

Ecosocial consequences and policy implications of disease management in East African agropastoral systems

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International research and development efforts in Africa have brought ecological and social change, but analyzing the consequences of this change and developing policy to manage it for sustainable development has been difficult. This has been largely due to a lack of conceptual and analytical models to access the interacting dynamics of the different components of ecosocial systems. Here, we examine the ecological and social changes resulting from an ongoing suppression of trypanosomiasis disease in cattle in an agropastoral community in southwest Ethiopia to illustrate how such problems may be addressed. The analysis combines physiologically based demographic models of pasture, cattle, and pastoralists and a bioeconomic model that includes the demographic models as dynamic constraints in the economic objective function that maximizes the utility of individual consumption under different level of disease risk in cattle. Field data and model analysis show that suppression of trypanosomiasis leads to increased cattle and human populations and to increased agricultural development. However, in the absence of sound management, these changes will lead to a decline in pasture quality and increase the risk from tick-borne diseases in cattle and malaria in humans that would threaten system sustainability and resilience. The analysis of these conflicting outcomes of trypanosomiasis suppression is used to illustrate the need for and utility of conceptual bioeconomic models to serve as a basis for developing policy for sustainable agropastoral resource management in sub-Saharan Africa.

bioeconomics | meta-tools | physiologically based models | cattle
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For >50 y, international donors have funded research and development (R&D) on many pressing issues of human and ecosystem health in sub-Saharan Africa. One of these research areas has been trypanosomiasis in cattle (and humans) that restricts husbandry across large part of sub-Saharan Africa (1). The causal agents of trypanosomiasis are species of parasitic protozoan of the genus *Trypanosoma* vectored principally by adults of several species of tsetse flies (*Glossina* spp.). Most programs against trypanosomiasis have been motivated by eradication and control objectives and have had only weak links to the environmental and social science research (1) required to formulate sustainable development policy (2). Here, we examine some of the ecosocial consequences of the suppression of trypanosomiasis on sustainability of an agropastoral community in southwest Ethiopia.

Goodland's (3) clarion call for ecological, economic, and social sustainability recognized that sustainability can be achieved only by keeping the scale of the human economic system within the biophysical limits of the ecosystem. Furthermore, we have learned that the self-repairing capacity of ecosystems cannot be taken for granted because ecosocial change may exceed system resilience (4, 5), which C. S. Holling (6) defined as the magnitude of disturbance a system can experience before it shifts to a different stability domain with different controls on system structure and

function. In application, this implies the need to sustain desirable pathways and ecosystem states and to avoid undesirable system configurations (7) in the face of continuous change (8, 9) that can have unexpected and unwanted consequences (10). Most studies on ecosocial resilience in managed systems have been theoretical and/or lacked conceptual and analytical models to access the interacting dynamics of the ecological, economic, and social components of ecosocial systems (11).

We propose 2 general modeling approaches to resolve some of these issues: Weather-driven physiologically based ecosystem models of energy/mass flow in trophic chains and webs including the economic consumer (12–14) and bioeconomic models that includes dynamics of the renewable resource to be managed and the resource manager, i.e., as dynamic constraints in the objective function (15, 16) that maximizes the utility of consumption by individuals under different levels of risk (17, 18). In economics, consumption is the hedonistic use of revenues in ways that do not contribute to firm growth, whereas in nature, consumption is the use of energy in a manner that, on average, does not contribute to growth (e.g., excess reproductive capacity in *r*-selected species and parental care in *K*-selected species) (18) but does contribute to adaptedness. A full suite of economic analogies for resource acquisition and allocation at all levels of natural and human economies, including the conflicting notions of biological and economic demand, consumption, and risk, has been proposed (17–19).

