Grazing Management, Resilience, and the Dynamics of a Fire-driven Rangeland System

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ABSTRACT

We developed a stylized mathematical model to explore the effects of physical, ecological, and economic factors on the resilience of a managed fire-driven rangeland system. Depending on grazing pressure, the model exhibits one of three distinct configurations: a fire-dominated, grazing-dominated, or shrub-dominated rangeland system. Transaction costs and costs due to shrub invasion, via their effect on grazing decisions, strongly influence which stable configuration is occupied. This, in turn, determines the resilience of the rangeland system. These results are used to establish conditions under which management for profit is consistent with the maintenance of resilience.

Key words: resilience; rangelands; multiple states; complex systems.

INTRODUCTION

This paper explores the idea of resilience in the context of a managed fire-driven rangeland system. Resilience, as originally defined in an ecological context, is the ability of an ecological system to maintain its integrity when subject to disturbances (Holling 1973). The term "resilience" is now being used more widely in the context of social ecological systems in what might be called resilience-based management approaches (see, for example, Berkes and Folke 1998; Walker and Abel forthcoming). Traditional economic-based management aims for efficient management regimes that is, the maximization of discounted returns from a resource base. Under certain conditions, economic-based management suggests that destruction of the resource base is optimal (Clark 1973). Resilience-based management, on the other hand, explicitly acknowledges the existence of multiple stable states in ecological economic systems, some of which are more desir-

able than others. Over time, a system may move from such a preferred state into another, less preferred state due either to changes in system dynamics induced by economic activity or the influence of external variability. Resilience-based management attempts to build adaptive capacity in a system to cope with the possibility of such shifts.

Management *per se* is not our main focus. This paper is motivated by the fact that resilience can be a difficult concept to work with in the context of managed ecological economic systems. Resilience is measured by the size of the displacement the system can tolerate and yet return to a state where a given function can be maintained. In purely ecological systems, this function, such as the ability of a system to capture and store resources, is fairly easy to define. In social ecological systems, defining this function can be more difficult. Brock (1998) provides some ideas on quantifying resilience in ecological economic systems and suggests that much research is needed in this area. Others argue that the concept of resilience does not offer new insights for economic and social systems (Hanley 1998).

To gain a better understanding of resilience in the context of social ecological systems, we developed a model that captures the essential features of a fire-driven rangeland system and yet is simple enough for resilience to be clearly defined. With the model, we explore how ecological, economic, and management factors influence the resilience of the system. Specifically, it is shown how economic factors can reduce the resilience of the system by driving the desirable configuration to the edge of its basin of attraction. Further, the model suggests that transaction costs are the main difficulty in applying resilience-based management in such a system. First, the ecological model is developed and its physical properties are analyzed. Later, the effects of economic and management factors on the resilience of the system are analyzed.

BACKGROUND

For a particular landscape–soil combination, the essential components of a rangeland ecosystem are communities of annual grass, perennial grass, woody shrub populations, and the external factors that drive them—rain, fire, and herbivory (Noy-Meir 1973; Westoby 1979/80). Grasses and shrubs compete for scarce water resources. Grazing and fire exert differential selective pressure on grasses and shrubs. By suppressing grass growth, grazing selects for shrubs. Fires, which consume dead grass shoots as fuel, cause significant shrub mortality and thus select against them. Rangeland ecology is characterized by shifting balances between these competing forces.

An important property of rangelands is that they can occupy multiple stable states (Westoby 1979/80). Depending on the external drivers of fire, rainfall, or grazing, rangelands can occupy a stable configuration dominated by perennial grasses with few shrubs or one dominated by shrubs with little grass. Thus, management practices have the potential to push a rangeland from a productive and sustainable state to an unproductive state.

It is generally accepted that since European settlement, the fire regimes in most Australian ecosystems have changed significantly (Luke and MacArthur 1978; Gill and others 1981). Grazing pressure on rangelands was lower, and in many areas, such as western New South Wales, fires may have been more frequent. The Europeans introduced commercial animals, along with artificial watering points that also promoted the expansion of wild animal populations. Grazing pressure on rangeland vegetation was thus very high, leading to a reduction in grass cover and consequently a re-

duction of the frequency of fire in rangeland systems (Noble and Grice forthcoming). Commercial animals such as sheep and cattle are primarily grazers rather than browsers and do not suppress shrubs. Their grazing acts as a selective pressure for the increase of woody plants and thus a decline in grass production per unit of rainfall (Stafford Smith and Pickup 1993).

Rangeland managers have to decide when to reduce grazing pressure to allow a system to recover and if and when to use fire management to suppress woody plants. Managers have to cope with uncertain rainfall patterns, fluctuations in wool prices, imperfect knowledge of the ecological system, and changing regulatory environments. Among the various approaches that have been used to characterize this situation are optimization (Perrings and Walker 1997), simulation (Stafford Smith and Foran 1992), and complex adaptive systems analysis (Janssen and others 2000).

There are a few integrated models focusing on the interaction of ecological systems, managers, and regulators that depart markedly from the standard optimal control approach so common in the policy literature (see, for example, Janssen and others 2000; Carpenter and others 1999a, 1999b). Their aim is to explain the dynamics of regulators, managers, and ecosystems as they might actually interact at the regional scale, while emphasizing the importance that uncertainty, lags, stochasticity, and nonlinear ecological dynamics play in the formation of management strategies. In this paper, we continue this line of research by examining how nonlinear ecological dynamics, economic structure, and existing management strategies influence the resilience of a rangeland system.

A STYLIZED RANGELANDS MODEL

This section has three objectives. First, we describe the conceptual model that underlies the mathematical model. Next, we outline the framework and scope of the analysis. Finally, we develop the mathematical model.

The Conceptual Model of the System

Rangeland ecological dynamics are strongly event-driven and occur across a wide range of spatial and temporal scales. The trigger-transfer-reserve-pulse model of Ludwig and others (1997b) is a useful tool for conceptualizing these processes. For example, water from a rain event (trigger) is transferred to different parts of the
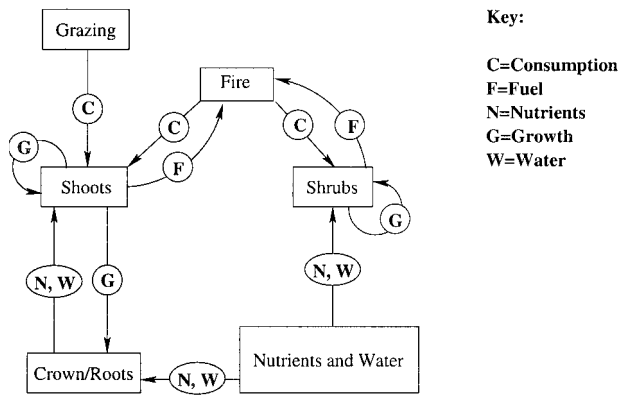
Figure 1. The conceptual model. The letters in the circles indicate the actions or flows indicated in the key; for example, fire consumes shrubs and grass shoots, which both provide fuel for fire. The figure shows the relationship between the state variables captured by the mathematical model.

landscape, where it enters the soil profile and a pulse of growth occurs. We abstract from such a detailed description and attempt to capture the qualitative behavior of the system as described by the state-and-transition model of Westoby and others (1989). In this model, the system can occupy one of several stable configurations and is driven from one configuration to another by key transition processes.

To study resilience, we must explicitly model the dynamic processes that generate the states and the transitions between them. To this end, we develop as simple a dynamic model as possible that will generate the observed behavior of rangeland ecosystems. The model is shown schematically in in Figure 1. The boxes contain state variables, and the arrows indicate interactions between state variables of the type indicated by the circled letters. There are four state variables that are explicitly modeled: grass shoot biomass, grass crown (growing points and roots) biomass, woody shrub biomass, and fire consumptive capacity. Grazing is treated as a parameter. Nutrients and water are modeled implicitly via competition and carrying capacity terms. The interactions between the state variables are based on basic ecological models of competition and herbivory (Bulmer 1994; Keshet 1986). They include aspects particular to rangelands (Walker and others 1981; Ludwig and others 1997a) as extended to include the interaction between the above- and belowground components of perennial grass plants.

The key driver in the system is the interaction between grass shoot biomass, grass crown biomass, and grazing. Crowns (growing points and roots) are essential for the capture of the water and nutrients necessary for the growth; shoots are needed to capture the solar energy required for growth. Thus, there is a tight feedback loop between shoots and crowns—that is, between productivity and the ability to capture resources. Grazing affects this feedback loop by reducing shoot biomass (productivity). This, in turn, reduces the ability of the plant to maintain the crown (the ability to capture resources), causing the slow death of the plant.

The role of shrubs in the system is to create a "lock-in" effect. Without shrubs, a heavily grazed grass system could recover if grazing pressure was removed. The competitive effect of shrubs can prevent grass recovering from very low biomass levels. Thus, heavy grazing pressure can lock the system into a state dominated by shrubs. Without fire in the system, shrub encroachment is inevitable. The role of fire is to keep shrub growth in check. Thus, as illustrated in Figure 1, fire and grazing mediate the competition between grass and shrubs and the interaction between the above-ground and below-ground portion of the grass plant. In an effort to increase the clarity of our presentation, we will develop the mathematics that describes each of these interactions separately before analyzing the full model.

Finally, we make two additional simplifying assumptions. First, the model describes the ecology and the management at the subproperty scale—that is, on the order of 1000 ha. We do not account for spatial heterogeneity in soil conditions or the spatial distribution of grass, shrubs, or fire within the subproperty. Second, we describe the system at an annual time scale. That is, we aggregate the effect of an average number of trigger events over the year and do not consider within-year variability in the model.

Framework and Scope of the Analysis

It is important to emphasize that it is not our objective to accurately model the dynamics of a particular rangeland system. Rather, we are interested in understanding the qualitative behavior of a *representative* rangeland model based on the Australian experience. Nor are we making prescriptions for management practice. The goal of the analysis presented here is to understand the influence that management practice, ecological factors, and economic factors have on the qualitative behavior of the model. The most powerful framework for

achieving our goal is the use of continuous time dynamical systems theory.

By developing a dynamical systems type rangeland model, we exploit two useful mathematical techniques: bifurcation analysis and scaling. Bifurcation analysis allows us to divide parameter space into regions in which the model exhibits the same qualitative behavior. Scaling is the technique of expressing the model in an equivalent form using dimensionless variables. For example, instead of measuring grass in kilograms per hectare, we measure it as a proportion of the maximum grass biomass. This allows the model to be expressed more meaningfully with parameters expressed as combinations of the original parameters. As we shall see, the qualitative behavior of the model is determined by *ratios of parameters* rather than *absolute* parameter values. This is important for ecosystems where absolute parameter values may vary widely across land types while ratios of parameters remain the same. Where important, we have attempted to provide an empirical basis for certain parameter (or ratios of parameter) values.

These combined techniques allow the study of resilience in a fairly transparent manner (Ludwig and others 1997a). Domains of attraction and their size can be clearly identified, giving an unambiguous measure of resilience. The cost of such clarity is simplification, so that resilience described in the model may bear little relation to that of the real system. This type of analysis is best used along with historical analysis and more complex applied models through an iterative process.

Grass

To capture the essentials of grass dynamics, the different effects of fire and grazing must be addressed. We do this by considering the grass plant as consisting of two parts, the crown and the shoots. Growth occurs through the interaction of these two parts. The crown provides the potential for growth and water and nutrient uptake abilities during growth. Shoots allow the plant to capture solar energy to grow and maintain the structure of the crown. The shoots are presumed dead when fire occurs so that translocation to the crown is complete and the loss of the shoots has little or no effect on the plant. After a fire, the shoots, depending on the tillering potential of the crown, can recover quite quickly.

