7. Implications of spatial heterogeneity of grazing pressure on the resilience of rangelands

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7.1 INTRODUCTION

Due to the scarcity of reliable surface water supplies, grazing pressure has been low for most of recent Australian evolutionary history. Fires set by Aboriginal people or lightning were relatively frequent in many ecosystems. These systems were also adapted to highly variable rainfall in both time and space (Friedel *et al.*, 1990). Following the establishment of water points after European settlement, wild (native and feral) and commercial animals combined to exert high grazing pressure on rangeland vegetation. This increased pressure has reduced grass cover, and thus the build up of fuel. This, in turn, has reduced the frequency of fire in many rangeland systems. Sheep and cattle are primarily grazers, rather than browsers, so they do not suppress shrubs. These changes have combined to cause woody plants to increase (Noble, 1997), and grass production per unit of rainfall to fall.

Rangeland managers must decide when to reduce grazing pressure in order to let the system recover, and if and when to use fire to suppress shrubs. The manager is confronted with many uncertainties: rainfall patterns, prices, imperfect knowledge of the ecological systems, and possible change in regulations. An important property of an ecological system such as a rangeland is the possibility that the system may occupy one of multiple states (Walker *et al.*, 1981). Depending on the management of the system, the rangeland can flip from a productive and sustainable state to an unproductive state. Ideally rangeland managers maintain the resilience of the system, that is, they will minimize the probability that the system flips to another (less productive) state due to a surprise (for example, a period of low rainfall).

Abrupt shifts among a multiplicity of very different stable domains are plausible in various different regional ecosystems. The likelihood of such shifts is determined by the resilience of these states as measured by properties of their stability domains. The costs of such shifts depend on the length of time spent in such states and their relative productivity. Since these features were first described for ecosystems (Holling, 1973), it has become evident that alternating states arise in a wide variety of ecosystems, such as lakes, marine fisheries, benthic systems, wetlands, forests, savannas, and rangelands. Although dynamics on different scales are explicitly included in the resilience analysis of ecosystems, spatial heterogeneity is usually neglected in the formal models which describe ecosystems with multiple stable states (though see Van de Koppel *et al.*, 1997).

Spatially explicit predator–prey models can show a reduction of oscillations compared with traditional predator–prey models (Jansen and de Roos, 2000). Given this ability of space to fundamentally change the dynamics of ecological systems, the question is, whether space can affect the resilience of ecosystems. The aim of this chapter is to explore the consequences of spatial heterogeneity for the resilience of rangelands. We show that including space can make the system even more vulnerable (i.e. it can be destabilizing), in contrast to studies in which space tends to be a stabilizing force (Grenney *et al.*, 1973; Pacala and Levin, 1997; Durrett and Levin, 1998).

In this chapter we analyse the implications of non-uniform grazing. The model is based on the stylized integrated model of rangeland ecosystem and management interactions from Anderies *et al.* (2002). With this model, Anderies *et al.* assessed the conditions under which the system flips from a healthy state to an unproductive shrub state. The model in Anderies *et al.* (2002) did not address space explicitly. In fact, a mean-field model was used for the rangeland system. The mean-field assumption can be a good approximation when the environment is homogenous and the population is well mixed and interacts over long distances. This assumption might be reasonable for many applications in physics and chemistry, but it often does not hold in ecology (Dieckmann *et al.*, 2000).

Using an agent-based model, we use the same framework as the Anderies *et al.* model but simulate individual sheep on a spatial lattice, and analyse the consequences for different assumptions related to the behavior of sheep, such as herding and the location of waterpoints.

The chapter is developed as follows. First, the importance of heterogeneity in rangeland ecology and rangeland management is discussed. Then, we briefly discuss the key equations of the Anderies *et al.* model. In the sections thereafter, the agent-based model is introduced and simulation results are discussed, which are analysed in more detail by a two-region model. The last section concludes.

7.2 SPATIAL HETEROGENEITY IN RANGELANDS

Spatial heterogeneity is a fundamental characteristic of rangelands due to their low level of productivity, which results in management units (like paddocks) having to be large relative to the underlying landscape heterogeneity. As a consequence, unlike high productivity pastures where different landscape units can be readily fenced off and managed differently, rangeland managers must focus on managing the heterogeneity *within* a management unit. This has long been recognized in management (e.g. Lange *et al.* (1984) report management investment in the 1890s to allow for this) as well as in range ecology (Coughenour, 1991), where space has been considered mainly in relation to the way soils and plants function within a landscape and in relation to animal behavior.

Work on landscape function has focused on resource re-distribution (e.g. Noy-Meir, 1975, further developed by Pickup, 1985, and a series of papers from Tongway and Ludwig, 1990 to Ludwig *et al.*, 2000, and, to a lesser extent, the interactive effects of plant competition (e.g. Archer *et al.*, 1988), usually at the landscape scale of ~1–100 ha. By contrast, animal behavior concerns have generally addressed a larger scale of ~1–100 km^2. The most notable spatially explicit models in this case were Goodall (1967) and Noble (1975), built on by the work of Senft *et al.* (1983), Stafford Smith (1984, 1988), Pickup and Chewings (1988), Stafford Smith and Foran (1990), and Coughenour (1992). Most of these models were aimed at specific implications of spatial grazing behavior on land degradation and paddock design, with a limited ability to link this to animal production. Further development of improved models of pasture and animal production has proceeded with point models that neglect most spatial processes (e.g. SPUR – Hanson *et al.*, 1988; GRASP – McKeon *et al.*, 1990). Although some effort has been made to place these in a spatial context (e.g. Pierson *et al.*, 1999; Milne *et al.*, 1999; Reynolds and Wu, 1999), none of these models have been explicitly used to explore the question of whether spatial heterogeneity and spatial processes per se confer more or less resilience on rangelands, and whether there are then lessons for management in different systems. Indeed most of the models were not formulated with this goal in mind, so that their simplistic use to test such questions would be doubtful.