An East African Grassland System

The flow of energy in an East African grassland/wild herbivore/predator system including the biological analog of consumption in each trophic level is illustrated in Fig. 1A. These grasslands have largely been converted to agropastoral systems with cattle becoming the dominant herbivore and pastoralists assuming the top position in the food chain with animal trypanosomiasis (tryp) being a major constraint in many areas (Fig. 1B) (20). An example of such an agropastoral system is the Gurage ethnic agropastoral community at Luke in the sparsely fertile and semimountain region of southwest Ethiopia (21, 22). In 1995, the Luke villagers initiated a program to reduce the prevalence of trypanosomiasis by treating infected cattle with trypanocidal drugs and by suppressing populations of the tsetse fly vector using odor baited traps. Ecosocial data on the project were also collected and analyzed (22, 23). Tick-borne diseases (tbd) in cattle and malaria in human, among others, are of concern in this area as are the changing patterns of land allocation to agriculture, declining soil fertility, the vagaries of environmental variables (Fig. 2).

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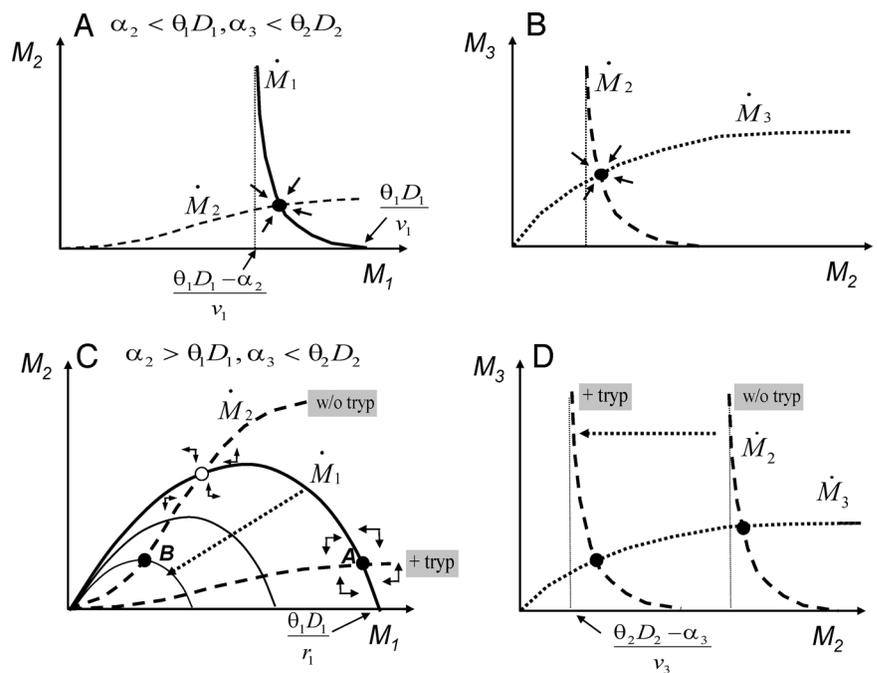


Fig. 3. Isoclines for an East African grassland (M_1), herbivore (M_2), and predator (M_3) system. (A) The grassland, herbivore phase plane. (B) The herbivore, predator phase plane, and a pasture/cattle/pastoralist system under trypanosomiasis (tryp) pressure. (C) The pasture, cattle phase plane with (+tryp) and without (w/o tryp) trypanosomiasis. (D) The cattle, pastoralist phase plane. • indicates stable equilibrium, and ◦ indicates an unstable one, and the dotted arrow in C indicates a decline in soil fertility.

The function $D_i h(u_i)$ is a ratio-dependent concave per-unit functional response model that includes interspecific competition in the exponent and the possibility of utilizing several resource species each having different α s and consumer preferences. The term $D_i M_i$ is the maximum population demand, and $D_i M_i h(u_i) \leq \alpha_i M_{i-1}$ is the rate of resource depletion by the i th level, where $\alpha_i \leq 1$ sets the limits on the extraction by level i from resource level $i-1$. If α_i is sufficiently small compared with the assimilation efficiency of the lower level [$\alpha_i \leq \theta_{i-1} D_{i-1} - v_{i-1}(D_{i-1})$], then the lower trophic level will survive any population size and demand rate of its consumer. The model (Eq. 1) has been used to study resource allocation dynamics at the individual, population, metapopulation and regional levels (14).

