

Plant productivity and soil nitrogen as a function of grazing, migration and fire in an African savanna

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Summary

1 Herbivores can play a key role in affecting ecosystem function, but their direct and indirect effects are often confounded with each other and have rarely been dissected. Predictions for open systems, i.e. those with cross-habitat nutrient fluxes and dispersal, may differ from those expected in closed systems, where no such transfers occur, but these differences have only recently begun to be characterized.

2 We present a theoretical model of plant productivity and soil nitrogen (N) based on the Serengeti ecosystem in order to investigate the interplay among herbivore movement, nutrient transport across habitats (spatial subsidies), the fire regime and the effects of herbivores on N cycling.

3 Model results suggest that the fire regime and herbivore migration are key determinants of primary productivity and fertility, and that the impact of these factors depends on grazing intensity. At low intensity, high grass biomass leads to extensive fires and N volatilization, but this effect is reduced at high grazing intensity. Without migration, the model predicts that primary productivity and fertility initially increase, then decline with increasing grazing intensity. Conversely, seasonal migration decouples the growing and grazing seasons, leading to a monotonic increase in productivity with grazing intensity. Cross-habitat N transport has a relatively modest effect on N dynamics, and the magnitude of the seasonality effect outweighs the spatial subsidy effect.

4 Our model suggests that herbivores and fire may play key interactive roles in regulating producers and determining ecosystem functional properties in grazing systems, both through consumption and via indirect effects on nutrient availability. The direction and magnitude of these effects could potentially vary greatly among ecosystems with resident vs. migratory herbivores, suggesting that spatial coupling through animal movement can be important at both the population and ecosystem levels.

5 This study suggests that the degree to which trophic interactions influence ecosystem function may be strongly modulated by whether systems are open or closed. It also suggests that direct and indirect effects of consumers on their resources (top-down effects) may be far more important than nutrient subsidies in open terrestrial systems.

Key-words: fire effects, fire–herbivore interactions, grazing optimization, migratory ungulates, nitrogen loss, nutrient cycling, primary productivity, Serengeti, spatial subsidies, wildebeest

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Introduction

An increasing emphasis has been placed on spatial processes in ecological systems over the past couple of decades (Tilman & Kareiva 1997). For example, meta-population theory shows that in open systems (those with dispersal among patches), the conditions for persistence of populations are very different from those in closed systems, where no cross-habitat movements occur (Levin 1976). Similarly, fluxes of nutrients or energy across habitat boundaries can have important consequences for ecosystem function (Polis *et al.* 1997). Simple theoretical models show that the dynamics and equilibria of ecosystems may vary considerably when these processes are considered independently vs. acting simultaneously, and in spatially open vs. closed systems (Loreau & Holt 2004). Relatively few studies, however, have explored the spatial dimension of ecosystem dynamics mediated by trophic and other interactions (Loreau *et al.* 2003; Loreau & Holt 2004), and the models exploring this theme have tended to be abstract and not tailored to realistic features of any particular natural ecosystem.

Grassland-grazer ecosystems provide potential case studies for the exploration of these issues. Grasses may be limited by resources such as nitrogen (bottom-up control) or by herbivores (top-down control), or by both, so both trophic and ecosystem constraints may potentially be important for plant population dynamics. The process of consumption itself, plus other direct and indirect effects of herbivory such as fire suppression (Hobbs *et al.* 1991), changes in nitrogen (N) cycling rates (Pastor *et al.* 1993), and trampling (Cumming & Cumming 2003), may all affect plant populations and/or ecosystem function. In open systems, consumers may move between habitats, thus transporting N and having effects that differ considerably from those expected in closed systems (Frank *et al.* 1994; Stapp & Polis 2003; Walker *et al.* 2003; Maron *et al.* 2006). A considerable amount of attention has been devoted to analysing the effects of grazing on grassland productivity and fertility (Ruess & McNaughton 1987; McNaughton *et al.* 1988; Hobbs *et al.* 1991; Seagle *et al.* 1992; Milchunas & Lauenroth 1993; Frank *et al.* 1994; Biondini & Manske 1996; Biondini *et al.* 1998; Augustine *et al.* 2003; Schoenecker *et al.* 2004), but few studies have attempted to tease apart the various components and indirect effects that summed together comprise the net effect of herbivores on these ecosystems (Hobbs 1996). Herbivores may affect N cycling (McNaughton *et al.* 1997; de Mazancourt *et al.* 1998; Ritchie *et al.* 1998), transport N between habitats (Frank *et al.* 1994; Augustine *et al.* 2003; Walker *et al.* 2003; Schoenecker *et al.* 2004) or alter the rate of N loss from ecosystems (Ruess & McNaughton 1988; Hobbs *et al.* 1991). In open systems with a large biomass of migratory grazing ungulates, long-distance nutrient transport could potentially play a significant role in local ecosystem functioning. Cross-system spatial subsidies have been documented in various ecosystems

(Frank *et al.* 1994; Anderson & Polis 1999; Helfield & Naiman 2001; Seagle 2003; Stapp & Polis 2003; Maron *et al.* 2006), but few studies (e.g. Frank *et al.* 1994; Walker *et al.* 2003) have investigated the effects of such fluxes on ecosystem function, particularly in terrestrial habitats (Polis *et al.* 1997).

In addition to herbivores, fire plays a potentially important role in the N dynamics of many ecosystems (Robertson & Rosswall 1986; Turner *et al.* 1997; Reich *et al.* 2001), but relatively few studies have investigated the combined effects of grazing and fire (e.g. Hobbs *et al.* 1991; de Mazancourt *et al.* 1999). Fire may cause N loss in savannas (Robertson & Rosswall 1986; Ojima *et al.* 1994), and its impact is only likely to expand as human populations continue to increase. Although the effects of herbivores on soil nutrients are less clear-cut than those of fire (see Milchunas & Lauenroth 1993), it is apparent that ungulate herbivores can have a strong indirect effect on N dynamics by limiting the extent of biomass burning (McNaughton *et al.* 1988; Hobbs 1996), thus promoting nutrient retention (Hobbs *et al.* 1991).

THE SERENGETI ECOSYSTEM

The Serengeti ecosystem is described in detail elsewhere (McNaughton 1985; Ruess & Seagle 1994). For our purpose, it may be broadly divided into two habitats: short-grass plains in the south-eastern portion of the ecosystem, and tall-grass wooded grasslands in the north and west. Wildebeest (*Connochaetes taurinus* Burchell), the numerically dominant herbivores in this system, migrate seasonally from nutrient-rich plains, which they occupy during the wet season, to the wooded grasslands. Given that the protein content of forage is at its lowest during the dry season, wildebeest can experience an N deficiency in their dry-season range, with N excretion exceeding intake (Sinclair 1977; McNaughton *et al.* 1988). This can result in a net transfer of N from plains (gained during the wet season) to wooded grasslands. The wildebeest population grew from a quarter million to over a million animals in the latter half of the 20th century, and went from being regulated by disease (rinderpest) to being regulated by its food supply (Mduma *et al.* 1999). The resulting effect of increased herbivory on standing grass biomass in the system also led to a reduction in area burned in the system (McNaughton *et al.* 1988). As fire influences N dynamics (Robertson & Rosswall 1986; Hobbs *et al.* 1991), these changes in wildebeest abundance could exert indirect (fire-mediated) and direct (consumption, excretion, and subsidy) effects on the N cycle.

