Center for Nonlinear Dynamics in Economics and Finance

CeNDEF Working Paper 26-03

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Resilience of Time-Constant Livestock Management of Savannas Facing Woody Encroachment

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9th February 2026

Abstract

Savanna ecosystems cover a large proportion of the Earth's surface and house a rapidly growing proportion of the world's population and livestock. An often overlooked but urgent threat to tropical savannas is woody encroachment, by which woodland encroaches upon grasslands used for livestock production, the principal means of subsistence in these areas. This paper analyses the impact of time-constant livestock and fire management on the resilience of savannas against woody encroachment in a well-known dynamic savanna model with tipping points. We study the sensitivity of savanna resilience to economic rather than geophysical parameters. We find that higher livestock prices incentivize management that lowers the resilience of the system, eventually leading to its collapse. We also find that, under general conditions on the livestock dynamics, the amount of vegetation biomass is not an indicator of proximity to the tipping point, as the level of vegetation is constant over livestock prices, while the resilience of the savanna regime decreases. Fire use makes the resilience of the savanna against woody encroachment more sensitive to changes in livestock prices if fixed livestock offtake and grazing intensity are chosen optimally.

Keywords: rangeland management, ecosystem resilience, dynamical systems, woody encroachment

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1 Introduction

Woody encroachment is an often overlooked but increasingly urgent threat to savanna ecosystems worldwide (Moleele, Ringrose, Matheson, & Vanderpost, 2002; Stevens, 2017). Savannas, characterized by the co-dominance of grasslands and scattered woody vegetation, cover a large proportion of the Earth's surface, housing a rapidly growing proportion of the world's population and livestock (Scholes & Archer, 1997). Through the process of woody encroachment, most generally defined as the increase in woody cover in savanna ecosystems (O'Connor, Puttick, & Hoffman, 2014), woody plant species grow at the expense of herbaceous grass cover necessary for livestock production.

While woody vegetation provides many resources to humans living in tropical savannas, livestock production is often the main agricultural activity and principal means of subsistence in these areas (FAO, 2019; Walker & Janssen, 2002). Livestock production interacts with woody vegetation through two, apparently counteractive processes: on the one hand, it incentivizes the direct clearance of woodland and shrubland to make way for productive grasslands (FAO, 2019). On the other hand, the removal of herbaceous species through grazing indirectly enables the growth of woody species, which compete with herbaceous species for water (Dos Santos Rabelo et al., 2023; Tomlinson et al., 2019). Fire mediates this effect: in the absence of grazing, fuel load builds up through grass biomass, which increases the probability and intensity of fires, causing greater damage to woody vegetation. Hence, grazing further exacerbates woody encroachment by removing the fuel load that would have otherwise served to keep woodland at bay through burning.

A precise understanding of the ecology of the system is needed to understand the context of decision making related to livestock production. The positive feedback loop between grazing, fire, and woody production has been modeled explicitly (Van Langevelde et al., 2003; Van Langevelde, van de Vijver, Prins, & Groen, 2019). Van Langevelde et al. (2003) argue that the positive feedback effect drives the discontinuous changes in grass and woody biomass observed in savanna ecosystems: through disturbances such as overgrazing and drought, the

system can 'tip' from a situation in which grassland and woody vegetation coexist to a situation in which woodland dominates, from which it is difficult to return. A central implication of Van Langevelde et al. (2003) is that fire increases the resilience of the savanna by allowing for an additional savanna equilibrium where there had only been a woodland equilibrium in the absence of fire.

Woody encroachment would not be a problem were it not for the economic incentives attached to livestock production, which are not yet explicitly taken into account by Van Langevelde et al. (2003, 2019). The main question considered in this paper is how the resilience of savanna ecosystems against woody encroachment is affected by time-constant livestock and fire management, assuming linear preferences over herd size and herd extraction. Utility is maximized over fire frequency, offtake, and grazing time, subject to the system being in a (locally) stable steady state. We then determine the resilience of the resulting savanna regime, adding a dynamic dimension to an otherwise static optimisation problem.

We find that the resilience of the savanna regime generally decreases with livestock prices if time-constant levels of cattle offtake and grazing intensity are chosen optimally and in conjunction. Higher livestock prices incentivize higher grazing intensity to enable higher cattle offtake levels, leading to decreased resilience against woody encroachment. This is in contrast with other rangeland management papers, which often look at cattle offtake in isolation and find that the resilience of the savanna is improved with higher livestock prices, as it incentivizes the alleviation of pressure on the savanna by taking animals out of the system (Langelaan, Van Langevelde, & Wagener, 2026; Stigter & Van Langevelde, 2004). We find that the grass biomass level resulting from time-constant optimal livestock management is unaffected by livestock prices under general conditions related to the herd population model. Finally, we find that more frequent fire use makes the resilience of the savanna more sensitive to livestock prices.

2 Theoretical Framework

2.1 Socio-economic drivers of woody encroachment

The areas affected by woody encroachment are tropical savanna ecosystems which are too humid to risk desertification, but too dry to develop into closed-canopy tropical forests. Instead, these areas develop into a dry, woodland ecosystem consisting of short trees and shrubs. Such savannas are found all over the world: they cover more than half the area of Africa and Australia, 45% of South America, and 10% of India and Southeast Asia (Werner, 1991, as cited in Scholes and Archer, 1997). They are characterized by a Mean Annual Precipitation (MAP) between 350 mm and 1000 mm (Sankaran et al., 2005), with soil types ranging from clayey (little groundwater runoff) to sandy (high water runoff). Woody encroachment is facilitated by higher rainfall levels and sandier soils, as woody plant species have a competitive advantage over grasses under these conditions (Knoop & Walker, 1985). We are primarily interested in socio-economic factors contributing to woody encroachment, which we will briefly review in the following.

2.1.1 Livestock production

In the case of the savannas of southern and eastern Africa, livestock holding has been the principal means of subsistence since before European settlement in the nineteenth century. Traditionally, however, these savannas were grazed by many different species of native ungulate and by cattle of semi-nomadic herdsmen, with much lower intensity (Barnes, 1979). Grazing was irregular and dependent on rainfall, and grazing areas were, on average, only lightly stocked by cattle, due to the migratory behavior of the herdsmen and their tribes, the latter of which were, moreover, smaller in number (Barnes, 1979).

Following European settlement from the mid-1800s onwards, savanna rangelands in especially eastern and southern Africa were subjected to increased strain by the introduction

of commercial ranching, in which grazing areas were fenced off and artificial watering points were introduced, allowing – at least temporarily – for increased cattle stocks [SOURCE] (Walker & Janssen, 2002). Although there had always been an incentive to keep livestock numbers as high as possible as a symbol for wealth and prestige, these developments incentivized excessive stocking rates in the short run. This has led to the degradation of African savanna rangelands in the long run, with woody encroachment being one of the main forms of degradation (Walker & Janssen, 2002).

Currently, livestock production is still the main form of agricultural production in the savanna ecosystems of western, eastern, and southern Africa. Traditional, rotational pastoralism still dominates in West Africa, while it is also active, sometimes in direct competition with commercial ranchers, in East Africa. In southern Africa, livestock production is almost exclusively commercial and static (Greyling, Vink, & Mabaya, 2015). Subsistence farmers and commercial smallholders generally have larger herds, while large commercial farmers are more interested in cattle offtake (Zantsi, Cloete, & Möhring, 2021). The main levers of livestock management are offtake strategies and grazing time [SOURCE].

2.1.2 Fire

It is argued that rangeland degradation has been further exacerbated by increased fire suppression efforts since the early twentieth century, especially in southern and eastern Africa (Belayneh & Tessema, 2017; O'Connor et al., 2014; Veenendaal et al., 2021). Anthropogenic burning has been common practice among traditional herdsmen operating in savanna rangelands for centuries (Bowman et al., 2009), as an instrument of fuel reduction to avoid more devastating wildfires (Walker, Ludwig, Holling, & Peterman, 1981) and as a way to manage wildlife and stimulate pasture regeneration (Bowman et al., 2009). Colonial governments in southern Africa held a negative view on fire and actively sought to suppress it through legislation (O'Connor et al., 2014). This negative view is argued to be rooted in uninformed

European attitudes towards fire as a primarily destructive force, haphazardly applied to the context of African savannas (Pyne & Goldammer, 1997). Although it was an attitude inappropriate for the rotational and nomadic way of life of traditional savanna inhabitants, it is becoming more appropriate for the increasingly adopted static form of living introduced by Europeans (Pyne & Goldammer, 1997). Relatedly, the potential of prescribed burning to suppress woody vegetation is further reduced by the increased unpredictability of fire through the increased variability of droughts due to climate change.

Increased democratization in southern and eastern Africa from the 1990s onward has led to the reinstatement of some of the traditional fire practices. Fire is again widely used as a means to suppress woody vegetation, both on rangelands and in wildlife reserves (Hudak, Fairbanks, & Brockett, 2004). Currently, the annual area burned in savannas is substantial and accounts for 75% of the total annual burned area of the Earth's surface, although savannas only account for 20% of the global landmass (Andela & Van der Werf, 2014; Archibald, 2016). Only about 10% of the fires are lit through 'natural' incidents such as lightning.

Still, fire management objectives vary across savannas and are sometimes even in conflict with one another within a particular region. Relatively recent concerns about greenhouse gas emissions are added to the mix of pros and cons of fire and add a global dimension to a formerly regional problem (Archibald, 2016).

2.2 Modeling grazing-induced woody encroachment in savanna ecosystems

Woody encroachment of tropical savannas has been modeled in several ways. Many current models refer back to the seminal work of Walker et al. (1981) and Walker and Noy-Meir (1982), who model the co-existence of woody vegetation and grasses typically observed in savanna ecosystems by invoking Walter's two-layer hypothesis (1971). Under this hypothesis, grasses and woody vegetation share infiltrated water in the upper layer of the soil, whereas woody vegetation alone has access to a deeper subsoil layer. The model illustrates that over-

grazing can exogenously cause woody encroachment. For low grazing levels, the system has two locally stable equilibria: a savanna equilibrium characterized by a co-existence of woody vegetation and grasses, and a woodland equilibrium dominated by woody vegetation. Once the grazing level is increased beyond a certain threshold, the savanna equilibrium vanishes. As seen in practice, it is then difficult to return to the mixed equilibrium, even after livestock is removed.

Van Langevelde et al. (2003, 2019) extend the model by Walker et al. (1981) to fire-driven savanna rangelands. The model explicitly incorporates the positive feedback loop between fire and grazing: grazing reduces herbaceous biomass, which lowers the fuel load for fires, leading to less damage to woody plants. On sandier soils with higher rainfall, this results in an open field for woody vegetation, driving out herbaceous biomass even further. Through this effect, fire enables the co-existence of two stable equilibria – one savanna state, one woodland state – where, without fire, there would have been only woodland.

Management of the savanna system, in the form of grazing intensity or burning, is strictly exogenous in the model by Van Langevelde et al. (2003, 2019), and offtake is not incorporated. In other savanna models, however, efforts have already been made to incorporate economic incentives. Perrings and Walker (1997) provide a savanna model with logistic growth functions for herbaceous, woody, and grazer biomass, in which welfare depends on revenues from grazer offtake, herd maintenance costs, and access charges to the range. In contrast to Van Langevelde et al. (2003, 2019), fire is not entirely exogenous: it ignites once the fuel load in the form of grass biomass is exceeded beyond a certain threshold. Optimal management paths show cyclical trends in offtake as well as in the vegetation and grazer stocks. Janssen, Anderies, and Walker (2004) find similar results for savannas in New South Wales, Australia. These results are extended in Perrings and Walker (2004), in which it is found that it can be optimal to shift between the previously found, cyclical 'conservation' strategy and a different, 'exploitation' strategy, depending on discount rates. A systematic analysis of the qualitative and quantitative effects of time-fixed livestock management of

fire-driven tropical savannas is, however, lacking, while such efforts have been undertaken for semi-arid grazing systems (Langelaan et al., 2026).

Modeling resilience

Both Janssen et al. (2004) and Perrings and Walker (2004) highlight the importance of maintaining some measure of resilience in optimal rangeland management. As defined by Holling (1973), resilience is a measure of a system's persistence and ability to absorb change and disturbance and still maintain the same relationships between populations or state variables. In the cases of Janssen et al. (2004) and Perrings and Walker (2004), this measure is represented by the size of the stability domain corresponding to some attractor.

