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Spatially Explicit Modeling of Savanna Processes

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CONTENTS

Introduction

Savannas are inherently spatially variable regardless of where they occur (Sinclair and Fryxell, 1985; Jeltsch et al., 1997; Wiegand et al., 2000a; Ward 2009; Figure 14.1). Therefore, models of savanna processes and patterns often explicitly address spatial variation. In this chapter, we will first give an overview of the features of savannas that show spatial variation. We will then present evidence for the importance of spatial variation in savannas, because presence of spatial variation does not necessarily imply importance for savanna dynamics. In the main part of the chapter, we will explain the spatial modeling techniques that have been applied to savannas, give examples of their application, and discuss their strengths and limitations.

Small-scale features that affect spatial variation in savanna structure include geology and soil, rainfall, elevation and topography, fire, intra- and interspecific competition, propagule pressure, and herbivory (Table 14.1). Regarding geology and soil features, Britz and Ward (2007) found that there were significant differences in the densities of *Acacia mellifera* on adjacent rocky and sandy soil substrates less than 100 m apart. McNaughton (1983)

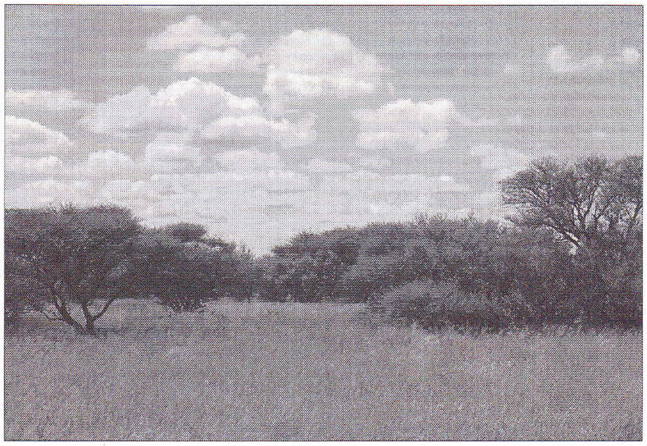

FIGURE 14.1
(**See color insert following page 320.**) Spatial structure in a semiarid savanna.

found that lawn grass patches occur in the Serengeti savanna (Tanzania) and may be associated with sodic soils or fertile locations. Scholes and Walker (1993) have shown that termite mounds and areas where people have lived and/or livestock corralled are more fertile (due to higher levels of nitrogen there), which has led to changes in savanna structure, shifting to *Acacia*-dominated savanna in an area dominated by broad-leaved trees.

TABLE 14.1

Major Spatial Processes in Savannas and Their Effect on Savanna Plant Mortality, Reproduction, and Growth; Their Direction; and the Scales They May Cover

	Effect[a] on Plant …				
Spatial Processes	**Mortality**	**Reproduction**	**Growth**	**Direction[b]**	**Scale[c]**
Abiotic Processes					
Rain events	–	+	+	h	100 m–10 km
Fire	+	–/+	0	h (+v)	10 m–10 km
Nutrient availability	–	+	+	h (+v)	1 mm–10 km
Biotic Processes					
Grazing	+	–	–/+	h	1 m–10 km
Termite mound degradation	0	0	+	h	10 cm–100 m
Belowground competition	+	–	–	v + h	1 cm–10 m
Facilitation via hydraulic lift	–	+	+	v	1 cm–10 m
Dispersal	–	0	0	h	1 cm–10 km

[a] Plants include trees, shrubs, and grasses; 0: neutral effect, –: negative effect, +: positive effect, –/+: negative and positive effects.
[b] Predominant direction of spatial variability; h: horizontal, v: vertical.
[c] Approximate scales covered by the process.

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Reid and Ellis (1995) found that livestock increased seed densities of *Acacia tortilis* trees by 85 times inside corrals compared with similar areas outside of corrals. In the Kruger Park of South Africa, the dominant savanna vegetation patterns follow variation in climate, fire, geology, and soils (Scholes et al., 2003). In the western Llanos of Venezuela, Silva and Sarmiento (1976) (quoted by Sarmiento, 1996) have shown that species richness per 1000 m^2 can vary between 53 and 84 species in a single soil catena and is strongly related to water availability.

With regard to spatial variation in rainfall, there is a negative correlation between mean annual rainfall and its coefficient of variation (see e.g., Sharon, 1981; Ward, 2009), leading to large spatial variation in savanna structure and function as mean annual rainfall declines. Although rainfall is often considered as a large-scale feature, rainfall events can be highly localized, particularly as mean annual rainfall declines (Sharon, 1981).

