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REVIEW

Spatial perspectives in state-and-transition models: a missing link to land management?

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Summary

1. State-and-transition models (STMs) synthesize and communicate knowledge about the alternative states of an ecosystem and causes of state transitions. Data supported narrative descriptions within STMs are used to select or justify management actions. State transitions are characteristically heterogeneous in space and time, but spatial heterogeneity is seldom described in STMs, thereby limiting their utility.

2. We conducted a review that indicates how spatially explicit data can be used to improve STMs. We first identified three spatial scales at which spatial patterns and processes are manifest: patches, sites and landscapes. We then identified three classes of spatial processes that govern heterogeneity in state transitions at each scale and that can be considered in empirical studies, STM narratives and management interpretations.

3. First, spatial variations in land-use driver history (e.g. grazing use) can explain differences in the occurrence of state transitions within land areas that are otherwise uniform. Secondly, spatial dependence in response to drivers imposed by variations in soils, landforms and climate can explain how the likelihood of state transition varies along relatively static environmental gradients. Thirdly, state transition processes can be contagious, under control of vegetation-environment feedbacks, such that the spatiotemporal evolution of state transitions is predictable.

4. We suggest a strategy for considering each of the three spatial processes in the development of STM narratives. We illustrate how spatial data can be employed for describing early warning indicators of state transition, identifying areas that are most susceptible to state transitions, and designing and implementing monitoring schemes.

5. *Synthesis and applications*. State-and-transition models are increasingly important tools for guiding land-management activities. However, failure to adequately represent spatial processes in STMs can limit their ability to identify the initiation, risk and causes of state transitions and, therefore, the appropriate management responses. We suggest that multi-scaled studies targeted to different kinds of ecosystems can be used to uncover evidence of spatial processes. Such evidence should be included in STM narratives and can lead to novel interpretations of land change and improved management.

Key-words: Chihuahuan Desert, contagion, Iceland, monitoring, patch dynamics, regime shift, southern Great Plains, spatial dependence, thresholds

Introduction

The occurrence of alternative states and thresholds has become a central issue at the interface of basic and applied ecology (Beisner, Haydon & Cuddington 2003; Hobbs & Cramer 2008). Alternative states (or regimes) represent major shifts in ecosystem function. The shifts are due to changes in the abundance and composition of dominant species and associated biological and physical processes. Alternative states tend to be recognized when ecosystem changes have societal significance

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and are persistent with regard to management timeframes (Suding, Gross & Housman 2004). Thresholds describe the changes in drivers and their interactions with local conditions that result in alternative states (Scheffer & Carpenter 2003; Suding & Hobbs 2009).

State-and-transition models (STMs) describe states, thresholds and management conditions leading to the formation of alternative states (state transitions). Although such models were first formalized for rangeland management (Westoby, Walker & Noy-Meir 1989), STMs (and similar conceptual models) have become a common means to synthesize information about state transitions in a variety of terrestrial ecosystems (see examples in Archer 1989; Milton *et al.* 1994; Bestelmeyer *et al.* 2004; Chartier & Rostagno 2006; Hobbs & Suding 2009; Zweig & Kitchens 2009). In south-western Australia, for example, land managers use STMs to assist with the restoration of jarrah forest in areas mined for bauxite (Grant 2006). In the United States, federal land management and assistance agencies have formally adopted STMs as a means to set management benchmarks and recommend practices to achieve desired conditions in rangelands and forests (http://www.fs.fed.us/biology/soil/Signed_RIESM_2010.pdf).

State-and-transition models for terrestrial ecosystems are typically developed using some combination of informal historical observations, expert knowledge, inventories of states with space-for-time substitution assumptions, monitoring of state transitions and controlled experiments (Briske, Fuhlendorf & Smeins 2003; Bestelmeyer *et al.* 2009). Reference (e.g. historical, desired or non-degraded) states and alternative (e.g. degraded) states are defined based on persistent differences in plant community productivity, composition and soil function. Narrative descriptions of transitions describe how management actions and environmental conditions interact to produce alternative states. The transition narratives are often a basis for on-the-ground actions. Observational or experimental data supporting the STMs are usually gathered at a limited number of points without thorough consideration of scale and spatial heterogeneity. Such non-spatial approaches yield valuable information about the possible alternative states and the mechanisms underlying transitions in broad ecosystem types (e.g. Brown & Archer 1999; Beckage & Ellingwood 2008; Okin, D'Odorico & Archer 2009).

Non-spatial approaches, however, miss important information about state transition processes. Transitions are often patchy and asynchronous (Van Nes & Scheffer 2005; Bestelmeyer, Ward & Havstad 2006). For example, within a landscape of 50 000 ha, state transitions may be localized to certain areas. This spatial pattern in state transitions might be partly a reflection of spatial variation in historical driver intensity including grazing pressure, deforestation rates, fire ignitions or localized drought (Pickup, Bastin & Chewings 1998; Foster *et al.* 2003; Jasinski & Payette 2005). Variation in soils and landforms filter the effects of drivers, compounding the spatial variation in state transitions (McAuliffe 1994; Fensham & Holman 1999). Spatiotemporal patterning in transitions may be evident at various scales. Localized state transitions may occur as fine-scale changes at the level of plant patches that gradually accumulate or transitions may radiate to broad areas from points of initial impact. These effects can be caused by feedbacks between patch spatial patterns at different scales and disturbance, resource redistribution or even climate (Peters *et al.* 2004; Rietkerk & Van De Koppel 2008). The combination of scale dependent and spatially overlapping processes produces the complex spatial patterns in alternative states typically observed in managed landscapes. Investigations of these spatial patterns could provide insights to improve monitoring and management that would not arise from simpler, non-spatial models (Pringle, Watson & Tinley 2006).