Grazing, on the other hand, works on a slower time scale than fire. Animals consume live shoots and can have a negative effect on the crown. They can keep the aboveground live biomass of the plant low for an extended period; during this time, the plant is unable to maintain its crown component. The crown component then dies, and the grass is lost from the system. Incorporating the relationship between shoots and crowns yields the following model:

$$\dot{c} = r_c s - \delta_c c \qquad (1)$$

$$\dot{s} = c(a_c + r_s s)\left(1 - \frac{s}{s^*}\right) - \gamma_g s \qquad (2)$$

where $c(t)$ and $s(t)$ represent crown (root plus growing points) and shoot biomass at time t, respectively. The parameter s^* is the maximum shoot biomass per unit area set by the soil nutrient level and water regime, and γ_g is the (constant) fraction of shoots removed by grazing pressure. It is important not to confuse what we have called "grazing pressure" with the grazing pressure exerted by one animal. The parameter γ_g represents the total grazing pressure exerted by several animals per unit area per unit time. To maintain γ_g at a constant level would, in the terminology of rangeland management, require a "perfectly reactive strategy" aimed at maintaining a constant utilization rate. We will discuss this in more detail later.

The crown grows at a rate $r_c s$ when shoots are present and declines at a rate δ_c. One might argue that the growth rate of the crown should depend on the interaction of shoots and crown biomass—that is, $r_c s c$. A moment's reflection reveals that this representation is flawed: This expression would allow the root system to grow at high rates when there is almost no aboveground shoots as long as there is very high root biomass. This simply does not occur; the main driver of crown growth is shoot biomass (Richards 1993). The form of Eq. (1) captures this fact.

The tiller potential, a_c, measures the shoot biomass growth rate per unit of crown biomass and captures that portion of shoot growth dependent only on the crown. The term r_s measures the shoot biomass growth rate per unit of crown biomass per unit of shoot biomass, capturing the portion of shoot growth dependent on the interaction between the crown and shoots. Note here that we are not keeping track of live and dead shoots separately, just total biomass. If the shoots are not grazed off, they will become fuel for fire (when we add fire dynamics to the model).

We can explore the dynamics of the system through simple phase-plane analysis. As discussed in the previous section, nondimensionalizing the equations will make the analysis more clear and meaningful. Throughout we use "$\hat{x}$" to indicate the nondimensionalized version of "x." Let

$$\hat{c} = \frac{r_s c}{r_c}, \quad \hat{s} = \frac{s}{s^*}, \quad \tau = \delta_c t \qquad (3)$$

These combinations were chosen by examining the units in the original model; for example, r_s has units of (biomass units $\times$ time)$^{-1}$, r_c has units of (time)$^{-1}$, and c has biomass units so that $\hat{c}$ has no units. The variable $\hat{c}$ measures the crown in units of potential shoot growth supplied by a unit of crown biomass to the potential crown growth provided by a unit of shoot biomass. When $\hat{c}$ is greater than 1, a unit of root biomass is generating more growth potential for a unit of above-ground shoot biomass than it receives from that unit. The point is that shoot and root biomass are not key drivers of model dynamics; rather, the growth potential they generate is. This is made more salient in the nondimensional variables. The variable $\hat{s}$ is the shoot biomass measured as a fraction of the maximum possible; thus, it is a number between 0 and 1. Finally, the passage of a day in the model is less meaningful than the passage of a period of time in which an event important to the dynamics of the model occurs. The variable τ measures how many half-lives (the time it takes for root biomass to halve from one period to the next) of the crown and roots have passed.

To remind the reader that time has been rescaled we use the short hand $\hat{c}'$ to mean $\frac{d\hat{c}}{d\tau}$ in the same way we used $\dot{\hat{c}}$ to mean $\frac{d\hat{c}}{dt}$. To change variables, first solve Eq. (3) for c and s in terms of $\hat{c}$ and $\hat{s}$ and substitute these into the right-hand sides of Eq. (2). Next, compute $\dot{c}$ and $\dot{s}$ in terms of the rescaled time using the chain rule, that is:

$$\dot{c} = \frac{d}{dt}\left(\frac{r_c\hat{c}}{r_s}\right) = \frac{d}{d\tau}\left(\frac{r_c\hat{c}}{r_s}\right)\frac{d\tau}{dt} = \frac{d}{d\tau}\left(\frac{r_c\hat{c}}{r_s}\right)\delta_c = \left(\frac{r_c\delta_c}{r_s}\right)\hat{c}'$$
$$(4)$$

with an analogous expression for $\dot{s}$. Substitution of these expressions for $\dot{c}$ and $\dot{s}$ on the left-hand sides of Eq. (2) and a little algebra yields:

$$\hat{c}' = \hat{r}_s\hat{s} - \hat{c} \qquad (5)$$

$$\hat{s}' = (\hat{a}_c\hat{c} + \hat{r}_c\hat{c}\hat{s})(1 - \hat{s}) - \hat{\gamma}_g\hat{s} \qquad (6)$$

where

$$\hat{r}_s = \frac{r_s s^*}{\delta_c}, \quad \hat{a}_c = \frac{r_c a_c}{s^* r_s \delta_c}, \quad \hat{r}_c = \frac{r_c}{\delta_c}, \quad \hat{\gamma}_g = \frac{\gamma_g}{\delta_c} \qquad (7)$$

Notice that the new parameters are ratios of the original parameters, which allows the model to be

studied without specifying absolute values for parameters. These parameters make it clear that the model dynamics are not determined by, for example, the intrinsic growth rate of shoots, but rather the rate of shoots growth relative to the rate of root decay (the parameter $\hat{r}_s$). This makes intuitive sense—if $\hat{r}_s$ is small, roots decay relatively faster than shoots grow. This means that less crown biomass can be maintained per unit of shoot biomass (that is, the more shoot biomass is required to keep the plant alive.) Thus $\hat{r}_s$ has a nice direct management interpretation: High or low $\hat{r}_s$ corresponds to high or low grazing tolerance, respectively. The parameter r_s alone does not have such a direct interpretation. The interpretation of the other nondimensional parameters will be discussed shortly.

To simplify still further, some parameter values can be fixed. The term δ_c in Eq. (1) represents the natural mortality of the crown (that is, of the perennial grass plant). An empirical study of the demographics of *Danthonia caespitosa* (Williams 1970), a common palatable perennial grass species in western New South Wales, indicated that its survival time is roughly linear on a log scale. Half-lives when above-ground shoots are depleted vary widely but fall within a range of 2–20 months. Given that we measure time in years, choosing $\delta_c = 1$ implies a half-life of between 8 and 9 months and is thus consistent with the observations of Williams (1970). Further, by setting Eq. (1) equal to zero and solving for the equilibrium ratio of crown to shoot biomass (that is, the root-to shoot ratio for a mature ungrazed plant), we see that $\frac{c}{s} = \frac{r_c}{\delta_c}$. In his work on the primary production of Australian grass communities, Christie (1978) recorded a root-to-shoot ratio of 0.9 at the end of the summer growing period for native C_3 grassland. Based on this, we assume $\frac{r_c}{\delta_c} = 1$; combined with our choice of δ_c, this implies that r_c is also 1. Finally, we can choose the area and biomass units so that s^* is 1 (that is, if the maximum aboveground shoot biomass is 5 tons per hectare, we can choose biomass units in tons and areal units of 0.2 hectare). By doing so, we are assuming that our model represents the dynamics on one block of characteristic size determined by s^*. Now we have:

$$\hat{r}_s = r_s, \quad \hat{a}_c = \frac{a_c}{r_s}, \quad \hat{r}_c = 1, \quad \hat{\gamma}_g = \gamma_g \qquad (8)$$

Figure 2 illustrates the model behavior for $\hat{r}_s = 3$, and $\hat{a}_c = 0.1$ (shoot growth potential generated by the crown is approximately 10% of that generated by shoots). The basis for these parameter choices
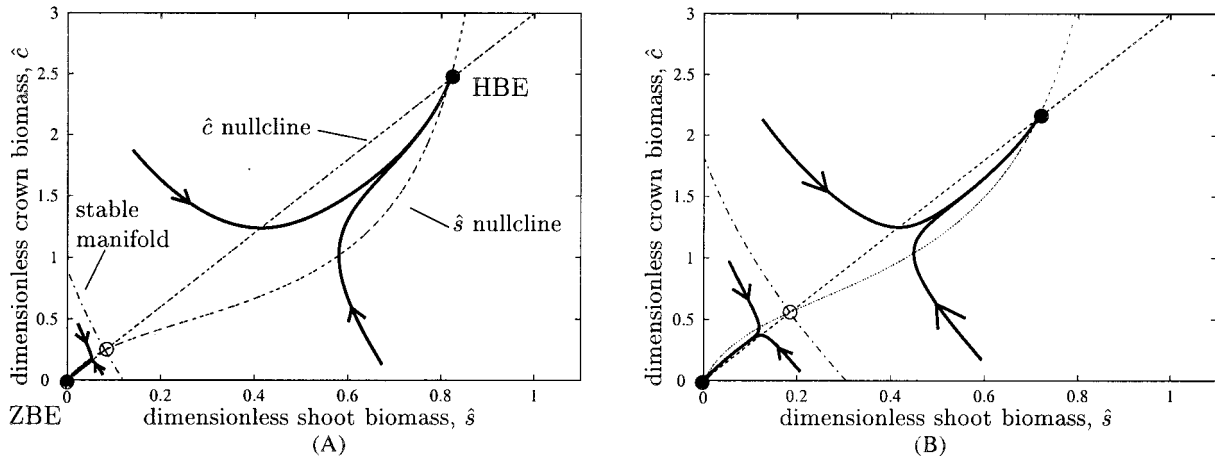
Figure 2. **A** shows the phase plane with $\hat{r}_s = 3$, $\hat{a}_c = 0.1$, and $\hat{\gamma}_g = 0.5$. **B** is the same as **A**, except with $\hat{\gamma}_g = 0.7$. In each case, the lighter dotted lines show the nullclines and stable manifold. The labels in **A** also apply to **B** but have been suppressed for clarity. ZBE = zero biomass equilibrium, HBE = high biomass equilibrium. Stable equilibria are shown with solid circles; unstable equilibria are shown with open circles. The heavy lines with arrows show the trajectories followed by the system over time. These trajectories will evolve either to ZBE or HBE, depending on the initial condition.

will be discussed in detail when the full model is analyzed. The $\hat{c}$-nullcline labeled in the figure is made up of points at which $\hat{c} = 0$. For values of $\hat{c}$ above this line, $\hat{c}'$ is less than 0. For values of $\hat{c}$ below it, $\hat{c}'$ is greater than 0. Each of the four heavy lines are trajectories that show how the shoot and crown biomass evolve over time from initial conditions in the different regions of phase space. Notice how the upper trajectory in Figure 2 starting from $(\hat{s}, \hat{c}) \approx (0.15, 1.9)$ slopes downward in the region above the $\hat{c}$-nullcline (that is, $\hat{c}' < 0$), is horizontal when it crosses it (that is, $\hat{c}' = 0$), and slopes upward when it is below it (that is, $\hat{c}' > 0$). The $\hat{s}$-nullcline has a similar interpretation. When the nullclines intersect, both $\hat{c}$ and $\hat{s}$ are zero and the system is in equilibrium.