This has not prevented pastoralists and extension agencies from continuing to develop management procedures that ideally should be based on the answers to these questions. For example, it continues to be contentious in northern Australia whether one should seek to fence to separate vegetation based on low and high productivity soils (so that they can be managed separately) or deliberately fence a diversity of vegetation in together (so the animals can actively select what is 'best for them' at different times) (see Ash and Stafford Smith, 1996). There is a considerable literature of recommendations based on perceived ideal waterpoint distributions for even grazing, which is in conflict with the desire to leave some areas un-grazed to preserve biodiversity that is incompatible with grazing disturbance (James *et al.*, 1999). Thus the issue remains in need of considerable clarification.

Based on the simple graphical models of Noy-Meir (1975) and the understanding arising from the many studies mentioned above, it is possible to assert that the answer to the question of whether spatial processes enhance or reduce resilience in rangelands is unlikely to be simple. For example, building on general observations made during the Responses of Savannas to Stress and Disturbance (RSSD) program (Frost *et al.*, 1986), Ash and Stafford Smith (1996) made explicit predictions about circumstances when one or another outcome might be expected, in the context of the management response that would then be sensible (see Table 7.1). In addition, Cridland and Stafford Smith (1993) have argued that the effects of spatial grazing behavior is driven mainly by differences between vegetation units in small rangeland paddocks, whilst in large paddocks distance to water becomes a more dominating driver; the definitions of 'small' and 'large' depend on the grazing animal, being distinguished by maximum distances to water that are smaller or larger than about 3–4 km for sheep and 5–7 km for cattle.

This chapter now sets out a preliminary model to explore these types of predictions in a theoretical sense, with the intent of sharpening up the quantification of conditions under which different responses might be expected. There are a number of different types of degradation responses which can occur, including loss of perennial forage species, increase in woody competitors, loss of local soil quality, and changes to landscape redistribution processes, any of which can reduce net productivity. This chapter focuses on changes in the grass/tree balance.

Table 7.1: Relationships between forage production and quality at the landscape scale and likely implications for production and management: predictions from Ash and Stafford Smith (1996) for a paddock which has two types of vegetation in it, where the vegetation types may grow at the same time or different times, where they may be more or less resilient to grazing pressures which are higher than the average in the paddock (in this paper, more or less likely to experience woody weed encroachment), and where one is preferred by the grazing animal over the other but both are edible. Column 3 indicates the predicted net result. This table neglects the effects of distance from water, which is an additional spatial factor within each vegetation type if the paddock is large enough. In this paper we analyse only conditions related to the last prediction.

Forage growth and quality between landscape elements	Preferred vegetation units	Impact on animal production and vegetation	Management implications
Asynchronous	Resilient	Enhanced animal production, vegetation stable through time	Paddock sizes can be large to take advantage of forage diversity with less risk of localized degradation
Asynchronous	Susceptible	Enhanced animal production but preferred areas at significant risk of degradation	Maintain large paddocks but strategic use of spelling fire, location of water and supplement points to reduce pressure on most preferred units. Scenario with the biggest trade-off between production and sustainability.
Synchronous	Resilient	Little production advantage in trying to exploit diversity, vegetation stable through time	More intensive stock management e.g. supplementation to achieve production targets
Synchronous	Susceptible	Little production advantage in trying to exploit diversity, preferred areas at risk of degradation	Smaller paddock size, preferred vegetation units in particular to be fenced off.

7.3 A STYLIZED MODEL OF RANGELANDS

The model describes the interactions between perennial grass, shrubs, fire and commercial stock in a stylized way, based conceptually on the functioning of semi-arid woodlands and shrublands in western New South Wales (cf. Ludwig *et al*., 1997). Here a brief overview is given. A detailed description and analysis of the model can be found in Anderies *et al.* (2002). Four state variables are defined as outlined below. The state variables are scaled in order to derive dimensionless equivalent forms. For example, instead of measuring grass in kilograms per hectare, it is measured as a proportion of the maximum grass biomass.

It is assumed that the pastoralist will adjust sheep density in order to maximize income. Decisions concerning sheep density are also assumed to be related to ecological factors, in this case, the amount of shrubs on the land. Furthermore, the pastoralist can suppress the occurrence of fire to a certain degree and thus control its effect on the competition between grass and shrubs.

The grass plant consists of two parts: the crown and the shoots. By crown we mean the root system and growing points. The shoots are the above-ground grass portion of the plant. The biomass of grass shoots is denoted by *s*, and basically follows a traditional logistic function. The crown promotes growth of the shoots according to the tiller potential ca_c independent of grass biomass, and through its interaction with above ground biomass via the term *cs*. Competition between woody shrubs and grass reduces the grass growth. This is captured by the term $\alpha_{us}w^{\beta}$, where α_{ws} is a competition coefficient, and where β (>1) leads to a growth reduction effect of woody shrubs that does not kick in until shrubs reach a relatively high density. Grass is removed by grazing pressure via the term $\gamma_g s$. Finally, grass biomass can be consumed by fire *I*, which has a general response function of form *f()*.

$$\frac{ds}{dt} = c\cdot(\alpha_c + s)\cdot(1 - s - \alpha_{ws}\cdot w^{\beta}) - \gamma_g\cdot s - I\cdot f(s;a_s,b_s) \qquad (7.1)$$

The response curve is formulated in general terms in equation (7.2), containing a variable *k* and parameters *a* and *b*. If $b = 1$, *f()* is a monotonically increasing function bounded above by 1; if $b > 1$, the function is sigmoidal. The parameter *a* controls the location of the point where *f* is half its maximum value, and *b* controls the steepness of the increasing portion. The larger the value of *b*, the more rapid is the switching.

$$f(k;a,b) = \frac{k^b}{a^b + k^b} \qquad (7.2)$$

The crown biomass c grows at rate $r_c s$ and dies at a rate 1. The grass growth is dependent on the presence of the crown.

$$\frac{dc}{dt} = r_c \cdot s - c \tag{7.3}$$

In the context of the consumption response of sheep, b =1 to capture the fact that at high grass biomass, sheep are limited by their ability to process grass, not grass biomass (constant offtake) while at low biomasses, search times become limiting and consumption drops off. The case is similar with fire.