The importance of scale and pattern-process linkages in land management has long been recognized and general theory is well developed (e.g. Wu & Loucks 1995; Liu & Taylor 2002 and chapters therein). Nonetheless, multi-scale spatial perspectives have not been widely incorporated into STMs and managers do not always appreciate the significance of spatial patterns. We propose that STMs can be improved by including data-supported information on spatial processes in STMs. We suggest that three classes of spatial processes should be recognized in studies of state transitions: (i) spatial variation of land use drivers, (ii) spatial dependence in response to drivers imposed by soils and landforms, and (iii) spatial contagion in responses to drivers due to vegetation-environment feedbacks. Consideration of each class is required to robustly translate STMs into land-management applications.

We begin our review with a hierarchical perspective on STMs that can facilitate consideration of multi-scale spatial processes. Each class of spatial processes is then reviewed and illustrated with empirical examples from the rangelands we study. Simulation and mathematical modelling applications derived from such empirical examples are described elsewhere (e.g. Wiegand *et al.* 2003). The review asks: What governs the distribution and abundance of alternative states across a landscape or region? How are spatial patterns related to transition mechanisms within a site?

To conclude, we discuss how traditional STMs could be improved with spatial perspectives and we explore the implications of such changes for management and monitoring. Our assessment suggests that spatially informed STMs would enhance ecosystem management while simultaneously providing a framework within which to interpret basic ecological studies of state transitions.

A SPATIAL HIERARCHY FOR STATE-AND-TRANSITION MODELS

A practical scheme to account for multiple scales must be devised to integrate spatial processes with STMs. Associating spatial processes with fixed spatial scales is problematic because different ecosystems (or even the same ecosystem) may experience a particular process at different measured scales. For example, the scale of important soil variations might occur over tens of metres or hundreds of metres. 'Domains of scale' or scale domains focus attention on characteristic pattern–process interactions within certain ranges of measured scale (Wiens 1989). Although the specific scales may vary among ecosystems, the hierarchical relationships among domains should be general. Qualitatively different pattern–process relationships occur in different scale domains.

We suggest that three scale domains (hereafter 'scales') usefully characterize the way scientists and managers perceive vegetation dynamics in terrestrial (especially rangeland) ecosystems (Fig. 1). We start with the middle scale of sites based on soils and landforms within an area of uniform climate that support similar ecosystems at their potential (i.e. the reference state). The term 'site' is used operationally throughout the world to recognize how variations in soils and topographic position create differences in plant community production/composition across a landscape (e.g. Illius & O'Connor 1999; Sasaki *et al.* 2008) via differences in water and nutrient availability and rooting substrate (McAuliffe 1994; Fensham & Holman 1999). Grazing pastures often subdivide or encompass one or more distinct sites, whereas a property or grazing area usually contains a variety of sites. Site has been formally recognized by US federal land management agencies as units called 'ecological sites'. These are subdivisions of the landscape based on soil map unit components (i.e. soil series phases of US soil classification; Bestelmeyer *et al.* 2009). STMs are usually developed for specific ecological sites and define the reference and alternative states for each site. Thus, a mapped delineation of an ecological site (e.g. at a 1 : 5000 scale) could be observed in one or more states.

At the finer patch scale, a given state can feature distinct types, abundances and spatial arrangements of patches. Depending upon the system and processes involved, a patch might be a grass tussock or group of tussocks, a clump of shrubs or trees, or a vegetation band characterized by both plant cover and surface soil properties (Ludwig & Tongway 1995). State changes that managers recognize at the site scale are built upon the rapid, dynamic processes of change in vegetation and surface soils occurring at the patch scale. For example, managers often recognize incipient state change in a site via the expansion of bare ground or invasion of shrubs occurring at the scale of centimetres to metres.

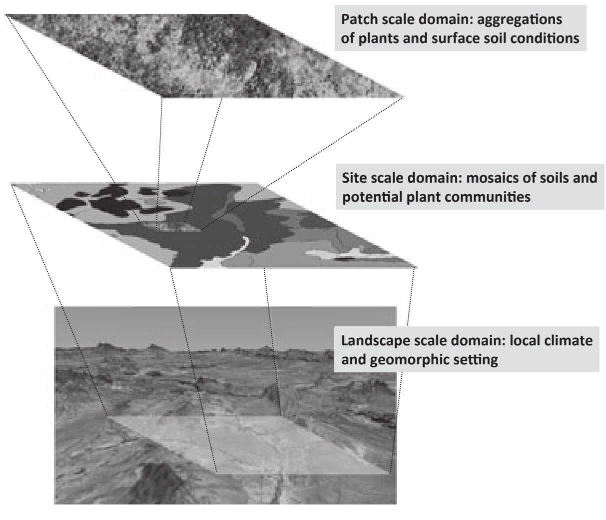

Fig. 1. A spatial hierarchical framework identifying three scale domains that characterize the dominant processes used by scientists and managers to explain dynamics in managed terrestrial ecosystems.

At the broadest scale of the landscape, sites occur in an area of similar local climate and co-occur with other sites to create a mosaic structured by slow geomorphic processes and long-term patterns of land use. Subtle variations in meteorology and the potential for lateral hydrological/eolian interactions among sites influence the net flux of resources and disturbances to and from a site. These fluxes influence the states that a particular site exhibits, all else being equal. For example, changes in the states surrounding a site can affect the magnitude of erosive sheet flow or likelihood of fire spread experienced by the site (Okin *et al.* 2009). Thus, managers sometimes recognize the landscape context of sites with the axiom 'look across the fence to see what is coming at you'.

We now illustrate how spatial patterns within these scale domains interact with three classes of spatial processes to produce spatial heterogeneity in alternative states. We review these processes in relation to traditional STMs.

SPATIAL VARIATION OF DRIVERS

Management-related drivers of state transitions in STMs, especially grazing intensity, are usually described in general terms (e.g. 'overgrazing') without reference to spatial variation. While it has been common to use gradients in grazing intensity from water points to estimate the magnitude of livestock activity needed to induce state transitions (Pickup, Bastin & Chewings 1998; Sasaki *et al.* 2008), STMs have seldom addressed how varying land-use histories in discrete management units (e.g. pastures or properties) influence variations in state transitions across a landscape (Turner, Wear & Flamm 1996). Different land users can vary in their application of drivers for social and economic reasons (e.g. degree of dependence on ranch income; Gentner & Tanaka 2002). Sequences of historical events (both natural and cultural) interact with these drivers to amplify or attenuate their effects (Lunt & Spooner 2005). Thus, spatially referenced, historical reconstructions of the motivations and events giving rise to variation in state transitions can provide great explanatory power in STMs (Foster 1992; Todd & Hoffman 2009).