Fire is considered a major determinant of spatial variation in savanna structure, particularly in mesic savannas (Higgins et al., 2000), although Australian studies indicate that fire can be important at rainfall values as low as 250–300 mm per annum (McKeon et al., 2004). Fires can result in increased space for trees to germinate en masse (Bond, 2008) or they can cause trees to be removed, resulting in a more open savanna (McKeon et al., 2004; Ward, 2005). Due to the large variation in fuel loads caused by differences in rainfall and soil type, fire intensity and duration vary considerably, resulting in considerable variation in spatial structure (Bond, 2008).

With regard to interspecific competition, Smith and Goodman (1986) have shown that *Acacia tortilis* and *Euclea divinorum* compete for space in the mesic Mkhuze reserve (South Africa); whereas Schleicher et al. (unpublished data) have shown that two species (*Tarchonanthus camphoratus* and *Acacia mellifera*) may compete for space in the semiarid area near Kimberley (South Africa). Propagule pressure may also show spatial structure. A spatially explicit simulation model by Jeltsch et al. (1996) showed that rooting niche separation might be insufficient to allow coexistence under a range of climatic situations. However, Jeltsch et al. (1998) found that introducing safe sites for seedling establishment by simulating the effects of various small-scale heterogeneities allowed coexistence. Grazing is widely purported to be the main factor affecting increases in tree density (Walker et al., 1981; Ward, 2005). This is largely ascribed to heavy stocking by domestic livestock, creating gaps for mass recruitment of trees. Piosphere formation (see e.g., Smet and Ward, 2006) and fenceline effects (e.g., Hendricks et al., 2005) are also a major source of the spatial variation in savannas, caused largely by heavy grazing near water holes and differential effects of animal densities on either side of a fence.

Even though savannas are often thought of as a homogeneous grass layer interspersed with trees, the grass component is also expected to be spatially heterogeneous (e.g., O'Connor, 1991; Fowler, 2002; Augustine, 2003; Wiegand et al., 2005). Jurena and Archer (2003) provided evidence that, in

Texas, there are always gaps in the grass for some *Prosopis* plants to germinate and establish. Spatial heterogeneity of the grass layer may thus facilitate woody invasion in grasslands. Such patterns are generally modified by grazing and fire, both of which are known to be highly patchy and to interact in spatially complex ways (e.g., Archibald et al., 2005; Getzin, 2007).

Large-scale spatial variation in savannas may occur too. In some cases, vast areas are affected. For example, Sinclair and Fryxell (1985) consider the Sahel, which covers 10 countries immediately south of the Sahara, as being subject to large changes due to a change from migratory livestock to fixed patterns of livestock control. Migratory ungulates use nutritious but seasonal food and probably maintain larger populations as a consequence. In the 1950s and 1960s, pastoralists were forced to settle with their livestock. This caused heavy grazing near these wells (leading to piosphere formation) and has resulted in frequent famines since this time (Sinclair and Fryxell, 1985). In North America, Schmitz et al. (2002) found that substrate heterogeneity in pine savannas in Florida, measured as variation in elevation, may influence species richness at larger spatial scales.

Evidence for the Importance of Space in Savannas

Patterns are the outcome of processes that have acted over time and space. Consequently, patterns are indicators of the processes that have shaped them, and spatial patterns indicate the presence of spatial processes. Thus, as a simple rule of thumb for model development, if there is at least one spatial pattern observed at the range of scales relevant to the question being studied, one should consider developing a spatial model. Arguably, this means that one should virtually always consider developing spatial models, because spatial patterns abound in our spatial world. The omnipresence of spatial patterns also makes it often easier to think spatially than nonspatially and to translate field knowledge into spatial rather than nonspatial models. Notwithstanding this, once spatial models have been thoroughly analyzed and have improved our understanding, it may well be possible to simplify the model and to remove the spatial components (e.g., Adler and Mosquera, 2000; Wiegand et al., 2004a). Most spatial savanna models presume that space is important without having explicitly tested the importance of space. A few exceptions exist and will be reviewed in the remainder of this section, but future research will need to clarify the level of spatial detail needed.

A common observation in savannas is the nonrandom spatial distribution of trees. However, whether the distribution is aggregated, random, or regular may change with age of savanna trees. This emphasizes the importance of space for explaining age-related phenomena. For example, small trees may be clumped whereas large trees are randomly or even regularly spaced

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(e.g., Skarpe et al., 1991; Meyer et al.
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(Table 14.1). The intricate mixture
using spatial models.

FIGURE 14.2
Example of spatial pattern of savanna pl
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E 24°29′), 30 km north of Kimberley, South
eter. *G. flava* is significantly more frequent
Schleicher, unpublished data and analyses).