The fire consumption index is governed by the following dynamics. A fire will break out when the grass biomass s grows a little beyond a_x. The term δ_I denotes the rate at which the fire begins to die out. The parameter r_I represents the rate of increase of the fire consumption index once sufficient fuel is present.

$$\frac{dI}{dt} = I \cdot r_I \cdot (f(s; a_I, b_I) - \delta_I) \tag{7.4}$$

Woody shrubs are simply defined as a logistic growth function, where r_w represents the intrinsic growth rate of shrubs. Furthermore, fire can consume woody shrubs as denoted by the last term of the equation:

$$\frac{dw}{dt} = r_w \cdot w \cdot (1 - w) - \gamma_{Iw} \cdot w \cdot f(I; a_w, b_w) \tag{7.5}$$

Table 7.2: Parameter values of the rangeland model

Initial values	Ecosystem parameters	Response function parameters
$c_0 = 0.3252$	$r_c = 3$	$a_s = 0.1$
$s_0 = 0.1262$	$r_I = 60$	$a_I = 0.5$
$w_0 = 0.4647$	$r_w = 0.1$	$a_w = 1$
$I_0 = 1\text{E-}9$	$\delta_I = 0.1$	$b_s = 1$
	$a_c = 0.1$	$b_I = 3$
	$\alpha_{us} = 0.5$	$b_w = 8$
	$\beta = 3$	
	$\gamma_{Iw} = 1$	

7.4 THE IMPLICATIONS OF NON-UNIFORM GRAZING

In this section we discuss the implications of non-uniform grazing of sheep on the biomass for grass and shrubs at the paddock level. Properties are typically 40000 ha, made up of about 20 paddocks. The stylized model is implemented in a spatial multi-agent simulation language Cormas (Bousquet, *et al.*, 1998). The paddock is split up into 100 cells (10 x 10) of about 20 ha each. Each cell contains equations (1) to (5). The starting conditions of the model correspond to a point in the stable cycle. The simulated periods are 100 years.

If a uniform grazing pressure is assumed ($\gamma_g = 0.25$) and a time step of 1/50 year, then the results are identical to the differential equation model (Figure 7.1). The model follows a stable cycle of about 9–10 years. The grass biomass and the shrub biomass grow until enough fuel is available to start a natural fire. The fire consumes the grass biomass almost completely, and reduces the shrub biomass significantly.

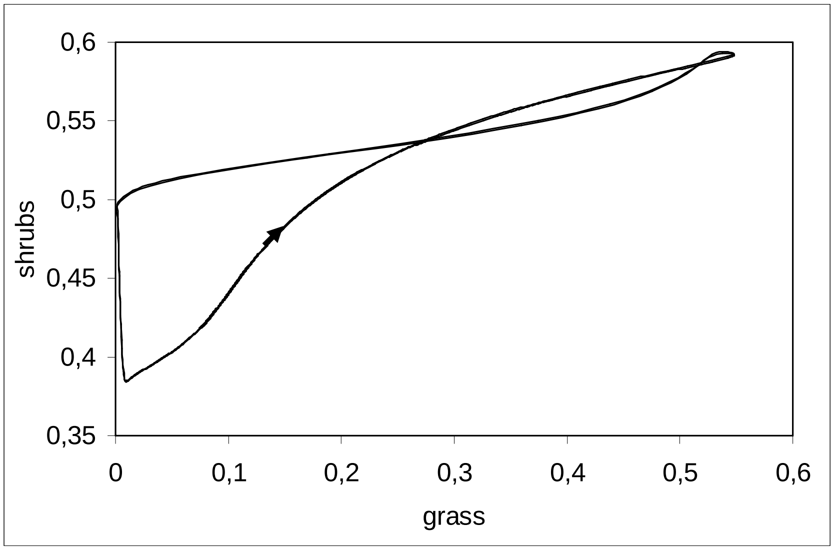

Figure 7.1: The trajectory that grass and shrubs follow due to periodic fires. This figure is based on the assumption of a uniform grazing pressure

The next step is to introduce sheep as individuals. A 2000 ha paddock might have around 250–300 sheep. The model is equipped with 300 agents representing the sheep. Initially, the sheep are randomly distributed over the paddock. When sheep move randomly in weekly time steps, the moving average of shrub biomass is similar to the experiment with uniform grazing, but the cyclic behavior over time vanishes (Figure 7.2). The levels of grass and shrubs continue to cycle within the same domain as for uniform grazing. For very short time steps and very small grazing units, the model simulations converge to the results of the mean-field differential equation model. However, with weekly time steps and 300 sheep, the results are not equivalent to a cloud of grass-eating, well mixed particles moving continuously over the landscape as is assumed by differential equation models. Therefore, the aggregated behavior of the systems includes some random behavior in a limited domain.

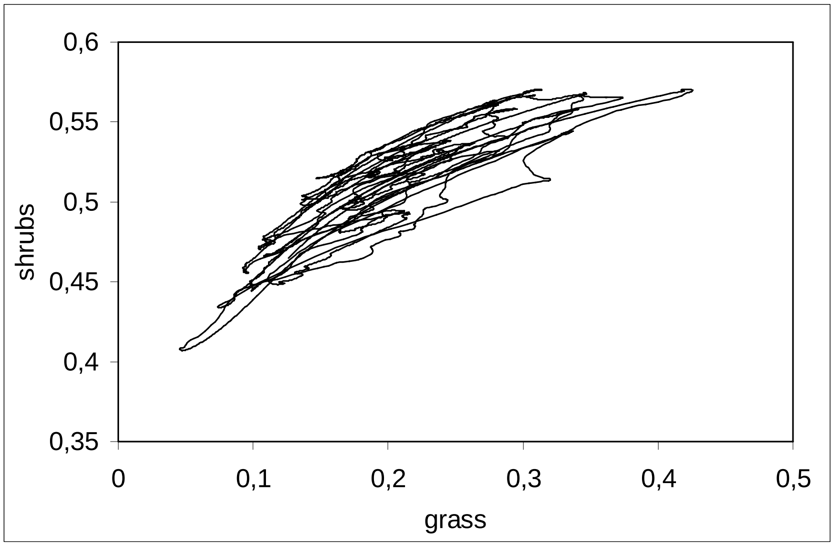

Figure 7.2: When sheep move randomly, over the paddock on a weekly time step, the resulting aggregated dynamics follows this erratic pattern