In a recent paper by Dakos and Kéfi (2022), resilience is defined more formally, specifically for systems with multiple attractors. They define it as the distance from a stable equilibrium to the threshold of its basin of attraction. This definition then spawns multiple resilience measures, depending on the measure of 'distance' used. The most straightforward measure and the one used in this paper is the distance from an attractor to the threshold of its basin of attraction in only one of the system's dimensions (see Figure 3 below). This is generally unequal to the minimal Euclidean distance from the attractor to the threshold of its basin of attraction. In systems with one stock, the two measures of resilience are equivalent: they are simply the difference between one attractor and the repeller separating its basin of attraction from another attractor's basin of attraction. In systems with two stocks and two attractors, the measure of resilience used in this paper is the distance between one of the attractors and the stable manifold of the saddle equilibrium between the two attractors (fig. 3b). For higher-dimensional systems with multiple attractors, the measure of resilience becomes difficult to illustrate, as basins of attraction are at least three-dimensional, and are separated by surfaces instead of curves.

An important takeaway from Dakos and Kéfi (2022) is that resilience is necessarily a property of a locally stable equilibrium. As such, when we apply this measure of resilience

to the context of savannas facing woody encroachment as modeled in Van Langevelde et al. (2003, 2019), we look at the resilience of a locally stable savanna equilibrium. Resilience then amounts to the size of a perturbation to the savanna equilibrium in either the grass, wood, or grazer stock that leads to the system's convergence to the woodland equilibrium. If there is no stable savanna equilibrium, there is no resilience. Hence, resilience is created by the use of fire, which establishes conditions under which a stable savanna equilibrium can exist alongside a stable woodland equilibrium.

In this paper, we will extend the work of Van Langevelde et al. (2003, 2019) by investigating the sensitivity of savanna resilience to time-constant optimal livestock management in the form of grazing intensity and extraction. The current analysis provides a tropical savanna counterpart to the analysis of the resilience of semi-arid grazing systems undertaken by Langelaan et al. (2026) and Vignal, Baudena, Mayor, and Sheratt (2023), while in addition taking into account the effect of grazing time, which is not studied in said papers.

3 Model

3.1 Ecosystem Dynamics

We build on the model by Van Langevelde et al. (2003, 2019). The three state variables that we are interested in are the biomass densities of grass (H), wood (W), and grazers (G), all measured in grams per square meter.

Following the two-layer hypothesis (Walter, 1971), which states that grasses and woody vegetation take root in different layers of the soil, total water infiltration w_{in} is divided between the upper grass root layer the lower tree root layer. Water in the topsoil layer is denoted by w_t, and water in the subsoil layer by w_s. Following Van Langevelde et al. (2003), water that percolates to the lower layer is modeled as

$$w_s = \max\{\alpha(w_{in} - \beta), 0\} \tag{1}$$

where β is the soil moisture content in the grass root zone above which water starts to percolate to the tree root zone. Water in the topsoil layer is the residual infiltrated water that does not percolate to the subsoil layer:

$$w_t = w_{in} - w_s \tag{2}$$

We depart from Van Langevelde et al. (2003, 2019) to a minor extent when we model water use in the grass root zone. Van Langevelde et al. (2003, 2019) adopt the model of Walker et al. (1981) and Walker and Noy-Meir (1982), in which topsoil water is split between uptake by grasses, uptake by woody vegetation and evaporation. The relative utilization of topsoil water per unit of grass biomass U_H is

$$U_H = \frac{\theta_H}{\theta_H H + \theta_W W + e} \tag{3}$$

where θ_H is the rate of water uptake per unit biomass of grass vegetation, and e the loss of water by evaporation. Analogously, the relative utilization of topsoil water per unit of woody biomass U_W is then

$$U_W = \frac{\theta_W}{\theta_H H + \theta_W W + e} \tag{4}$$

where θ_W is the rate of water uptake per unit biomass of woody vegetation. The following relation should hold:

$$w_t = U_H H + U_W W + e \tag{5}$$

Van Langevelde et al. (2003, 2019) alter this equation by replacing evaporation e with water in the subsoil layer w_s. However, this is inconsistent with the definition of w_t as the amount of infiltrated water that is left after percolation to the subsoil layer.

We propose to model the relative utilization of topsoil water as done by Walker et al. (1981) and Walker and Noy-Meir (1982), with the simplification that evaporation is zero. We consider this admissible since Walker et al. (1981) have argued that the effect of evaporation on the dynamics of the system is insignificant.

The rates of change in herbaceous and woody biomass per year are then represented by

$$\dot{H} = r_H w_t \frac{H}{H + uW} - d_H H - \tau c_H G H - k_H n H, \qquad H \geq 0 \tag{6}$$

$$\dot{W} = r_W \left[w_t \frac{uW}{H + uW} + w_s \right] - d_W W - k_W n a H W, \qquad W \geq 0 \tag{7}$$

All parameters and their associated interpretation, unit, and reasonable value range are given in Table 1. The first term in equations 6-7 represents water use. Depending on relative vegetation biomass and relative rates of water uptake, denoted by $u = \frac{\theta_W}{\theta_H}$, water in the topsoil layer w_t is divided over herbaceous vegetation and woody vegetation, whereas woody vegetation has exclusive access to water in the subsoil layer w_s. Each vegetation type has a different water use efficiency r_H or r_W, and grasses have a comparative advantage over woody plants in this respect ($r_H > r_W$) as well as in water uptake rate ($u < 1$).

Both vegetation types have their own natural death rate, d_H and d_W, and both are affected by fire, as captured by the last term of both equations. Fire frequency is denoted by n, and can range between 0 (no fires) to 1 (one fire per year). In contrast to other savanna models, fire is kept strictly exogenous. We argue that this modeling choice is justified since we are dealing with a model that spans a large surface area over a long horizon, in which, on average, it will always be possible to light a sufficiently destructive fire at some point within a year. This is a different setting compared to, for instance, Perrings and Walker (2004), who look at changes between months. The regime shifts Perrings and Walker (2004) find beyond the seasonal cycles of dry and wet periods are what we are interested in. Specific losses due to fire in grasses and woody vegetation are denoted by k_H and k_W, and losses in woody biomass due to fire increase with fuel load, in the form of grass biomass. The increase in fire intensity due to grass biomass is represented by a.

Finally, grass biomass is affected by grazing. Grazing is incorporated by a linear functional response term containing grazer biomass G and a biophysical consumption coefficient c_H, which captures how much grass grazers consume per unit of grazer biomass per year. We add a factor τ to the model by Van Langevelde et al. (2003, 2019), which we shall henceforth call 'grazing intensity', which regulates how long the herd is allowed to graze. If $\tau = 0$, the animals are kept 'in the pen', in which they will not affect the pasture. The situation in which $\tau = 1$ represents the 'unmanaged' situation studied in Van Langevelde et al. (2003, 2019) in which animals roam free. For values of $\tau \in (0, 1)$, grazing time is restricted. We argue that $\tau = 1$ is not necessarily an upper bound to τ in the managed setting, as the animals could find their way to greener pastures more easily when they are guided by herdsmen, and are thus able to consume more grass than in the unmanaged setting.

The grazing term returns in the rate of change in herbivore dynamics, based on Van Langevelde et al. (2019):

$$\dot{G} = \tau c_H e_H G H - d_G G^2 - E, \qquad G \geq 0 \tag{8}$$

Here, e_H represents the conversion efficiency of consumed plant biomass into herbivore biomass, and d_G represents the loss rate of grazer biomass due to mortality. The choice of a quadratic rather than linear mortality rate is justified by an observed increased mortality at high cattle-densities [SOURCE]. Finally, E represents herbivore offtake, or livestock that is removed from the population to be sold on the market. As we keep E fixed in our analysis, we impose that $\dot{G} = 0$ for $G = 0$ to ensure $G \geq 0$.

3.2 Economic incentives

The savanna rangelands are inhabited by different economic agents. We will restrict our attention to two main types: traditional subsistence farmers, who value large herd sizes while also extracting part of their herd for their own consumption, and large, commercial farmers, who are principally interested in herd offtake to be sold on the market. These two types constitute the two ends of the spectrum describing average preferences of livestock holders within the system. These preferences are represented by the following utility function

$$U(G, E; p) = G + pE \tag{9}$$

The situation in which $p = 0$ corresponds to the subsistence end of the spectrum, whereas we move farther and farther to the commercial end of the spectrum as we increase p.

We look at the maximization of utility over the relevant management parameters, subject to the system being in equilibrium:

$$\max_{n,\tau,E} U(G, E; p) \quad \text{s.t.} \quad \dot{H} = \dot{W} = \dot{G} = 0 \tag{10}$$

This problem is equivalent to the optimal control problem with zero discounting.

	Interpretation	Units	Values	Sources
Stocks				
H	grass biomass	g/m^2	$0-400$	
W	woody biomass	g/m^2	$0-1000$	
G	herbivore biomass	g/m^2	$0-30$	
Management parameters				
n	frequency of fires per year	1/yr	$0-1$	
τ	grazing intensity		$0-1.5$	
E	grazer offtake	g/m^2yr	$0-2$	
Physical parameters				
w_{in}	annual amount of infiltrated water	mm/m^2yr	$0-1000$	
β	soil moisture content in the grass root zone above which water starts to percolate to the tree root zone	mm/m^2yr	$200-500$	
w_t	rate of moisture recharge in the topsoil layer	mm/m^2yr	$w_{in}-w_s$	
w_s	rate of moisture recharge in the subsoil layer	mm/m^2yr	$\max\{\alpha(w_{in}-\beta),0\}$	
α	proportion of excess water that percolates		0.8	
Grass parameters				
r_H	water use efficiency of grasses	g/mm	1.0	
U_H	proportion of water uptake per unit grass biomass	m^2/g	See Eq. (3)	
θ_H	rate of water uptake per unit grass biomass	mm/g yr	1.0	
d_H	specific loss of grass biomass due to mortality	1/yr	0.9	
k_H	specific loss of grass biomass due to fire	1/yr	0.1	
Wood parameters				
r_W	water use efficiency of woody vegetation	g/mm	0.5	
U_W	proportion of water uptake per unit woody biomass	m^2/g	See Eq. (4)	
θ_W	rate of water uptake per unit woody biomass	mm/g yr	0.6	
u	ratio of the rate of uptake of water by woody vegetation to that by grasses		0.6	
d_W	specific loss of woody biomass due to mortality	1/yr	0.4	
k_W	specific loss of woody biomass due to fire expressed per unit energy	1/W	0.01	
a	coefficient for the increase in fire intensity with grass biomass	$W/m^2/g$	0.5	
Herbivore parameters				
c_H	consumption coefficient of grass biomass by grazers	$m^2/g/yr$	0.02	
e_H	conversion efficiency of grass biomass by grazers		0.05	
d_G	specific loss of herbivore biomass due to mortality	1/yr	0.02	

Table 1: List of parameters and variables used with their interpretation, units, and estimated values. Parameter values are taken from Van Langevelde et al. (2003, 2019) and references therein.

4 Model analysis under exogenous management

4.1 The grass-wood system without grazers

We begin our analysis by an examination of the grass-wood system without grazers (eqs. (6)-(7), $G = 0$), as it represents the status quo of the system without livestock production. Geophysical conditions under which this system has a stable equilibrium with positive grass biomass, represented by levels of water infiltration w_{in} and percolation threshold β, constitute the boundary conditions for livestock production in the full system with dynamic grazers. In particular, the grass-wood system has three types of stable equilibria, as defined in Definition 4.1.

Definition 4.1 (Stable equilibrium types)**.**

- A **grassland** equilibrium is an equilibrium $(\bar{H}, \bar{W})$ of the grass-wood system (eqs. 6-7) such that $\bar{H} > 0$ and $\bar{W} = 0$.
- A **savanna** equilibrium is an equilibrium $(\bar{H}, \bar{W})$ of the grass-wood system (eqs. 6-7) such that $\bar{H} > 0$ and $\bar{W} > 0$.
- A **woodland** equilibrium is an equilibrium $(\bar{H}, \bar{W})$ of the grass-wood system (eqs. 6-7) such that $\bar{H} = 0$ and $\bar{W} > 0$.

Only equilibria with a positive grass biomass are suited for livestock production, and will be called 'grazing equilibria'.

Definition 4.2 (Grazing equilibrium)**.** A grazing equilibrium is an equilibrium $(\bar{H}, \bar{W})$ of the grass-wood system (eqs. 6-7) such that $\bar{H} > 0$.