(e.g., Skarpe et al., 1991; Meyer et al., 2008). This transition is readily explained by intraspecific competition leading to increased mortality of trees with many neighbors. However, other explanations may be possible such as in the case of *Acacia raddiana* trees in the Negev desert. At the seedling stage, these trees were clumped, changing to a random distribution thereafter (Wiegand et al., 2000a). In a spatially explicit simulation model, the breakup of the clumped pattern was explained by both density-dependent mortality (competition) or relatively high, yet density-independent, seedling mortality (Wiegand et al., 2000a). The lesson that one pattern may have more than one explanation is also true for the example of the clumping of fleshy-fruited *Grewia flava* relative to *A. erioloba* in the Kalahari and Kimberley Thorn Bushveld (Dean et al., 1999; Figure 14.2). Both facilitation and directed seed dispersal by birds and mammals are equally likely explanations. Spatial heterogeneity, for example, in soil resources, may also play a role, and further modeling is required to sort out these possibilities. These examples show that spatial patterns are key to better understand spatiotemporal processes (Table 14.1). The intricate mixture of space and time can be captured only by using spatial models.

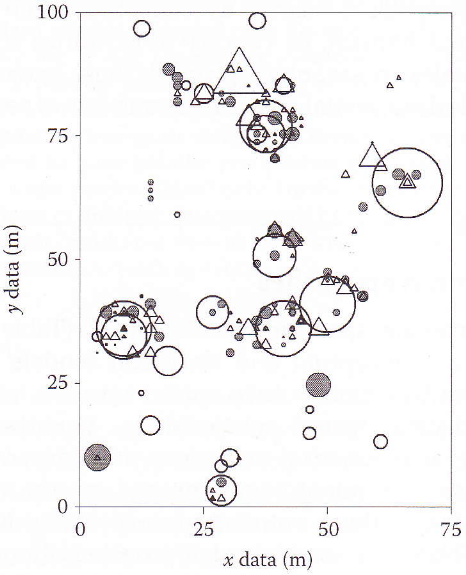

FIGURE 14.2
Example of spatial pattern of savanna plants. Spatial distribution of *Acacia erioloba* (open circles), *Grewia flava* (solid circles), and *Ziziphus mucronata* (triangles) at Pniel Estates (S 28°35′, E 24°29′), 30 km north of Kimberley, South Africa. Symbol size is proportional to canopy diameter. *G. flava* is significantly more frequently found beneath *A. erioloba* than in the open (Jana Schleicher, unpublished data and analyses).

Recently, empirical and modeling evidence for explaining savanna tree–grass coexistence with hierarchical patch dynamics has accumulated (e.g., Wiegand et al., 2005; Meyer et al., 2007b; Moustakas et al., 2009). Wiegand et al. (2005) investigated patterns of local tree size distributions across an *Acacia reficiens* savanna landscape in Namibia. Local tree size frequency distributions indicated that one or two age cohorts were present; whereas, at the landscape scale, a multitude of cohorts were detected after a negative exponential tree size–frequency distribution and reflecting an overall birth-death equilibrium (Wiegand et al., 2005). Using paleoecological techniques, Gillson (2004) found that patterns of vegetation change differed among micro, local, and landscape spatial scales, with the most rapid changes at the micro scale. In patch dynamic savannas, infrequent recruitment events generate even-aged stands at the local level. Competition at the micro level leads via self-thinning (Wiegand et al., 2008) from dense localized tree patches to open savanna with a few large trees. If the local recruitment events are not correlated in space and time, then a stable savanna emerges (Gillson, 2004; Wiegand et al., 2005, 2006). Other predictions of patch dynamics are supported by model results. Models show that mass recruitment driven by overlapping localized rain events in combination with self-thinning are the main drivers in arid savannas (Figure 14.3). In humid savannas, recruitment bottlenecks are more often mediated by fire (Higgins et al., 2000), whose spatial patchiness can drive patch dynamics as well. Since patch dynamics is a spatial scale-explicit mechanism, its validity in savannas supports the importance of spatial scales in savannas. Overall, these examples highlight the importance of including spatial structure in models of savanna dynamics.

Spatial Modeling Approaches

Models can incorporate space in various ways (Table 14.2). Descriptive approaches such as conceptual and statistical models or applications of remote sensing and GIS contribute to spatial savanna modeling by formalizing and quantifying spatial relationships. Equation-based modeling approaches require mathematical extensions to incorporate space explicitly, such as in the case of moment equations and matrix models. Grid-based approaches including cellular automata are specially designed to capture spatial processes. Therefore, grid-based approaches offer probably the greatest flexibility in describing, understanding, and predicting the impact of spatial relationships on savanna patterns and dynamics. Since grid-based modeling has been the most common approach in *spatial* savanna modeling thus far, we will present this approach in more detail a little later. Each modeling approach has strengths and limitations and should be applied accordingly to the savanna processes involved (Table 14.2).