Of course, most grazing animals do not behave entirely randomly. Sheep select which part of paddock to graze in at various scales (Stafford Smith, 1988). First, they are obliged to return to the waterpoint at least once a day in hot weather (most of the year), so at least once a day they may choose to move to a different grazing location with minimal marginal investment of energy (that is, they are forced to make a major movement for water anyway, and moving to a different location is a marginal additional investment on top of this). The options that are available for this depend on the physical layout of the paddock, and in the absence of other stimuli sheep often move out into the wind. More locally, sheep also make minute-by-minute choices as they move during grazing, and these choices can also add up to significant movements at a broader scale. Here we examine the effects of various types of behavior which are observed in the field:

1. The sheep return individually to approximately the same area of the paddock each day but choose the best local cell within that area (with all parts of the paddock equally accessible);
2. As for 1. but the sheep prefer to be near others so that their behavior shows some contagion or flocking behavior;
3. Areas closer to the waterpoint are in fact accessed more easily and often, so we assume these are more attractive (for energetic reasons) and that activity is concentrated concentrically around the water;
4. We assume that the sheep know the state of the vegetation throughout the paddock and that preference for areas with greater forage overwhelms the effects of distance to water (i.e. vegetation preferences dominate movement choices.

1. Instead of moving randomly, we now assume that every time step, the sheep moves to the best of the nine cells centered on its current position. Given the weekly time step, this is akin to assuming that individual sheep prefer to return to the same location each day, but slowly adjust their preference. This process is simulated by comparing the state of the nine cells below and around the sheep. Interestingly, the resulting system behavior is similar to the case of uniform grazing (Figure 7.3). In fact, assuming that sheep will move to the cell with the relative highest level of grass biomass leads to a very efficient grazing of the paddock. Due to the existence of 300 independent sheep on 100 cells, the resulting grazing becomes similar to uniform grazing, especially since all cells start with the same conditions and have the same parameter values. This result shows that even in multi-agent models, the results might follow the results of the mean-field approximation. The interesting question is then, for which behavioral rules can the mean field results be replicated, and for which not?

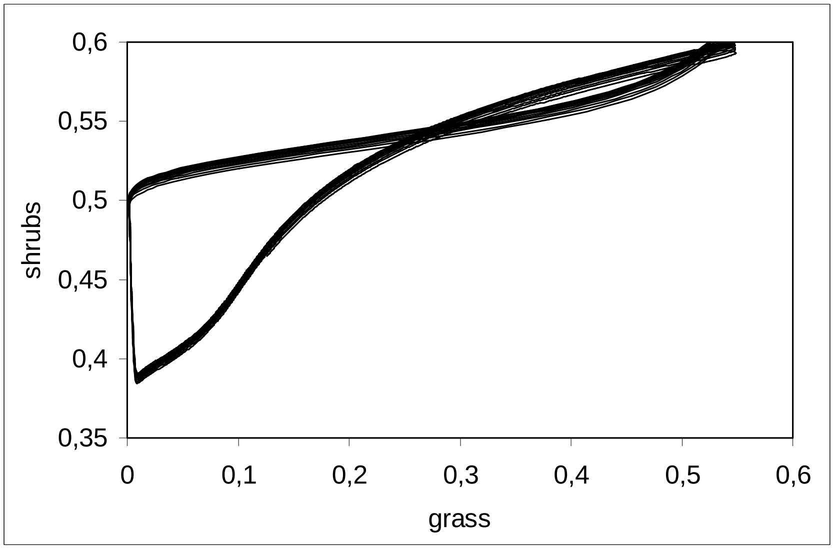

Figure 7.3: When sheep move to the neighboring cell with the relative highest grass biomass, the resulting pattern follows a similar figure as uniform grazing

2. To include more realistic sheep behavior in line with observation, we next include the impact of contagion. Sheep have a greater tendency to occur in larger flocks when conditions are good (Dudzinski *et al.*, 1978; Stafford Smith, 1984). This is implemented by defining an indicator of attractiveness of the neighboring cells. This indicator takes into account the amount of grass biomass and the relative distance to the waterpoints and the number of sheep in the neighboring cells:

$$rp = \beta \cdot s \cdot d + (1-\beta) \cdot p$$

where (7.6)

$$\beta = e^{-\alpha \cdot s}$$

and where *rp* is the relative preference, $d \in [0,1]$, the relative location of waterpoint ($d = 1$ is the waterpoint, $d < 1$ means not at the waterpoint. The lower *d* the further away from the waterpoint). *p* is the percentage of neighboring cells where other sheep are located. Including herding (with $\alpha = 0.04$) leads to a higher concentration of grazing pressure, and therefore increasing degradation of the paddock for a given grazing pressure (Figure 7.4). Flocks of sheep move around on the paddock while overgrazing local cells, which in the end leads to an irreversible effect at the paddock level. The system begins with shrub density cycling between approximately 0.43 and 0.55 between fire events; at the same time, grass varies between 0.08, just after a fire, up to 0.45, just before a fire. As the system becomes degraded, less grass (fuel) builds up between fire events (i.e. the width of the 'pyramid' decreases), fires are less intense and thus less effective at suppressing shrubs. Shrub density increases, adding further competitive stress on grass, i.e. the trajectory moves upward over time. Finally, the system can no longer carry a fire, the cyclic behavior ceases and the system converges to a shrub-dominated state and constant grass biomass. This process shows the flip from a fire-dominated to a shrub-dominated system.