The model is used to describe the dynamics of the East African pastoral system where M_1 is pasture biomass, M_2 is cattle biomass, and M_3 is the pastoralists (Eq. 2)

$$\begin{aligned} \dot{M}_1 &= \theta_1 M_1 D_1 h(u_1) - v_1 (D_1) M_1 - M_2 D_2 h(u_2) S_{\text{trypt}} S_{\text{tbd}} \\ \dot{M}_2 &= \theta_2 M_2 D_2 h(u_2) S_{\text{trypt}} S_{\text{tbd}} - v_2 (D_2) M_2 - M_3 D_3 h(u_3) S_{\text{malaria}} \\ \dot{M}_3 &= \theta_3 M_3 D_3 h(u_3) S_{\text{malaria}} - v_3 (D_3) M_3 \end{aligned} \quad [2]$$

Survivorship terms for trypanosomiasis (S_{trypt}) and tick-borne diseases (S_{tbd}) in cattle and malaria in pastoralists (S_{malaria}) are included as constants indicating the level of disease pressure (i.e., 0–1) due to the combined effects of morbidity and mortality. For specific field application, the density-dependent effects of each disease can be estimated from field data as k value functions (24), and the other parameters of the model can be estimated from field and/or laboratory data. This enables the model to be used to analyze changes in various agropastoral regions by using weather and the dynamics of soil nutrients and water as forcing variables (12–14). Below, we analyze the general stability properties of natural and managed East African grasslands to assess the ecological consequences of human interventions.

Analysis of a Natural Grassland/Wild Herbivore/Predator System

Wildlife is tolerant of trypanosomiasis ($S_{\text{trypt}} \approx 1$) but may carry high levels of infection (20) (Fig. 1A). The shapes of the zero isoclines and the equilibrium properties of Eq. 2 depend on the value of the apparency rate (α_{i+1}) of the renewable resource to

the consumer relative to the maximum per-capita growth rate of the resource ($\theta_i D_i$) (13). The inequalities for the natural grassland system are $\alpha_2 < \theta_1 D_1$ and $\alpha_3 < \theta_2 D_2$ yielding the zero isoclines for levels M_1 and M_2 depicted in Fig. 3A. The direction of the inequality $\alpha_2 < \theta_1 D_1$ is due to the high per-unit biomass growth rate of grass relative to the ability of wild herbivores to consume it. Similarly, the biomass growth rate of herbivorous wildlife is high relative to the predation pressure (i.e., $\alpha_3 < \theta_2 D_2$) yielding the zero isoclines in the (M_2, M_3) phase plane (Fig. 3B). The resource species have a maximum population at $(\theta_i D_i)/v_i$ and cannot be driven below the vertical asymptotes at $(\theta_i D_i - \alpha_{i+1})/v_i$. Stable equilibrium (•) occur in both the (M_1, M_2) and (M_2, M_3) phase planes.

Analysis of a Managed Grassland/Cattle/Agropastoralist System

In contrast to natural systems, trypanosomiasis pressure in agropastoral systems (+tryp) is high, and cattle are susceptible resulting in a low value for $S_{\text{trypt}} \rightarrow 0$. When healthy, cattle have an efficient search behavior and a larger per-capita demand rate than wild herbivores (i.e. $\alpha_2 > \theta_1 D_1$), and hence the shape of the isoclines for the pasture (M_1) is humped (Fig. 3C) as proposed by Noy-Meir (25). Pastoralists view herd size as a measure of wealth, and as insurance during periods of drought or high incidence of disease, and hence prefer not to consume or sell them (26). For this reason, the shape of the M_2 isoclines (Fig. 3C) is sigmoid as in Fig. 3A (e.g., $\alpha_3 < \theta_2 D_2$).

Under high trypanosomiasis pressure ($S_{\text{trypt}} \rightarrow 0$; +tryp), cattle density (M_2) is low ($>(\theta_2 D_2 - \alpha_3)/v_2$) (Fig. 3D), and pasture level (M_1) is high, yielding a stable equilibrium at point A (•, Fig. 3C). However, suppression of tsetse/trypanosomiasis drives $S_{\text{trypt}} \rightarrow 1$ and allows cattle populations to increase resulting in an unstable equilibrium (◦) that leads to overgrazing and the depletion of soil nutrients. This causes the M_1 isocline to contract leftward (dotted arrow, Fig. 3C) resulting in a new stable equilibrium at low M_1 and M_2 (point B, •, Fig. 3C). This is a demonstration of exceeding resilience capacity that takes the system to a new but unfavourable stable point (6).