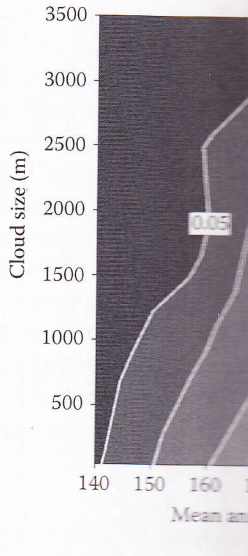

FIGURE 14.3
Tree–grass ratios as a function of precipitati
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are developing a simulation model combini
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Conceptual Models

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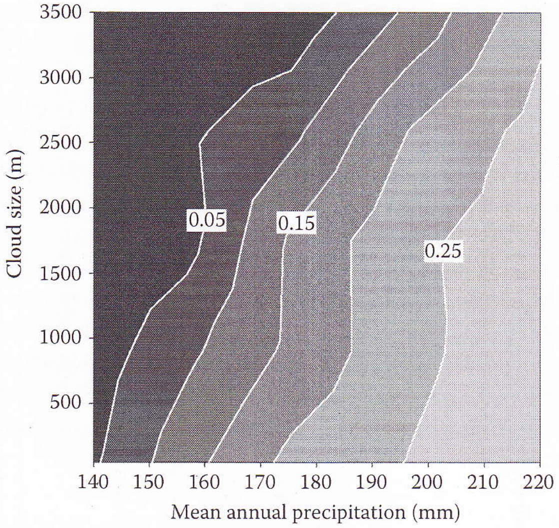

FIGURE 14.3

Tree–grass ratios as a function of precipitation cloud size (length) and mean annual precipitation. To test the hypothesis that local recruitment driven by localized rainfall and self-thinning may be major drivers of patch dynamic arid savannas, Eisinger, Wiegand, and Ward (in prep.) are developing a simulation model combining self-thinning of local shrub cohorts (Wiegand et al., 2008) with localized rainfall. (Adapted from Eisinger, D., and K. Wiegand 2008. *South African Journal of Science* 104, 37–42.) The shading indicates tree–grass ratio in terms of tree cover. Values below 0.05 indicate grassland, savanna extends from 0.05 to 0.25, and values beyond 0.25 indicate open woodland. This preliminary result shows that, given a fixed amount of mean annual precipitation, tree–grass ratios shift toward greater tree cover if rainfall is more patchily distributed in space (smaller precipitation cloud size). Especially in very dry areas, savannas occur under patchy rainfall only. Further preliminary results show that the spatial distribution of trees of different sizes generated by the model is in agreement with the patch-dynamics hypothesis (results not shown). Thus, tree–grass coexistence is indeed possible in a framework of hierarchical patch dynamics.

Conceptual Models

Conceptual models organize information, represent hypotheses and theories, and are particularly useful for capturing spatial relationships. For example, Walter's two-layer hypothesis explained tree–grass coexistence in savannas with a spatial segregation of rooting depths to access water (Walter, 1971), which was originally formulated as a conceptual model. Subsequent empirical and theoretical tests of Walter's hypothesis were based on this spatial conceptual model, yielding equivocal results (e.g., Knoop and Walker, 1981; Walker and Noy-Meir, 1982; Wiegand et al., 2005). In another spatial conceptual model, patch dynamics were mooted as a spatially explicit mechanism underlying tree–grass coexistence (Wiegand et al., 2006; Meyer et al., 2009). The explicit formulation of a conceptual model facilitated the derivation of specific predictions from the patch-dynamics mechanism such as the

TABLE 14.2

Major Spatial Processes in Savannas and Examples of How They Can Be Addressed in Spatial Modeling Approaches[a]

	Modeling Approaches						
Spatial Processes	**Conceptual Models**	**Remote Sensing**	**Spatial Statistics[b]**	**Moment Equations**	**Matrix Models**	**Cellular Automata**	**Grid-Based Models**
Abiotic Processes							
Rain events	Box	Possible	CV vs. average, autocorr	Forcing or input	Perturb or sub	Trans prob = f(rain)	Input + algorithm[e]
Fire	Box	Possible	Autocorr	Forcing or input	Perturb or sub	As cell state that can change trans probs	Input + rules
Nutrient availability	Box	Only indirectly[c]	Autocorr	Forcing or input	Perturb or sub	Trans prob = f(nutrient availability)	Input + rules
Biotic Processes							
Grazing	Arrow	Only indirectly[c]	Gradient analysis	Forcing or input	Perturb or sub	As cell state that can change trans probs	Input + rules
Termite mound degradation	Arrow	Only aerial photos	Autocorr	Forcing or input	Perturb or sub	As cell state that can change trans probs	Input + rules
Belowground competition	Arrow	Impossible	Point, NN	NN effect via equ[d]	Sub (if at all)	Trans probs between cells	Rules (+ input)
Facilitation via hydraulic lift	Arrow	Impossible	Gradient analysis	NN effect via equ[d]	Sub (if at all)	Trans probs between cells	Rules (+ input)
Dispersal	Arrow	Impossible	Cluster processes	Distr	Sub	Trans probs between cells	Rules+/distr (+ input)

Note: CV—coefficient of variation—refers to amount of rain in different with locations as at one point in time; autocorr—spatiotemporal autocorrelation analysis; point—point pattern analysis; NN—nearest-neighbor statistics; forcing—forcing function; input—input parameter; distr—distribution (e.g., Gaussian, Cauchy); perturb—via perturbation matrix approach; sub—via submatrix approach; trans prob—transition probability; *f*(*x*)—function of *x*.