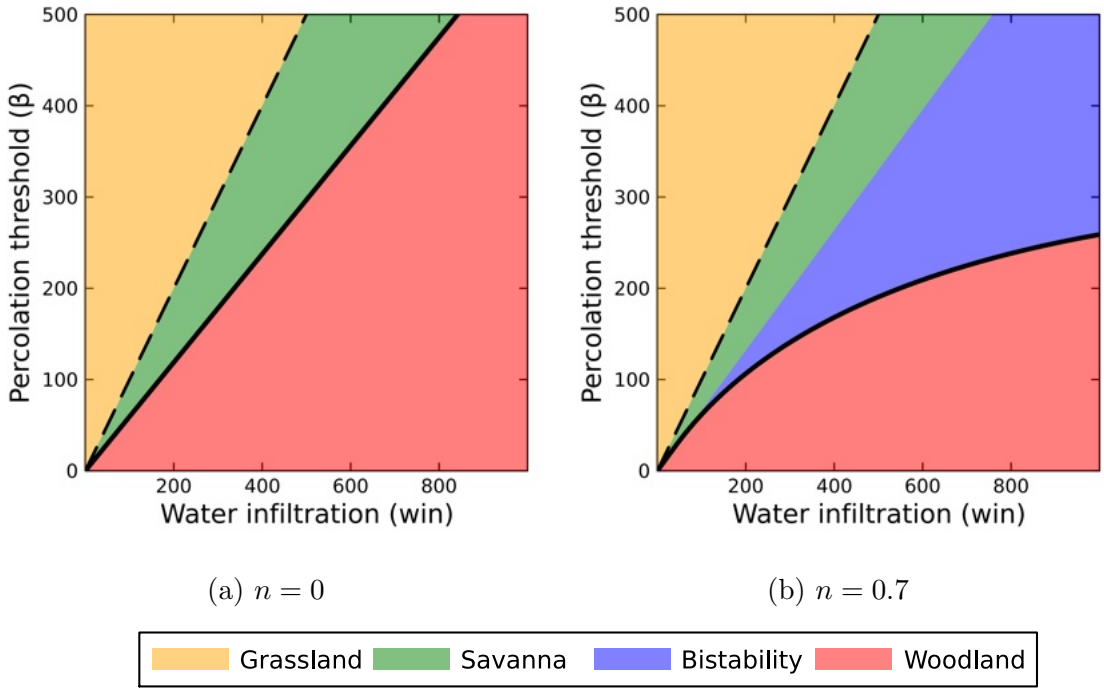
In the absence of fire, the system will have a single, globally stable equilibrium (Van Langevelde et al., 2003). Which type of equilibrium results, depends on geophysical conditions w_{in} and β. Grassland dominates in case there is no percolation ($w_{in} < \beta$), in which case all water

stays in the topsoil layer, which is shared between grasses and woody vegetation. Grasses are assumed to be more competitive than woody vegetation: they both take up more water than woody vegetation ($\theta_H > \theta_W$) and convert water into biomass more efficiently than woody vegetation ($r_H > r_W$), outweighing the relatively higher death rate of grasses ($d_H > d_W$). As soon as there is percolation to the subsoil layer ($w_{in} > \beta$), there is niche separation between the grasses and the woody vegetation. Woody vegetation is then able to persist, as it has exclusive access to subsoil water. This either results in a savanna equilibrium (low percolation) or a woodland equilibrium (high percolation).

Figure 1a maps the three globally stable equilibrium types in the absence of fire onto geophysical conditions. Figures (2a)-(2c) show the associated phase diagrams corresponding to each equilibrium type.

Van Langevelde et al. (2003, 2019) have shown that, in the presence of fire, a bistable configuration emerges in which two locally stable equilibria coexist, a savanna equilibrium and a woodland equilibrium. The configuration exists under some geophysical conditions at which either a unistable savanna or a unistable woodland existed in the absence of fire. Figure 1b maps this bistable configuration onto geophysical conditions, along with the unistable configurations, for a specific fire frequency. The bistability region emerges mostly at the expense of the woodland region, making formerly unproductive conditions potentially productive for raising livestock. The phase diagram associated with the bistable case is shown in Figure 2d.

The savanna equilibrium in the bistability region is, however, vulnerable. A large negative shock in the grass stock, due to e.g. a temporary drought, might shift the system to the woodland equilibrium. In contrast with the unistable savanna configuration, less than the entire grass stock needs to be destroyed before the system shifts to a woodland, making it hard for a rangeland manager to predict whether the savanna will be able to bounce back after a shock. The largest magnitude of a shock that can be withstood before the system shifts is given by the distance of the savanna equilibrium to the boundary of its basin of



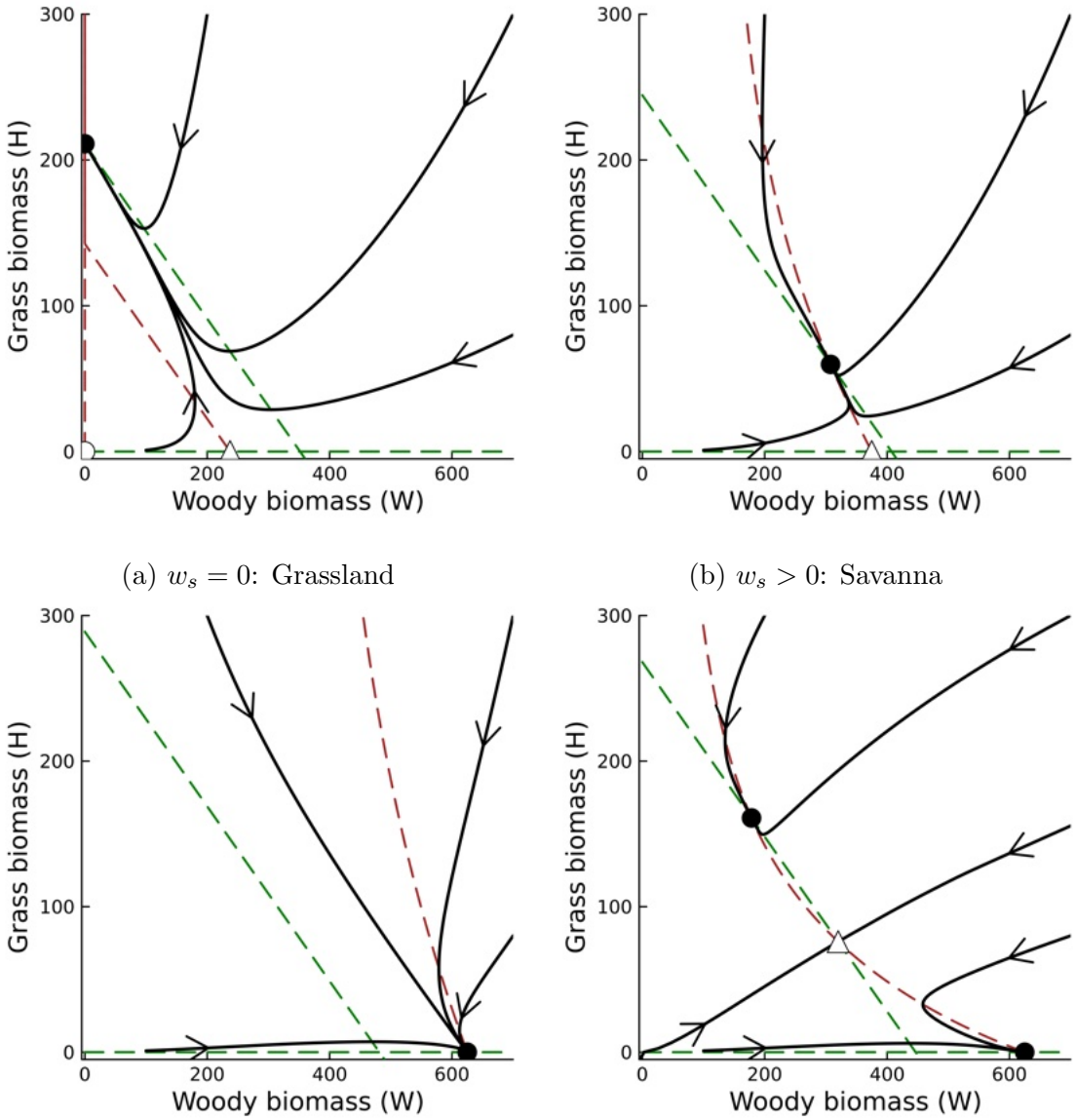
(a) $n = 0$ (b) $n = 0.7$

Figure 1: Two-dimensional bifurcation diagrams in w_{in}, β parameter space representing rainfall and soil type combinations admitting different vegetation configurations in the grass-wood system without grazing ($G = 0$), without fire (a), and with moderate fire (b). Parameter values are as in Table 1. The dashed line represents the percolation threshold $w_{in} = \beta$. The area above the solid line represents conditions suitable for livestock production.

attraction. The basin of attraction of the savanna equilibrium in the grass-wood system is given by the stable manifold, or separatrix, of the saddle equilibrium between the savanna and woodland equilibria. Only negative shocks in the grass biomass and positive shocks in the wood biomass can trigger a regime shift from savanna to woodland (Figure 3). As only a negative shock in the grass stock has a relevant real-world interpretation, we shall limit our attention to resilience to this type of shock. We shall call the corresponding resilience measure 'H-resilience'.

Definition 4.3 (H-resilience; grass-wood system)**.** The H-resilience of a grazing equilibrium is equal to the minimal negative shock in the H-stock to the grazing equilibrium after which the system converges to a woodland equilibrium.

In the unistable case, H-resilience will be equal to the equilibrium value of the grass stock.



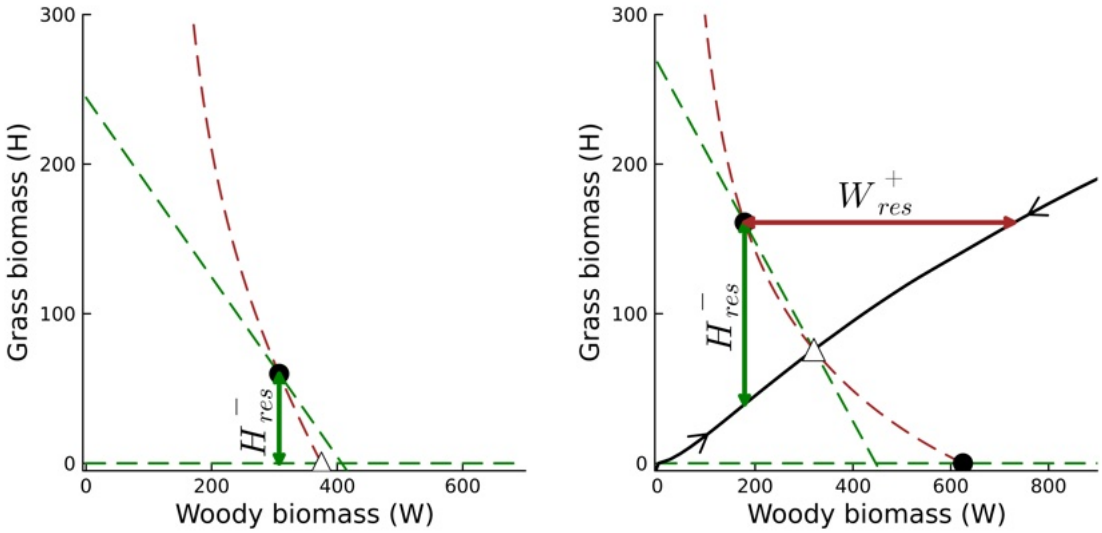
(a) $w_s = 0$: Grassland

(b) $w_s > 0$: Savanna

(c) $w_s \gg 0$: Woodland

(d) $w_s \gg 0$, $n > 0$: Bistability

Figure 2: Phase diagrams showing trajectories, equilibria (solid circle: stable, open circle: unstable, triangle: saddle) and nullclines (dashed green: $\dot{H} = 0$; dashed red: $\dot{W} = 0$) for the grass-wood system with no grazers ($G = 0$) and parameter values as in Table 1, with $\beta = 200$ and $w_{in} \in \{190, 300, 500\}$, and $w_{in} = 500$, $\beta = 200$, $n = 0.7$ in (d).



(a) Unistable: resilient

(b) Bistable: vulnerable

Figure 3: Illustration of the measure of resilience used in the grass-wood system. Parameter configurations correspond to right column of Figure 2.

Preconditions for livestock management

We can then subdivide geophysical characteristics into three main regions relevant to livestock management. A certain configuration of geophysical conditions w_{in}, β and fire frequency n either leads to the existence of a globally asymptotically stable grazing equilibrium (either grassland or savanna), two locally asymptotically stable equilibria including one grazing equilibrium and one woodland equilibrium, or one globally asymptotically stable woodland equilibrium. The first configuration will be called 'Stable Grazing' (SG), the second 'Vulnerable Grazing' (VG), and the last 'Woodland' (W), as defined below.[1]

$$\text{SG} = \{(w_{in}, \beta, n) | \text{ there is a globally stable grazing equilibrium}\} \tag{11}$$

$$\text{VG} = \{(w_{in}, \beta, n) | \text{ there is a loc. stable grazing eq. and a loc. stable woodland eq.}\} \tag{12}$$

$$\text{W} = \{(w_{in}, \beta, n) | \text{ there is a globally stable woodland equilibrium}\} \tag{13}$$

[1]Throughout this paper, 'globally stable' will mean 'globally asymptotically stable' and 'locally stable' will mean 'locally asymptotically stable'.