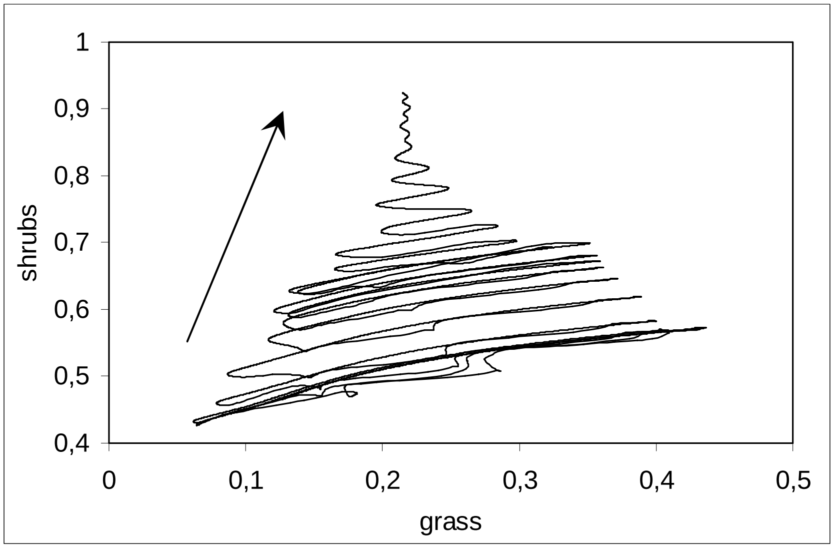

Figure 7.4: As Figure 7.3, but now including the assumption that sheep prefer also to be near each other. The herding effect has a destabilizing effect. The arrow depicts the direction of the system in time.

3. Now consider the effect of distance to water on grazing. Assume that the waterpoint is located in the middle of the paddock. Since the sheep have to go to the waterpoint every day, they have a preference for grazing near the waterpoint. Therefore we include an indicator related to the distance of the waterpoint. Two situations are modeled: The attractiveness of the point most distant from the waterpoint is reduced by 10% (modest effect) and 33% (strong effect), respectively (these correspond to different assumptions about the effects of scale on animal behavior; see Cridland and Stafford Smith,

1993). Initially the sheep are distributed near the waterpoint. The stronger the attraction of the waterpoint, for example due to high temperatures or salty forage and a consequent frequent need to drink, the faster the system will flip into a shrub-dominated case (Figure 7.5 and Figure 7.6). In this case where sheep are dependent on the waterpoints, the result is selective pressure around the waterpoint, and a degradation of these cells. The sheep have to move further away, putting pressure on a further set of cells. This eventually leads to a shrub-dominated property.

4. The final type of experiment focuses on the distribution of grass (now ignoring the effects of distance to water). If the carrying capacities of different cells are assumed to vary (by 10% (modest heterogeneity) and 50% (strong heterogeneity)), the system flips into a shrub-dominated state (Figure 7.7 and Figure 7.8). This is caused by the fact that the most favorite spots are grazed totally in the initial years, leading to lower potential biomass for the same amount of sheep.

To conclude, spatial heterogeneity in conjunction with specific assumptions about the movement of sheep can increase the risk of overgrazing. This is caused by localized pressure on cells which become overgrazed and which flip into an unproductive state. Although these model runs are merely illustrations of the consequences of spatial heterogeneity for specific parameter values, they clearly show the importance of including this heterogeneity in the analysis of management strategies. The results in this paper are in line with Jansen and de Roos (2000) who studied predator-prey systems and concluded that when the movement of the predator is homogenous, the system behaves like the differential equation variant, while when the predator moves diffusively, leading to local clusters, the dynamics differ.

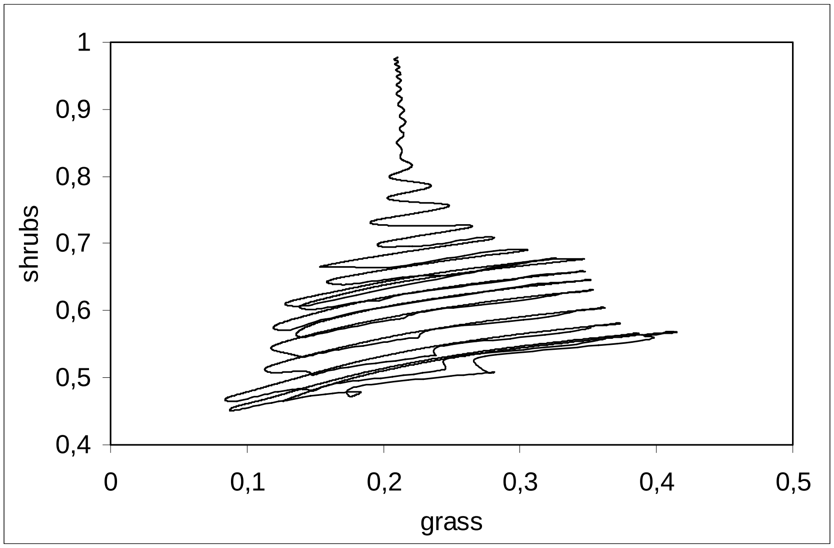

Figure 7.5: As Figure 7.4, but now including a modest effect of the availability of a waterpoint in the center of the paddock

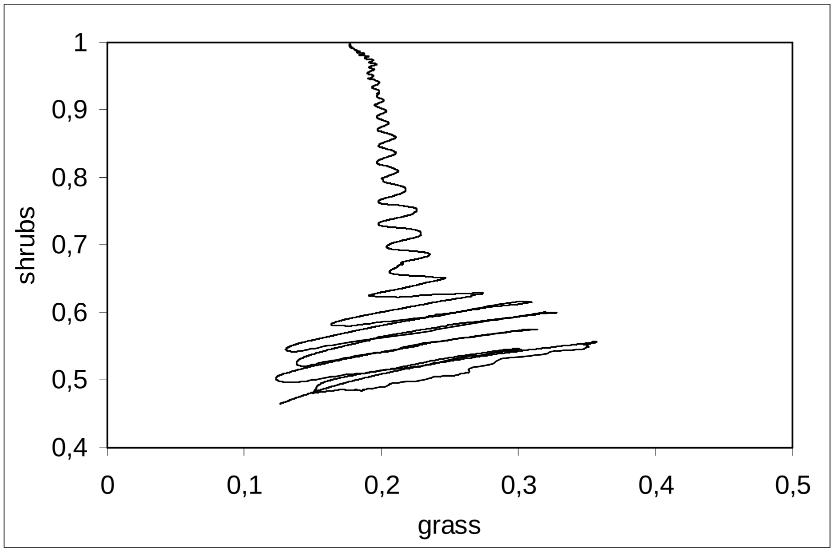

Figure 7.6: As Figure 7.4, but now including a strong effect of the availability of a waterpoint in the center of the paddock