We here develop and explore a simulation model of N dynamics in the Serengeti that incorporates these effects of herbivory and fire. Our aim is to develop a model that captures a range of realistic ecosystem processes known to matter in N dynamics in the Serengeti and other grassland ecosystems. The model allows us to investigate the role of herbivores as agents of long-distance nutrient transport, as scaled against other impacts of

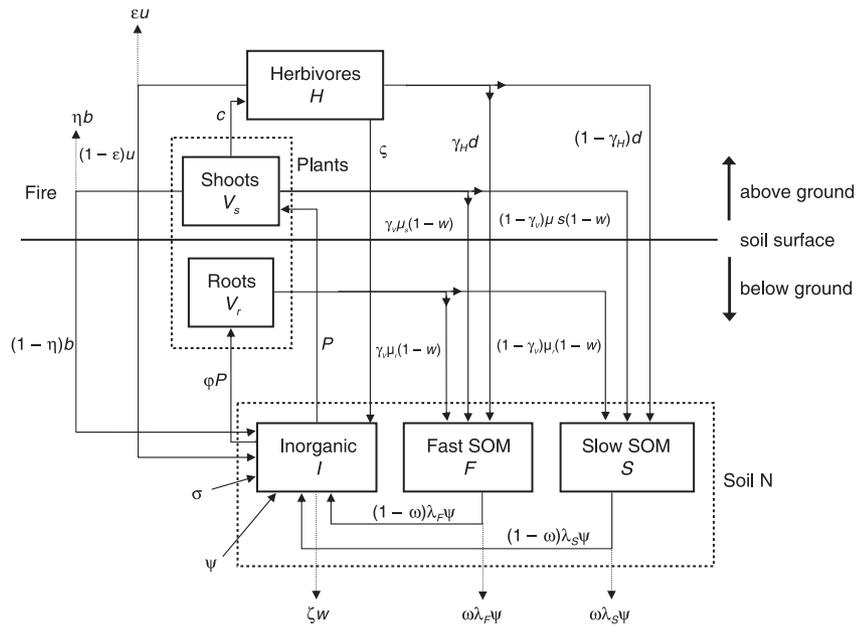


Fig. 1 Compartments and flow pathways for the Serengeti N cycling model. The compartments are above-ground (shoot) N (V_s), below-ground (root) N (V_r), herbivores (H), fast (F) and slow (S) soil organic N compartments, and inorganic soil N (I). The rate constants used in the model are shown. The consumption and plant production functions c and P are depicted in bold to differentiate them from the other terms, which are given as rate constants.

herbivory. The Serengeti provides an ideal study system for the investigation of the combined effects of highly mobile herbivores and fire in a natural ‘open’ ecosystem, as defined above. Simulating herbivory and fire effects in this system can allow general insights into the importance of migratory herbivores, spatial subsidies, and herbivore–fire interactions in controlling N dynamics. The Serengeti is one of the few ecosystems where ungulate herbivores have been shown repeatedly to increase N cycling (Seagle *et al.* 1992; McNaughton *et al.* 1997), in contrast to other systems (Ritchie *et al.* 1998; Singer & Schoenecker 2003), and it is an essentially open ecosystem that has historically not been subjected to managed fire control. Thus a key question driving our model is: To what extent do the openness and fire regime of the Serengeti modulate the positive effect of herbivores on the nitrogen cycle?

We use the model here to address the following questions: (i) What are the independent and combined effects of herbivory and fire on soil N and above-ground net primary productivity (ANPP) in the wooded grasslands? (ii) How do grassland productivity and fertility differ between resident and migratory strategies? (iii) What is the effect of N subsidies from plains to wooded grasslands as a result of migration?

Materials and methods

NITROGEN CYCLING MODEL

Model description

In the present paper, we focus on the wooded grassland habitat of the Serengeti. We developed an N cycling

model consisting of five differential equations describing the dynamics of key system components. The state variables in the model are (Fig. 1): herbivores (H), above-ground (V_s) and below-ground (V_r) plant N, fast (F) and slow (S) soil organic matter or SOM N pools, and soil inorganic N (I). We assume an additional soil N pool is present (passive SOM), but that its size does not vary over the time frame of the simulation because of its slow dynamics (de Mazancourt *et al.* 1998; Pacala & Kinzig 2002) (we take its size into account when estimating total soil N). This framework loosely follows the ‘common ecosystem model’ proposed by Pacala & Kinzig (2002), which is in turn a simplification of the CENTURY model (Parton *et al.* 1987). The model specifies all state variables in N units; we assume that C : N ratios are fixed. Unlike the common ecosystem model and CENTURY, the present one incorporates herbivory and fire. As protein content of forage varies widely between wet and dry seasons, and this variation affects N retention by herbivores (Sinclair 1977; Mould & Robbins 1981), we assume that the C : N ratio of the portion of plant biomass consumed varies seasonally, even though the overall C : N ratio of V_s remains constant. This does not alter the N balance in the system: we essentially assume that, during the dry season, plants reabsorb some of their N and store it below ground; this stored N then becomes available for growth at the onset of the following wet season. In the model, the shift in C : N ratio of V_s occurs instantaneously, while in actuality it is a continuous process. Still, given the rapid rate at which high-quality green grass dries out at the onset of the dry season (McNaughton 1985), our simplification seems reasonable. We further assume that grazing does not significantly alter the grass C : N

ratio in the model; even though rotational-passage grazing can lead to localized flushes of high-quality regrowth (McNaughton 1985; McNaughton & Banyikwa 1995), we assume that averaged over large scales, forage protein content is fixed, but seasonally variable.

The model is characterized by N transfers among the various compartments, plus external inputs (atmospheric deposition and N fixation) and losses (leaching, denitrification, volatilization and pyrodenitrification), as shown schematically in Fig. 1. In most of our simulations we assume no feedbacks of the vegetation on herbivore population density H or migratory behaviour, and treat herbivory as a fixed independent variable. Under these conditions, the system of equations defining the model is given by

$$\begin{aligned} \frac{dV_s}{dt} &= P - \mu_s V_s (1 - w) - cH - bV_s \\ \frac{dV_r}{dt} &= P\phi - \mu_r V_r (1 - w) \\ \frac{dF}{dt} &= \gamma_V (\mu_s V_s + \mu_r V_r) (1 - w) + \gamma_H dH - \lambda_F F m \\ \frac{dS}{dt} &= (1 - \gamma_V) (\mu_s V_s + \mu_r V_r) (1 - w) \\ &\quad + (1 - \gamma_H) dH - \lambda_S S m \\ \frac{dI}{dt} &= \sigma + \psi - \zeta I w + (1 - \epsilon) u H \\ &\quad + (1 - \omega) (\lambda_F F + \lambda_S S) m \\ &\quad - P(1 + \phi) + (1 - \eta) b V_s + \zeta H \end{aligned} \quad \text{eqn 1}$$