The SG region can be seen as the union of the grassland and savanna region in Figure 1, the VG region corresponds to the bistability region, and the W region corresponds to the woodland region. Livestock production is feasible in the SG and VG regions. The union of these regions will thus be called 'Feasible Livestock Production' (FLP).

$$\text{FLP} = \text{SG} \cup \text{VG} \tag{14}$$

The analysis by Van Langevelde et al. (2003) suggests that if $(w_{in}, \beta, n_1) \in$ FLP, then $(w_{in}, \beta, n_2) \in$ FLP if $n_1 \leq n_2$. That is, the region of (w_{in}, β) that admits livestock production increases with n. Similarly, the woodland region in the (w_{in}, β)-plane decreases with n. We shall call combinations of (w_{in}, β) in the region $\mathcal{R}_{\text{W}} \cap \{n = 1\}$ the 'Always Woodland' (AW) region, as in this region can never be made feasible for livestock production through n or otherwise.

$$\mathcal{R}_{\text{AW}} = \mathcal{R}_{\text{W}} \cap \{n = n_{\max} = 1\} \tag{15}$$

Figure 4 illustrates SG, VG, and FLP for $n = 0.7$.

Finally, the FLP region is important for livestock management both in the system with fixed grazers (eqs. 6-7) as well as in the system with dynamic grazers (eqs. 6-8).

Lemma 1 (Livestock management in FLP region; grass-wood system)**.** For all (w_{in}, β, n) on the interior of the FLP region, there exists some $G > 0$ for which there is a grazing equilibrium in the grass-wood system (eqs. 6-7).

This is proven by the fact that the grazing equilibrium is hyperbolic on the interior of the FLP region, such that the implicit function theorem applies and there will be a grazing equilibrium for parameter values of G in a neighbourhood of $G = 0$, as the system is continuous and differentiable in G.

In the full system, the relevant equilibria are those in which the equilibrium grazer stock is positive, which will be called 'grazer equilibria':

Definition 4.4 (Grazer equilibrium)**.** A grazer equilibrium is an equilibrium $(\bar{H}, \bar{W}, \bar{G})$ of the full system (eqs. 6-8) such that $\bar{G} > 0$.

Grazer equilibria will also be persistent under perturbations in livestock parameters τ and E on the interior of the FLP region.

Lemma 2 (Livestock management in FLP region; full system)**.** For all $(w_{in}, \beta, n) \in$ FLP, There exists some (τ, E), $\tau > 0$, $E \geq 0$, for which there is a grazer equilibrium in the grass-wood-grazer system (eqs. 6-8).

The proof of Lemma 2 is analogous to the proof of Lemma 1.

In the sequel we shall limit our attention exclusively to geophysical conditions in the FLP region.

4.2 Ecosystem transitions induced by livestock production

4.2.1 Fixed grazer stock

As a step between the empty savanna and the savanna with dynamic grazers, it is useful to analyze the grass-wood system with a fixed grazer stock, in the absence and in the presence of fire. Figure 5 illustrates the effect of increasing the grazer stock on the grazing equilibrium and its associated H-resilience. Each column represents a different geophysical condition at $n = 0.7$: SG with no percolation (a), SG with percolation (b) and VG (c). The top row corresponds to the situation without fire, the bottom row to the situation with moderate fire. Combinations of (w_{in}, β) such that $(w_{in}, \beta, n = 0.7) \in \mathcal{R}_{\mathrm{W}}$ are left out, as for these combinations the woodland equilibrium is the only globally asymptotically stable equilibrium, with and without fire, and with and without grazing.

In the absence of fire, the grass stock decreases with grazer stocking level in SG, and is nonexistent in VG. In case of no percolation, the grassland transitions to woodland discontinuously, while the savanna transitions gradually to woodland in the case of percolation. An increase in the grazer stocking level is equivalent to an increase in the death rate of the

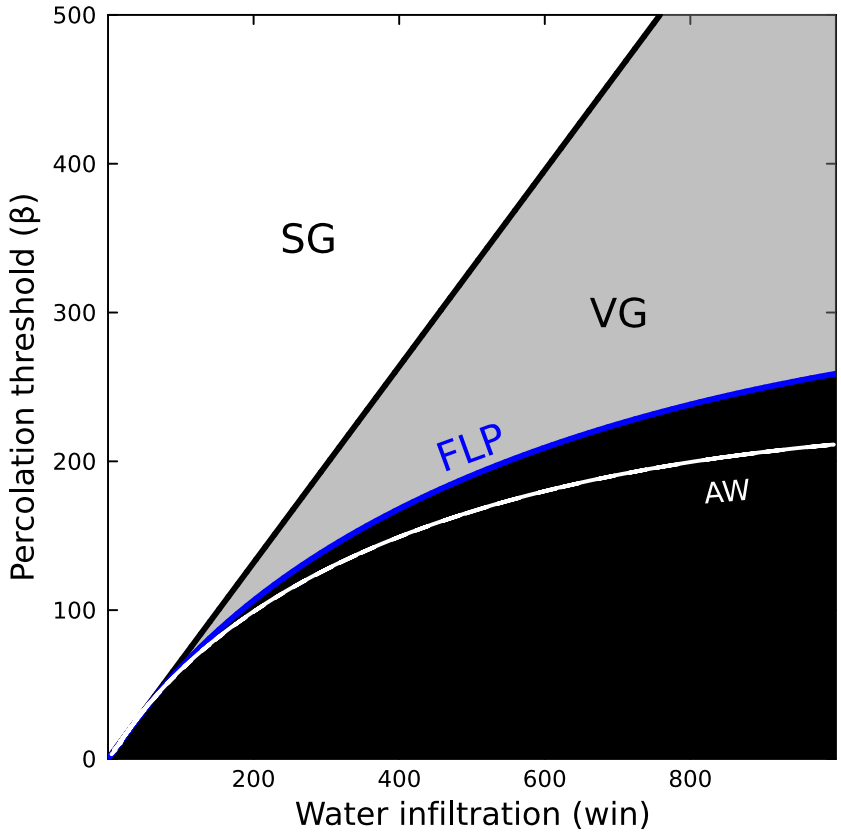


Figure 4: Stable Grazing (SG), Vulnerable Grazing (VG), Woodland conditions (black) in the grass-wood system, with $n = 0.7$ and $G = 0$. Other parameter values as in Table 1. Feasible Livestock Production (FLP): above blue line. Always Woodland (AW): below white line.

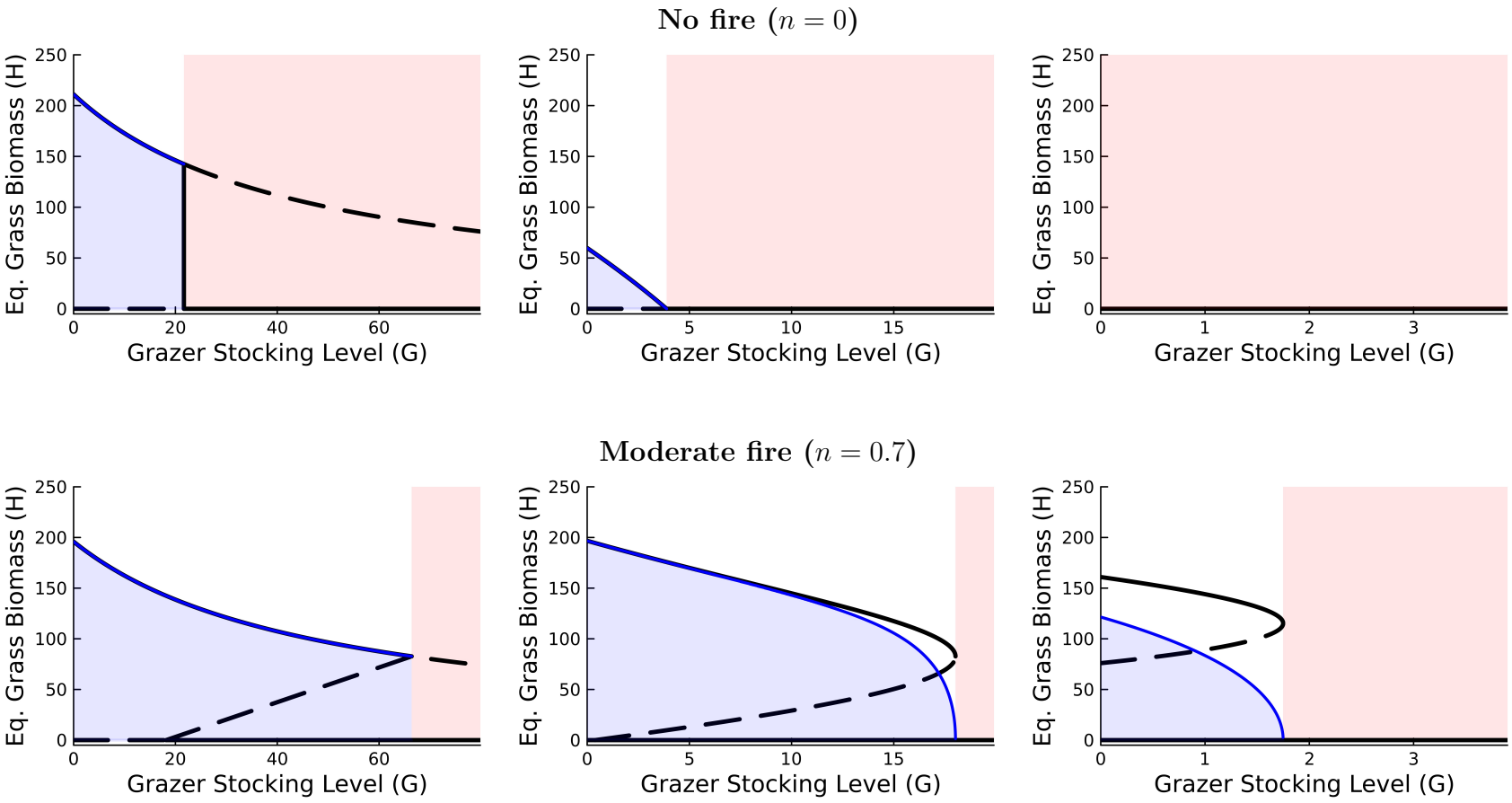
grasses; in the no percolation case, this means that at some grazing level G the dominant position shifts from the grassy vegetation to the woody vegetation, after which the regime shifts. In the percolation case, woody vegetation already has some dominance in the absence of grazing, and the grasses are pushed out more gradually. The H-resilience of the grazing equilibrium is equal to the grass stock in the grazing equilibrium, as it is the single, globally attracting equilibrium in the system.

Through fire use, the grazer stock until which a grazing equilibrium can be maintained is extended in all cases, by an interval in which both a grazing equilibrium and a woodland equilibrium are locally asymptotically stable. The grazing equilibrium discontinuously transitions to a woodland beyond the grazing threshold in each case. The transition is dis-

continuous in the sense that the system converges from a strictly positive equilibrium grass biomass to zero grass biomass when the stocking level exceeds the grazing threshold, making it hard for a rangeland manager to glean how close the system is to collapse by observing the grass stock, in case it can be assumed to be in equilibrium.

The H-resilience of the grazing equilibrium tracks the equilibrium grass stock in the SG case without percolation; in this case, the grazing equilibrium corresponds to a grass equilibrium, in which there is no woody biomass and no water in the subsoil layer, such that woody vegetation cannot establish a foothold, even if the grass equilibrium is subjected to a large shock. Hence, even if the system is bistable for some interval of grazer stock G, it does not affect the resilience of the system. In the SG case, the resilience of the grazing equilibrium gradually falls short of the equilibrium grass stock after tracking it for low grazer stock, while it is significantly lower than the equilibrium grass stock, even without grazers, in the VG case.

Importantly, fixed grazers create bistability between a grazing equilibrium and a woodland equilibrium, even in SG conditions. In addition, although H-resilience decreases with the grazer stock under all conditions, the gap between H-resilience and equilibrium grass stock is most significant in VG conditions.



(a) SG, $w_{in} < \beta$ (b) SG, $w_{in} > \beta$ (c) VG

Figure 5: Parameter-state diagrams showing ecosystem transitions by varying grazer stocking level, for three types of geophysical conditions at $\beta = 200$: Stable Grazing without percolation ($w_{in} = 190$) (a), Stable Grazing with percolation ($w_{in} = 300$) (b), and Vulnerable Grazing ($w_{in} = 500$) (c). Top row: no fire use ($n = 0$); bottom row: moderate fire use ($n = 0.7$). Other parameter values are as in Table 1. Color codes correspond to those in Figure 1. Overgrazing occurs in red regions (woodland); vulnerable livestock production occurs in blue regions (bistability); stable livestock production occurs in yellow (grassland) and green (savanna) regions.