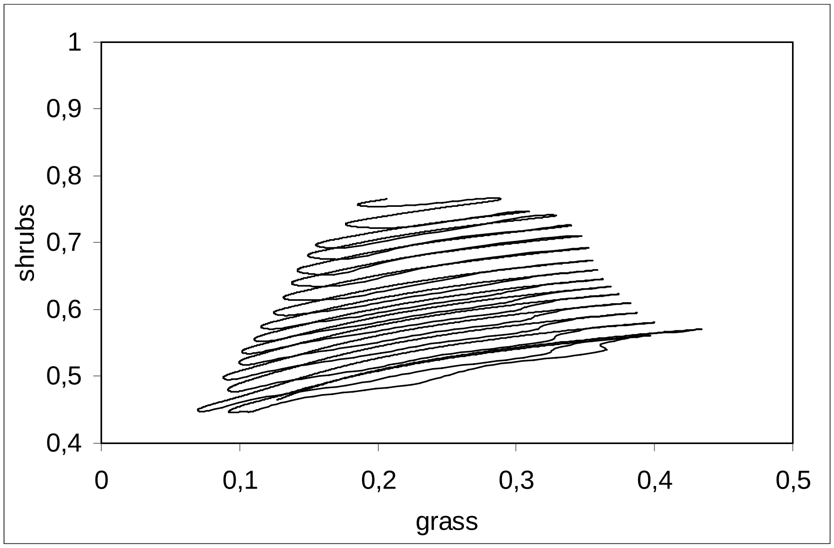

Figure 7.7: As Figure 7.4, but now assuming modest heterogeneity of the local carrying capacity of grass biomass

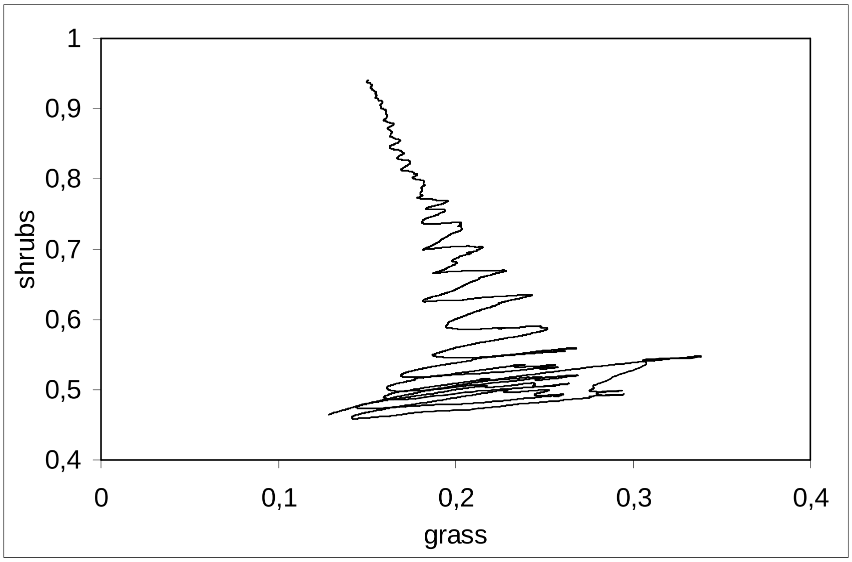

Figure 7.8: As Figure 7.4, but now assuming strong heterogeneity of the local carrying capacity of grass biomass

When herding behavior makes a difference

One of the key results of including space in ecology is its stabilizing role (Grenney *et al.*, 1973; Pacala and Levin, 1997; Durrett and Levin, 1998; Bascompte and Solé, 1998; Jansen and de Roos, 2000). However, the results in the previous section suggest that spatial factors can also play a destabilizing role in rangeland systems, as has long been suggested on empirical grounds (e.g. Ash and Stafford Smith, 1996; Table 7.1). An important difference between our rangeland model and the studies on predator–prey systems, is our presumption of the existence of multiple stable states (cf. Westoby *et al.*, 1989). We conclude our analysis by exploring the rangeland system in more detail through a simplified model. In line with Jansen and de Roos (2000) we developed a two-region model of the rangeland system, where livestock are assumed to migrate between two regions of a paddock. In order to use the simplest model possible, we exclude fire and shrub dynamics and focus only on the interaction of grass and grazing dynamics. The behavior of the sheep is modeled with simple rules to mimic flocking behavior.

The resulting model can be described as:

$$\frac{dc_j}{dt} = r_c \cdot s_j - s_j \tag{7.7}$$

$$\frac{ds_j}{dt} = c_j \cdot (a_c + s_j) \cdot (1 - s_j) - \gamma_{g_j} \cdot f(s_j, a_s, b_s) \tag{7.8}$$

where the index j refers to the j^{th} region of the paddock, here $j = 1,2$. The sheep behavior is based on searching for food, and flocking behavior. Define $g() = 1 - f()$ where f is as defined as above (equation (7.2)). Then,

$$\begin{aligned}\frac{d\gamma_{g_1}}{dt} = {} & r_m \cdot [\gamma_{g_2} \cdot g(s_2, a_m, b_m) - \gamma_{g_1} \cdot g(s_1, a_m, b_m)] \\ & + r_f \cdot [\gamma_{g_2} \cdot \max(\gamma_{g_1} - \gamma_{g_2}, 0) - \gamma_{g_1} \cdot \max(\gamma_{g_2} - \gamma_{g_1}, 0)]\end{aligned} \tag{7.9}$$

$$\gamma_{g_2} = \gamma_{g_t} - \gamma_{g_1} \tag{7.10}$$

The term $g(s_2, a_m, b_m)$ captures the idea that as grass density falls below the threshold a_m (with sharpness b_m) in region 2, the number of sheep there (γ_{g2}) will decline (at a maximum rate r_m) and transfer to region 1 – i.e. in migration to region 1. This decision does not depend on the density of grass in region 1, because sheep rely on local information to make their decisions. With just two spatial blocks, they are too large for a sheep to see the other region, the sheep must go there to investigate. In the previous model, the paddock was split up into 100 blocks so that the sheep could obtain knowledge of nearby patches during their daily movements.