There are three equilibria where the nullclines meet. The stability properties are determined by examining whether trajectories starting nearby these points tend to move away from or toward them. Based on this analysis, Figure 2 shows that the intermediate equilibrium point is unstable and the lower and upper equilibria, which we will call the zero and high biomass equilibria (abbreviated ZBE and HBE, respectively) are stable. The unstable point is a saddle point, which means that the system can move toward this point for a period before eventually moving away from it. This behavior is illustrated by the heavy lines shown near the saddle point that collapse toward it before eventually moving off to the left. Whether the trajectory will eventually veer off to the left or right depends on its initial condition. There is a special trajectory called

a "stable manifold" (see Figure 2) that veers neither to the left or right but approaches the unstable point. The slightest perturbation from this path, however, will cause the system to veer off either to the left or right. Thus, the stable manifold (also called the "separatrix") divides the plane into two basins of attraction—one to the lower equilibrium, where the shoots and crowns die out; one to the upper point, where the shoot biomass is nearly 80% of maximum. For further details on the analysis of planar dynamical systems see Edelstein-Keshet (1988), Clark (1990), Murray (1989) and Bulmer (1994).

Figure 2(B) (in which the labels have been suppressed for clarity) shows the case where the grazing pressure has been increased by 40% from 0.5 to 0.7. This causes the $\hat{s}$ nullcline to shift up and to the left, which results in the unstable point and HBE moving closer together. This, in turn, causes the size of the ZBE basin of attraction to increase at the expense of the HBE basin of attraction. We are now in a position to define resilience in the context of the model. First note that resilience does not apply to a system, it applies to states within a system. Therefore, in our model thus far, it is sensible to refer to the resilience of two states, the ZBE and HBE. The resilience of either state is measured by the size of their respective basins of attraction, which is a proxy for the size of a perturbation that the system can tolerate and still return to the given state. The case shown in Figure 2A could absorb a larger perturbation (such as a drought) and still recover to the HBE than the case in Figure 2B.
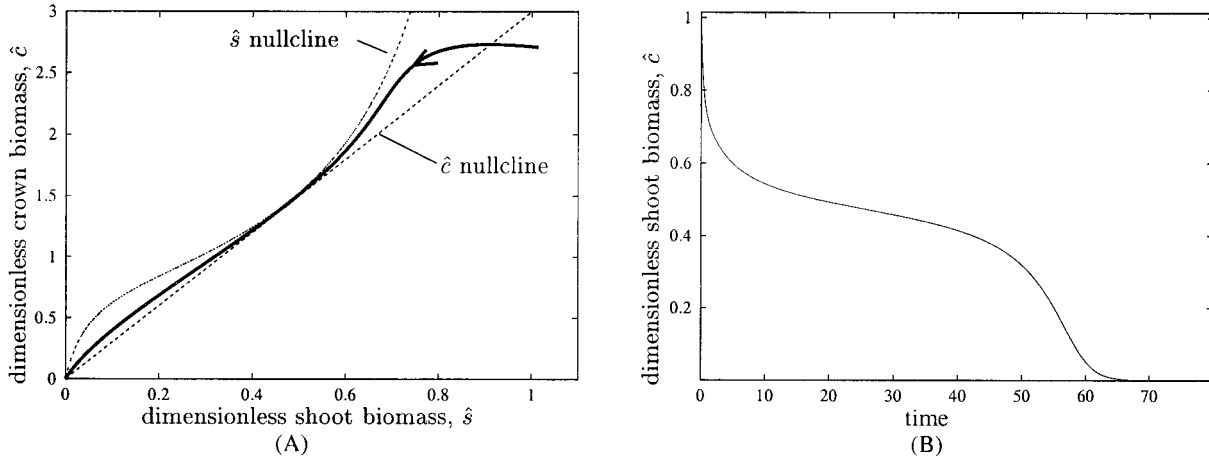
Figure 3. A shows the phase plane with $\hat{r}_g = 3$, $\hat{a}_c = 0.05$, and $\hat{\gamma}_g = 0.5$. The interpretation is exactly as in Figure 2. **B** shows the evolution of grass biomass over time.

Thus, we can say that grazing reduces the resilience of the HBE (the desirable state) to perturbations such as drought. This example illustrates how introducing the symbiotic relationship between above-ground and below-ground biomass introduces a threshold, the existence of which is of great importance to resource managers.

The ratio $\dfrac{a_c}{r_s}$ is an important determinant of the location of the separatrix and thus the size of the HBE and ZBE basins of attraction. Reducing this ratio moves the separatrix up and to the right, which increases the size of the ZBE basin of attraction and decreases the size of the HBE basin of attraction. This decreases the resilience of the desirable state of the system. This ratio has a nice physical interpretation: The stronger the ability of crown to send up shoots relative to their reliance on photosynthesis for shoot growth (larger value of $\hat{a}_c$), the greater will be the plants ability to survive in spite of being grazed off. This illustrates the utility of the nondimensionalized parameters.

Finally, the distance between the $\hat{c}$- and $\hat{s}$-nullclines governs the rate of change of the state variables. Figure 3 depicts a situation where grazing animals are introduced into a rangeland area with maximum shoot biomass. The grazing pressure is 0.84, just above the maximum sustainable level with $\hat{r}_s = 3$ and $\hat{a}_c = 0.05$. The rangeland is being grazed unsustainably, but there is a bottleneck between $\hat{s} = 0.6$ and $\hat{s} = 0.4$ where the system is degraded very slowly. The existence of such a bottleneck depends on the shape of the $\hat{s}$-nullcline being concave up over some range of shoot biomass. The only assumptions required to get such a shape is that at higher shoot biomass levels, the

grass shoots become the dominant growth limiting factor. The point is that the manager cannot look at the phase plane shown in Figure 3A; instead, he or she sees only data in the Figure 3B. The shoot biomass drops precipitously just after the introduction of the stock. For the period from year 10 to year 40, the shoot biomass declines very slowly—indeed, imperceptibly, as viewed from the time scale of a human lifetime. During this period, the root system is slowly degrading, but this process is unobservable (remember, the manager cannot see the phase plane). The system begins to change rapidly in year 45 and is completely degraded in 15 years.

Suppose that in year 55, after a 10-year period in which shoot biomass dropped by a factor of two, the manager decides to reduce stock to allow the system to recover. It must be reduced enough so that the present state (approximately $\hat{s} = 0.2$, $\hat{c} = 0.6$) lies within the HBE basin of attraction. This depends critically on the tiller potential of the crown. A look at Figure 2 suggests why. If the tiller potential is relatively high as in the case of Figure 2, a reduction in grazing pressure from 0.84 to 0.7 is just sufficient to expand the HBE basin of attraction to include the point (0.2, 0.6), and a reduction to 0.5 will certainly expand it to that point. If there is no tiller potential, the unstable manifold would be shifted up and to the left, and a reduction to 0.5 will not be sufficient. For example, if $\hat{a}_c = 0$, a reduction in grazing pressure of more than half to 0.4 is required to sufficiently expand the HBE basin.

Reducing grazing pressure to capture the present state in the HBE equilibrium is only part of the story. The other part is the time it takes for the

system to recover—that is, the relaxation time. For the parameter set for the case in Figure 3, if the grazing pressure were set to zero, the system would require 4 years to recover—a short period on a time scale relevant to landscape ecology but a long period on a time scale relevant to the financial viability of a pastoralist.

Woody Shrubs

By treating grass plants as the interaction between shoots and crowns, we have captured the potential for nonreversible dynamics through positive feedback between productivity and the ability of the plant to capture resources. However, if grazing pressure is reduced, the grass can always recover. This can be seen in Figure 2. Reducing grazing pressure moves the $\hat{s}$-nullcline down, causing the unstable equilibrium to collide with the ZBE. This makes the ZBE unstable, which allows the system to recover. This scenario is unrealistic for two reasons. First, we have not (yet) accounted for the possibility of invasion by competing species. Second, we have not taken into account plant–soil feedbacks. Loss of vegetation can cause the loss of soil and soil nutrients, thus further aggravating vegetation loss.

Our interest here is the frequently observed tendency of rangeland systems to flip from one desirable state to another undesirable state caused by shifts in the competitive advantage between different species. In this case, grass is replaced by shrubs; there is no loss of soil structure or nutrients, only a loss in economic productivity. We are not suggesting that slow soil degradation is not an important consideration for the resilience of rangeland systems, but rather that the shift from grass to shrubs is more important for managers in Australian rangelands. Further, the ability to properly capture changes in the capacity of the landscape to capture, concentrate, and conserve water and nutrients would require a model far beyond the scope of this paper (for a discussion of the Australian rangelands see Ludwig and others (1997b).

We include in the model the two strongest competitive interactions between shrubs and grass:

- Shrubs exert competitive pressure on grass via water. Over most of their life histories, grass and shrubs differentially compete for water at different horizons in the soil. Grass outcompetes shrubs in the upper layers, whereas the reverse is true in lower layers (compare Walker and others 1981).

- Grass exerts a competitive effect on shrubs through fire. Fire can stimulate seeds for germi-

nation in shrubs; but for germination to succeed, the correct conditions must be present just after the fire. This effect depends on the rainfall, and in the semi-arid rangelands, it is not as significant as the negative effect fire has on shrubs.

Grass also competes with shrubs for water, but explicitly including it does not change the qualitative behavior of the model. Under these assumptions, the model becomes:

$$\dot{c} = r_c s - \delta_c c \tag{9}$$

$$\dot{s} = c(a_c + r_s s)\left(1 - \frac{s}{s^*} - \alpha_{ws}\left(\frac{w}{w^*}\right)^\beta\right) - \gamma_g s \tag{10}$$

$$\dot{w} = r_w w\left(1 - \frac{w}{w^*}\right) \tag{11}$$

where w is shrub biomass, r_w is the intrinsic growth rate of shrubs, w^* is the maximum shrub biomass per unit area, and $\alpha_{ws}\left(\frac{w}{w^*}\right)^\beta$ models the competitive effect of shrubs on grass. The parameter β measures the relative nonlinearity of this effect. If β is 1, this competitive effect rises linearly with woody shrub biomass. If β is greater than 1, the effect of shrubs on grass increases slower than linearly at low biomass and faster than linearly when shrub biomass is relatively high, which is consistent with observation (Noble 1999). Here we rescale c and s as before, and we rescale shrub biomass by letting $\hat{w} = \frac{w}{w^*}$. This yields:

$$\hat{c}' = \hat{r}_s \hat{s} - \hat{c} \tag{12}$$

$$\hat{s}' = (\hat{a}_c \hat{c} + \hat{c}\hat{s})(1 - \hat{s} - \alpha_{ws}\hat{w}^\beta) - \hat{\gamma}_g \hat{s} \tag{13}$$

$$\hat{w}' = \hat{r}_w \hat{w}(1 - \hat{w}) \tag{14}$$

where $\hat{r}_w = \frac{r_w w^*}{\delta_c}$. As before, we set $\delta_c = r_c = 1$.

Figure 4 illustrates the impact shrubs have on the system when $\hat{r}_s = 3$, $\hat{a}_c = 0.1$, $\alpha_{ws} = 0.5$ (the maximum competitive effect of shrubs on shoots is 50% of the maximum intraspecific competitive effect in shoots), $\hat{r}_w$ is 0.1 (the maximum growth rate of shrubs is considerably less than for shoots), and $\beta = 3$. Shown is the $\hat{s}$-nullcline when $\hat{w} = 0.3$ (bold dotted line) and $\hat{w} = 0.825$ (light dotted line), which occurs after 25 years of unchecked shrub growth. The effect of shrubs is to move the $\hat{s}$-nullcline up and to the left, which in turn moves the separatrix up and to the right. This moves the
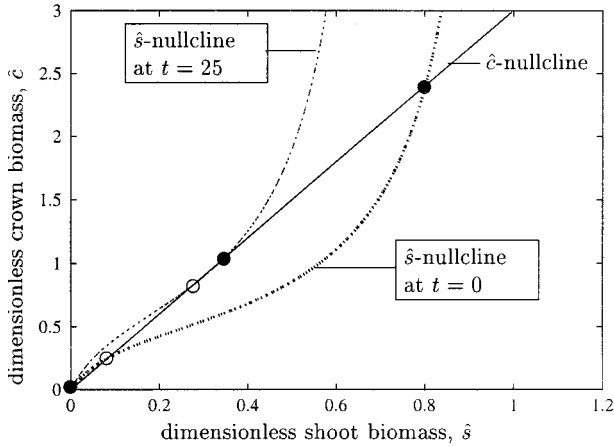
Figure 4. The influence of woody weed invasion on the shoot/crown system. As woody shrubs invade the system over time, the shoot nullcline is forced upward and to the left. The two isoclines shown in the figure show the position of the $\hat{s}$-nullcline for two different cases. The solid and open circles indicate the locations of stable and unstable equilibria, respectively. The lower right curve corresponds to a shrub density of 0.3 at $t = 0$. After 25 years have passed, the invasion of shrubs has pushed the isocline to the new position shown in the upper left curve.