4.2.2 Dynamic grazers with fixed grazing intensity τ

We now turn to the more realistic scenario in which grazer biomass varies with grass availability. The equilibria of the full system with dynamic grazers are given by the intersection between the equilibria of the grass-wood system studied previously and the solutions of nullcline $\dot{G} = 0$. In the case without extraction, the nullcline is given by

$$H = \frac{d_G G}{\tau c_H e_H} \tag{16}$$

and hence is linear in G. We can learn about the equilibria of the full system by superimposing the nullcline of the grazer equation onto the equilibria of the grass-wood system in Figure 5. Figure 6 illustrates this for $n = 0.7$ and critical levels of grazing intensity τ, for the same combinations of (w_{in}, β) as in Figure 5.[2] Figure 7 shows the total effect of grazing intensity τ on the equilibria of the full system, again for the same combinations of (w_{in}, β), at $n = 0.7$. It also shows the associated H-resilience, which is defined slightly differently for the full system compared to the grass-wood system.

Definition 4.5 (H-resilience; full system)**.** The H-resilience of a grazer equilibrium is equal to the minimal negative shock in the H-stock to the grazer equilibrium after which the system converges to an attractor that is not a grazer equilibrium.

The difference with H-resilience in the grass-wood system is that in the full system, the system may shift to a savanna equilibrium that does not support grazers after a shock, not just to a woodland equilibrium. The empty savanna equilibrium, however, is only locally stable when $E > 0$.

In the system with dynamic grazers, the qualitative difference between SG and VG conditions becomes apparent. In contrast with the fixed-grazer system, the dynamic-grazer

[2]Without fire, there will not be any discontinuous transitions brought on by variations in grazing intensity in the full system. Grazing stock is maximised in the no percolation case as soon as the nullcline intersects the grass-wood equilibrium at the kink. In the percolation case, the grazer stock is maximized for some interior τ. See 8a.

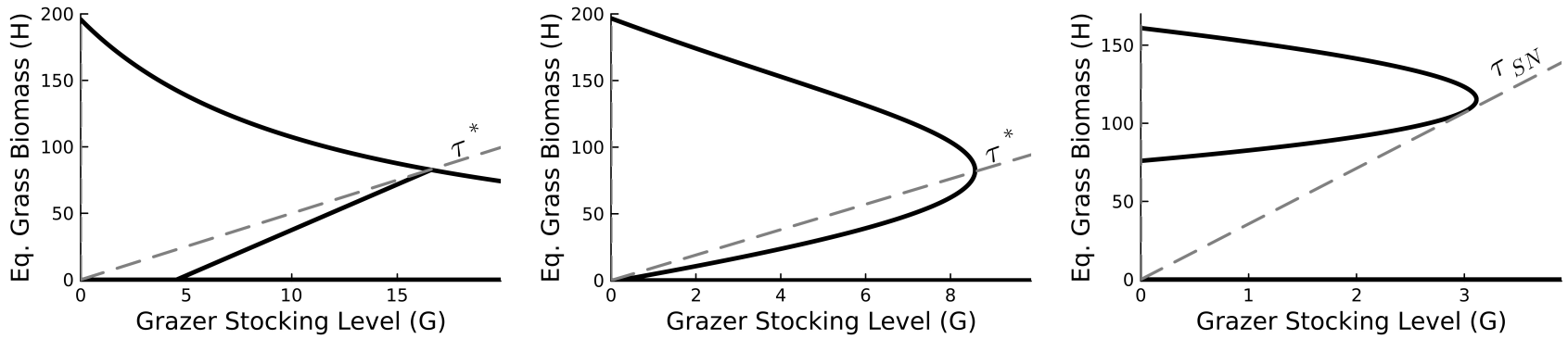
system cannot transition to woodland through livestock production under SG conditions. The grazer stock will converge to a level at which some positive level of grass biomass can be maintained, although both grazer and grass biomass will become very low for very high levels of grazing intensity (fig. 6a), or the globally stable grazer equilibrium will bifurcate into a globally stable limit cycle with positive grazer stock (fig. 7b). The woodland equilibrium is not stable under SG conditions, and its stability is not affected by grazing intensity.

Under VG conditions, the woodland equilibrium is locally stable and becomes globally stable when grazing intensity becomes excessive, through a saddle-node bifurcation of the grazer equilibrium. This is a case of what we shall call 'ecological overgrazing'.

Definition 4.6 (Ecological overgrazing)**.** Ecological overgrazing occurs when an excess in grazing intensity τ causes a (locally) stable grazer equilibrium to lose stability (only in case $E > 0$) or disappear (only in case $E = 0$).

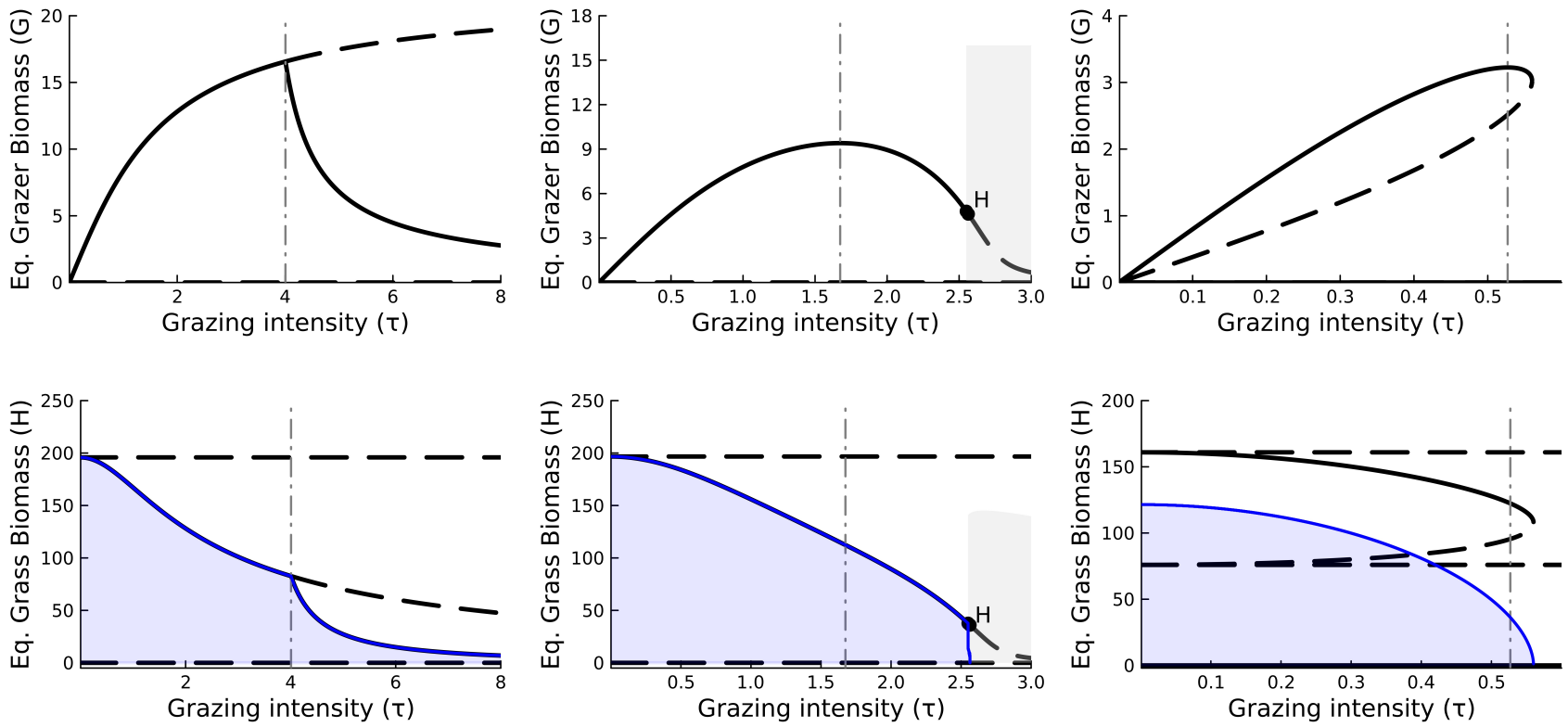
This should be distinguished from 'economic overgrazing/undergrazing', which is the case in which grazing intensity is set sub-optimally with respect to the utility maximization problem. The two types of overgrazing generally do not coincide when herd size is the only source of utility. Figure 7 shows levels of τ at which herd size is maximized. Under SG conditions, the herd-maximizing level of τ significantly exceeds the 'natural' grazing intensity of unmanaged livestock, $\tau = 1$. Under VG conditions, herd-maximizing grazing intensity and the grazing intensity at which the system shifts to a woodland are lower than the unmanaged level; the system is vulnerable and/or close to collapse for realistic values of τ.

Similar to the fixed-grazer case, Figure 7 shows that H-resilience is decreasing in grazing intensity. This is intuitive, as grazing intensity represents the degree of pressure or 'predation' by grazers on the grass. In the dynamic-grazer system, however, H-resilience completely tracks the equilibrium grass stock in both SG cases, although there is, again, a resilience gap under VG conditions.



(a) SG, $w_{in} < \beta$ (b) SG, $w_{in} > \beta$ (c) VG

Figure 6: Parameter-state diagrams showing intersections between equilibria of grass-state model (solid) with nullclines $\dot{G} = 0$ (dashed) for different τ, for three types of geophysical conditions at $\beta = 200$, $n = 0.7$: Stable Grazing without percolation ($w_{in} = 190$) (a), Stable Grazing with percolation ($w_{in} = 300$) (b), and Vulnerable Grazing ($w_{in} = 500$) (c). Other parameter values are as in Table 1. Overgrazing occurs in VG case when $\tau > \tau_{SN}$.



(a) SG ($w_{in} < \beta$) (b) SG ($w_{in} > \beta$) (c) VG ($w_{in} \gg \beta$)

Figure 7: Parameter-state diagrams showing G-equilibria (top) and H-equilibria (bottom), as well as H-resilience of the productive equilibria (bottom, in blue) of full model with dynamic grazers for three types of geophysical conditions at $\beta = 200$, $n = 0.7$: Stable Grazing without percolation ($w_{in} = 190$) (a), Stable Grazing with percolation ($w_{in} = 300$) (b), both leading to Stable or Stable Cyclical Production (S(C)LP), and Vulnerable Grazing ($w_{in} = 500$) (c), leading to Vulnerable Production (VP). Other parameter values are as in Table 1.

4.2.3 Dynamic grazers with extraction

It may be profitable to 'extract' animals from the herd to be sold on a livestock market. Extraction E naturally presses down the equilibrium value of the herd, which, in turn, alleviates pressure on the grass stock. Equilibrium herd biomass will therefore be decreasing in extraction, while equilibirum grass biomass will be increasing. Importantly, however, there is a lower bound to the grazing intensity τ that needs to be exceeded for a grazer equilibrium to be sustainable at any positive level of E. Overextraction occurs when a grazer equilibrium cannot be sustained at a certain level of extraction:

Definition 4.7 (Overextraction)**.** Overextraction occurs when an excess in grazer extraction E causes a (locally) stable grazer equilibrium to lose stability or disappear.

This type of unsustainable livestock management is analogous to the concept of 'overfishing' in fishery models. In this rangeland system, however, it is not as urgent a problem, as we do not assume any Allée effect by which the herd needs a minimal, positive level of biomass to survive, and it is unrealistic for a rangeland manager to extract their last animal. Within the current analysis, the concept of overextraction is useful as a limit beyond which a time-constant extraction strategy is not sustainable. As such, it applies more to the capacity to sustain itself of the herd than of the savanna, and has little to do with woody encroachment. The system will transition from a grazer equilibrium to an 'empty savanna' equilibrium rather than a woodland equilibrium, from which it is easy to return to a grazer equilibrium by lowering E.