The term $1 - f(s_1, a_m, b_m)$ captures out-migration from region 1. The term r_f $[\gamma_{g2}(\max(\gamma_{g1}-\gamma_{g2},0) - \gamma_{g1}(\max(\gamma_{g2}-\gamma_{g1},0))$ captures flocking behavior. If γ_{g1} is larger than γ_{g2}, sheep in region 2 will flock towards the larger population and migrate to region 1 and vice versa. The 'propensity to flock' is given by r_f. If we keep the total grazing pressure constant, the 'conservation' law makes a differential equation for γ_{g2} unnecessary, i.e. it is given by expression (7.10).

With this simple model, a stable limit cycle for sheep migrating back and forth between the two blocks of a paddock has been constructed. The requirements are: a fairly sharp threshold for when to move, i.e. $b_m = 8$ or more, and that sheep move very fast relative to ecological dynamics – which is reasonable, i.e. $r_m = 30$ or more. The model is rather sensitive to the threshold value a_m. If the sheep eat too much, they severely degrade the paddock block they are in before they move. They then severely degrade the other block and return before the one they left initially has recovered. Then the whole system is degraded. If they move after eating just a small amount of grass, this acts like diffusion and the model converges to the non-spatial version – i.e. $\gamma_{g1} = \gamma_{g2}$. This is compatible with some of the proposals in Table 7.1, depending on the resilience of the vegetation types.

In order to compare the resilience of the spatial and non-spatial systems, we attempted to compare the grazing pressure at which the equilibrium becomes unstable. In the non-spatial case, the equilibrium becomes unstable when $\gamma_g \approx 0.58$. For a two-patch model made up of identical copes of the non-spatial model (with no migration, i.e. $\gamma_{g1} = \gamma_{g2}$ always) then the equilibrium would become unstable when $\gamma_{gt} \approx 1.16$. The question is, then, at what grazing pressure does the model with spatial migration become unstable?

The system has two stable attractors. If the initial conditions are identical in both regions, the system remains at this stable point. The slightest perturbation will move the system to a periodic orbit (Figure 7.9). These results show how migration can reduce the resilience of the system. A periodic solution is shown in Figure 7.9 with $a_m = 0.2$, b_m , $r_m = 30$ and $r_f = 0.1$, super imposed on the isoclines for the non-spatial system. The average root and shoot biomass are less than they would be with uniform grazing. Using numerical experiments, we find that the periodic solution becomes unstable at $\gamma_{gtot} = 1.02$. Thus the spatial model is less resilient – it can support about 13.5% less grazing pressure for these assumptions.

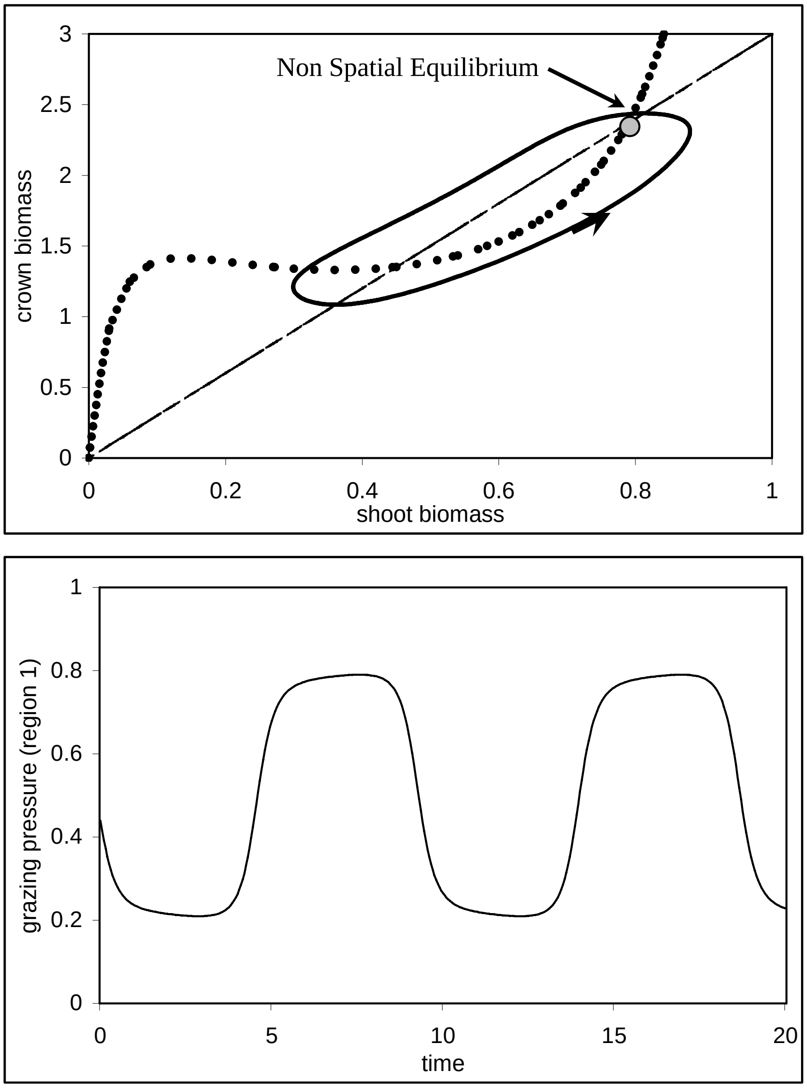

Figure 7.9: Shoot-crown phase plane for two-compartment model (above), and grazing pressure in region 1 over time (below)

To understand how the tendency to flock may reduce the resilience of the system, we performed an additional experiment. By comparing the dynamics of the systems for different levels of flocking tendency r_f , we determined that the key mechanism that reduces resilience is the degradation of the crown portion of the plant. Specifically, increasing r_f from 0.1 to 1 does not reduce the average shoot biomass, it just shortens the period of the cycles. However, it does reduce the average crown biomass. The relatively fast process of the analysis thus seems to show up the fact that flocking behavior is more detrimental to the relatively slower variable of crown biomass (note that, as modeled, grass dynamics are three times faster than crown dynamics and flocking dynamics are ten times faster again than grass dynamics).