HBE closer to the unstable equilibrium and closer to the boundary of the HBE basin of attraction. This shrinks the HBE basin of attraction and reduces the resilience of the desirable state suitable for grazing.

The only mechanism to stop the progressive loss of resilience of the desirable state is fire. In an ungrazed situation (for example, prior to European settlement), natural periodic fires would help prevent woody vegetation from dominating the system (Noble and Grice forthcoming). As grazing pressure increased, fire regimes changed, possibly resulting in the encroachment of native shrubs into formerly productive grassland areas (Noble 1996). Fire has the potential to maintain the structure of both natural and managed rangeland systems.

Fire

In the model, we make no attempt to model the complex spatial process associated with fire. Our only concern is the the aggregate effect in terms of the quantity of shoots and shrubs consumed during a fire event at the subproperty spatial scale. In simplest terms, we need only model fire as an "outbreak" process as a function of fuel loads. The model we use is based on some ideas from a recent more complex model of fire in a savanna system developed by Ludwig and others (1997a) that as-

sumes that the probability of fire is strongly dependent on fuel loads. Once sufficient fuel loads are present, eventual ignition is certain via either lightning strikes or human action.

To model the aggregate effect of fire for a given quantity of fuel, we define the fire index $I(t)$. This unitless variable has no physical meaning on its own; but when combined with other variables, it determines the biomass of shoots or shrubs consumed during a fire event. To attach some physical intuition to I, it can be thought of as the consumptive capacity of a fire. When the fuel load exceeds a critical level, I will increase rapidly (the fire will flare up) and consume the fuel. Once the fuel is consumed, I will decrease rapidly (the fire will burn out). A very simple and effective way to model the dynamics of I is:

$$\dot{I} = I(r_I f(s; a_I, b_I) - \delta_I) \qquad (15)$$

where the function f is the functional response of the fire to the shoot biomass, r_I is the rate of increase of I once sufficient fuel is present, and δ_I measures the minimum fuel requirement for the maintenance of a fire. A convenient general form for f is:

$$f(s; a_I, b_I) = \frac{s^{b_I}}{a_I{}^{b_I} + s^{b_I}} \qquad (16)$$

where a_I controls the location of the point where f is half its maximum value and b_I controls the rate of increase of f. The function f satisfies $0 \leq f < 1$ and models "switching on" type dynamics that we will use repeatedly in the model.

The effect of fire on shoots and shrub biomass is included by modifying Eqs. (10) and (11) to read:

$$\dot{s} = c(a_c + r_s s)\left(1 - \frac{s}{s^*} - \alpha_{ws}\left(\frac{w}{w^*}\right)^{\beta}\right) - \gamma_g s$$
$$- \gamma_{Is} I f(s; a_s, b_s) \qquad (17)$$

$$\dot{w} = r_w w\left(1 - \frac{w}{w^*}\right) - \gamma_{Iw} w f(I, a_w, b_w) \qquad (18)$$

where the expressions $\gamma_{Is} f(s; a_s, b_s)$ and $\gamma_{Iw} wf(I, a_w, b_w)$ measure the shoots and shrub biomass consumed for a given consumptive capacity I, respectively. Notice that we use the same function f but with different parameters than in Eq. (15). The role f plays in the shoot and shrub dynamics is slightly different. In reality, fuel would be consumed at a roughly constant rate until depleted. In Eq. (17), we approximate this process using f with $b_s = 1$ and $a_s = 0.1$. Figure 5 shows the shape of $f(s, 0.1, 1)$. In Eq.
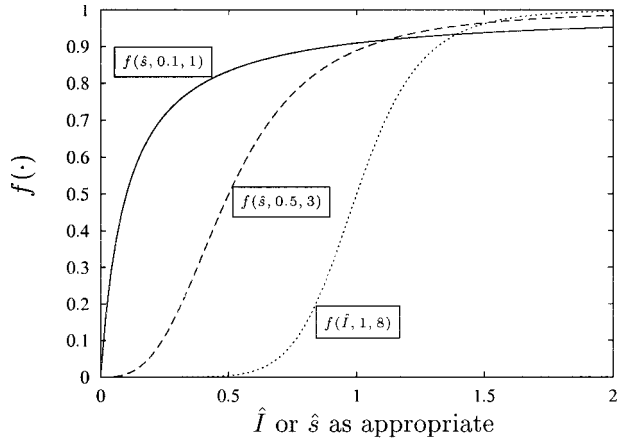
Figure 5. Instances of *f* used in the model. Recall that the function *f* has two parameters: one that governs the value of its argument at which *f* is one-half of its maximum value and one that governs the steepness of the slope of *f*. The function *f* appears three times in the full model (Eqs. [21], [22], and [23]). The curves in this graph show the shape of *f* for each of these cases used in the model.

(18), *f* captures the fact that a higher fire index is required to burn shrubs than shoots. We can model this threshold using *f* where a_w defines the fire index threshold for combustion of shrubs, b_w defines the sharpness of the threshold, and γ_{Iw} is the rate at which shrubs are consumed for a given fire index. The parameter choices for each case are discussed in more detail in the next section.

Analysis of the Full Model

We now have a full model for crown, shoot, shrub, and fire dynamics given by Eqs. (1), (17), (18), and (15). The first step is to nondimensionalize the system by letting:

$$\hat{c} = \frac{r_s c}{r_c}, \quad \hat{s} = \frac{s}{s^*}, \quad \hat{I} = \frac{I\gamma_{Is}}{\delta_c s^*}, \quad \hat{w} = \frac{w}{w^*}, \quad \text{and } \tau = \delta_c t$$

(19)

As before, we let $\delta_c = r_c = s^* = 1$. Changing variables yields:

$$\hat{c}' = \hat{r}_s \hat{s} - \hat{c}$$

(20)

$$\hat{s}' = (\hat{a}_c \hat{c} + \hat{c}\hat{s})(1 - \hat{s} - \alpha_{ws}\hat{w}^\beta) - \hat{\gamma}_g \hat{s} - \hat{I}f(\hat{s}; 0.1, 1)$$

(21)

$$\hat{I}' = \hat{I}\hat{r}_I(f(\hat{s}; a_I, b_I) - \hat{\delta}_I)$$

(22)

$$\hat{w}' = \hat{r}_w \hat{w}(1 - \hat{w}) - \hat{\gamma}_{Iw}\hat{w}f(\hat{I}; a_w, b_w)$$

(23)

where the three new nondimensional parameters are $\hat{r}_I = \frac{r_I}{\delta_c}$, $\hat{\delta}_I = \frac{\delta_I}{r_I}$ and $\hat{\gamma}_{Iw} = \frac{\gamma_{Iw}}{\delta_c}$.

We must now estimate reasonable parameter values for the model. It is important to remind the reader that we are analyzing how the *qualitative* behavior of the model changes as a subset of parameters are held fixed while others are varied. Based on extensive analysis, the model exhibits the same qualitative behavior over a wide range of parameter values. In the few instances where data are available to estimate parameters, we have used it. The remaining parameters have been chosen to produce the best qualitative match to rangeland dynamics in western New South Wales.

To determine reasonable values for these parameters, we ignore shrubs for the moment (that is, $\alpha_{ws} = 0$) and focus our attention on Eqs. (20), (21), and (22), which govern fire dynamics. In the model, endogenous fire outbreaks are generated via a limit cycle that emerges from what is known as a "Hopf bifurcation" (see Murray 1989). Thus, for some parameter combinations, the model will exhibit fire outbreak behavior; whereas for others, it will not.

Two other key aspects of fire that are important to capture are the frequency and duration of fire events and the minimum fuel load necessary to carry a fire. With no grazing, a fire frequency of 5–10 years is reasonable. A reasonable fuel load required to carry a fire is 30%–70% of the maximum shoot biomass, that is, when the nondimensional variable $\hat{s}$ is around 0.5 to 0.7 (K. Hodgkinson personal communication). With $\hat{r}_s = 3$ and no grazing, this leaves five parameters we can choose to capture this qualitative behavior: $\hat{a}_c$, δ_I, $\hat{r}_I$, a_I, and b_I. Analysis suggests that b_I has very little effect on the qualitative behavior of the model. All that is important is that *f* exhibit threshold behavior, so we set $b_I = 3$. Any value of a_I between 0.3 and 0.7 will cause fire to break out in the fuel load range given above. We set $a_I = 0.5$. The form of *f* for these parameter choices is shown in Figure 5.

For the model to produce a reasonable duration of a fire event, $\hat{r}_I$ must be large that is, fires must flare up and die out very quickly. If $\hat{r}_I$ is too small, fires burn for several years which, of course, is not very realistic. To get fire times on the order of days, $\hat{r}_I$ must be on the order of 500, which makes the numerical analysis intractable. As a reasonable compromise, we set $\hat{r}_I = 60$.

This leaves two parameters; δ_I and $\hat{a}_c$, which control two things—whether the model exhibits a limit cycle and, if so, its period (that is, the fire frequency). Because $0 \leq f < 1$, to be mathematically sensible, $\hat{\delta}_I$ must be between 0 and 1. The higher $\hat{\delta}_I$, the
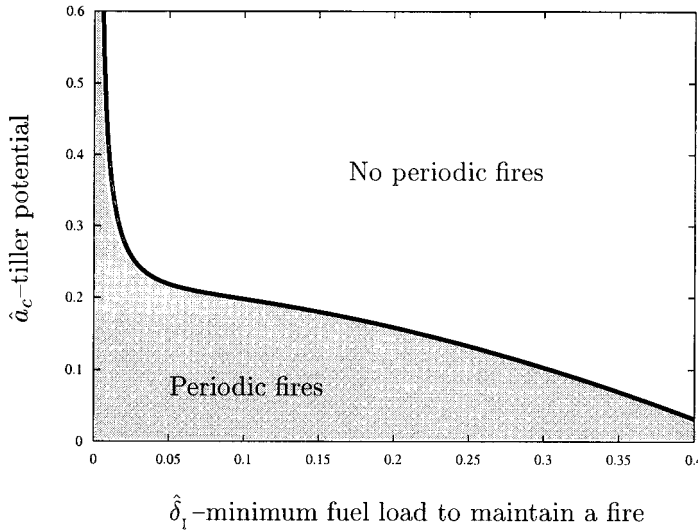
Figure 6. The heavy line shows the location of Hopf bifurcations as a function of the parameters $\hat{a}_c$ and $\hat{\delta}_I$. In the gray-shaded region, the model exhibits periodic fire outbreaks; in the unshaded region, it does not. The closer to the heavy dividing line that divides up parameter space, the longer the period between fire events.

higher $\hat{s}$ must be for $\hat{I}'$ to remain positive—that is, the more fuel is required to maintain a fire. If $\hat{\delta}_I$ is too high, fires will burn out before consuming the fuel, and the model will converge to a stable equilibrium with very small fires burning all the time without ever consuming the fuel. This is clearly unrealistic. With $\hat{a}_c = 0.1$, the model exhibits a Hopf bifurcation at $\hat{\delta}_I = 0.3048$ below which the model exhibits periodic fires. Increasing $\hat{a}_c$ increases the speed of recovery of shoots (fuel) after fires, which in turn allows more frequent fire events. Using the powerful bifurcation software, Auto, developed by Doedel (1981), we can track how the location of the bifurcation changes as $\hat{a}_c$ is varied, as shown in Figure 6. For parameter combinations in the shaded region, the model exhibits periodic fire outbreak dynamics. In the unshaded region, the model exhibits unrealistic continuous low-intensity fires. The period of the fire outbreak cycles ranges from 35 years, when $\hat{\delta}_I = \hat{a}_c = 0.03$, to 4 years, when $\hat{\delta}_I = \hat{a}_c = 0.15$. We set $\hat{\delta}_I = \hat{a}_c = 0.1$ for roughly a 10-year fire cycle when there is no grazing.