Here, Greek letters are fixed parameters, whereas Latin characters denote state variables and functions or parameters that vary seasonally (Table 1 compiles the model parameters and variables). P is net above-ground primary production (ANPP). The quantity b is the amount of area burned, c , d and u are consumption, defecation and urinary losses by herbivores, respectively, and ζ is herbivore mortality. The function w is a binary variable that takes on the values 0 and 1 in dry and wet seasons, respectively, and so acts as a switch that controls shoot (μ_s) and root (μ_r) litter production and leaching ζ of inorganic N. The function m governs the maximum rate of organic matter decomposition of the SOM fractions (λ_S and λ_F). The constants σ and ψ represent atmospheric N deposition and fixation, respectively, and ϵ , ω , and η are the rate of N volatilization due to urine deposition, denitrification and burning, respectively. Finally, the parameters γ_V and γ_H control the fractions of plant and herbivore detritus that enter the fast SOM pool, respectively, and ϕ scales below-ground production as a proportion of above-ground production (see Fig. 1).

In equation 1, the herbivores are considered to be a 'forcing function', whose dynamics are driven by processes external to the system being modelled. This assumption of an open system may capture some of the

reality of the Serengeti, where the number of wildebeest present in a given tract of wooded grassland may be determined by processes in the plains, disease outbreaks such as rinderpest, and poaching pressure (Sinclair 1979). At the other extreme, however, herbivore numbers could be governed by *in situ* dynamics. To examine the implications of this, we also considered a model for a closed system. To this effect, we coupled the following equation to equation 1:

$$\frac{dH}{dt} = (c - d - u - \zeta)H \quad \text{eqn 2}$$

where ζ is the maximum rate of mortality, estimated from Mduma *et al.* (1999), and c , d and u are defined above.

Plant production

We assumed that plant productivity P is a function of rainfall (R), soil inorganic N (I), and above-ground plant N (V_s):

$$P = \frac{rRI(V_s + \rho)}{I + K_N} \left(1 - \frac{V_s}{K_V} \right) \quad \text{eqn 3}$$

This expression qualitatively captures many features of grassland above-ground biomass dynamics, including co-dependence upon rainfall and N availability, self-limitation, and the presence of a root mass permitting recovery of above-ground plants. The expression assumes that ANPP is linearly related to rainfall, as suggested by the empirical results of McNaughton (1985). In our numerical studies, we assumed that rainfall switches seasonally between two constant values, R_{wet} and R_{dry} , determined from rain gauge data spanning the period 1960–2001. The effect of N on growth follows a Monod function (McGill *et al.* 1981; Pacala & Kinzig 2002). When N is not limiting, growth is a logistic function of standing plant biomass, which allows for self-shading effects. K_V and K_N are, respectively, the maximum shoot biomass and the half-saturation constant for plant N uptake. We estimated these parameters from the literature (McGill *et al.* 1981; McNaughton 1985). The parameter ρ allows for growth when $V_s = 0$ (Fryxell *et al.* 1988), due to the continual presence of roots below ground, and we assigned it a small value, simply to prevent grass extinction. We make the simplifying assumption that production of below-ground plant N (V_r) is a fixed proportion of above-ground production, given by the above- to below-ground biomass ratio ϕ . We estimated a value for ϕ of 1.15 from a known empirical relationship between precipitation and above- to below-ground production (Parton *et al.* 1987). We further assume that root and shoot litter production occur during the dry season. Although root litter production may occur year-round, the adopted model structure is approximately consistent with seasonal patterns of production and decay, and the removal of this seasonal switch in litter production was found to have little effect on model behaviour.

Table 1 Model variables, functions and parameters with their values, units, and the sources and methods used to derive them

Quantity	Interpretation	Units	Value(s)	Source(s) or equation(s)
H	Herbivore N	g N m ⁻²		Equations 1 & 2
V_s	Above-ground plant N	g N m ⁻²		Equation 1
V_r	Below-ground plant N	g N m ⁻²		Equation 1
F	Fast soil N pool	g N m ⁻²		Equation 1
S	Slow soil N pool	g N m ⁻²		Equation 1
I	Soil inorganic N	g N m ⁻²		Equation 1
P	Above-ground production	g N m ⁻²		Equation 3
m	Effect of soil moisture on decomposition			Equation 4
c	Consumption	week ⁻¹		Equation 5
d	Defaecation	week ⁻¹		Equation 6
u	Urination	week ⁻¹		Equation 7
R_{wet}, R_{dry}	Rainfall	mm ⁻¹ week ⁻¹	23.5, 6.7	Serengeti rain gauge data
r	Plant intrinsic growth rate	mm ⁻¹ week ⁻¹	0.986	Estimated by model fitting
K_N	N uptake half-saturation constant	g N m ⁻²	0.05	McGill <i>et al.</i> (1981)
ρ	Minimum value of V_s	g N m ⁻²	0.01	See text
K_V	Maximum shoot biomass	g N m ⁻²	6.0	Fryxell <i>et al.</i> (1988)
ϕ	Root : shoot ratio		1.15	Parton <i>et al.</i> (1987)
μ_s	Shoot decay rate	week ⁻¹	0.04	McNaughton (1985); Parton <i>et al.</i> (1987)
μ_r	Root decay rate	week ⁻¹	0.03	Personal observation
α	Maximum cropping rate	week ⁻¹	10.81	Shipley <i>et al.</i> (1994)
β	Cropping half-saturation constant	g m ⁻²	27.3	Wilmshurst <i>et al.</i> (2000)
$\delta_{wet}, \delta_{dry}$	Digestive constraint (wet and dry season)	week ⁻¹	7.76, 4.62	Wilmshurst <i>et al.</i> (2000)
v_{wet}, v_{dry}	Wet and dry season shoot [N]		0.02, 0.01	Murray & Illius (2000); Sinclair (1977)
ξ_0, ξ_1	N retention in herbivores		0.0216, 0.65	Mould & Robbins (1981)
s	Maximum N retained	week ⁻¹	0.01	Estimated by model fitting
κ_0, κ_1	Area burnt intercept and slope		0.939, 0.662	A.R.E. Sinclair (unpublished data)
f_V	Plant biomass fraction to fast soil pool		0.5	Scholes & Walker (1993); Parton <i>et al.</i> (1987)
f_H	Animal dung fraction to fast soil pool		0.67	Parton <i>et al.</i> (1987); Ruess & McNaughton (1987); Estimated by model fitting
λ_F	Fast soil pool mineralization rate	week ⁻¹	0.00667	Estimated from λ_F and Ruess & McNaughton (1987)
λ_S	Slow soil pool mineralization rate	week ⁻¹	0.00079	Estimated from λ_F and Ruess & McNaughton (1987)
θ	Potential evapotranspiration	mm week ⁻¹	17.1	Thornwaite (1948)
$\iota_0, \iota_1, \iota_2$	Constants in SOM decomposition function		0.20, 0.99, 0.31	Parton <i>et al.</i> (1987)
σ	Atmospheric N deposition	g N m ⁻² week ⁻¹	0.0077	Ruess & McNaughton (1988); Augustine <i>et al.</i> (2003)
Ψ	N fixation	g N m ⁻² week ⁻¹	0.0144	M. Ritchie (unpublished data)
ζ	Leaching rate	week ⁻¹	0.017	Estimated by model fitting
ε	Urine volatilization		0.2	Ruess & McNaughton (1988)
ω	Denitrification		0.075	M. Coughenour (unpublished data)
η	Pyrodenitrification		0.75	Kuhlbusch <i>et al.</i> (1991); Crutzen & Andreae (1990); Scholes & Walker (1993)
ς	Herbivore mortality	week ⁻¹	0.0019	Mduma <i>et al.</i> (1999)