Spatial variation in driver histories can be expressed at several scales. Contrasting policies between countries, such as the implementation of grazing regulations in the USA and not in Mexico in 1934, can create different distributions of states at landscape scales (Bryant *et al.* 1990). For STMs aimed at management, however, it is especially useful to map and reconstruct management histories that have varied within specific ecological sites. For example, fence-line contrasts between grassland and shrub-dominated, sparse grass states are commonly observed in broad areas of the sandy ecological site in the Chihuahuan Desert, New Mexico, USA that includes several pastures and landowners (Fig. 2). Historical investigation of these units reveal that the mosaic of alternative states originated in 1915–1922 when the New Mexico State University College Ranch (CR) and the Jornada Experimental Range (JER) were isolated from public land now administered by the

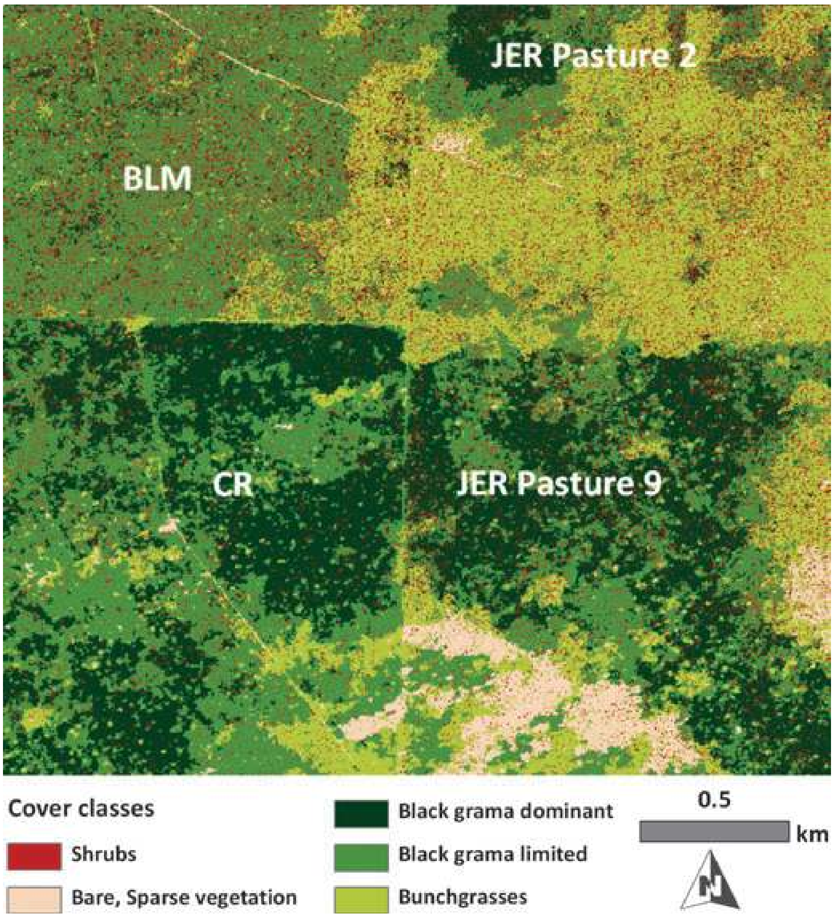

Fig. 2. Chihuahuan Desert vegetation states on a single ecological site (Sandy) near Las Cruces, NM, USA, on two management units (Pastures 2 and 9) at the western boundary of the Jornada Experimental Range (JER); on the adjoining New Mexico State University Chihuahuan Desert Rangeland Research Center (CR); and on U.S. Bureau of Land Management (BLM) land. Units were separated by fences to manage livestock grazing. Vegetation was classified from a Quickbird satellite image (October 2003) using eCognition software following Laliberte *et al*. (2004). Classes are patch types of a state-and-transition model produced for the area (Bestelmeyer *et al*. 2004) that includes black grama *Bouteloua eriopoda* Torr.-dominant, black grama limited (i.e. sparse cover), bunchgrass, and bare ground. Mesquite *Prosopis glandulosa* Torr. shrubs were classified separately (red). Increased bare ground and shrub density within pasture 9 (right of image) is associated with a water point. The image classification was produced by Caiti M. Steele.

U.S. Bureau of Land Management (BLM). Subsequently, average utilization (an estimate of the percentage of plant biomass removed by livestock grazing) was 15–55% lower on CR than BLM through the drought period of the 1950s and afterwards (Holechek *et al*. 1994). The heavier livestock grazing on BLM landscapes during this drought period triggered the extirpation of grasses, erosion and transition to a shrub-dominated state.

The imagery (Fig. 2) also reveals how subtle differences in pasture management within JER influenced state transitions. Pasture 9, in which extensive grasslands have been maintained, was fenced in 1928 and has been managed as a reserve pasture with light summer stocking rates, whereas Pasture 2 experienced higher (but normal for the time period) stocking rates (Jornada Experimental Range Document Archives, unpublished data). The historical reconstruction suggests that relatively minor differences in long-term grazing management can be responsible for the patchy pattern of alternative states among management units that typifies the sandy site. This result highlights the sensitivity of this site to management variations and how difficult it can be to manage stocking rates to avoid state transitions.

State-and-transition models could readily include (i) a characterization of the typical patterning of states at site and landscape scales, and (ii) descriptions of the historical circumstances giving rise to the pattern of states (Swetnam, Allen & Betancourt 1999; Briggs *et al*. 2006). Information on specific decisions and motivations underlying those decisions would provide an even deeper understanding of state transitions (Brunson & Shindler 2004; Fensham, Fairfax & Archer 2005).