Finally, we set $b_w = 8$ to model a reasonably sharp fire threshold above which fire consumes (kills) shrubs (see Figure 5). This threshold, determined by a_w, cannot be too low or shrubs will be easily eliminated from the system by fire; nor can it be too high, or fires will have no effect. Again, experiments with the model show that $a_w = 1$ produces plausible results. The parameters are summarized in Table 1. We will vary $\hat{\gamma}_{Iw}$ and $\hat{\gamma}_g$ as part of the analysis.

Grass exerts competitive pressure on shrubs through fire via $\hat{\gamma}_{Iw}$; whereas shrubs exert pressure on grass through competition for water via α_{ws}. Figures 7 and 8 summarize the behavior of the model for $\hat{\gamma}_{Iw} = 1$ without and with grazing, respectively. As shown in Figure 7A, over a cycle, the grass and shrub biomass increase from their low point just after a fire (lowest, leftmost point on the cycle) to their high point just before fire (highest, rightmost point on the cycle). A fire event then reduces their biomass back to the postfire low point. The narrow shape is due to the fact that the time scale of shoot dynamics is much faster than that for shrub dynamics. In Figure 7B, the highest, rightmost point on the cycle again represents the system just before a fire event. During a fire event, the system follows the almost horizontal trajectory along which shoot biomass is reduced to almost zero and crown biomass changes very little. After the fire, because of the lack of above-ground shoots, the root system begins to decay but then recovers as the shoot cover returns. The system then returns to the prefire state. Notice how the fire dynamics keep the shrub biomass low—below 35% of the maximum. As the grazing pressure is increased, the system exhibits three distinct configurations:

1. Frequent fires, stable but fluctuating shoot and shrub biomass as shown in Figure 7, with low grazing pressure

2. No fire, low shoot biomass, and high shrub biomass with intermediate grazing pressure (Figure 8A)

3. No fire, no grass, and dominant shrubs after sustained high grazing pressure (Figure 8B)

The sensitivity of the system to grazing pressure is governed by the choice of $\hat{\gamma}_{Iw}$ and α_{ws}. As one might expect, the system becomes more sensitive to grazing as $\hat{\gamma}_{Iw}$ decreases (shrubs affected relatively less

Table 1. Parameter Interpretations and Values for the Model Analysis

Parameter	Interpretation	Reasonable Range	Value used in the Analysis
Original model parameters			
r_c	Crown intrinsic growth rate	0.5–3	1
δ_c	Crown decay rate	0.5–3	1
a_c	Tillering potential	See $\hat{a}_c$	—
r_s	Shoot intrinsic growth rate	See $\hat{r}_s$	—
$s*$	Maximum shoot biomass	Arbitrary	1
γ_g	Grazing rate	See $\hat{\gamma}_g$	—
r_ω	Shrub intrinsic growth rate	See $\hat{r}_\omega$	—
$w*$	Maximum shrub biomass	Arbitrary	1
r_I	Rate of change of fire index	See $\hat{r}_I$	—
δ_I	Minimum fuel load required to maintain a fire	See $\hat{\delta}_I$	—
γ_{Is}	Effect of fire on shoots	See a_w	—
γ_{Iw}	Effect of fire on shrubs	See $\hat{\gamma}_{Iw}$	—
Nondimensional parameters			
$\hat{r}_s$	Ratio of shoot growth rate to crown decay rate	1–10	3
$\hat{a}_c$	Ratio of tillering potential to shoot growth rate	0–1	0.1
$\alpha_{\omega s}$	Competitive effect of woody shrubs on grass	0–1	0.5
β	Nonlinearity of the shrub competitive effect	>1	3
$\hat{\gamma}_g$	Ratio of grazing rate to crown decay rate	0–1	Variable
$\hat{r}_I$	Ratio of fire index growth rate to crown decay rate	50–500	60
a_I	Controls fuel load at which fire flares up	0.3–0.8	0.5
b_I	Sharpness of fuel load threshold	>1	3
$\hat{\delta}_I$	Minimum fuel load required to maintain a fire	0–1	0.1
$\hat{r}_\omega$	Ratio of shrub growth rate to crown decay rate	0–1	0.1
$\hat{\gamma}_{Iw}$	Ratio of effect of fire on shrubs to crown decay rate	1–10	Variable
a_ω	Shrub consumption by fire threshold relative to effect of fire on shoots	0.5–2	1
b_ω	Sharpness of shrub consumption threshold	>1	8

The top of the table shows the original model parameters. The bottom shows the nondimensional parameters whose values are actually set in the model.

by fire) and α_{ws} increases, and both conditions tend to give shrubs the edge in the competition.

Figure 8 shows the system behavior in shoot/shrub phase space under two different grazing regimes, $\hat{\gamma}_g = 0.25$ and 0.35, respectively. The heavy lines are the stable limit cycles. The lighter lines show the transient trajectory as the system moves from one configuration to another. The cycle shown by the heavy line in Figure 8A shows the location of the stable limit cycle when $\hat{\gamma}_g$ is increased from 0 to 0.25. Two things have happened: The average shrub biomass has increased (the limit cycle has shifted upward as compared to 7A), and configuration (1) has become less resilient. The trajectory shown in the lighter line results when the system is perturbed slightly away from the stable limit cycle. Shrub biomass steadily increases, the consumptive capacity of fire events diminishes (amplitude of fluctuations in shoot biomass decreases), and the system converges to configuration (2). If grazing pressure

is increased still further from 0.25 to 0.35, the system will evolve along the lighter trajectory toward configuration (3) as depicted in Figure 8B.

If managers recognize the changing landscape dynamics associated with increasing grazing pressure, they can reduce grazing pressure to allow the system to recover. However, the system will not bounce back to the zero grazing state depicted in Figure 7. Figure 9 illustrates this point. The graph in Figure 9A shows the recovery from configuration (2). Burning is possible, but because of insufficient fuel, the fire will not significantly reduce the shrubs. They will again invade the system before there is enough fuel for a second burn. Only after 20 years and three burns can the shrubs be brought back under control. As shown in Figure 9B, the recovery from configuration (3) is even slower. Here, shrubs dominate for almost 25 years until enough shoot biomass builds up to allow fire back into the system.
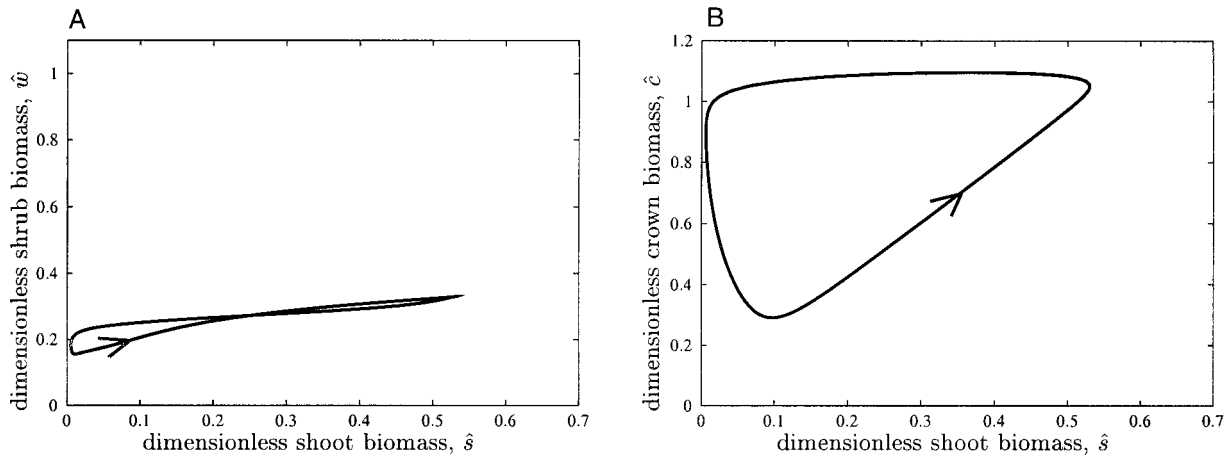
Figure 7. **A** and **B** show the shrub/shoot and crown/shoot phase planes, respectively. As in previous diagrams, the heavy line traces out the trajectory of the state variables over time. The arrow indicates the direction of movement. The time it takes for the system to traverse around the cycle— that is, the period—is 10 years.
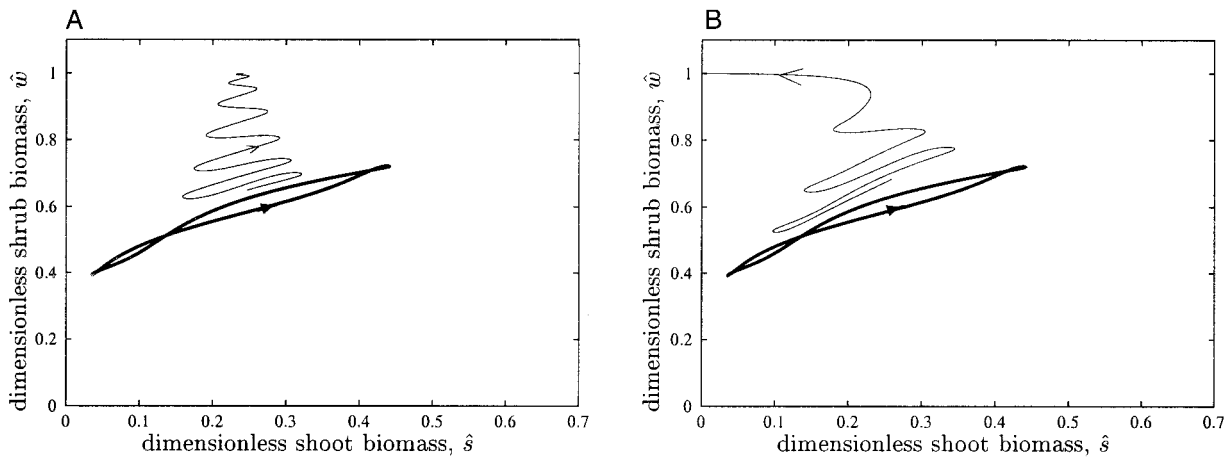

Figure 8. **A** and **B** show the the analogue of Figure 7A for two different levels of grazing pressure, $\hat{\gamma}_g = 0.25$ and $\hat{\gamma}_g = 0.35$, respectively.

MANAGEMENT, ECONOMIC FACTORS, AND RESILIENCE

In this section, we examine how management options and external economic factors affect the resilience of the system. We first discuss the effect of three different management options on resilience, then we turn our attention to economic factors. When we discuss the different models for grazing, the units on the variables and parameters must be spelled out carefully. For this purpose, we will use the original variable and parameter names. When we present the results of our analysis (carried out on the nondimensionalized version), we will use their dimensionless counterparts (with the "hat" notation).