[a] See text for more details on the modeling approaches.

[b] Examples of possible statistics, not conclusive.

[c] Via Normalized Differenced Vegetation Indices (NDVI).

[d] Effect of nearest-neighbor via additional equation.

[e] For example, SERGE. (Adapted from Eisinger, D. and K. Wiegand 2008. *South African Journal of Science* 104, 37–42.)

occurrence of cyclical successions
level (Meyer et al., 2009). State-an
conceptual models that classify ve
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Remote Sensing, GIS, and Spatial

After the formulation of conceptual
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interactions. By applying nearest-ne
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depends on the resolution of the im
savannas, the combined use of high-
appropriate than using either of the

occurrence of cyclical successions of grass and tree dominance at the patch level (Meyer et al., 2009). State-and-transition models comprise a range of conceptual models that classify vegetation into multiple stable states and formulate probabilities for transitions between states. Transitions can be triggered by natural disturbances such as fire or by management actions such as grazing or wood harvesting. State-and-transition models have, for example, been used for the conceptual modeling of range management (Westoby et al., 1989) and bush encroachment (Dougill and Trodd, 1999), albeit not dealing with space explicitly. These examples illustrate the usefulness of conceptual models as a first step in the investigation of a new theory and for improving the communication between scientists, range managers, and the public. However, these models have the disadvantage that the applicability of conceptual models is limited to this early stage, because they are either purely descriptive or make only qualitative and not quantitative predictions.

Remote Sensing, GIS, and Spatial Statistics

After the formulation of conceptual models, remote sensing techniques such as satellite imagery or aerial photography can provide large-scale information on spatial patterns required to parameterize and validate subsequent modeling procedures (see also Section 3). Before this information can serve as input or validation for models, it needs to be processed to quantify the spatial patterns. Therefore, remote sensing is frequently used in combination with other descriptive techniques such as GIS and spatial statistics. The GIS capture spatial data in layers that can be superimposed and related to each other (Wiegand et al., 2000b). Spatial statistics cover a broad spectrum of techniques ranging from neighborhood analyses to spatial point pattern methods. These techniques are mainly used to describe spatial patterns of savanna vegetation and to infer the underlying processes.

Combining series of remotely sensed images, GIS, and spatial statistics can give insights into spatiotemporal patterns of savanna tree demography and help identifying their underlying drivers such as competitive or facilitative interactions. By applying nearest-neighbor and spatial point pattern analyses to remotely sensed data processed by a GIS to identify individual trees, Moustakas et al. (2008) found cyclical transitions between clumped, random, and regular tree patterns over time. Smaller nearest-neighbor distances and less clumped spatial point patterns coincided with high mortality, thus indicating the predominance of competitive interactions (Moustakas et al., 2008). Couteron (2002) found remote sensing followed by spectral analysis with Fourier transforms suitable for the description of patterned semiarid vegetation. The suitability of remotely sensed data for spatial savanna studies depends on the resolution of the images. To create maps of burned areas in savannas, the combined use of high- and low-resolution images seems more appropriate than using either of the two (Maggi and Stropiana, 2002).

Remote sensing, GIS, and spatial statistics have all, either alone or in combination, fruitfully been coupled with equation- or grid-based modeling approaches. To reconstruct land cover distributions in savannas, GIS have been combined with predictive land cover models for the analysis of pollen distributions (Flantua et al., 2007). In a Zambian savanna, land cover change has been predicted by linking remotely sensed data and a matrix model, indicating the continuation of a trend toward increasing proportions of bare and cultivated soils under unchanged environmental conditions (Petit et al., 2001). In contrast, a rule-based expert system fed with remotely sensed and GIS-processed data predicted canopy closure between woody clusters for a mesquite savanna in Texas, in the absence of management (Loh and Hsieh, 1995). Applying spatial point–pattern analysis to the output of various grid-based simulations of major savanna processes, Jeltsch et al. (1999) determined general relationships between patterns and processes that were subsequently used to infer the most likely processes generating the spatial tree patterns on remotely sensed images of the Kalahari in South Africa and Botswana. There, clumped tree patterns were promoted by grass fires, whereas random tree patterns arose from randomly distributed establishment patches (Jeltsch et al., 1999). However, the statistical analyses of the model output also showed that the spatial pattern observed in the aerial photographs from the Kalahari, that is, regular distributions at small scales and random or clumped distributions at intermediate scales, was diagnostic both for persistent open savannas and open savannas in transition toward woodlands. These combined approaches are particularly strong, because they benefit from the quantification strength of descriptive techniques and the predictive capabilities of equation- or grid-based models. The disadvantage of remote sensing, GIS, and spatial statistics approaches is their static nature. This could be overcome by combining them with dynamic approaches or by investigating temporal sequences of data (e.g., Moustakas et al., 2008).