The function m incorporates the effect of soil moisture on the rate of decomposition of F and S , and is a function of temperature, rainfall R , and potential evapotranspiration θ (Parton *et al.* 1987). Given that mean monthly temperature shows little seasonal variation in the Serengeti (Sinclair 1977), we ignored temperature effects on decomposition. The empirical relationship between the ratio R/θ and the effect of soil moisture on decomposition m derived by Parton *et al.* (1987) can be approximated well with a quadratic function:

$$m = \tau_0 + \tau_1 \frac{R}{\theta} + \tau_2 \left[\frac{R}{\theta} \right]^2 \quad \text{eqn 4}$$

We estimated the parameters τ_0 – τ_2 from Parton *et al.* (1987) and calculated a mean value for θ using the method proposed by Thornwaite (1948). We used a single value for θ irrespective of season because the estimated annual coefficient of variation in potential evapotranspiration is low in the Serengeti (11%).

N cycling

For both plant litter and animal dung, we assumed that a proportion γ of decaying organic N was incorporated into the fast pool F , and that a proportion $(1 - \gamma)$ decayed into the slow soil pool S (Pacala & Kinzig 2002). The

values of γ_V (plant component) and γ_H (animal component) are a function of the N : lignin ratios of the decomposing matter (Parton *et al.* 1987), which we obtained from Scholes & Walker (1993). An N : lignin ratio was not available for dung, but we estimated it from C : N ratios in dung relative to litter (Ruess & McNaughton 1987), assuming that the proportion of C comprised of lignin does not vary between litter and dung. For simplicity, we assumed that root and shoot N : lignin ratios are the same. Two other avenues of N return to the soil are animal urine and carcasses. We assumed that both these N sources become readily available for plant uptake, given that in the Serengeti animal carcasses are rapidly disposed of by scavengers and probably return to the soil as N-rich carnivore urine and faeces.

We obtained N inputs from atmospheric deposition and N losses due to urine volatilization, denitrification and pyrodenitrification from the literature (Table 1). We obtained a value for N fixation from recent field measurements conducted in the Serengeti (M. Ritchie, unpublished data). For a few parameters, there were no published values that could be applied directly to the model, so we estimated them by fitting the dynamic model to published values for productivity (McNaughton 1985) and soil N (Ruess & McNaughton 1987) using a simulated annealing approach (Press *et al.* 1992; Hurtt & Armstrong 1999). These fitted parameters were as follows: r , the maximum plant growth rate; the leaching rate ζ ; and the SOM decomposition rates λ_F and λ_S . A degree of freedom was regained by the fact that the ratio λ_F/λ_S can be estimated (Parton *et al.* 1987). Ruess & McNaughton (1987) report a soil N-value of 0.17% (*c.* 192 g N m⁻²) for a site in northern Serengeti receiving 798 mm of rain per annum. Assuming that 30–40% of this N is passive SOM (Parton *et al.* 1987), the remainder is partitioned into fast or microbial SOM, slow SOM and inorganic N. Measured values for inorganic N and microbial biomass allowed the remaining terms to be calculated. We fitted the model with these values to obtain the remaining parameters.

Herbivory

We assumed that herbivore consumption is recipient-controlled (de Mazancourt *et al.* 1998). The intake function combined a type II functional response (the cropping constraint) with a digestive constraint $\delta(t)$ that depends on forage quality (Wilmshurst *et al.* 2000):

$$c = \min \left[\frac{\alpha V_s}{\beta + V_s/v(t)}, \delta(t)v(t) \right] \quad \text{eqn 5}$$

where forage N concentration $v(t)$ converts units of total plant biomass into units of plant N. Both v and δ vary seasonally. We assumed that $v_{wet} = 0.02$ and $v_{dry} = 0.01$ (Sinclair 1977; Murray & Illius 2000). We obtained the parameters α and β from allometric equations derived

by Shipley *et al.* (1994) and Wilmshurst *et al.* (2000), respectively (Table 1). An allometric relationship between maximum daily voluntary intake of forage (δ) and grass neutral detergent fibre (NDF) content was produced by Wilmshurst *et al.* (2000). We applied this relationship to a 136-kg wildebeest consuming wet and dry season forage of 45% and 65% NDF, resulting in values of δ_{wet} and δ_{dry} equal to 7.76 and 4.62, respectively (Wilmshurst *et al.* 1999).

Like consumption (c), the defecation (d) and urination (u) rates depend on the N concentration and biomass of forage. The net N balance of herbivores depends on N intake (Mould & Robbins 1981). When feeding on a low-N diet, as occurs during the dry season in the Serengeti dry-season habitat, herbivores may undergo a period of negative N balance, during which losses in dung and urine exceed N intake from forage (Sinclair 1977). These losses are derived from metabolic N resulting from the breakdown of lean mass (Mould & Robbins 1981; Hobbs 1996). In addition to affecting the N balance, the rate of N intake affects the ratio of faecal to urinary N loss (Hobbs 1996). This ratio has consequences for N cycling because, on the one hand, urinary N is more susceptible to volatilization, and therefore losses, than faecal N (Ruess & McNaughton 1988), but on the other, urinary N is in mineral form and therefore more readily available for plant uptake. To derive a relationship between N intake and retention for wildebeest, we used a data set collected by Mould and Robbins (1981) for elk. They measured N retention per kg of body mass; we fitted a regression model to these data to predict N excretion (dung d plus urine u) as a function of intake c for a 136-kg wildebeest, arriving at: $d + u = \xi_0 + \xi_1 c$, where $\xi_0 = 0.0216$ and $\xi_1 = 0.65$. This relationship suggests that an intake below 0.062 (or 21.8 kg N wildebeest⁻¹ year⁻¹) would result in $d + u > c$ and a net N deficiency, and vice versa. When N intake is high, this relationship can lead to a high rate of N retention, leading to rates of herbivore biomass increase that are unrealistic. We thus constrained the relationship between $d + u$ and c with the following equation: $d + u = \max[\xi_0 + \xi_1 c, c - s]$, where $s = 0.01$, and is defined as the maximum amount of N that can be retained. We estimated s by fitting the model with a maximum likelihood procedure to a data set consisting of 40 years of wildebeest census data (Pascual *et al.* 1997). We also estimated the ratio of N excreted in urine vs. dung as a function of dietary N concentration from empirical functions developed by Hobbs (1996). Our assumption of forage N concentrations of 0.02 and 0.01 in the wet and dry seasons resulted in estimated urine : dung ratios $N_{u:d}$ of 1.2 and 0.45, respectively. The functions d and u are given by:

$$d = \max[\xi_0 + \xi_1 c, c - s] / (1 + N_{u:d}) \quad \text{eqn 6}$$

and

$$u = d N_{u:d} \quad \text{eqn 7}$$

In addition to a net input of N into the wooded grasslands due to N deficiency during the dry season, we used the mean wildebeest mortality rate (ζ in equation 1) reported by Mduma *et al.* (1999) to estimate the rate of N flow from plains to wooded grasslands due to wildebeest mortality. Given that wildebeest gain body mass primarily during the wet season (when they are in the plains), dry season mortality represents a net addition of N for the wooded grasslands.