Management Options and Resilience

An important part of rangeland management occurs through adjusting the stocking rate. Given that managers decide when to mate their ewes and rams and when to buy, sell, and move their stock, we can assume that these adjustments are stronger determinants of the stock dynamics than natural population dynamics. This is not to say that managers do not utilize the reproductive capacity of the sheep to adjust the stock and do not suffer costs when sheep die naturally. However, these processes can be captured with adjustment costs rather than adding another stock variable to the model. To keep the model as simple as possible, we assume that pastoralists can adjust stocking rates instantaneously. Although this is not the case, the acts of buying,
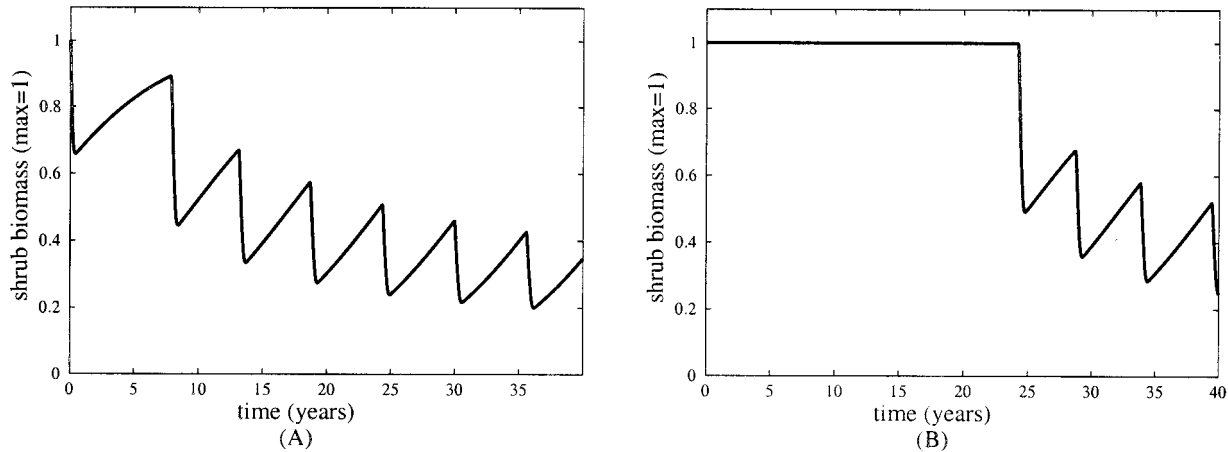
Figure 9. **A** and **B** show the woody shrub dynamics over time recovering from different initial conditions. **A** shows how the system recovers from the state in which shrubs dominate but there is a small amount of grass biomass; **B** shows how it recovers from the state in which shrubs dominate and there is no grass biomass.

selling, and moving sheep happen almost instantly compared to the long time scale of the natural ecological system.

Here we will compare three cases: the maintenance of a constant grazing pressure with fire suppression, the maintenance of a constant stocking rate with fire suppression, and the maintenance of a constant grazing pressure with periodic burning. The first case refers to a situation in which a constant grass biomass offtake is maintained by adjusting the stock. The second refers to a situation in which a constant number of animals per unit area is maintained. Actual rangeland management falls somewhere between these two extremes. The last case represents a strategy that is not commonly practiced but nonetheless has the potential to increase the resilience of the system.

Constant Grazing Pressure with Fire Suppression

Recall that grazing pressure, by which we mean the proportional shoot biomass offtake per unit area due to grazing, has so far been treated as a constant, γ_g. In practice, γ_g is almost certainly not constant. To keep γ_g constant would require a "perfectly reactive strategy" aimed at maintaining a constant utilization rate. Land managers working in terms of stocking rate would, based on their observation of available shoot biomass, constantly adjust the number of animals per unit area in order to maintain:

$$\gamma_g = \text{animals per unit area}$$

$$\times \frac{\text{shoot biomass eaten per animal}}{\text{unit of standing shoot biomass}} \quad (24)$$

at a constant level. Of course managers do not practice such a precise strategy; however, they might try to adjust stock on an annual basis to try to maintain a constant utilization rate. We analyze the resilience properties of this perfectly reactive case to serve as a benchmark with which to compare the more realistic case of constant stocking rate. The key difference between these two strategies is the cost associated with adjusting stock numbers.

Without fire, shrubs will invade the system and reach their maximum biomass of 1.0, as shown in Figure 8A. The difficulty from the management perspective is that the transition in shoot biomass as grazing pressure is increased does not occur uniformly in time (recall Figure 3). This is depicted in Figure 10. The parameter values are those shown in Table 1 with $\hat{\gamma}_{Iw} = 1$. Figure 10A and B shows the long-run equilibrium shoot and crown biomass as a function of the grazing pressure. The heavy line indicates that the equilibria are stable; the light line indicates that they are unstable. The arrows indicate the direction the system will move if perturbed a small distance away from the equilibrium. Notice that for grazing pressures below 0.15 there is a single domain of attraction. If the system is perturbed away from equilibrium by, for example, a period of drought, the system will recover. For grazing pressures above 0.15, a second domain of attraction around the zero shoot biomass state appears. In this case, if the system is perturbed so that both the shoot and crown/root biomass fall below the light line, the system will fall into the no shoot, no crown, all shrub state. That is, unless there is a way to generate income with shrubs, the financial
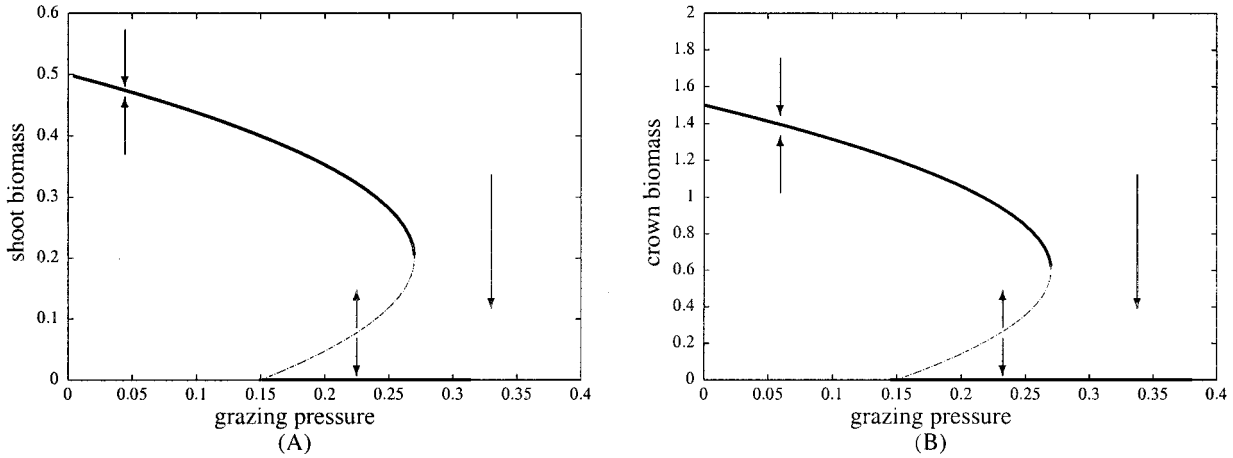
Figure 10. **A** shows the long-run equilibrium grass biomass with complete fire suppression and $\alpha_{wg} = 0.5$. **B** shows the same for the below-ground biomass.

productivity of the rangeland will be lost. The distance between the heavy and light lines is a representation of the resilience (as measured by the ability of the rangeland to produce feed for livestock) of the system. As $\hat{\gamma}_g$ is increased to around 0.27, the heavy and light lines meet at a bifurcation point (called a "limit point" in this case). Beyond this point, there is only one stable state—the ZBE. In this case, the system is permanently locked in the degraded state. This caricature roughly matches the history of rangelands where in some cases, grazing pressure has been maintained at a level near the bifurcation point and the occurrence of drought pushed the system into the region where eventual degradation was almost certain.

Constant Stocking Rates with Fire Suppression

Up to now, we have assumed that managers are perfectly reactive to shoot biomass and maintain a constant utilization rate. This assumption is unrealistic. Land managers do adjust stocking rates according to the available shoot biomass but not continuously—perhaps once or twice per year. A more common strategy is to maintain a constant number of animals per unit area. To model this properly, we must now take into account how sheep actually consume shoots.

Above a certain critical shoot biomass, sheep consume shoots at a roughly constant rate determined by gut capacity. When shoot biomass falls below a critical level of a few hundred kilograms per hectare, search and processing times increase resulting in decreased rates of consumption (Short 1985). A reasonable model for shoot consumption is:

$$\frac{\text{grass consumption}}{\text{area} \times \text{unit time}} = \gamma_g f(s; a_{sc}, 1) \qquad (25)$$

where γ_g is now interpreted as the maximum amount of shoot biomass consumed per unit time (= number of sheep per unit area times a per-animal maximum consumption rate of around 1.3 kg per day (Short 1985) and f, the "functional response curve," has the form shown in Figure 5 for $b = 1$. The parameter a_{sc} controls the shoot biomass below which consumption begins to fall off. Values of a_{sc} in the range 0.05–0.1 cause f to stay near 1 until $\hat{s}$ drops below 0.2, then drops off precipitously (compare the shape of f when $b = 1$ in Figure 5 to Figure 5 on page 440 of Short [1985]).

Figure 11 is the analogue of Figure 10A with $\hat{\gamma}_g \hat{s}$ replaced with $\hat{\gamma}_g f(\hat{s}; 0.1, 1)$ in Eq. (21) showing the long-run equilibrium shoot biomass versus grazing pressure. Recall that in the previous model grazing pressure was given directly by $\hat{\gamma}_g$. Here, because of the changed interpretation of $\hat{\gamma}_g$, grazing pressure (proportional offtake) is given by $\dfrac{\hat{\gamma}_g f(\hat{s}; 0.05, 1)}{\hat{s}}$. The only difference between the two figures is the point at which the equilibrium becomes unstable—at a grazing pressure of about 0.23 in the constant stocking rate model versus 0.27 in the constant grazing pressure model. The reason for this difference is that in the constant grazing pressure case, the manager is very responsive to perturbations. If the shoot biomass is reduced by a perturbation, such as a drought, the manager destocks immediately. In the constant stocking rate case, managers are less responsive to perturbations. For example, during the onset of a drought, managers often
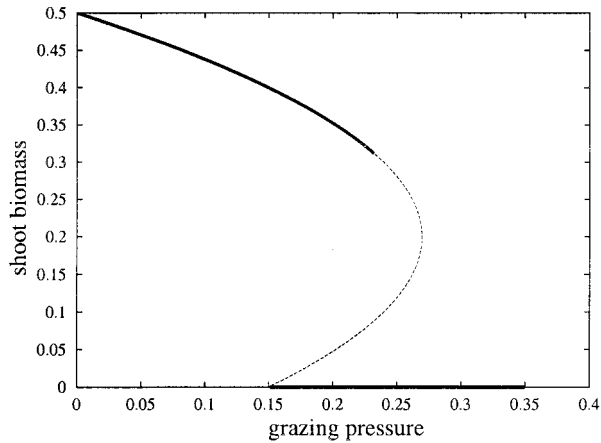
Figure 11. Long-run equilibrium grass biomass versus grazing pressure for the constant stocking model.

maintain their stock in the hope that rain will come. The adaptive capacity in the constant grazing pressure (that is, the perfectly reactive, constant utilization rate) model allows a higher proportional shoot offtake while maintaining stability and resilience than does the constant stocking rate model.

Constant Grazing Pressure with Periodic Fires

Thus far, we have been studying the resilience of stable equilibrium configurations. In both of these cases, the disturbance of fire has been removed from the system. In this section, we examine how reintroducing this disturbance affects the resilience of the system.