Which levels of E constitute overextraction necessarily depends on grazing intensity τ, just as overgrazing levels of τ depend on the level of extraction E. When the system does not face overextraction or overgrazing, livestock production is sustainable. We distinguish a number of cases. We shall call combinations of (τ, E) for which there is a globally asymptotically stable grazer equilibrium 'Stable Production' (SP); combinations of (τ, E) for which there is a globally asymptotically stable limit cycle with positive grazers 'Stable Cyclical

Production' (CSP). The union of both sets is non-empty for all $(w_{in}, \beta, n) \in \mathcal{R}_{SG}$.

$$\mathcal{R}_{\text{SP}}(w_{in}, \beta, n) = \{(\tau, E)| \text{ grazer equilibrium globally stable}\} \tag{17}$$

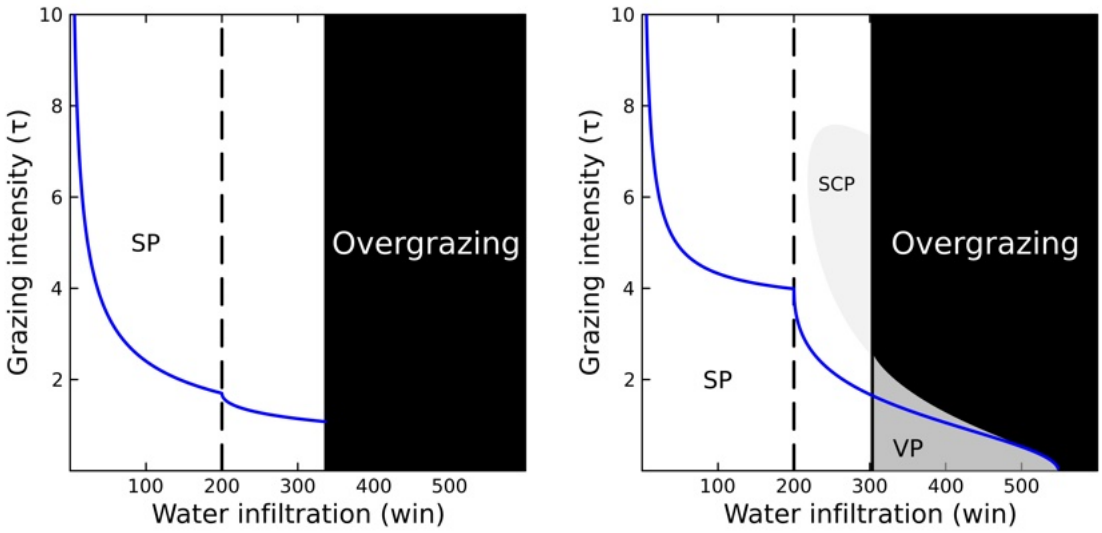
$$\mathcal{R}_{\text{SCP}}(w_{in}, \beta, n) = \{(\tau, E)| \text{ limit cycle with } G > 0, \text{ globally stable}\} \tag{18}$$

We then define livestock management levels (τ, E) as Vulnerable Production (VP) when there is at least one locally stable grazer equilibrium and one locally stable equilibrium with zero grazers and positive woodland at that combination of (τ, E), for some w_{in}, β, and n. This set is only non-empty for combinations of $(w_{in}, \beta, n) \in \mathcal{R}_{VG}$.

$$\mathcal{R}_{\text{VP}}(w_{in}, \beta, n) = \left\{(\tau, E)| \text{ eqs. } \bar{G}_1 > 0, \bar{G}_2 = 0, \bar{W}_2 > 0 \text{ loc. as. stable}\right\} \tag{19}$$

Any optimal combination of (τ, E) has to be in the union $\mathcal{R}_{SP} \cup \mathcal{R}_{VP}$ and any combination of (τ, E) outside the union of all three regions is either ecological overgrazing or ecological overextraction.

Figure 8 illustrates the different management outcomes for $n = 0$ and $n = 0.7$, keeping extraction E zero. Optimal choices of τ are superimposed in blue, in case equilibrium herd size is the only objective. For $n = 0$, livestock production is either stable (low water infiltration), or it is in the overgrazing region (high water infiltration). For moderate fire frequency $n = 0.7$, livestock production stays stable for water infiltration below the percolation threshold as grazing intensity is increased, from stable to cycle-stable for moderate percolation, and from vulnerable to overgrazing for high water infiltration. The optimal grazing intensity decreases with water infiltration, and approaches the cycle-stable and vulnerable region boundaries with increasing water infiltration, tracking it very closely for very high levels of water infiltration. As we are most interested in scenarios in which ecological overgrazing is possible, the remainder of the analysis will be focused livestock management under geophysical conditions in the VG region.



(a) $n = 0$ (b) $n = 0.7$

Figure 8: Classification diagram in water infiltration and grazing intensity for $\beta = 200$ and $n = 0$ (a) and $n = 0.7$ (b), showing Stable Production (SP), Cycle-Stable Production (SCP), Vulnerable Production (VP) and overgrazing levels of τ for each w_{in}. Herd-maximizing levels of grazing intensity are given by the blue line. Percolation threshold $w_{in} = \beta$ is given by the dashed line. Other parameters as in Table 1

Effect of livestock extraction E under vulnerable conditions

Figure 9 illustrates combinations of $(\tau, E) \in \mathcal{R}_{VP}$, under vulnerable geophysical conditions $(w_{in}, \beta, n) \in \mathcal{R}_{VG}$, along with overextraction production and overgrazing production. Herd-size maximizing levels of grazing intensity for each extraction level are again superimposed in blue.

Sustainable combinations (τ, E) form a right-skewed triangle, bounded from above by a saddle-node bifurcation and bounded from the right by a subcritical Hopf (dashed line) and saddle-node bifurcation. The outermost point of the triangle is a Bogdanov-Takens point, in which the saddle-node and Hopf bifurcation coincide. Within the triangle, there are three locally asymptotically stable equilibria: a savanna with grazers, a woodland equilibrium, and a savanna without grazers. Above the triangle, the grazer-savanna disappears, while it only loses stability to the right of the triangle (without gaining a stable limit cycle). The empty savanna and woodland equilibria are locally asymptotically stable for all $(\tau, E > 0)$

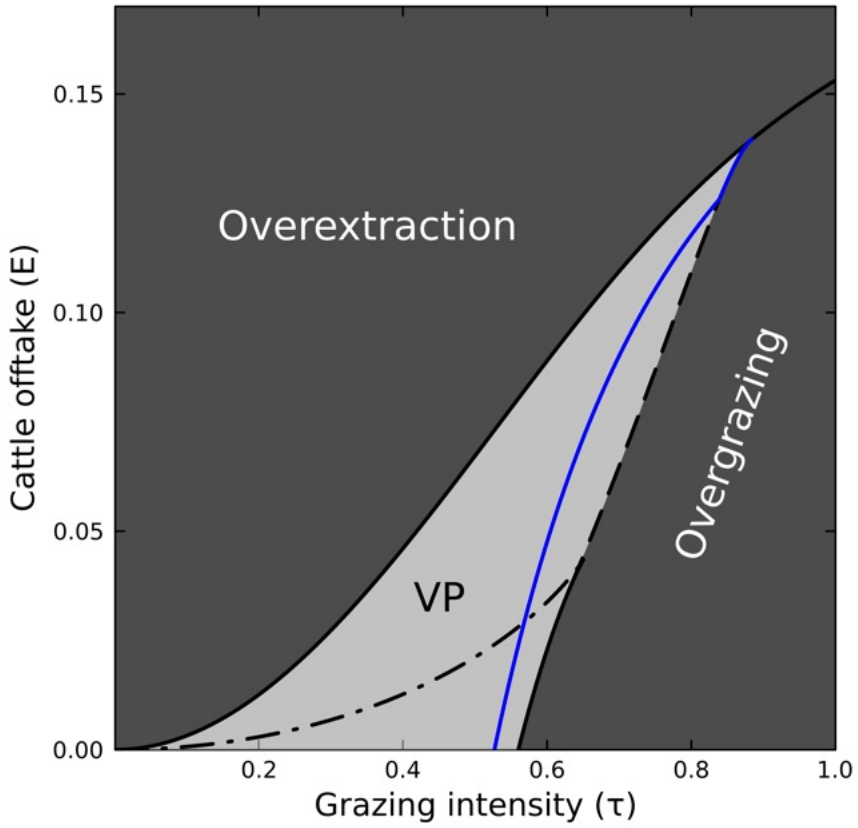
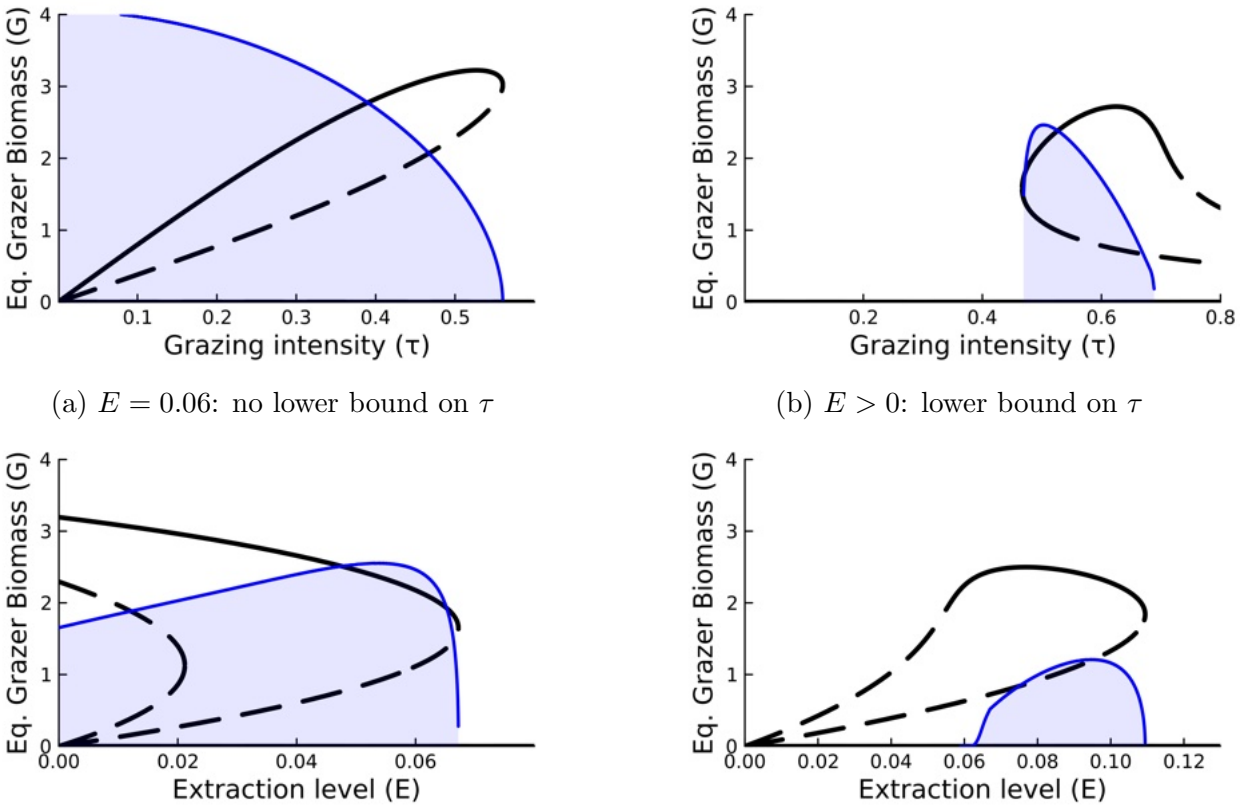


Figure 9: Classification diagram in grazing intensity and extraction for $\beta = 200$, $w_{in} = 500$, $n = 0.7$ ($(w_{in}, \beta) \in \mathcal{R}_{VG}(n = 0.7)$), showing Vulnerable Production (VP) levels (τ, E), and overextraction and overgrazing levels. Optimal grazing intensity for fixed level of E given by blue line. Saddle-node bifurcations given by solid and dash-dotted line. Hopf bifurcation given by dashed line. Other parameters as in Table 1.

when $(w_{in}, \beta) \in \mathcal{R}_{VG}$. Herd-maximizing grazing intensity is generally on the interior of the VP triangle, except at high extraction levels, where optimal grazing intensity coincides with the Hopf-bifurcation line. The productive equilibrium is only semi-stable here.