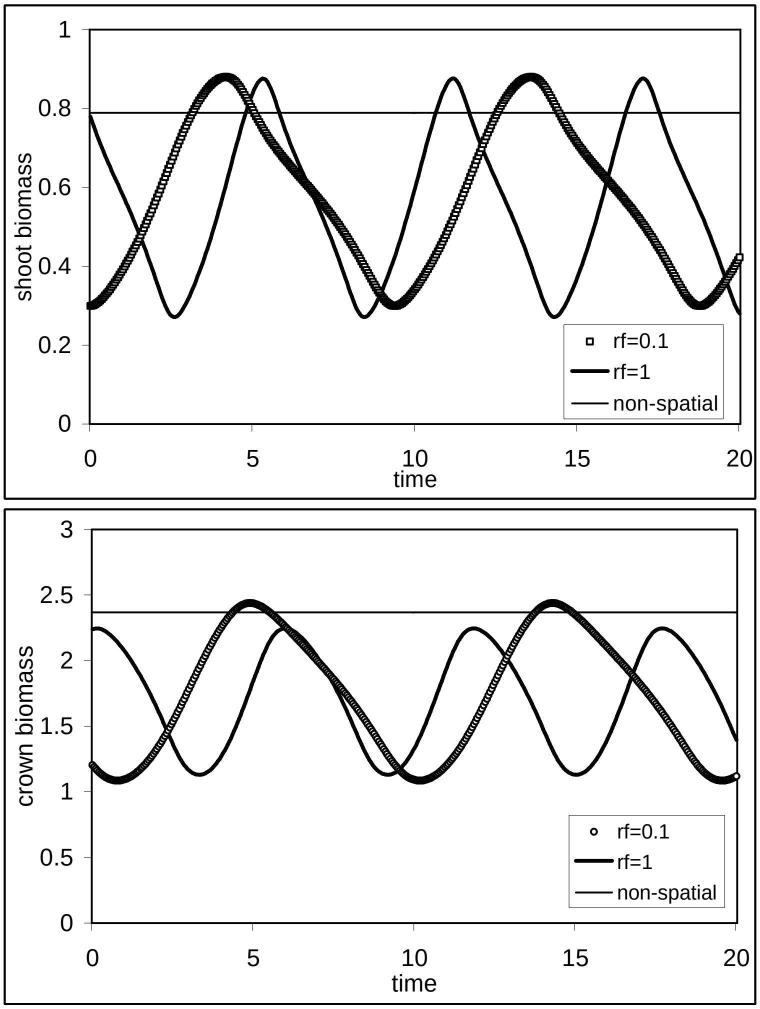

Figure 7.10: Shoot and crown biomass over time for different tendencies to flock. The horizontal line is the non-spatial case, the dotted curve is for r_f *= 0.1, and the solid curve for* r_f *=1*

7.5 DISCUSSION

In this chapter we have explored the consequences of a spatially explicit analysis of the resilience of rangelands. When sheep do not graze a paddock in a uniform way, but cluster due to herding behavior or physical attractants like waterpoints and preferred areas of vegetation, the results of our analysis show that this particular system will flip to a degraded state at a lower grazing pressure than in the same analysis without spatial explicit grazing.

Thus, in this case, inclusion of spatial heterogeneity makes the rangeland system more likely to end up in a degraded state for a larger set of parameter values. This means that a more realistic description of the rangeland system will support less optimistic stocking rates if resilience of the rangeland is too maintained.

This finding is compatible with some of the suggestions made in Table 7.1 on the basis of empirical observations. The practical experience of range management in Australia and other rangelands of the world show that ecosystem change has occurred suddenly and unexpectedly in some circumstances. The changes have been ‘unexpected’ compared with what might have been predicted from the experiences of higher productivity, smaller paddocks, or from the resilience of small grazing trials (see review in Ash and Stafford Smith, 1996), almost all of which suggest that higher rather than lower stocking rates should be attainable in rangelands. Indeed the practical experiences of the more conservative pastoral managers often suggest that lower stocking rates are attainable in rangelands than scientific evidence drawn from small plot trials would imply. This analysis begins to identify the potential role that spatial factors may have to play in this process of surprise.

However, Table 7.1 also provides some hints of the conditions under which this finding might not be general. An extensive literature has appeared in recent years suggesting that there are circumstances where rangelands may be said to be very much more resilient than the small plot evidence would suggest (see review in Illius and O’Connor, 1999). Whilst some of this literature relates to the purpose of production and therefore the significance of any change of ecosystem state, other elements probably relate to a genuinely buffering effect of spatial factors, particularly the selective behavior of herbivores, as noted by Ash and Stafford Smith (1996). In this regard, the detailed conclusions of this chapter are tentative since not all spatial oriented processes are included (e.g. seed dispersal, wildlife movements, heterogeneity of soil conditions). Even for those factors we have considered, not all possible combinations have been included, but this must remain a task for the future. What can be said confidently from the simulation experiments is that spatially explicit rangeland management is likely to be very important in some circumstances and should not be ignored in future modeling of these systems.

Understanding the implications of spatial processes is vital in the large open paddocks of rangelands; however, it is likely that these processes are also important in a perhaps more subtle way in other environments. Dealing with spatial heterogeneity has become an important part of range management in recent years (e.g. Coughenour, 1991), of equal significance as managing for temporal variability. The challenge in fact is to ascertain what spatial and temporal factors in what combinations create significant impacts, as well as when they do not; the comprehensive analysis of this question is the challenge for another study.

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