SPATIAL DEPENDENCE IN RESPONSE TO DRIVERS

Whether or not a driver causes a state transition depends on how inherent (or slow changing) geophysical properties filter the effects of the driver (Swanson *et al*. 1988). Accounting for this filter has been accomplished in many areas of the US through the development of STMs for different ecological sites. Interpretation of such STMs, however, usually assumes that ecological sites are internally homogeneous with respect to soils and that mapped ecological site delineations do not vary in climate across the region for which they are developed. In arid and semi-arid rangelands, this is often not the case. For example, the spatial pattern of shrub infilling (Archer 1995) and alternative states (Bestelmeyer, Ward & Havstad 2006; Browning *et al.* 2008) can be patchy or exhibit gradients at scales of metres to hundred of metres. These patterns are controlled by subtle variations in soil properties such as subsurface clay content. High subsurface clay content simultaneously favours perennial grasses by retaining water and nutrients near the soil surface while limiting deep root penetration by shrubs, thereby negating their advantage (McAuliffe 1994). Historical aerial photographs indicate that some grass-dominated patches in an area mapped as the loamy ecological site in the Chihuahuan Desert have been highly stable while other patches on the same landscape and under similar management have undergone transitions between vegetated and non-vegetated states. The patches that are now vegetated or bare are aggregated in certain portions of the site, forming an ecotone in vegetation (Fig. 3a). Soil sampling revealed a limiting–factor relationship between persistent grass cover and subsoil clay content, wherein increasing clay content placed an increasing upper bound (90th quantile) on the amount of grass cover (Fig. 3b). Thus, while relatively high subsoil clay content did not guarantee grassland resilience, it permitted it to occur in discrete areas.

Subtle spatial variations in static soil properties (such as depth) can locally filter drivers that are uniform at site scales and help to produce patchy or gradient patterns of state transitions (Fuhlendorf & Smeins 1998). Similarly, landscape-scale gradients in climate can alter the likelihood of transition in otherwise similar soils (Jasinski & Payette 2005). Thus, local measurements of soil profiles and climate are often needed to properly contextualize individual measurements of state transitions in STMs (Didham, Watts & Norton 2005), even in areas assigned to a single ecological site. Such data can reveal that the likelihood of transitions within STMs is a combined function of driver intensity and gradual variations in geophysical properties.

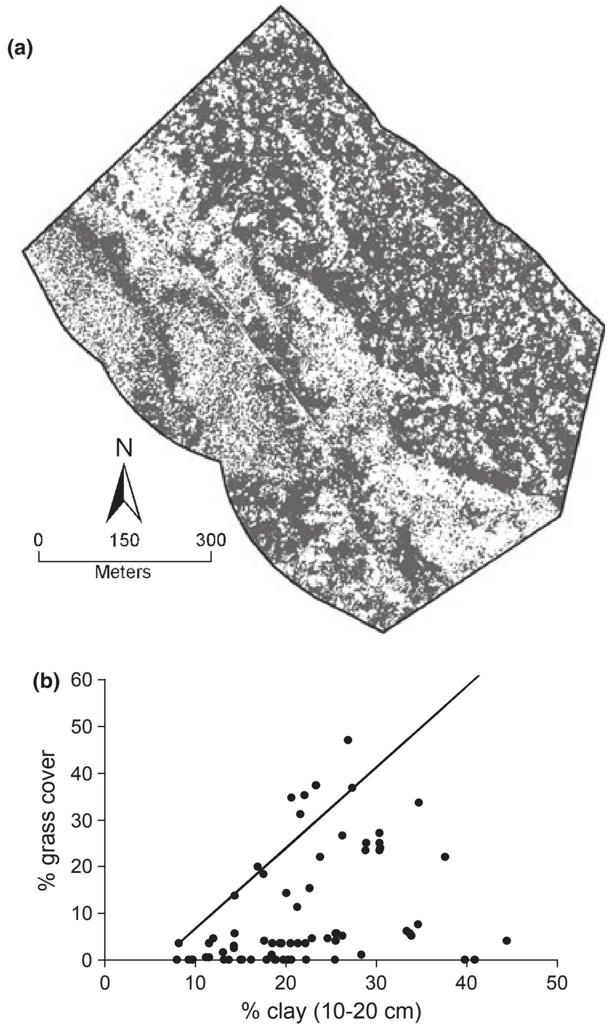

Fig. 3. (a) A map of grassy, vegetated (grey) and shrub-dominated, sparsely vegetated (white) patches in a management unit of the Coralitos Ranch, New Mexico, USA. (b) Grass cover vs. % clay in the subsurface soil. The line fits a least absolute deviation regression of the 90th quantile using Blossom version W2008.04.02 software (Cade & Richards 2005). The probability that the line's slope is zero is 0·019 based on a nonparametric permutation test. Data from Bestelmeyer, Ward & Havstad (2006).

SPATIAL CONTAGION AND FEEDBACKS

Spatial contagion here refers to the spread of localized state-transitions to adjacent areas due to feedbacks between plant growth, survival and dispersal with local environmental conditions, independent of driver intensity in the adjacent areas (Watt 1947; Peters *et al.* 2004). Traditional STMs tend to treat mechanisms of state transitions as due to point-based, vertical processes involving an external driver interacting with specific plant patches and local soil/topographic properties. Horizontal processes (contagion), however, can be important components of state transition mechanisms at patch, site and landscape scales.