The triangle is skewed to the right: extraction allows for higher grazing intensity τ. Extraction is a double-edged sword, however, as it also requires a higher grazing intensity for the herd to be sustained to make up for lost biomass that would have otherwise contributed to the growth of the herd, imposing a lower bound on grazing intensity in addition to the upper bound. This is illustrated in the top row of Figure 10, along with the associated H-resilience of the grazer equilibria. For positive extraction, H-resilience is no longer



(a) $E = 0.06$: no lower bound on τ

(b) $E > 0$: lower bound on τ

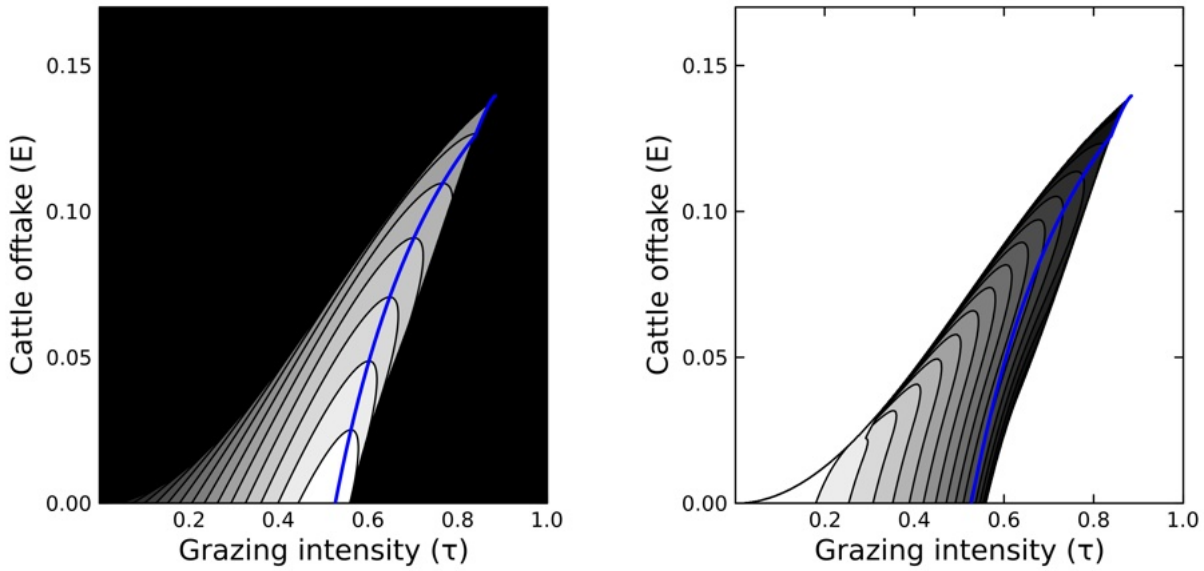
(c) $\tau = 0.5$: no underextraction

(d) $\tau = 0.7$: underextraction

Figure 10: Grazer biomass in equilibrium as a function of τ (a-b) and E (c-d) (black); H-resilience/30 (blue), for $n = 0.7$, $w_{in} = 500$, $\beta = 200$. Other parameter values as in Table 1.

monotonically decreasing in grazing intensity. The bottom row of Figure 10 shows that, conversely, a higher grazing intensity τ requires a positive level of extraction for the grazer equilibrium to be sustainable.

Figure 11 shows contour lines for the grazer biomass (a) and H-resilience (b) achieved in the grazer equilibrium that results from management decision (τ, E), again with grazer-maximizing levels of τ for each E superimposed in blue. There is a clear trade-off between H-resilience (high for generally low levels of τ) and herd size (high for generally high levels of τ). For higher levels of E, the herd-maximizing level of τ generally results in a lower level of resilience.



(a) Herd size

(b) H-resilience

Figure 11: Contour plots for herd size (a) and resilience (b), with optimal combinations of E and τ for varying p (blue). $w_{in} = 500$, $\beta = 200$, $n = 0.7$.

5 Resilience versus economic efficiency

We now turn to optimization of fixed livestock management and investigate its effect on the resilience of the system.

5.1 Extraction management with fixed grazing intensity

Existing rangeland management literature often focuses on extraction as the single management parameter, keeping grazing intensity fixed. The optimization problem then reads

$$E^*(p) = \arg\max_E U(G, E; p) = \arg\max_E G + pE \quad \text{s.t.} \quad \dot{H} = \dot{W} = \dot{G} = 0 \tag{20}$$

Depending on the grazing intensity and geophysical parameters, at $p = 0$, in which case benefits of extraction are zero and herd size is the only objective, E^* will be zero (low grazing intensity, e.g. fig. 10c) or positive (moderate grazing intensity, e.g. fig. 10d), or there will be no sustainable extraction (high grazing intensity). The direction of the effect is

the same when varying w_{in}, and the opposite when varying β and n. $E^*(p)$ will trace out a vertical line within the VP triangle from Figures 9 and 11. In the moderate grazing intensity case, $E^*(p = 0)$ is not necessarily on the overgrazing bound; we have seen in Figure 10d that the herd-maximizing level of E is away from it.

Figure 12 shows $E^*(p)$ along with the associated H-resilience and herd size. $E^*(p)$ is increasing in p. The resulting H-resilience is non-monotonic in p, but does not collapse to zero, which would be the case if $E^*(p)$ were equal to the overextraction threshold. $E^*(p)$ approaches the overextraction boundary in the VP triangle, but does not coincide with it for finite p. Herd size is non-increasing in p.

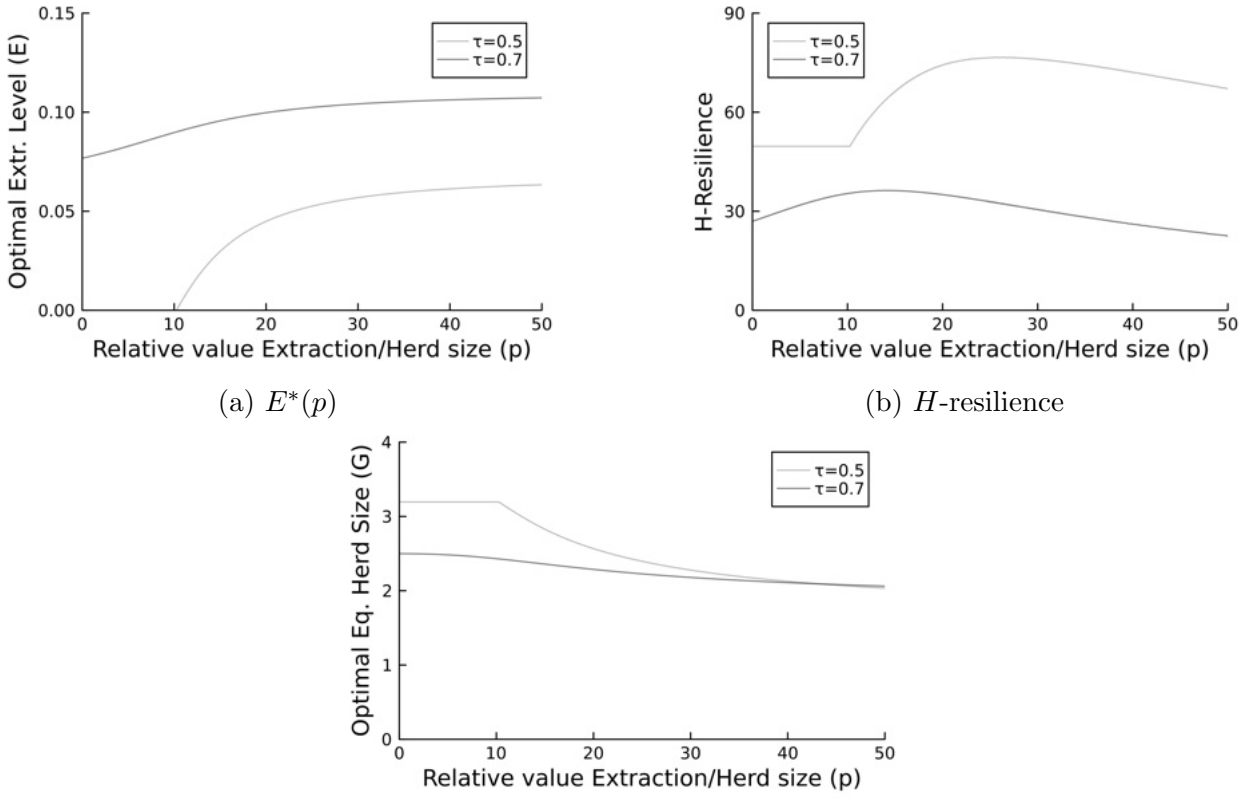
We can conclude that, in this system, woody encroachment cannot be a consequence of time-constant livestock management that exclusively optimizes over extraction level. No matter the level of p, management optimally steers clear of the overgrazing boundary.

5.2 Complete, time-constant livestock management

In the complete, time-constant livestock management case, τ^* and E^* are chosen by maximizing utility

$$(\tau^*, E^*) = \arg\max_{\tau,E} U(G, E; p) = \arg\max_{\tau,E} G + pE \quad \text{s.t.} \quad \dot{H} = \dot{W} = \dot{G} = 0 \tag{21}$$

$(\tau^*(p), E^*(p))$ traces out the blue curve from Figures 7 and 11 for varying p. If p is zero, only the herd size is valued. Managers will not extract any animals and will set some interior level of grazing intensity. As p is increased, the optimal combination of E and τ walks up along the blue curve in the interior of VP region, until it hits the Hopf-bifurcation line marking the frontier of the ecological overgrazing region. The optimal combination of E and τ then walks along this Hopf-line until it hits the upper-rightmost corner of the VP region at the Bogdanov-Takens point. In the H-resilience contour plot, this walk corresponds to a general decrease in H-resilience of the savanna, which becomes equal to zero as soon as the optimal



(a) $E^*(p)$

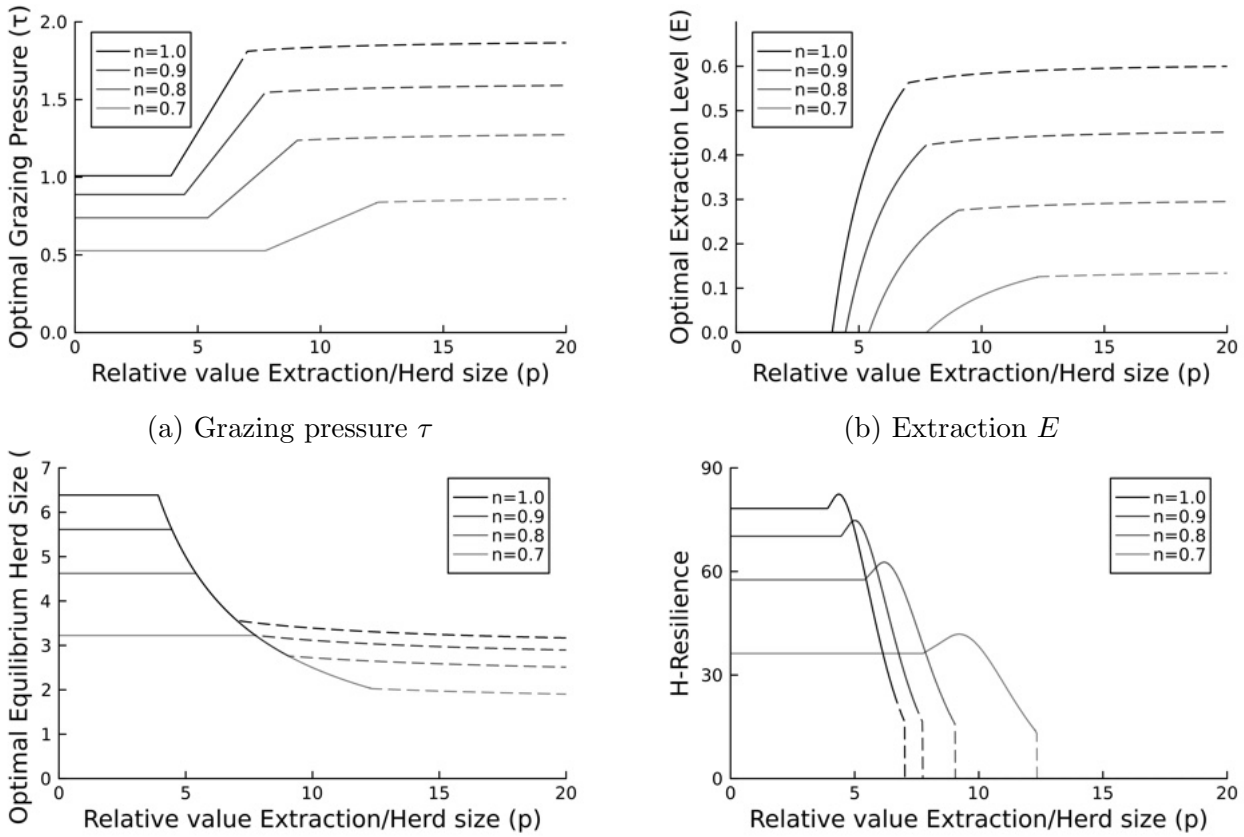
(b) H-resilience

(c) $G(E^*(p))$

Figure 12: Optimal values resulting from fixed extraction management E^*, keeping τ fixed at $\tau \in \{0.5, 0.7\}$. $w_{in} = 500$, $\beta = 200$, $n = 0.7$. Remaining parameter values are as in Table 1.

combination of E and τ hits the right-hand VP boundary. On this boundary, ecological and economic overgrazing coincide. In contrast with the extraction-only management case, in case both extraction and grazing intensity are managed, optimal management leads to woody encroachment for high levels of p.

The p-curve is further illustrated in Figure 13, in which optimal grazing intensity (a), extraction (b) and corresponding herd size (c) and H-resilience (d) are plotted against relative preference for extraction p for different fire frequencies. Below some positive threshold value of p, it is optimal not to extract, and all management levels stay the same. Fire frequency allows for higher grazing intensity and a larger subsequent herd size at low levels of p. Beyond the threshold value of p, it becomes profitable to extract. H-resilience increases



(a) Grazing pressure τ

(b) Extraction E

(c) Herd size G

(d) H-resilience

Figure 13: Optimal values fixed management τ^* (a), E^* (b) and resulting herd size (c) and H-resilience (d).