Fire

We assumed that the function of loss of above-ground plant N (V_s) to fire b is related to fuel load and the occurrence of an ignition event (McNaughton *et al.* 1988), which occurs at the beginning of the dry season. Although data on grass biomass measurements over time in the Serengeti have not been published, A. R. E. Sinclair (personal communication) found a negative linear relationship between wildebeest numbers and the proportion of area burned in the northern Serengeti. Thus, we assumed that when $t = t_{ignite}$, the quantity $b = \kappa_0 - \kappa_1 H$, where κ_0 and κ_1 were estimated from Sinclair's data. At all other times of the year, b was set to 0. We derived approximate population densities for the most heavily used 5000 km² of the dry season range by analysing spatial occupancy data from detailed surveys conducted between 1969 and 1972, and used this occupancy pattern as a basis for converting historical estimates of the wildebeest population into average population densities (and into g N m⁻² for use in the model).

The proportion of plant N lost to the atmosphere as a result of burning (pyrodenitrification) has been estimated to vary between 50% in cool, low-intensity fires, and 100% in hot, intense fires (Crutzen & Andreae 1990; Kuhlbusch *et al.* 1991; Scholes & Walker 1993). We assumed an intermediate volatilization rate of 0.75. Although fire temperature (and thus pyrodenitrification) depends on fuel biomass (Stronach & McNaughton 1989), we assumed a fixed rate of N loss. The state variables, functions and parameters used in the model and the sources for parameter estimates are given in Table 1.

MODEL SCENARIOS

We first used the model to investigate the effect of wildebeest herbivory and fire on above-ground net primary productivity (ANPP) and total soil N in the wooded grasslands, with the rate of herbivory fixed. We then conducted a second set of simulations that incorporated feedbacks of the vegetation on the herbivore population. Given that the model is not analytically tractable (due to the seasonal transition effects), we solved it numerically. We used 100-year model runs to investigate the effects of fire, grazing intensity and occupancy scenarios. We used herbivore population density as a proxy for grazing intensity. We examined four factors, fire, herbivory, migratory behaviour (present year-round vs. present only during the dry season) and the spatial subsidy

effect, although not all combinations of these factors were investigated.

In the first two analyses we modelled a range of population densities to investigate the effects of the rapid expansion of the wildebeest population in the 1970s and 1980s following release from rinderpest. First, we considered the effect of grazing intensity on ANPP and soil N for two fire regimes (fire and no fire), and two wildebeest occupancy scenarios: (i) wildebeest resident year-round, and (ii) wildebeest present only in the dry season. The migratory case differed from the resident scenario in that H was set to 0 during the wet season in the former. In a second analysis, we tested the importance of the subsidy effect as a function of herbivore numbers with and without fire. In this case we assumed that the wildebeest are migratory (the default scenario). The purpose of this test was to estimate the relative importance of the local nutrient-cycling enhancement effect of grazers, vs. the effect of N input from the plains. The subsidy factor had two levels: present or absent. In the former case, d and u are given by equations 6 and 7, as described above. In the no subsidy and in the year-round occupancy cases, excretion is equal to intake, so equation 6 becomes $d = c/(1 + N_{w,d})$ and the N subsidy due to mortality is 0.

Finally, to simulate the system with feedbacks on the herbivore population, we allowed herbivores to respond to food availability with and without fire by adding equation 2 to the model. We restricted the analysis to a resident herbivore scenario because we did not model the resource dynamics of the plains habitat, a prerequisite for considering the migration case with herbivore population dynamics. We set the initial value of H at 0.2 (its estimated value before release from rinderpest) and allowed the simulation to run for 100 years, observing the transient dynamics of ANPP, soil N, standing vegetation biomass and herbivore population density for each fire regime. The main objective of this simulation was to investigate the sustainability of the system following the switch from top-down regulation of herbivory (through rinderpest, a disease) to bottom-up regulation (food availability), and to examine the effect of the fire regime on the herbivore population.

SENSITIVITY ANALYSIS

We conducted a sensitivity analysis to investigate the effect of different parameters on model behaviour. For a set of 16 parameters, we tested values of 80, 90, 100, 110 and 120% of the default value, while keeping all other parameters at their 'best' values. For this sensitivity analysis, we ran the model for 100 years under the following scenario: a present-day wildebeest population density (1.1 g N m⁻²) and no fire suppression. The purpose of this analysis was to investigate the robustness of model predictions under a scenario that preserves the set of conditions that have predominated in the Serengeti over the past few decades (i.e. a high wildebeest population and little or no fire management).

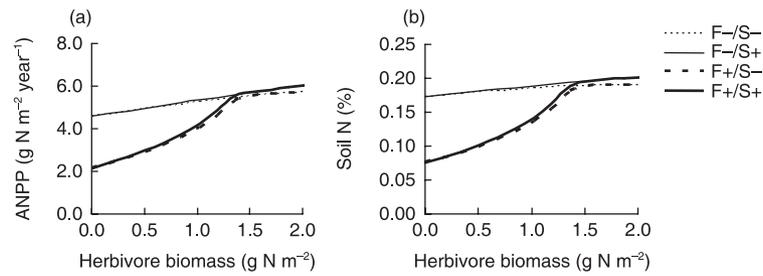


Fig. 2 Effect of fire and N subsidies from the Serengeti plains on (a) ANPP and (b) soil N as a function of herbivore population density after 100 years. The fire scenarios are uncontrolled burns (F+) and fire suppression (F-). In the 'subsidy' scenarios (S+), herbivore N retention is regulated by intake, and a net N flow occurs seasonally from the plains. In the absence of subsidies (S-), it is assumed that herbivore N balance is neutral.

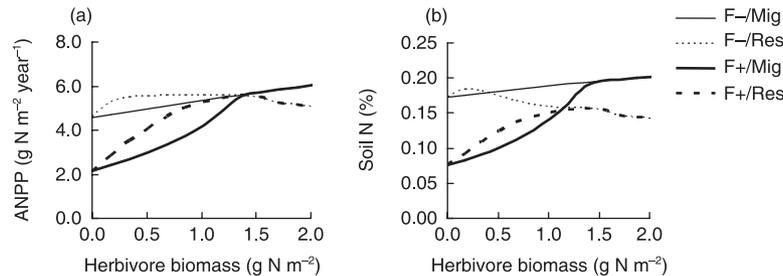


Fig. 3 Effect of herbivore migratory behaviour and fire on (a) ANPP and (b) soil N after 100 years. The fire scenarios are uncontrolled burns (F+) and fire suppression (F-). In the case of migration (Mig), herbivores are assumed to move out of the woodlands during the wet season. In the resident scenario (Res), the herbivores are assumed to occupy the woodlands year-round.