If fires are not suppressed, when the fuel load reaches the critical level in the neighborhood of 0.45, the manager destocks and allows a paddock to burn (that is, lights a fire.). Figure 12 shows the average shoot and shrub biomass over one cycle for two different values of $\hat{\gamma}_{Iw}$: $\hat{\gamma}_{Iw} = 1$ and $\hat{\gamma}_{Iw} = 1.4$. The solid circles indicate that the cycle is stable (periodic burns are sustainable); the open circles indicate that the cycle is unstable (periodic burns cannot be sustained). Above a critical grazing pressure, the system will move toward the no-fire equilibrium of no shoots, no fires, and shrubs at carrying capacity, as indicated by the arrows in Figure 12.

If we compare Figure 12 to Figure 10, it is evident that average shoot biomass is lower than with fire suppression and is less sensitive to grazing. This is because the dynamics are driven more by fire than by grazing pressure. The biggest difference between the two cases is the level of shrub encroachment. Without fire, the shrubs reach their carrying capac-

ity of 1.0. With fire, the shrub biomass is much lower. This is the key reason why the system with fire is more resilient. After a perturbation such as a drought, shoots have a better chance of recovering when the competitive pressure from shrubs is lower. Further, the importance of the parameter $\hat{\gamma}_{Iw}$ (effect of fire on shrubs) is clear. Increasing $\hat{\gamma}_{Iw}$ increases the maximum grazing pressure for which fire can be maintained and reduces the average shrub biomass in the system.

To compare the constant grazing pressure model with fire to one without fire, we measure resilience by the Euclidian distance between the equilibrium state and the boundary of its domain of attraction in shoot/crown space. The resilience, R, of the system with fire suppression ($w = 1$) is given by:

$$R = \sqrt{d_s^2 + d_c^2} \qquad (26)$$

where d_s and d_c are the distances between the bold upper line and light lower line (or the x-axis) in Figure 10A and B, respectively. Referring to Figure 10, below a grazing pressure of 0.15, the ZBE vanishes and there is only one stable equilibrium—the HBE. In this case, any perturbation will return the desirable state. Above a grazing pressure of 0.28, the HBE vanishes, leaving only the ZBE. In this case, any perturbation will return to the ZBE.

Periodic fire complicates things; it is more difficult to compute the basin of attraction boundary for a periodic orbit than for a fixed point. However, remember that fire events are infrequent and short-lived, so that most of the time the system is in a recovery stage with no fire. Recall that the curves in Figure 10 are computed for shrubs at carrying capacity. Reducing the level of shrubs greatly expands the size of the domain of attraction as shown in Figure 13A, which compares the equilibrium shoot biomass for two different levels of shrub encroachment, $\hat{w} = 1$ (fire suppression) and $\hat{w} = 0.4$ (a shrub density maintained by periodic burning with grazing pressure of 0.15). Thus, between fire events, shoot and crown biomass increase toward their no-fire equilibria. As shrubs encroach, the outer curve contracts toward the inner curve in Figure 13A. Because the system state and domain of attraction are both moving, computing the distance between them is difficult.

One approach is to compute the distance between the average shoot and crown biomass to the boundary computed for the average shrub density. Figure 13B illustrates the relationship between the resilience of a system with fire and one without fire. Up to a point, both systems exhibit only one stable
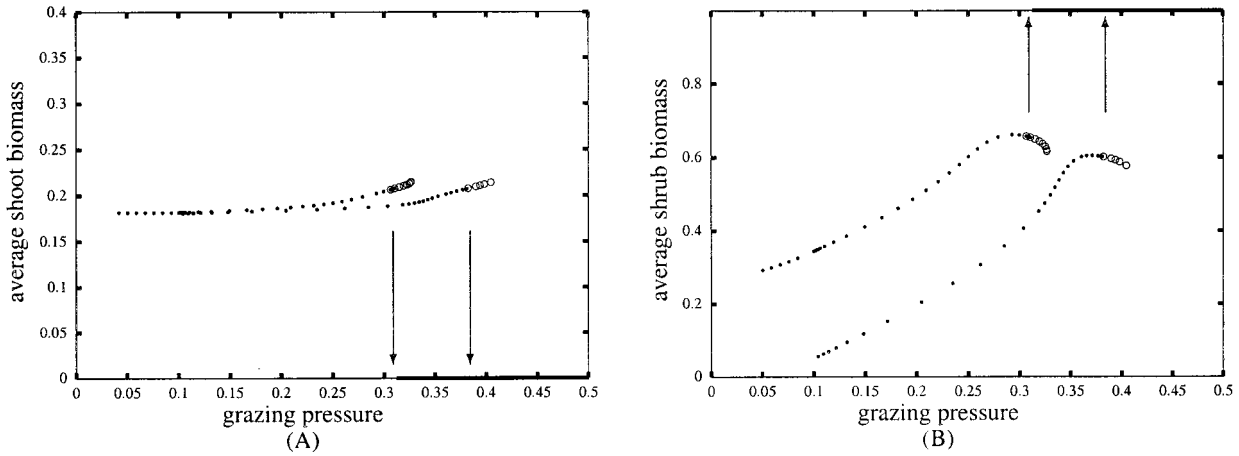
Figure 12. **A** shows the long-run average grass biomass per cycle. Solid circles indicate that the cycle that produced the average biomass shown is stable; open circles indicate that the cycles are unstable. The transition from solid to open circles marks the transition from sustainable grazing with periodic fires to a state where grazing pressure is too high for fires to be maintained. The system configuration then moves toward the shrub-dominated state, as shown by the arrows. The upper left sequence of circles in **A** correspond to $\hat{\gamma}_{Iw} = 1$; the lower right corresponds to $\hat{\gamma}_{Iw} = 1.4$. **B** is interpreted just as **A** but for shrub biomass.
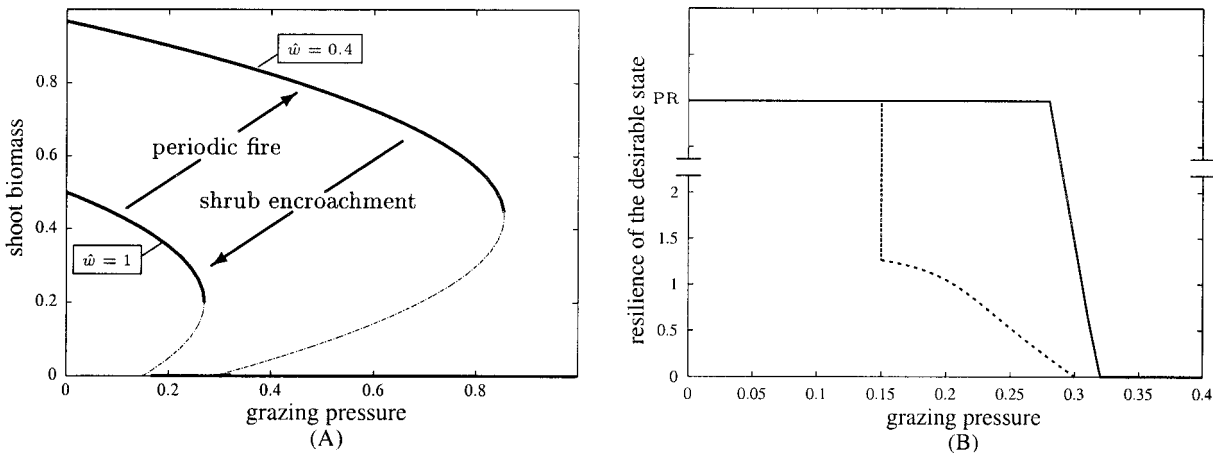

Figure 13. **A** illustrates the effect of shrub encroachment between fire events on the long-run equilibrium shoot biomass. The two cases shown are for $\hat{\omega} = 0.4$ (periodic burning) and $\hat{w} = 1$ (no burning, shrubs have reached carrying capacity). **B** shows the resilience of the case with fire (solid) and without fire (dashed).

configuration—the (desirable) HBE. In these cases, the system can withstand any size perturbation and return to the desirable state. In this case, we cannot assign a meaningful number to resilience; thus, we refer to the HBE as being "perfectly resilient." This is marked with the label "PR" in Figure 13B. In the system without fire, a definite boundary for tolerable perturbations appears at $\hat{\gamma}_g = 0.15$. This is indicated by the abrupt drop from the PR line to a value of approximately 1.25 in Figure 13B. As grazing pressure increases, the size of the domain of attraction for the desirable state shrinks to zero. With periodic burning, on the other hand, the sys-

tem remains perfectly resilient up to $\hat{\gamma}_g = 0.28$. Exceeding $\hat{\gamma}_g = 0.28$ precludes fire, and the resilience of the system drops off very rapidly. Figure 13B raises two interesting questions:

1. What ecological and economic conditions favor the periodic burning versus the fire suppression configurations?

2. If fire suppression is favored, what ecological and economic conditions favor the high- versus low-resilience regimes?

We address these questions with a simple economic model.

Economic Factors

Economic characterizations of resource systems are commonly cast as solutions to intertemporal optimal control problems (Clark 1990), which are highly dependent on discount rates. This type of analysis is beyond the scope of this paper. We are currently preparing a paper that explores this problem. Our economic characterization will focus on long-run sustainable income—that is, we act as a manager with a zero discount rate.

We examine this case for two reasons. First, the effect of discount rates on resilience in general is well known (Brock 1998). Managers with higher discount rates are less willing to forgo present income (wool production from grass shoots) to maintain resilience (save shoots for fuel). They would favor higher grazing rates, longer periods between fires, and reduced resilience. Second, discount rates are attributes of managers, not of the system. We are interested in how economic factors intrinsic to the system influence resilience. We thus examine the case in which managers have zero discount rates (that is, wish to maximize long-run sustainable income) knowing that managers with positive discount rates will choose to trade off resilience for present income.

For our purposes, it is sufficient to treat sheep and the wool property infrastructure as a black box that converts shoot biomass into revenue via wool production. Further, many of the costs associated with periodic burning and fire suppression are the same. We single out two of the main costs that will differ between the two strategies—the cost of adjusting stock associated with burning, C_a, and the costs associated with shrubs, C_w. We thus define the net revenue exclusive of these two costs by $R(\gamma_g s(t))$; that is, the sheep convert the shoots they eat per unit time $\gamma_g s(t)$ into $R(\gamma_g s(t))$ dollars per unit time after all costs except C_a and C_w are considered. To keep things as simple as possible, we assume that $R(\gamma_g s(t)) = R\gamma_g s(t)$ where R is a constant, and by choice of units, set $R = 1$. Thus, the instantaneous rate of profit per unit area, $\pi(\gamma_g, s(t), w(t))$, is given by the expression:

$$\pi(\gamma_g, s(t), w(t)) = \gamma_g s(t) - C_a(\gamma_g) - C_w(\gamma_g, w(t))$$
$$(27)$$

The main component of C_a is the cost of moving animals off and on the property through a burn-and-recovery cycle. The higher the grazing pressure γ_g, the greater the total number of animals that will have to be moved during the destocking/restocking process. Assuming a constant cost per animal, the

function $C_a(\gamma_g)$ can be approximated by $C_a \gamma_g$ where C_a is a constant of proportionality. In the case with fire suppression, $C_a = 0$.

The costs associated with shrubs include reduced wool cuts due to lower-quality feed, inefficient surveillance of lambing ewes, harbor for predator species in heavily shrubbed paddocks, and longer and incomplete "musterings" (MacLeod 1993). "Mustering" refers to locating and gathering animals on several occasions per season for, among other things, shearing and treatment for lice and blowflies. Incomplete musterings are costly because if an animal is missed and not treated, it can reinfect all those that were treated. As with adjustment costs, we assume a constant cost per unit of grazing pressure associated with shrub invasion that rises linearly with shrub density. Thus to a first approximation, $C_w(\gamma_g, w(t) = C_w \gamma_g w(t)$ where C_w is a constant.