Positive feedbacks between plant patches and resource availability are postulated to underlie transitions between highly and sparsely vegetated states in a variety of ecosystems (Rietkerk *et al.* 2004). In arid ecosystems, plants within vegetated patches (e.g. several metres across) facilitate one another by collectively harvesting and retaining water via improved infiltration and capture of overland flow. Plant mortality caused by drought or patchy grazing disturbance (e.g. Adler, Raff & Lauenroth 2001) leads to patch disintegration, the breakdown of positive feedbacks and ultimately a cascade of patch loss that is perceived as a transition between highly vegetated and sparsely vegetated states at the site scale (Davenport *et al.* 1998; Ludwig *et al.* 2005; Okin, D'Odorico & Archer 2009). Consequently, vegetation patch metrics are increasingly proposed to describe the structural changes and loss of resilience forewarning of state transitions (Ludwig *et al.* 2002; Bisigato *et al.* 2005; Kefi *et al.* 2007; Guttal & Jayaprakash 2009).

Patch-scale changes in vegetation can initiate contagious processes of state transition at the site scale via cross-scale interactions between large bare patches and broad-scale wind or water erosion (Peters *et al*. 2004; Pringle, Watson & Tinley 2006). For example, areas of shrub-dominated coppice dunes in the Chihuahuan Desert have been documented to expand, converting adjacent grasslands into coppice dunes (Fig. 4a,b). Coppice dune states result when long-lived stoloniferous grasses are selectively killed by drought and heavy livestock grazing (e.g. the resulting 'bunchgrass' and 'bare' classes in Fig. 2). The contagion of savanna- or grassland-coppice dune transition is mediated by mesquite recruitment coupled to sand burial of grasses in the prevailing direction of erosive winds (Okin *et al*. 2009).

Examples of contagious soil degradation are not restricted to warm, arid ecosystems, as is commonly assumed. A similar pattern of spreading soil erosion has also been observed in cold, humid environments such as those of Iceland (Fig. 5a), where grazing disrupts the vegetation thermal barrier. This, in turn, amplifies freeze–thaw dynamics that destabilize highly erodible Andisol soils, making them more prone to frequent, small-scale disturbances associated with frost boils, frost heaving and needle-ice formation (Fig. 5b; Archer & Stokes 2000; Thorsson 2008). These geophysical forces help create and reinforce the persistence of small bare patches, which expose the friable, thick (50–200 cm) mantle of volcanic soil to removal by wind and water (Arnalds 1998). As small eroded patches increase in density and gradually enlarge, coalescence occurs and the

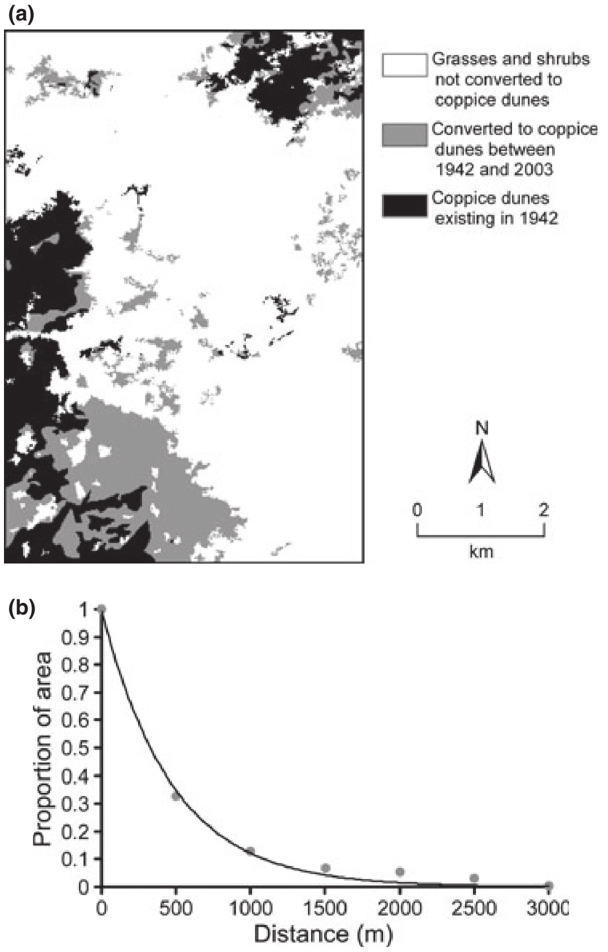

Fig. 4. Spatial contagion of grassland to coppice dune shrubland transitions in the Chihuahuan Desert, USA (Jornada Experimental Range, New Mexico). (a) Areas that were mesquite dunes in 1942, areas converted to dunes between 1942 and 2003, and areas that remain grassland or savanna as of 2003 (map shown is a subset of the modelled area). The 1942 map was hand digitized from an aerial photograph, the 2003 map digitized from a Quickbird satellite image. (b) The proportion of area that converted to mesquite dunes as a function of distance from dunes present in 1942 (fitted to a negative exponential function $P = 0{\cdot}9941^{(-0{\cdot}0021d)}$, where P = proportion of landscape converted to dunes and d = distance (m) from established dunes; $r^2 = 0{\cdot}99$).