Results

EFFECTS OF HERBIVORY AND FIRE

Fire exclusion is predicted to increase productivity and soil N, but this effect varies strongly with grazing intensity (Fig. 2). When herbivores are migratory, grazing increases ANPP and soil N, but although the effect is slight or even negligible in the absence of fire, it is very pronounced when fire is present, particularly at low grazing intensities (Fig. 2). Above a herbivore biomass of about 1.3 g N m^{-2} , little residual grass biomass remains at the end of the dry season to sustain fires, and N volatilization due to fire thus becomes negligible. The presence of fire in the model thus had a key impact on the behaviour of the system. The fact that fire affects both soil N and ANPP suggests that (beyond any constraints imposed by water availability) modelled productivity is limited by N, as the primary effect of fire in the model is to cause N loss from the system.

EFFECTS OF SPATIAL SUBSIDIES

The N subsidy from the Serengeti plains does not seem to contribute a substantial fraction of the positive effect that migratory herbivores exert on soil N and ANPP, suggesting that the principal impact of migratory herbivores on system productivity (other than their influence on fire) is derived from increases in nutrient turnover rather than N transport (Fig. 2). Although

the wildebeest migration is a dramatic feature of the natural history of the Serengeti, the main impact on N dynamics may be through modulation of fire regimes, rather than via direct transport of nutrients.

EFFECTS OF MIGRATORY BEHAVIOUR

When herbivores are migratory in an open system, the relationship between grazing intensity and ANPP and soil N is consistently positive (Figs 2 and 3). When herbivores are resident in a closed system, by contrast, the model results are consistent with the pattern predicted by the grazing optimization hypothesis (McNaughton 1979): ANPP and soil N initially increase and then decline as a function of grazing intensity (Fig. 3). At low grazing intensities, productivity is limited by N availability. As herbivory intensifies, N turnover and N availability are enhanced, resulting in greater productivity. However, as more biomass is consumed, grass growth (determined by the logistic function in the equation for P) slows, reducing ANPP, and N uptake declines, resulting in greater N losses to leaching from the system, which in turn results in an overall decline in soil N with increasing herbivory.

Thus, for the resident herbivore scenario, the grazing optimization curve is caused by the interplay of N limitation at low grazing intensity (bottom-up control) and by suppression of plant standing biomass at high grazing intensity (top-down control). Intermediate levels of grazing promote N recycling without sharply depressing

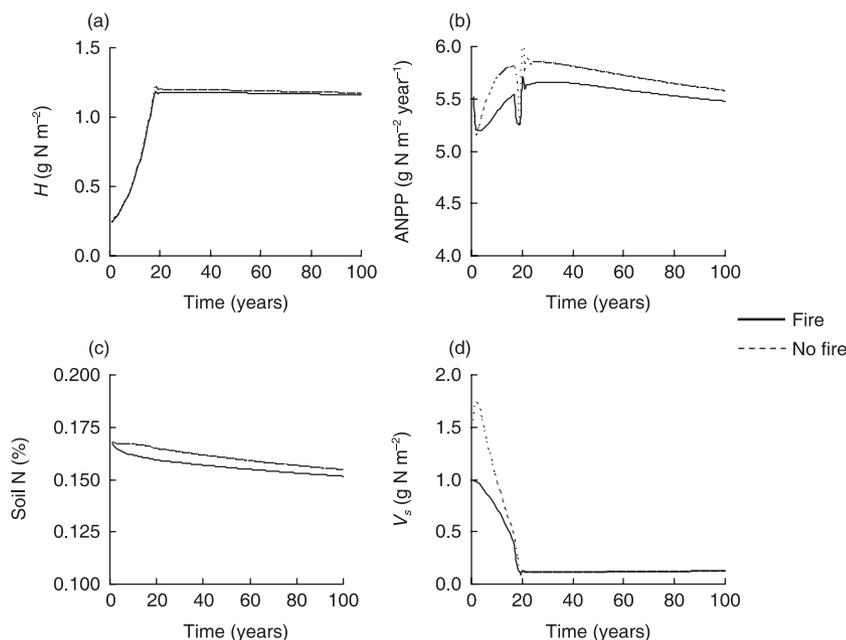


Fig. 4 Transient dynamics of (a) herbivore biomass H , (b) ANPP, (c) soil N, and (d) above-ground plant N (V_s) at the end of the dry season, with and without fire, assuming that herbivores are resident and regulated by food. The oscillatory behaviour in ANPP is driven by oscillations in soil inorganic N (not shown) that occur as H reaches steady state. These are in turn caused by oscillations in H , not visible due to the scale of the figure.

plant biomass. The peak of the curve is shifted to the left when fire is suppressed (Fig. 3), indicating that the positive effect of herbivores on N turnover reaches a maximum at a much lower intensity of grazing, so that the overall effect (beyond a low density) is negative. When fire is present, by contrast, herbivores continue to affect N availability positively at higher grazing intensities, because they minimize pyrodenitrification losses to the system.

In the migrant scenario, where herbivores are viewed as a forcing function, herbivory does not suppress grass growth (thus slowing N uptake) in the wooded grasslands during the growing season, when productivity is highest. As a result, at high grazing intensities, there is less build-up of inorganic N in the soil during the dry season in the migrant than in the resident scenario, and hence less N is exposed to leaching at the onset of the rains. Conversely, at low and medium population densities the resident scenario leads to higher productivity (Fig. 3). This occurs because by grazing in the wooded grasslands during the wet season, residents, unlike migrants, maximize N availability (through urinary and faecal N) at the time of the year when decomposition rates are also highest.

SYSTEM DYNAMICS WITH FEEDBACKS ON HERBIVORES

When herbivores are regulated by food availability, the model predicts a rapid increase from pre-rinderpest eradication population densities, with the population appearing to stabilize at present-day levels (Fig. 4). This shift is mirrored by a shift in plant above-ground

N (V_s). Productivity, after an initial decline, increases to a maximum as herbivore biomass H reaches a peak, and begins a gradual decline (Fig. 4). This decline in productivity is accompanied by a noticeable (but less pronounced) decline in soil N and H . ANPP and soil N are predicted to have lower values when fire is included than when fire is absent from the system, but the difference is small because herbivores suppress fire at steady-state (Fig. 4). The slow decline in ANPP and soil N is caused by a gradual loss of N from the system (both with and without fire), which also translated into a less pronounced decline in herbivore biomass (Fig. 4).