Moment Equations

Incorporating spatial relationships explicitly into equation-based models is not an easy task, because it always requires an extension of the model with additional equations or matrices. In plant population modeling, deriving moment equations has been found to be a useful approach to capture spatial processes (Bolker et al., 2003). Moment equations or pair approximations consist of a pair of equations where one equation represents average population dynamics and the other represents the spatial covariance of the population dynamics, that is, the spatial interactions between an individual and its direct neighbors (Bolker and Pacala, 1997). This technique may be powerful but has only very recently been applied to model spatial savanna dynamics (Calabrese et al. 2010). A problem of moment equations is moment closure, that is the fact that usually only the effect of the direct neighbors is incorporated but not the effect of the neighbors' neighbors, to reduce mathematical

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complexity. Another disadvantage
less strongly linked to empirical da
parameters that are difficult to pa
tions of moment equations benefi
analytical tractability, and their hi
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Spatial Matrix Models

Another mathematical approach to
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(Raventos et al., 2004), and to vali
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spatial matrix models have the ad
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can be used to investigate questions
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bilities need parameterization and
trade-off between the ease with
model can be found and the numb
temporal variation that can be con

Cellular Automata

In cellular automata, space is discre
discrete states, in the narrow defin
transition rules between the state
Transition rules depend on the direc
interactions only. The *direct neighbor*

complexity. Another disadvantage is that equation-based models are often less strongly linked to empirical data, because they often contain aggregated parameters that are difficult to parameterize. On the other hand, applications of moment equations benefit from the small data requirements, their analytical tractability, and their high potential for generalization. Therefore, their careful application to the spatially explicit modeling of savanna processes, probably in combination with other approaches, should be given more consideration. An example of a question suitable for moment equation modeling may be the extent to which local interactions matter for overall savanna dynamics.

Spatial Matrix Models

Another mathematical approach to spatially explicit savanna modeling is to add a spatial extension to matrix models. Matrix models often capture age- or stage-structured population dynamics and can be applied to implement state-and-transition models. Rows and columns of a matrix may refer to population states such as age or stage class and matrix entries to transition probabilities between the respective states. Nonhomogeneous matrix models can include perturbations to mean states and transitions due to spatial structure by adding an extra perturbation matrix. Another approach would be to create a matrix whose entries are submatrices, representing the transitions in each cell of a spatially discrete landscape. In savannas, the perturbation matrix approach has been used to predict land cover change (Petit et al., 2001), to evaluate individual plant architecture of fire-adapted species (Raventos et al., 2004), and to validate a new stability analysis method for nonhomogeneous Markov models (Li, 1995). The submatrix approach has been applied very rarely to savanna dynamics thus far (but see Miriti et al., 2001). In addition to the analytical tractability of an equation-based model, spatial matrix models have the additional advantage of capturing population structure when based on populations. Therefore, spatial matrix models can be used to investigate questions that focus on the demography of savanna plants as suggested by Sankaran et al. (2004). However, all transition probabilities need parameterization and are thus "data hungry"; and there is a trade-off between the ease with which an analytical solution of a matrix model can be found and the number of influencing factors such as spatial or temporal variation that can be concurrently analyzed.

Cellular Automata

In cellular automata, space is discretized into grid cells with a finite number of discrete states, in the narrow definition, only deterministic and synchronous transition rules between the states (Childress et al., 1996; Hogeweg, 1988). Transition rules depend on the direct neighborhood of a cell and represent local interactions only. The *direct neighborhood* is defined as the four cells sharing an edge with the focal cell (von Neumann neighborhood) or all eight cells touching the focal cell (Moore neighborhood). In the wider definition of cellular automata, stochastic and asynchronous transitions are also possible. The patterns that cellular automata produce can subsequently be compared with empirical data for validation. Spatial patterns emerging from cellular automata that have been successfully validated include the spread of prescribed fires (Berjak and Hearne, 2002); the distribution of crown heights and widths (Drake and Weishampel, 2001); and the spread of tree species depending on fire, demography, and seed dispersal (Hochberg et al., 1994). Cellular automata can be used to determine the importance and quality of spatial effects for the simulated patterns. In a sensitivity analysis of their cellular automaton, Drake and Weishampel (2001) found that spatial crown distributions were highly sensitive to spatially interactive parameters such as fire ignition, spread, and competition. A limitation of cellular automaton models is that they can quickly become highly complex, because all transitions between all possible combinations of states need to be described and parameterized from empirical data or expert guesses. To reduce this complexity, aggregation techniques are available, such as the voting system. In contrast to a unique neighbor system, in a voting system, only the number of cells in each state in a neighborhood is determined and not their exact location within the neighborhood (Childress et al., 1996). On the other hand, narrowly defined cellular automaton models are analytically tractable and very flexible due to the great range of possible cell identities from individual plants to pixels of satellite images (Childress et al., 1996).