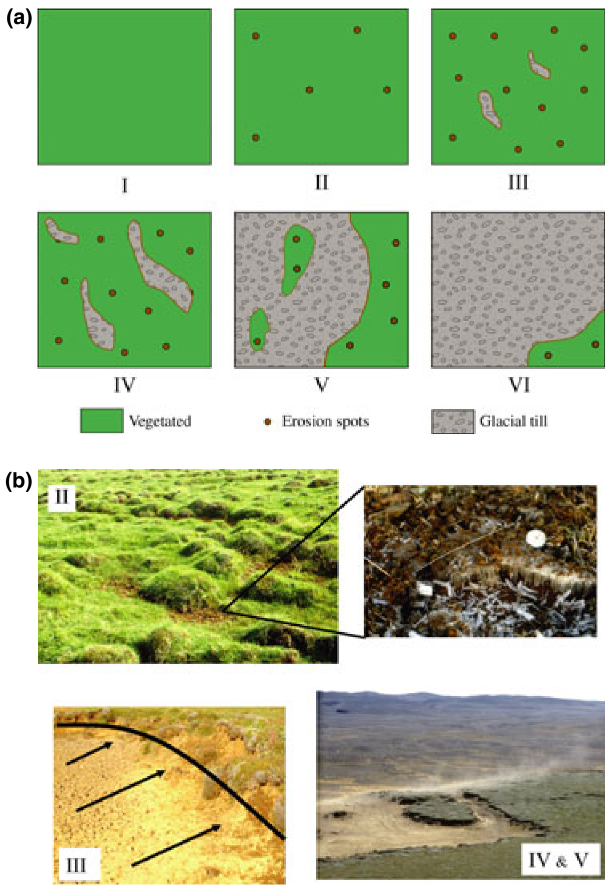

Fig. 5. Spatial contagion in high latitude birch woodland to desert pavement transitions in Iceland. (a) Conceptual diagram depicts six states on an Andisol soil, ranging from birch *Betula pubescens* Ehrh. woodland (I) to heathland with low (II) and high densities of small erosion patches beginning to coalesce (III), to heathland with large bare areas with erosion fronts (IV). Once in state IV, these fronts march unimpeded across the landscape due to erosion, leaving glacial till in their wake (V, VI). (b) Photos depict field examples of state II (showing hummocks and erosion spots, the latter being highly susceptible to frost heaving and needle-ice formation that further destabilize soils), state III (coalesced erosion patches with incipient erosion front) and a large erosion front on the move (states IV and V in the foreground, with state VI in the background). See Archer & Stokes (2000) and Thorsson (2008) for details.

length of exposed perimeter increases dramatically. This results in the creation of erosion fronts whose vertical faces are fully exposed to wind and water (Arnalds 2000). These elongated, wind-driven fronts can now advance rapidly across the landscape, leaving glacial till in their wake. As with arid coppice dunes, management practices to preserve the remaining vegetated zones do little to prevent the advance of these fronts.

Spatial contagion can also interact with static soil variation in complex ways across a landscape. Spatial variation in transitions from grass- to shrub-dominated states in the southern Great Plains occurs at a landscape scale, with the rates and patterns of these transitions dependent on subsurface variation in the development of argillic (clay pan) horizons (Fig. 6a,b). Spatial variation in runoff from these upland ecological sites, in turn, influences the patterns of grassland-to-woodland transition in the adjoining lowland ecological site (Fig. 6c). A similar example is that patterns of fire spread can be determined by where the spread was initiated relative to the spatial arrangement of ridges and valley bottoms (Swanson *et al.* 1988) as well as the local connectivity of fuel loads relative to the direction of spread (Allen 2007).

When state transitions have occurred over a sufficient spatial extent, a distinct set of cross-scale interactions can be initiated at the landscape scale that link even distant sites together. For example, vegetation clearing in upland areas of southern Australia has led to rising water tables and salinization in lower-lying ecological sites within the watershed that were not cleared (Yates & Hobbs 1997). Similarly, changes in land surface conditions can have a pronounced effect on weather, climate and local meteorology (Bryant *et al.* 1990; Pielke *et al.* 1998). The landscape-scale cover of highly vegetated- vs. poorly vegetated states can influence meso-scale climate via the influence of vegetation on dust aerosols and soil surface temperatures that intensify local drought and vegetation loss (Balling *et al.* 1998; Rosenfeld, Rudich & Lahav 2001; Cook, Miller & Seager 2009). Dust deposition can decrease snowpack albedo regionally, thus accelerating melt and potentially increasing summer drought stress in lower elevation ecosystems (Painter *et al.* 2007). There is little work to indicate the areal extent, continuity or nature of state change needed to initiate feedbacks at landscape and larger scales. Hodgson, Hatton & Salama (2004) provide an example predicting vegetation cover–salinization relationships using hydrological models in south-western Australia.

Several features of STMs have precluded the representation of contagious processes. With regard to patch- and site-scale contagion, STMs have typically relied exclusively on measurements of surface cover and have not used measures of patch size, arrangement, or spatiotemporal patterns of spread to characterize state transitions. With regard to landscape-scale contagion, STMs are typically developed for specific ecological sites rather than landscapes and are therefore incapable of linking state-transitions occurring in one place (or across an extent) to those occurring in another.

Elaborating STMs to account for spatial processes

State-and-transition models are synthetic tools that serve to link field observations of patterns in the geophysical setting,

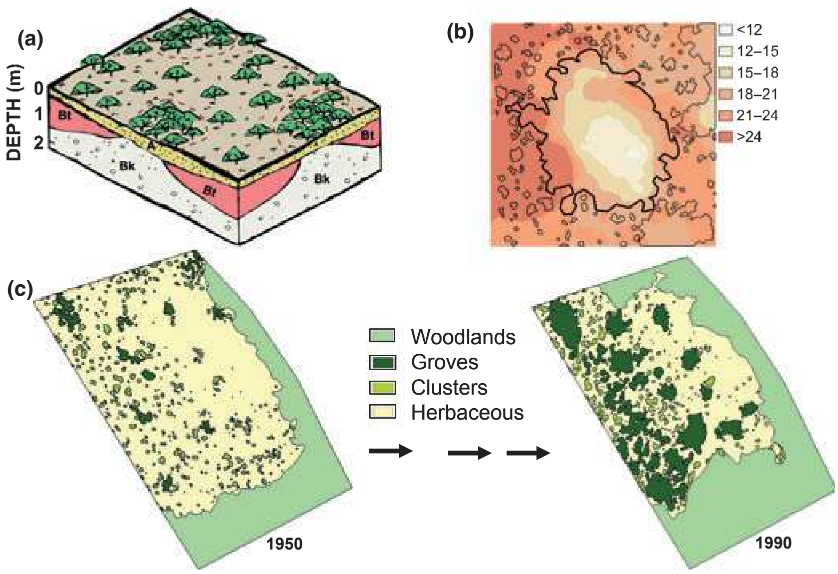

Fig. 6. Grass-shrub transitions in the southern Great Plains. (a) Groves (high densities of large shrubs) develop where the clay pan horizon is poorly expressed. Where the clay pan is well-developed, shrubs are smaller and sparser (from Archer 1995). (b) Canopy boundaries of groves developing on grassland (heavy black line) coincide with areas of relatively low (< 18%) subsurface clay content; grasses and small shrub clusters (fine black lines) occur where clay content is higher (from Stokes 1999). (c) Patterns of transition in adjoining ecological sites. Convex sandy loam uplands with patches of shrubs embedded within a grassy matrix grade (1–3% slopes) into closed-canopy woodlands of clay loam lowlands. Patterns of state change in uplands are governed by the distribution of low clay inclusions within the grassy matrix (panels a and b), whereas patterns of upslope migration of woodlands into grassland depends on spatial variation in runoff coming from adjoining uplands. Where surface runoff from uplands is low, woodland-savanna boundaries have been fairly static from 1950 to 1990 (right-hand side of the image); where runoff from uplands is greater, woodlands have migrated substantially upslope (bottom portion of the image; from Wu & Archer 2005).