SENSITIVITY ANALYSIS

The sensitivity analysis (Fig. 5) suggested that (given a high level of herbivory and the presence of fire in the system) two main groups of parameters exert dominant effects on the equilibrium values for ANPP and soil N. The first group is a set of parameters that control the inputs of external N (such as atmospheric deposition σ and fixation ψ), and losses of N from the system (pyrodenitrification η , and denitrification ω). These parameters exerted similar effects on soil N and ANPP, with stronger effects on the latter than on the former. The second group of parameters was associated with internal N cycling along the plant pathway (the rate of decomposition of the slow SOM pool λ_s , the ratio of above- to below-ground production ϕ , and the proportion of plant detritus going to the fast SOM pool γ_V). These parameters affected soil N rather than ANPP (Fig. 5). This second group of parameters affects the extent to which N in the system is shifted away from above-ground biomass and

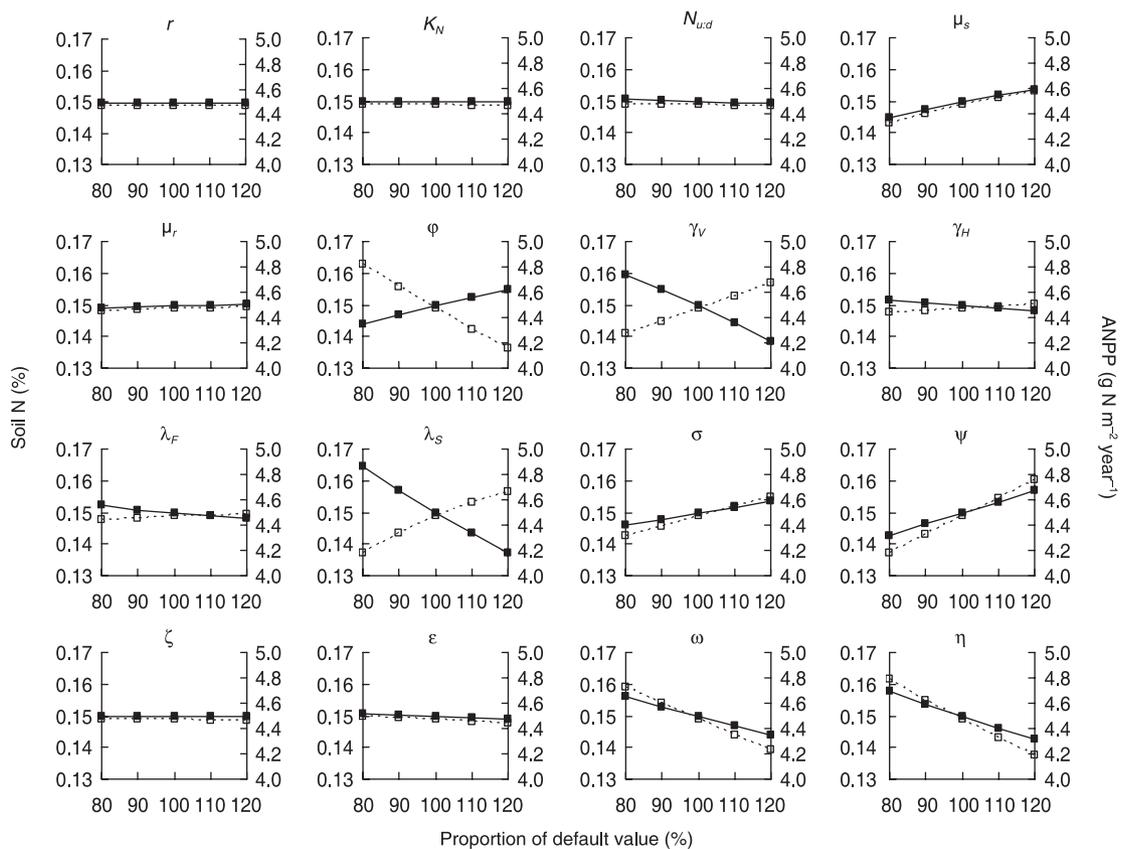


Fig. 5 Results of a sensitivity analysis on soil N (■) and ANPP (□) for 16 model parameters (refer to Fig. 1 and Table 1 for explanation of parameter symbols). The model was run for 100 years using five values of each parameter while all other parameters were kept at their default values.

kept in the slow N pool, where it is less readily subjected to losses from the system. With the exception of γ_H (the proportion of animal detritus going to the fast SOM pool), modifying the parameters associated with plant productivity and cycling through the animal pathway had only small or negligible effects on model equilibria (Fig. 5).

Discussion

THE EFFECTS OF FIRE, HERBIVORE POPULATION DENSITY AND MIGRATORY BEHAVIOUR

The model supports the hypothesis that fire may lead to N depletion from grassland and savanna ecosystems (Robertson & Rosswall 1986; Hobbs *et al.* 1991; Ojima *et al.* 1994), and suggests that fire and herbivory have antagonistic effects on N availability (Wedin 1995), although the magnitude of this effect depends on grazing intensity. The model also indicates a strong interaction between these two agents, driven primarily by decreasing pyro-volatile N losses as fuel loads are reduced by grazing. The indirect effect of herbivores via fire may be the principal mechanism through which grazers affect N dynamics in this ecosystem over long time periods. Interactions between grazing and fire have

been shown to be important in a number of ecosystems, both in terms of their effects on ecosystem function (Hobbs *et al.* 1991; Wedin 1995; de Mazancourt *et al.* 1999; Knapp *et al.* 1999; Kochy & Wilson 2005) and community structure and composition (Collins *et al.* 1998). This implies that the slight grazing optimization effect caused by enhanced N turnover with herbivore population density has a smaller magnitude than does the indirect effect of herbivores on N loss through fire. This is shown by the marked changes in productivity and soil N as a function of the fire–herbivore interaction compared with the modest optimization effects noted in the absence of fire (Fig. 2). This result is consistent with previous work conducted in a West African savanna (de Mazancourt *et al.* 1999). The role of herbivores as agents that mainly regulate pyro-volatile N losses is reinforced by the results of the sensitivity analysis. The latter shows that only a few parameters have strong effects on soil N and productivity, namely those that affect N inputs and outputs and those that regulate the recycling of plant N through the slow N pool. The only strong effect of herbivores occurs via the indirect reduction of pyrodenitrification through consumption.

The results also suggest that the system is relatively stable over the time-scales simulated here, although the gradual depletion of soil N under sustained heavy grazing (as indicated by the results with dynamic control over

the herbivore population) leads to a slow decline in the carrying capacity of the system. As with other models of plant-herbivore dynamics, a necessary condition for the system to be sustainable is that plants must be able to regrow reasonably rapidly following defoliation according to whichever growth equation pertains (logistic, in this case), regardless of their previous history of grazing. This could potentially lead to unrealistic behaviour at high grazing intensities: it is thus not clear that the present-day herbivore population density and high sustained rates of productivity (even when N is not limiting) could be achieved over long periods of time in the wooded grasslands of the Serengeti with year-round herbivory, as suggested by the simulation results. Moreover, we should caution that there clearly are other important processes (e.g. competition between trees and grasses) not included in the model.

