vegetation structure and composition play a role in the outcome of a local interaction. This makes sense if the vegetation is mostly shaped by processes acting on larger scales, such as climatic effects (evapotranspiration, rainfall), hydrology, and soil retention, as well as by some indirect effects (e.g., capacity of a system to sustain pollinators, seed disperses, predators of the herbivores). These two scenarios could be equally important across systems in reality, and we show that both can have the same qualitative behavior. Although the qualitative results of alternative stable states and early-warning signals were robust to the rather crude simplifications, follow-up work with more elaborate growth and survival models and with a more thorough exploration of the parameter space would be needed to simulate particular situations in more realistic detail.

As the irregular patch size distributions predicted by our model as well as the facilitative effects it represents are so widespread, our results suggests that, in a broad class of drylands, remotely sensed indicators of critical slowing

down might be used to assess the resilience of treeless and woody states and thus the likelihood of an upcoming transition.

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Above, a typical shrubland subject to desertification in Ningxia, western China. Photo by Chi Xu. *Below*, typical vegetation patterns in El Planerón, Belchite, a field site close to Zaragoza in northeastern Spain. Photo by Sonia Kéfi.