Grid-Based Models

Grid-based models consist of a grid of cells similar to the grid on which cellular automata are based, but they can capture interactions between any two or more cells. These interactions are not confined to a specific neighborhood such as in cellular automata. Cells of cellular automata can only be in one of a defined set of states, whereas grid-based models can have complex and structured dynamics within each cell. Thus, grid-based models can capture spatial structure of almost any complexity and are, therefore, probably the most flexible spatially explicit modeling approach. The cells of a grid-based model can represent individual organisms or aggregated information such as biomass or presence or absence of a species. When cells contain individual organisms, agent-based modeling is a common approach in which the modeled dynamics emerges from individual interactions and depends on individual properties such as canopy width or spatial location (Grimm and Railsback, 2005). In the grid-, agent-, and rule-based savanna patch model SATCHMO, shrub agents, whose seed output depended on the individual property of canopy size, competed with other shrub or grass agents (Figure 14.4, Meyer et al., 2007a). A 10 × 10 cm cell contained either a shrub seedling, a part of a shrub or grass canopy, a part of the water uptake zone of one of eight roots per shrub, or bare ground and a certain amount of daily updated

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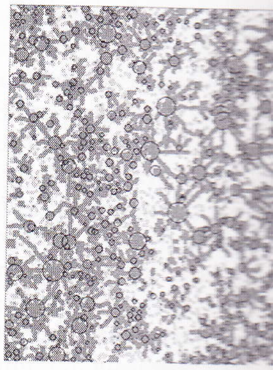

FIGURE 14.4
Overview of a typical model grid of an
section of the same grid (b). Grid-based
interactions such as, in this example,
covers about 500 × 500 m in reality and
interacting agents are shrubs and grass
aboveground (circles) and eight roots
by an uptake zone (dark gray) to model
uptake zones [cells with bold black edges
(light gray) and interact with shrubs
Meyer et al., 2007a. *Ecological Modelling*

soil moisture. Spatial processes
shrub-grass competition were
an empirical distribution around
according to the number of
a certain cell, respectively
tialized with one shrub
shrub and grass population and
truly emergent from the
validation procedure and
hand. Parameterized with field
fully validated against several
cyclical successions between
a setting typical of a semiarid
central prediction of
et al., 2009, Chapter 16).
Grid-based modeling is one of
explicit savanna modeling,
the prediction of NPP, water
the impact of shrub encroachment
simulation of spatial rain cloud
relationship between the
stocking rate in the SAVANNA

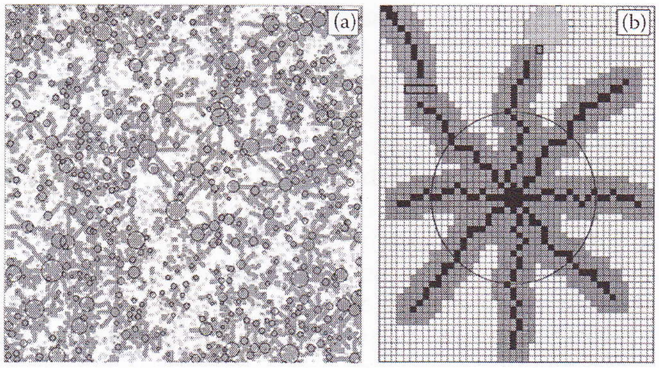

FIGURE 14.4
Overview of a typical model grid of an agent- and grid-based savanna model (a) and an enlarged section of the same grid (b). Grid-based models can be used to represent and analyse spatial interactions such as, in this example, water uptake and competition for soil moisture. The grid covers about 500 × 500 m in reality and consists of square cells with a side length of 10 cm. The interacting agents are shrubs and grass tufts. Each shrub is represented by its canopy extent aboveground (circles) and eight roots [black cells in (b)] below ground. Each root is surrounded by an uptake zone (dark gray) to model water uptake and competition for water in overlapping uptake zones [cells with bold black edges in (b)]. Grass tufts are represented by an uptake zone (light gray) and interact with shrubs when their uptake zones overlap. (Reprinted from K. M. Meyer et al., 2007a. *Ecological Modelling* 209, 377–391. © 2007. With permission from Elsevier.)