Despite the prediction of N depletion driven by fire, there is evidence from other systems that, over time, fire may indirectly increase microbial N immobilization, thus reducing N uptake by plants and the N content of labile soil pools, but not of the slower pools (Dell *et al.* 2005). This presumably occurs because N is removed from the portions of the cycling pathway where it may be particularly susceptible to volatilization, as plants allocate more resources to below-ground structures protected from fire (Wedin 1995). In support of this hypothesis, at least one study has found that fire does not reduce total soil N over time in a savanna environment (Aranibar *et al.* 2003). As a counterweight to the argument that fire may lead to N immobilization, burning could indirectly lead to increases in N mineralization by increasing phosphorus (P) availability (Hartnett *et al.* 2004). The tall grasses of the wooded grasslands of the Serengeti are very poor in P, and there is some evidence that this P deficiency contributes to limiting the availability of inorganic N (Ruess & Seagle 1994). Additional empirical research would be desirable to investigate the complex effects of fire on N immobilization and uptake.

The resident herbivore scenario of the model generates a pattern consistent with McNaughton's (1979) grazing optimization hypothesis, although this effect is quantitatively not very pronounced. Several studies have supported this hypothesis (McNaughton 1979; Georgiadis *et al.* 1989; Williamson *et al.* 1989; Turner *et al.* 1993), but it also has been the source of much controversy (e.g. McNaughton 1983; Belsky 1986; McNaughton 1986). Milchunas & Lauenroth (1993) summarized a large number of empirical studies in a meta-analysis, and found that although grazing does at times appear to increase productivity, in most cases it had a negative or neutral effect on plant growth. Our study suggests that the pattern observed may depend on the particular range of grazing intensities considered. The prediction of increased ANPP at low to moderate grazing intensity is observed in a number of empirical studies (McNaughton 1985; Williamson *et al.* 1989; Turner *et al.* 1993), prior computer simulation studies for

the Serengeti ecosystem (Coughenour 1984; Coughenour *et al.* 1984; Seagle *et al.* 1992), and from abstract theoretical models (chapter 6 in DeAngelis 1992; de Mazancourt *et al.* 1998).

THE ROLE OF CROSS-BOUNDARY SUBSIDIES

Our results do not support the hypothesis that herbivore effects on productivity and N availability are attributable to the openness of the Serengeti ecosystem, given that the resident scenario results in higher productivity than the migrant scenario for a wide range of population densities (Fig. 3). In our model, this occurs because the effect of high N turnover driven by resident herbivores during the wet season in the wooded grasslands outweighs the N subsidy effect that occurs when migration is permitted. Studies of spatial subsidies in other ecosystems have documented important effects of cross-ecosystem nutrient fertilization (e.g. Frank *et al.* 1994; Polis *et al.* 1997; Helfield & Naiman 2001; Walker *et al.* 2003). However, at an ecosystem-wide scale, our model results suggest that N transport by wildebeest in the Serengeti is unlikely to exert an important influence on productivity relative to other key processes. Although daily movements by large herbivores may generate significant cross-habitat N fluxes (Augustine *et al.* 2003; Seagle 2003), seasonal migrations generally tend to generate subsidies that are small compared with those produced by daily patterns of habitat use at small spatial scales (Seagle *et al.* 1992; Schoenecker *et al.* 2004). We initially expected to observe a strong subsidy effect, but our model results suggest that the effect is masked by other key ecosystem processes.

MODEL LIMITATIONS

It is possible that some of these conclusions could change were the model made more complex in realistic ways. For instance, to simplify the model, we did not explicitly model plant litter dynamics. Including terms for litter compartments may be potentially important, because litter accumulation can represent an important factor limiting plant productivity at low herbivore density (McNaughton *et al.* 1988; Seagle *et al.* 1992). We also assumed that N : C ratios within compartments are fixed; this could potentially bias our results, because the rate at which N and C are lost from the various compartments can vary differentially as a function of fire intensity, herbivory and rainfall. Furthermore, herbivory may directly affect the N content of plant tissues (Ritchie *et al.* 1998). Another potentially important factor is that plant community composition may shift over time when changing from an ungrazed to a grazed condition (McNaughton *et al.* 1988). Over time, given a trade-off between palatability and productivity across species (Coley *et al.* 1985; Pastor & Cohen 1997), selective grazing should lead to the replacement of palatable species by unpalatable ones, depressing system productivity and potentially slowing nutrient cycling (Pastor

et al. 1993; Pastor & Cohen 1997; Ritchie *et al.* 1998). This replacement may not be limited to grasses: heavy grazing leading to fire suppression can result in an increase in tree biomass (Dublin *et al.* 1990). Our model assumes that tree biomass (which is not modelled explicitly) is invariant, but a shift from grasses to trees may slow N cycling, given the higher content of lignin and secondary compounds in trees relative to grasses (Scholes & Walker 1993). Conversely, this shift in functional groups could enhance N cycling if trees are N fixers, as occurs in much of the Serengeti wooded grasslands.

In the future, we intend to explore the effect of relaxing these assumptions, adding feedbacks of the vegetation on herbivore biomass using the SAVANNA ecosystem model, which incorporates a rich array of ecosystem processes, including tree–grass interactions (Coughenour 1992; Boone *et al.* 2002).

CONCLUSIONS AND FUTURE DIRECTIONS

Our model suggests that ungulates may exert profound direct and indirect effects on ecosystem nutrient budgets, and that the interactions among these effects may be rather complex. Herbivory itself can potentially enhance N availability and productivity in grassland ecosystems by accelerating the rate of N turnover in the system, but the timing of grazing in relation to the growing season may also be critical in determining the shape of the relationship between grazing and ecosystem function. In the Serengeti, the effects of large-scale seasonal migrations may have consequences for productivity and N turnover that differ from those observed in closed ecosystems because of seasonal forcing in herbivory (although this migratory effect does not appear to explain the positive effects of herbivores on productivity in the wooded grasslands). Herbivory may also be a key factor moderating the potentially detrimental effects of fire on ecosystem nutrient balance, and indeed this effect may greatly outweigh the spatial subsidy effect that might be casually expected from the visual spectacle of the ungulate migration. Our modelling framework provides a useful platform from which to conduct a first-order analysis of these factors. Given the fact that testing some of these effects experimentally (e.g. retaining herbivory while eliminating spatial subsidies in the Serengeti) may be logistically impossible, simulation models such as that presented here can provide essential insights into ecosystem functions and feedbacks that are vital for making sound management decisions (e.g. in guiding controlled burning). We hope that our approach generates hypotheses amenable to testing in an experimental or comparative framework, and suggest that our synthetic ecosystem–vegetation–herbivore model highlights the potential importance of herbivore–fire interactions and system openness in modulating the impact of herbivores upon plant production, biomass and ecosystem dynamics.

More broadly, our results buttress the suggestion (e.g. see Loreau & Holt 2004) that there can be profound differences between spatially open and closed ecosys-

tems (here, determined by the presence or absence of migration in a dominant herbivore). Our model suggests that the impact of trophic interactions on ecosystem function can be strongly influenced by whether the ecosystem is open or closed.

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