vegetation and soil surface to ecological processes bearing upon management actions. They are used by managers to develop science-based predictions about ecosystem behaviour across broad land areas, most of which have not been (nor ever will be) intensively studied by ecologists. Given the focus on day-to-day management and the broad areas involved, it would be impractical to suggest managers should become fluent with GIS, the manipulation of high-resolution remotely sensed data or spatially explicit simulation models. Nonetheless, a body of detailed studies of spatiotemporal dynamics within different types of ecosystems (Bestelmeyer *et al.* 2009) could be used as benchmarks for developing spatially informed STMs.

As illustrated in the preceding empirical examples, we suggest that STMs can include data-supported narrative descriptions of spatiotemporal patterns and associated processes at patch, site and landscape scales. We suggest developing a matrix that focuses model developers on each of the three spatial processes (spatial variation in drivers, dependence and contagion) in each scale domain (Table 1). The matrix assists model developers in recognizing important spatial processes that have often been ignored in STMs.

In some cases, the matrix exercise may indicate that state transitions are coupled across a landscape. In these cases, it will be useful to develop landscape-scale conceptual models. The boundaries of the landscape can be delineated based upon the strength and extent of dominant spatial interactions among ecological sites and repeating patterns of those interactions across a geographic area [called 'ecosystem clusters' by Forman (1995) and 'soil-geomorphic systems' by Bestelmeyer *et al.* (2009)]. STMs developed for particular ecological sites can be linked by these interactions. For example, in the Jornada Basin of southern New Mexico (Fig. 7), we have postulated that transitions from grassland to bare states in broad drainages (inset fans; locally called Draw ecological sites) can accelerate transitions from grassland to shrubland or bare states on the piedmont slope (Loamy ecological site) below the drainages by increasing erosive overland water flow. These state transitions make more run-in water available to the margin of

Table 1. Elements of transition narratives for the sandy ecological site in southwestern New Mexico, USA, referencing spatial processes at each of three scale domains. Evidence is noted in superscripts

	Patch	Site	Landscape
Driver pattern	Grazing breaks up large patches resulting in more evenly distributed, smaller tufts[1]	State transitions have varied strongly among pastures on the same soils due to differences in grazing management in years preceding drought events[2]	No differences in management drivers/transition rates detected across the extent of sites in US, differences observed across US-Mexico border[6]
Spatial dependence	None detected	Soils with weaker development of argillic or calcic horizons have been more prone to transition[3]	No clear differences in the likelihood of transition within the range of climate observed for this site
Spatial contagion	Bare patches > 200 cm diameter are associated with evidence of increased erosion[4]	Shrubland states tend to spread laterally within sandy soils even when grazing pressure is reduced or eliminated[2,5]	Eroded sand deposits can bury surfaces of adjacent ecological sites that are downwind of prevailing erosive winds[6]

[1]Paulsen & Ares (1962); [2]Examples discussed in this paper; [3]D. Browning & M. Duniway, unpublished data; [4]Okin, Gillete & Herrick (2006); [5]Peters *et al.* (2006); [6]B. Bestelmeyer, personal observations.

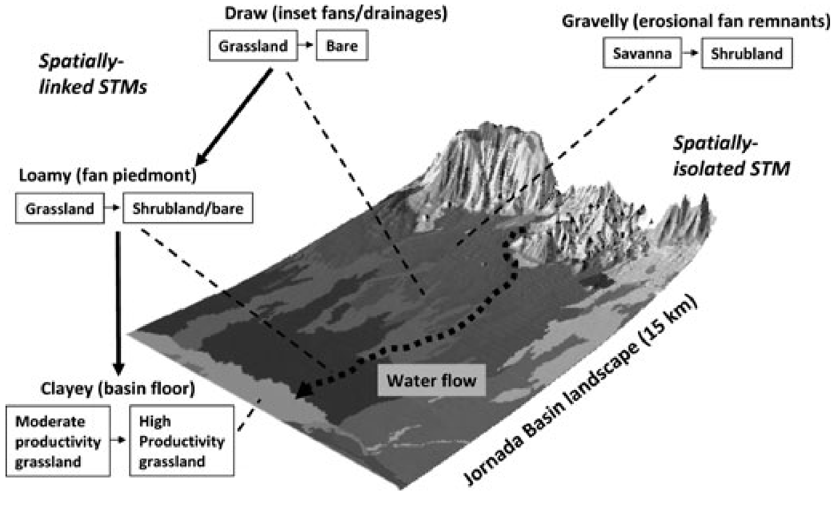

Fig. 7. A landscape level state-and-transition models (STM) for a portion of the southern Jornada Basin, New Mexico, USA. States (boxes) and transitions (fine arrows) for different ecological sites are located in the landscape figure using dashed lines. State transitions in the upslope Draw ecological sites in inset fans (drainages) affect state transitions in Loamy fan piedmont and Clayey basin floor sites via water flow and erosion; these linkages are illustrated using thick arrows. The Gravelly ecological site does not produce downslope effects.

the basin floor (Clayey ecological site), increasing grass production there (Herbel & Gibbens 1989). Other ecological sites, such as Gravelly sites on uplands (erosional fan remnants), are hydrologically isolated and their locally caused state transitions from savanna to shrubland are not believed to have off-site effects.