soil moisture. Spatial processes such as seed dispersal and shrub-shrub and shrub-grass competition were modeled by distributing seeds according to an empirical distribution around their parent and distributing soil moisture according to the number of individual shrubs and grass tufts overlapping in a certain cell, respectively (Meyer et al., 2007a). Since simulations were initialized with one shrub individual and 10 randomly distributed grass tufts, shrub and grass population and cover dynamics and spatial patterns were truly emergent from the simulations. These patterns were then used in a validation procedure and analyzed to yield conclusions about the question at hand. Parameterized with field data and a few expert guesses and successfully validated against several observed patterns, SATCHMO showed that cyclical successions between grassy and woody dominance can emerge from a setting typical of a semiarid savanna (Meyer et al., 2007b), corroborating a central prediction of patch-dynamics theory (Wiegand et al., 2006; Meyer et al., 2009, Chapter 16).

Grid-based modeling is one of the most common approaches in spatially explicit savanna modeling, addressing a large spectrum of questions such as the prediction of NPP, water fluxes, radiation absorption (Simioni et al., 2003), the impact of shrub encroachment on small mammals (Popp et al., 2007), the simulation of spatial rain cloud patterns (Eisinger and Wiegand, 2008), the relationship between the fragmentation of a grazed area and herbivore stocking rate in the SAVANNA model (Boone and Hobbs, 2004), or the ecological-socioeconomic assessment of management strategies in pastoral systems (Müller et al., 2007). Grid-based approaches are particularly useful in modeling spatial processes that range further than to the nearest plant neighbor, such as in the case of seed dispersal, fire, or grazing. Special emphasis has been placed on the role of grazing and herbivory for generating savanna dynamics and patterns (e.g., de Knegt et al., 2008). With a grid-based model whose grid cells were linked by seed dispersal and fire, Baxter and Getz (2005) showed that woody plant persistence was promoted by high tolerance to browsing by elephants, browsing-induced increase in germination success, and faster growth of woody plants. On the other hand, Jeltsch et al. (1996) found that persistence of tree clumps was promoted by intermediate values of grazing, fire, and moisture in their savanna modeling system. In an extension of this model, the effect of grazing on shrub encroachment depended on the time frame and became apparent at a century scale only (Jeltsch et al., 1997). Moreover, Weber et al. (2000) identified a threshold behavior of shrub cover response to grazing in their grid-based model, complicating predictions of grazing effects. However, predicting the effects of grazing is of major importance. For instance, grazing had a greater impact on shrub cover than climate change in a grid-based model of a southern African savanna (Tews et al., 2006, Chapter 15).

When compared with equation-based models, grid-based approaches do not have to make compromises with regard to complexity to ensure mathematical feasibility and are driven by and tightly linked to empirical data. Therefore, grid-based models are often structurally realistic (Wiegand et al., 2004b), which facilitates model parameterization and validation using qualitative expert knowledge that can sometimes be the only type of knowledge available in savannas. On the downside, they are very data hungry, which is alleviated by their great flexibility to adapt the level of modeled detail to data availability. Grid-based modeling is resource intensive regarding developing and computing time, and predictions are often difficult to generalize due to the lack of analytical solutions. First attempts to approximate the output of grid-based simulation models with analytical expressions (Calabrese et al., 2010) benefit from the full flexibility of one approach and the analytical tractability and general conclusions of the second.

Conclusions

Spatially explicit savanna modeling has focused on processes with strong spatial structure such as rainfall, fire spread, moisture fluxes, seed dispersal, competition, and grazing. This pool of spatial processes also provides the drivers of savanna tree–grass coexistence. Therefore, spatially explicit approaches, be they empirical or theoretical, are crucial to elucidate the

underlying mechanisms of tree–
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underlying mechanisms of tree–grass coexistence. The few existing spatially explicit theories of tree–grass coexistence emphasize the importance of spatial structure such as small-scale heterogeneities (Jeltsch et al., 1998) and the scale explicitness of patch dynamics (Wiegand et al., 2006; Meyer et al., 2009). These examples share another characteristic, that is, the combination of different approaches such as grid-based modeling and spatial statistics. Future studies will greatly benefit from placing more emphasis on combining different approaches. Moreover, since savannas span a great range of spatial scales, more scale-explicit approaches are needed in future spatial savanna modeling. For example, among the grid-based approaches, agent-based models can cover several spatial scales by predicting large-scale population dynamics from local interactions between plant and animal individuals. Given that many people depend on savannas for a living, ultimately, the challenge will be to apply the modeling results to develop management strategies that sustain savanna ecosystems and improve people's living. For example, management may gain from applying the principles of patch dynamics, which indicates that there is no single appropriate scale and that changes are "normal" within any given savanna (Wiegand et al., 2006).

This will further enlighten the importance of spatially explicit savanna modeling for describing, understanding, and predicting savanna processes, patterns, dynamics, and management.

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