In terms of the nondimensional variables, the instantaneous profit rate per unit area is:

$$\pi(\hat{\gamma}_g, \hat{s}(t), \hat{w}(t)) = \hat{\gamma}_g(\hat{s}(t) - C_a - C_w \hat{w}(t)) \quad (28)$$

Let π_c denote instantaneous profit in the fire suppression (constant stocking rate) configuration. In this case, $\hat{w}(t) \rightarrow 1$ and $\hat{s}(t)$ approaches its long-run equilibrium value which we denote by $\hat{s}^*$. Recalling that with fire suppression $C_a = 0$, Eq. (28) becomes:

$$\pi_c(\hat{\gamma}_g) = \hat{\gamma}_g(\hat{s}^* - C_w) \quad (29)$$

which is constant over time. In the periodic burning configuration, profit fluctuates over time. In this case, we compute the average rate of profit over one cycle and compare it to Eq. (29). Letting $\bar{\pi}_f$ denote the average profit rate with periodic burning over one cycle, we have:

$$\bar{\pi}_f = \frac{1}{T_2 - T_1} \int_{T_1}^{T_2} [\hat{\gamma}_g \hat{s}(t) - C_a \hat{\gamma}_g - C_w \hat{\gamma}_g \hat{w}(t)] dt \quad (30)$$

where $T_2 - T_1$ is the period of the burn-and-recovery cycle. Factoring out $\hat{\gamma}_g$, Eq. (30) becomes:

$$\bar{\pi}_f = \hat{\gamma}_g(\bar{\hat{s}} - C_a - C_w \bar{\hat{w}}) \quad (31)$$

where $\bar{\hat{s}} = \frac{1}{T_2 - T_1} \int_{T_1}^{T_2} \hat{s}(t) dt$ and $\bar{\hat{w}} = \frac{1}{T_2 - T_1} \int_{T_1}^{T_2} \hat{w}(t) dt$ are the average shoot and shrub biomass over one burn-and-recovery cycle, as shown in Figure 12.

By comparing these profit rates, we can see the interplay between ecological and economic parameters that favor each of the configurations. For a
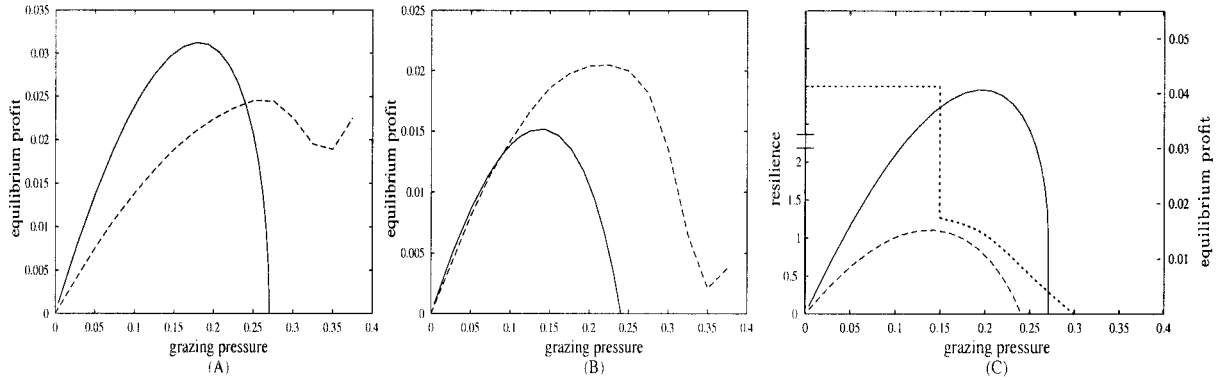
Figure 14. **A** Equilibrium profits for $C_\omega = 0.2$ and $C_a = 0.03$ for periodic burning (dashed) and fire suppression (solid). **B** Same as **A** except with $C_\omega = 0.3$ and $C_a = 0.02$. **C** Equilibrium profits with fire suppression for $C_\omega = 0.15$ (solid) and $C_\omega = 0.3$ (dashed) and resilience (bold dashed).

given $\hat{\gamma}_g > 0$, periodic burning is preferred if $\bar{\pi}_f > \pi$. That is:

$$\hat{\gamma}_g(\bar{s} - C_a - C_w\bar{w}) > \hat{\gamma}_g(\hat{s}^* - C_w) \Leftrightarrow \quad (32)$$

$$C_w(1 - \bar{w}) - C_a > \hat{s}^* - \bar{s} \quad (33)$$

This relation has a simple interpretation: The cost savings associated with shrub reduction, $C_w(1 - \bar{w})$, less the transaction costs necessary to achieve that reduction, C_a, must be greater than the lost revenue associated with burning, $\hat{s}^*-\bar{s}$. Thus, lower transaction costs and a high cost of shrub invasion favors periodic burning. The average shrub biomass over a cycle, $\bar{w}$, is determined by the ecological parameter $\hat{\gamma}_{Iw}$ (see Figure 12). The larger $\hat{\gamma}_{Iw}$ (that is, the more sensitive shrubs are to fire), the smaller $\bar{w}$. This tends to increase the left hand side of Eq. (33), which tends to favor the use of periodic burns.

Figure 14(A) and (B) illustrate the tradeoff between transaction and shrub invasion costs. Figure 14A shows sustainable profit as a function of grazing pressure with (dashed line) and without (solid line) periodic burning for $C_\omega = 0.2$ and $C_a = 0.03$. In this case, it is optimal to suppress fires and maintain a constant grazing pressure of about 0.175. Figure (14B) shows the case for $C_\omega = 0.3$ and $C_a = 0.02$— that is, higher shrub invasion and lower transaction costs than in Figure 14A. Here it is optimal to periodically burn and maintain a grazing pressure of 0.22. The interplay between transaction costs and shrub invasion costs strongly influences the resilience of the system.

Figure 14C provides an answer to the second question. If transaction costs are high and fire sup-

pression is favored, the shrub invasion cost determines whether the system occupies a high- or low-resilience regime. The dashed and solid curves correspond to $C_\omega = 0.3$ and $C_\omega = 0.15$, respectively. Maximum profit occurs in the high- and low-resilience regimes, respectively. The lower C_ω (or the less knowledge managers have of C_ω due to poor monitoring or understanding), the stronger the tendency to push the system close to a bifurcation boundary, causing a loss of resilience.

DISCUSSION

The analysis of our model highlights several points concerning how the economic, management, and ecological characteristics of a rangeland system affect its resilience:

- The model exhibits three distinct equilibrium configurations depending on grazing pressure: "balanced" perennial grass and shrub densities mediated mainly by periodic fires and to a lesser extent by grazing pressure ("fire-dominated"): no periodic fires, where shrubs dominate and shoot biomass is mainly regulated by grazing pressure ("grazing-dominated"); and no periodic fire, where shrubs dominate and there is no grass ("shrub-dominated").

- Measured by the ability of the system to generate economic returns via shoot production, resilience ratchets down as grazing pressure increases and the system moves from fire-dominated to grazing-dominated to shrub-dominated. A configuration allowing periodic fire disturbances has the highest resilience. It is important to emphasize that the measurement of resilience is context-dependent. If a means to

Table 2. Relationship among Key Model Parameters, Equilibrium Configuration, and Resilience

Parameter Combinations	Equilibrium Configuration	"Resilience"
$\hat{\gamma}_{Iw}$–high C_a–low C_w–high	Periodic burning, "fire-dominated"	Very high
$\hat{\gamma}_{Iw}$–low C_a–high C_w–high	No periodic burning, "grazing-dominated," low grazing pressure	High
$\hat{\gamma}_{Iw}$–low C_a–high C_ω–low	No periodic burning, "grazing-dominated," high grazing pressure	Low
$\hat{\gamma}_{Iw}$–low C_a–high C_w–low	Shrub-dominated, previously subject to high grazing pressure	Very high but very undesirable

generate economic returns via shrubs exists, or if resilience is measured by some other metric such as landscape function, the change in resilience of the system may be less marked.

- The equilibrium configuration and resilience of the system is strongly influenced by three parameters, $\hat{\gamma}_{Iw}$, C_a, and C_ω, as shown in Table 2. Lower transaction costs and higher shrub invasion costs favor the fire-dominated configuration and thus enhance resilience provided that $\hat{\gamma}_{Iw}$ (the sensitivity of shrubs to fire) is sufficiently high. High transaction costs favor the grazing-dominated configuration. In this configuration, the high or low cost of shrub invasion determines whether the resilience will be low or high, respectively. It is important to note that because our economic model includes only instantaneous cash flows, it does not capture the lost future income flows and lost option values associated with falling into the unproductive state. If sufficiently high, these costs may increase the economic appeal of the higher-resilience configurations.

- The comparison of the constant grazing pressure and constant stocking rate strategies in the case where fire is suppressed shows that resilience can be enhanced without periodic burning. However, the additional adjustment costs associated with maintaining constant grazing pressure may make it economically unattractive.

The main limitation of the model is that it is does not address spatial and temporal variability across different scales. Temporal variability both in rainfall and wool prices is a major issue faced by pastoralists

(Stafford Smith and Foran 1992). Such variability would increase transaction costs. For example, response to droughts requires a rapid change in the stocking rate during which animals have to be sold into a depressed market. Future work should focus on expanding the basic model developed here to include temporal variability, as well as external economic forces such as discount rates and prices. Smaller-scale spatial variability in productivity and the effect of fire would also influence our results. Local patches of very productive areas could improve resilience, whereas patchy burn events could reduce resilience. Nonetheless, there is still value in the deterministic model for strategic management. Buxton and Stafford Smith (1996) note that pastoralists have identified the strategic management of long-term stocking levels as one of three main areas where better information and training could help them cope with climatic variability. Increasing resilience through the strategic use of fire and grazing pressure could help to buffer against exogenous shocks.

In an effort to keep the model as simple as possible, we elected to not model changes in soil quality induced by changes in vegetation and the physical effects of grazing. The implication of this simplification is that our model overestimates the resilience of the system. Having said this, the soils in the Australian rangelands are very nutrient-poor compared to other arid systems around the world (Charley and Cowling 1968), and most nutrients in the system are locked-up plant biomass. The main driver in the system is the ability of plants to capture water resources as they flow through the sys-

tem rather than resources in the soil. We have built the model around this characteristic of the Australian rangelands. This, of course, limits the applicability of our results to other rangelands that may be more driven by soil nutrients.

Finally, it is important to point out the implications of assuming a zero discount rate in our economic characterization of the system. The purpose of building resilience is to maintain future income. Discount rates measure the willingness of a manager to trade off present income for future income. Our zero discount rate case illustrates how economic factors such as high adjustment costs and low costs of shrub invasion make the system less resilient in the most optimistic circumstances when managers care most about the future. Managers with positive discount rates would place less weight on lost future income due to shrub invasion. For such managers, an even higher C_ω and lower C_a would be necessary to induce them to operate in the higher-resilience configuration with periodic burning. Discounting does not alter our main result that higher C_ω and lower C_a enhance resilience; it just exaggerates it.

CONCLUSIONS

With wool production as the metric, we can conclude that the resilience of the system strongly depends on ecological parameters ($\hat{\gamma}_{Iw}$ or effect of fire on shrubs), economic parameters (C_a or stock adjustment costs and C_w or costs associated with shrub invasion), and management parameters ($\hat{\gamma}_g$ or stocking strategy) (Table 2. Resilience-based management would prescribe periodic destocking and burning to keep the system in the fire-dominated configuration. Economic-based management aimed at maximizing long-run sustainable income is consistent with resilience-based management if the costs of shrub invasion are high, transaction costs are low, or the cost and probability of falling into the unproductive state are high. Assuming that managers practice economic-based management, policies aimed at influencing C_a and C_ω could increase resilience by making economic- and resilience-based management more consistent.

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