Potential benefits of spatial STMs

It is important to ask whether the inclusion of information on spatial processes would improve the utility of STMs and management outcomes. Although we cannot provide direct evidence because such models are only now being developed and used, we describe some anticipated benefits of spatial STMs based on the literature and our experiences.

EARLY WARNING INDICATORS OF STATE TRANSITIONS

Theory suggests that changes in the statistical properties (e.g. patch size frequency distributions, variance or skewness) of patch size or biomass within states might indicate that state changes are imminent (Rietkerk *et al.* 2004; Guttal & Jayaprakash 2009). Empirically, there is evidence that a breakdown of scaling relationships (i.e. deviations from a power law distribution of vegetation patch sizes) is associated with increasing resource limitation or grazing impact in arid rangeland ecosystems (Kefi *et al.* 2007; Scanlon *et al.* 2007). The breakdown in scaling relationships is related to the fragmentation of large, interconnected vegetation patches. Similarly, increasing connectivity of bare ground between patches and changes in patch orientation towards the direction of wind or water vectors can signal a breakdown in the feedbacks supporting productive states (Ludwig *et al.* 2002; Ares, Del Valle & Bisigato 2003; Okin *et al.* 2009). Conversely, the preservation or recovery of resource-retaining patch structures could signal restoration opportunities.

These ideas suggest that information on patch size frequency distributions, patch shape or bare ground connectivity could be valuable additions to STMs, particularly in arid ecosystems. Managers typically rely on plot-scale estimates of vegetation cover to assess land condition relative to an STM. In some cases, reliance on cover alone can be misleading. Ludwig *et al.* (2007) found that a catchment featuring a large area of eroding bare ground and 54% grass cover had 43 times greater sediment loss than a catchment where the grass cover was less (43%) but more evenly distributed. This result suggests that, in some ecosystems, the spatial pattern of vegetation cover can be even more important than the average amount of cover in evaluating state transition processes. In other ecosystems, patch metrics may not have meaningful relationships to state transition mechanisms and could safely be ignored.

COMPARATIVE LIKELIHOOD OF STATE TRANSITIONS AMONG AREAS AND TIME PERIODS

While STMs developed for a set of ecological sites or ecosystems convey the mechanisms of state transitions and temporal patterns of change, they do not provide for comparisons of the risk of state transition (or restoration opportunity) across space. In addition to ecological site variation, there are geographic variations in the characteristics of dominant actors, management strategies and policies. STMs developed for ecological site classes may also circumscribe significant within-class heterogeneity in geophysical properties. We suggest that it would be useful to quantitatively (or even qualitatively) compare the likelihood of state transition among ecological sites, among geographic areas or along gradients within an ecological site. Such information could be used to prioritize management interventions or monitoring at landscape scales.

Statistical relationships between state transition occurrences within an ecological site (or similar unit) and drivers or spatial dependence (e.g. ownership class, administrative area, subtle differences in soil depth or regional climate) could be used to explicitly represent heterogeneity in state-transition processes (e.g. Fig. 3b). Interactions with temporal variables (e.g. drought vs. non-drought periods) should also be examined. A variety of methods discussed earlier, including inventory of states and repeat aerial photography, could be used to develop these statistical relationships.

SPATIALLY STRUCTURED ASSESSMENT AND MONITORING

Monitoring has frequently been advocated as a means to anticipate and detect state transitions or restoration opportunities. If not recognized, however, spatial processes can compromise the effectiveness of monitoring. Monitoring typically involves random placement of sampling units or stratification based on dominant vegetation. In Western Australia, monitoring data were shown to be of limited utility because monitoring locations in spatially dominant uplands were often divorced from the points of initial degradation in drainages – from which degradation eventually spreads to uplands (Pringle, Watson & Tinley 2006). Monitoring simulations for the area represented in Fig. 3a indicate that random sampling within an ecological site can underestimate or overestimate vegetation change when loss and recovery of vegetation is patchy (see Appendix S1, Supporting Information).

These examples suggest that even simple spatial models of state transition processes have the potential to vastly improve the deployment, cost-efficiency and effectiveness of monitoring schemes. We suggest that descriptions of spatial processes in each scale domain could be used to structure monitoring strategies across scales (Table 1). For example, measurements might focus on the diameter of bare (or vegetated) patches based on the hypothesis that change in patch size signals the initiation of a state transition. Sampling might focus on the ecotones between reference and degraded states at the site scale based on the hypothesis that degraded states tend to expand. Alternatively we could distribute monitoring across a landscape to detect cumulative effects on hydrology. Sampling could also focus on ecological sites or management areas expected to be at relatively high risk for state transitions during drought periods. Descriptions of transition processes in current STMs seldom enable these kinds of decisions.

Conclusions

The ability to predict and manage transitions in many ecosystems would be improved by knowledge of spatial processes. Nonetheless, empirical studies of transition mechanisms in terrestrial systems rarely include spatial variables. Our review points to a set of approaches for including information on spatial processes in the interpretation of land change and design of management actions. First and foremost, state transitions should be re-conceptualized as consequences of local point mechanisms characterized by traditional STMs (e.g. resource limitation, competition/facilitation interactions or disturbance effects) interacting with spatial patterns and processes. Secondly, spatially explicit and multi-scaled studies of state transitions, featuring the suite of approaches described in this review, should be conducted in different kinds of ecosystems (e.g. distinct landscapes or ecoregions) to provide empirical evidence for spatial processes. This evidence could support the production of spatial STMs that distil the evidence into narratives, indicators or map-based products. Spatial STMs would be of greater use for assessment, monitoring and forecasting than traditional STMs because they better enable natural resource professionals to recognize transition mechanisms and identify where, when and under what circumstances undesirable transitions or opportunities to promote desirable transitions are most likely to occur.

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Supporting Information

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

Appendix S1. Simulation of monitoring results based on random transects in a patchy rangeland environment.

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