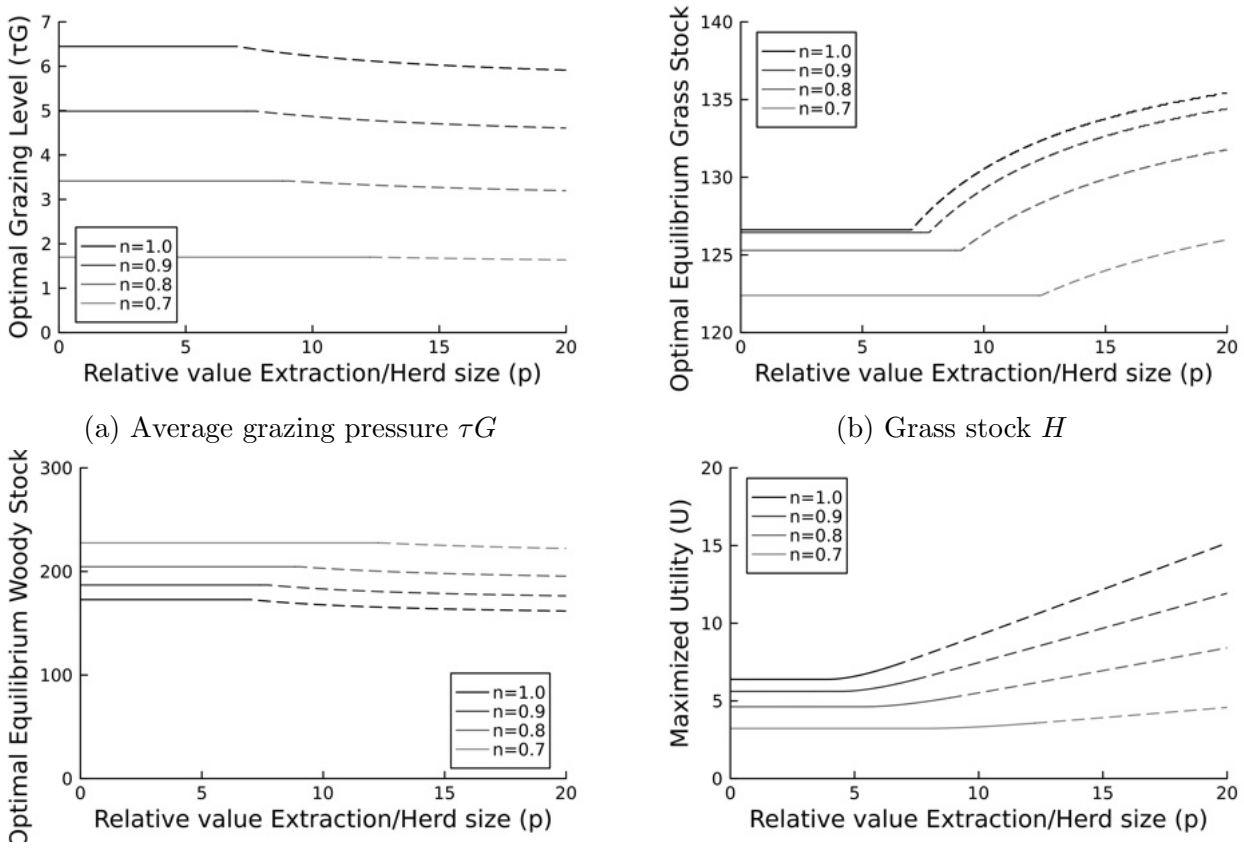
slightly as some pressure on the grass is alleviated by taking some animals out of the system through extraction. Optimal grazing intensity increases linearly with p, while the increase in extraction with p is sublinear. The resulting herd size decreases hyperbolically, suggesting that average grazing intensity τG does not change as p is varied. Beyond some level of p, the resulting equilibrium has zero resilience, which is represented by the dashed part of the curves. This corresponds to the part of the p-curve on the Hopf-bifurcation line. At that threshold value of p, the savanna system collapses to a woodland. Notably, the herd size resulting from optimal management tracks the same hyperbolic function in p at every fire frequency at those levels of p between the extraction threshold and collapse threshold.

Interestingly, for low levels of p, resilience is maximal for high levels of fire frequency. However, the extraction threshold for p – after which resilience quickly starts to drop off –

is lower for higher fire frequencies, such that the system will collapse sooner for an increase in p at higher fire frequencies.

Levels of other parameters and stocks for varying p are given in Figure 14. Figure 14a, showing average grazing pressure τG, confirms that τ is linear in p and G is hyperbolic in p, as τG does not change between the extraction and collapse thresholds of p. As the rate of change in the grass only depends on τ and G through τG, the resulting grass stock also stays the same for intermediate levels of p (fig. 14b), implying that the wood stock stays the same as well, which is indeed the case (fig. 14c). It is proven in Appendix 6 that the equilibrium grass stock under optimal management of τ and E is constant over p, under quite general circumstances. This is a crucial result, as it means that, under time-constant optimal livestock management, it is impossible to read from the equilibrium grass stock how close the savanna is to collapse.

As a final consideration, we can think about the optimal management of fire frequency. The analysis by Van Langevelde et al. (2003, 2019) suggests that more fire is always preferable, as it allows the feasibility of livestock production in areas in which woodland would dominate without it. The current results, on the other hand, suggest a drawback to fire use. For higher fire frequencies, the resilience of the savanna is more vulnerable to price changes.



(a) Average grazing pressure τG

(b) Grass stock H

(c) Wood stock W

(d) Utility

Figure 14: Optimal values average grazing pressure $\tau^* G^*$ (a), resulting grass stock (b), wood stock (c) and utility (d).

6 Discussion

This paper outlines under which geophysical conditions optimal time-constant livestock management leads to woody encroachment of savannas. It determines the resilience of the savanna against drought shocks, under optimal management for different livestock market prices. High livestock prices incentivize higher livestock extraction. If managers are only able to manage extraction, but not grazing intensity, woody encroachment does not result from time-constant optimal management, and the effect of livestock prices on the resilience of the savanna is non-monotonic. Conversely, if managers are able to control both extraction and grazing intensity, there will be a livestock price level at which the savanna collapses to a woodland, as higher extraction levels are able to be maintained by higher grazing intensity,

which leads to instability.

Under quite general conditions, we find that both grass and woody biomass levels resulting from time-constant management in extraction and grazing intensity stay constant over livestock prices until collapse. That is, there is a single, optimal level of vegetation biomass for every combination of geophysical conditions given by water infiltration, percolation threshold, and fire frequency, which is unaffected by livestock prices and associated optimal management. Hence, the vegetation of the savanna system does not demonstrate any (early) warning signals before collapse. However, the mean-field approach taken in this paper may gloss over any short-term fluctuations in vegetation biomass that could indicate a transition in reality.

Further results indicate that the sensitivity of the savanna to livestock prices increases with fire use. That is, the collapse of the savanna as a result of optimal time-constant management occurs at a lower livestock price at high fire frequencies than at low fire frequencies. This is while the resilience of the savanna is higher for higher fire frequencies when livestock prices are low.

- Further research
  - **Optimal control**: optimal trajectories of time-varying management controls τ, E converge to points on the p-curve. Under which conditions can these optimal equilibria be reached? Can they be reached from points outside the VP triangle?
  - **Feedback rules**: it is unrealistic for a livestock manager to extract their 'last animal'. More realistic would be if the manager stopped extracting at some lower bound on the herd size, which may increase the sustainable livestock management region.

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Appendix A. Proof grass cover resulting from optimal management of τ, E constant with respect to p

The following precisely formulated result shows that if pastoralists maximise a combined income stream $G + pE$, constituted of income proportional to herd size and income from selling offtake, grass cover and wood cover are independent of the selling price. As resilience decreases to zero with increasing p, this shows that monitoring the grass cover may be insufficient to obtain information about the resilience of the managed grazing system.

Let $D = \{(H, W, G) : H \geq 0, W \geq 0, G \geq 0\}$ and $M = \{(\tau, E) : \tau \geq 0, E \geq 0\}$. Introduce the state variable $X = (H, W, G) \in D$ and the parameter $\mu = (\tau, E) \in M$. Assume that the steady state equations read as $F(X, \mu) = 0$, where $F : D \times M \to \mathbb{R}^3$ is given as

$$\begin{aligned} F_1(X, \mu) &= f_1(H, W) - \tau\varphi(H, W, G) \\ F_2(X, \mu) &= f_2(H, W) \\ F_3(X, \mu) &= c\tau\varphi(H, W, G) - g(G, E). \end{aligned}$$

Theorem 3. *Assume F is twice continuously differentiable, and that (X_0, μ_0) is such that $F(X_0, \mu_0) = 0$ and $D_X F(X_0, \mu_0)$ is invertible. Introduce $\Phi(H, W) = (\frac{\partial f_1}{\partial H}\frac{\partial f_2}{\partial W} - \frac{\partial f_1}{\partial W}\frac{\partial f_2}{\partial H}, f_2)$.*

Consider the problem to maximise

$$U = G + pE,$$

with respect to X and μ, given the restrictions $F = 0$ and $(X, \mu) \in D \times M$. Denote the maximiser $(X^*(p), \mu^*(p))$, and assume that $(X^*(p_0), \mu^*(p_0)) = (X_0, \mu_0)$ and that (X^*, μ^*) is the unique maximiser for μ close to μ_0.

If the maximiser is interior for $p = p_0$, that is, if $(X^*(p_0), \mu^*(p_0))$ is an interior point of $X \times D$, and $\det D\Phi(H^*(p_0), W^*(p_0)) \neq 0$, then

$$\frac{\partial H^*}{\partial p}(p_0) = \frac{\partial W^*}{\partial p}(p_0) = 0$$

and

$$\frac{\partial}{\partial p}\tau^*\varphi(H^*, W^*, G^*) \Big|_{p=p_0} = 0.$$

Proof. As $D_X F(X, \mu)$ is invertible, by the implicit mapping theorem, there is a smooth

function $X(\mu)$, defined on an open neighbourhood N of μ_0, such that $F(X(\mu),\mu)=0$ for all $\mu \in N$.

Consider

$$U(\mu,p)=U(\tau,E,p)=G(\tau,E)+pE$$

as a function of μ. The first order conditions of maximising U with respect to μ yield that

$$\frac{\partial G}{\partial \tau}(\mu^*)=0, \qquad \frac{\partial G}{\partial E}(\mu^*)+p=0.$$

Writing $D_X F D_\tau X + D_\tau F = 0$ in components, we obtain for $\mu=\mu^*$ that

$$\begin{pmatrix} \frac{\partial f_1}{\partial H}-\tau\frac{\partial \varphi}{\partial H} & \frac{\partial f_1}{\partial W}-\tau\frac{\partial \varphi}{\partial W} & -\tau\frac{\partial \varphi}{\partial G} \\ \frac{\partial f_2}{\partial H} & \frac{\partial f_2}{\partial W} & 0 \\ c\tau\frac{\partial \varphi}{\partial H} & c\tau\frac{\partial \varphi}{\partial W} & c\tau\frac{\partial \varphi}{\partial G}-\frac{\partial g}{\partial G} \end{pmatrix} \begin{pmatrix} \frac{\partial H}{\partial \tau} \\ \frac{\partial W}{\partial \tau} \\ 0 \end{pmatrix} = \begin{pmatrix} -\varphi \\ 0 \\ c\varphi \end{pmatrix}. \tag{22}$$

As $c\tau\varphi = g > 0$ for interior points, the right hand side is not the zero vector; since $D_X F$ is invertible, it follows that that $(\frac{\partial H}{\partial \tau}, \frac{\partial W}{\partial \tau})$ is also not the zero vector if $\mu=\mu^*$.

Adding c times the first component to the third component of (22), and retaining the second component, we obtain

$$\begin{pmatrix} c\frac{\partial f_1}{\partial H} & c\frac{\partial f_1}{\partial W} \\ \frac{\partial f_2}{\partial H} & \frac{\partial f_2}{\partial W} \end{pmatrix} \begin{pmatrix} \frac{\partial H}{\partial \tau} \\ \frac{\partial W}{\partial \tau} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}. \tag{23}$$

As the vector $(\frac{\partial H}{\partial \tau}, \frac{\partial W}{\partial \tau})$ is non-zero, it follows that the matrix has nonzero kernel and therefore zero determinant, which yields the condition

$$\Phi_1(H^*,W^*)=0.$$

Combined with the condition

$$\Phi_2(H^*,W^*)=f_2(H^*,W^*)=0,$$

this determines H^* and W^* as constant functions of p since $D\Phi(H^*,W^*)$ is invertible. Equation $F_1(X^*,\mu^*)$ then implies that also $\tau^*(H^*,W^*,G^*)$ is constant. □