Viewing the isoclines in the (M_2, M_3) phase plane shows that trypanosomiasis suppression causes a rightward shift in the M_2 isocline that affects the level but not the shape of the M_3 isocline

(Fig. 3D). However, overgrazing causes a reversal or leftward shift in the M_2 isocline in the (M_2, M_3) phase plane that could be as extreme as the effects of high trypanosomiasis pressure (Fig. 3D) suggesting that solving the trypanosomiasis problem may lead an overgrazing problem. The ecosocial consequences of trypanosomiasis suppression were examined by ref. 26 and are reviewed and expanded below by using the bioeconomic model.

Bioeconomic Model of Managed Grassland/Cattle/Agropastoralist Systems

For clarity, Eq. 2 is simplified to represent the dynamics of M_2 and M_3 given a constant amount of forage M_1 (Eqs. 3 and 4) (see ref. 17):

$$\frac{dM_2}{dt} \equiv \dot{M}_2 = G(M_1, M_2) - v_2(D_2)M_2 - F(M_2, M_3) \quad [3]$$

$$\frac{dM_3}{dt} \equiv \dot{M}_3 = \theta \cdot F(M_2, M_3) - v_3(D_3)M_3 \quad [4]$$

where $G(M_1, M_2) = M_2 D_2 h(u_2)$ is the quantity of M_1 eaten by cattle, $F(M_2, M_3) = M_3 D_3 h(u_3)$ is the flux of M_2 harvested by pastoralists (M_3), and $v_2(D_2)M_2$ and $v_3(D_3)M_3$ are the respiration rates. The functions $G(\cdot)$ and $F(\cdot)$ satisfies the necessary concavity and positive marginal productivity conditions of economic models because both increase with resource levels and decrease with intraspecific competition among consumers [i.e., the exponent $-\alpha_i M_{i-1}/D_i M_i$ in $h(u_i)$, (Eq. 1)] (13). This biology in reduced form is included in the bioeconomic objective function (Eq. 5).

Bioeconomic Objective Function

In economics, the objective function for resource exploitation by all individuals of M_3 seeks to maximize the present value utility of individual consumption (C) from the revenue (energy) stream and is expressed as:

$$\max_{C, D} \int_0^{\infty} e^{-\delta_{\text{trypt}} t} M_3 U(C) dt \quad [5]$$

subject to the dynamics constraints of the managed resource M_2 (Eq. 3) and the pastoralists M_3 (Eq. 4), $e^{-\delta_{\text{trypt}} t}$ is the discount factor reflecting the level of risk of trypanosomiasis, t is time, and the per-capita demand (D) and consumption (C) rates are control variables (17). C is included in the model via the monotonically increasing concave utility function of individuals $U(C)$ that has properties $U'(C) > 0$, $U''(C) < 0$ and $U'(C) \rightarrow 0$ as $C \rightarrow \infty$.

By Pontryagin's maximization principle, the maximization of Eq. 5 by all consumers M_3 subject to population dynamics constraints (Eqs. 3 and 4) is equivalent to the maximization of the current value Hamiltonian (Eq. 6) (17, 27):

$$\mathcal{H} = U(C)M_3 + \lambda_1(g - F) + \lambda_2[\theta F - (vD + C)M_3] \quad [6]$$

where λ_1 and λ_2 are costate or auxiliary variables associated with the dynamic constraints. In particular, λ_1 is the Lagrange multiplier that represents the marginal utility of income from harvesting M_2 . The necessary conditions for an optimal solution of Eq. 6 are satisfied, $C^*(\delta)$ is an increasing function of δ , and because λ_1 and M_2 do not depend on M_3 and $\lambda_1 \leq U'(C^*)(\theta - v)$, this allows the analyses to be restricted to $[0, U'(C^*)(\theta - v)] \times [0, \infty]$ in the (λ_1, M_2) phase space. The extensive mathematical analysis is outlined in ref. 17 and is not reproduced here.

Two solutions arise: The optimal societal solution for resource exploitation by all pastoralists maximizes the present value utility of individuals expending from the revenue stream in ways that do not contribute to growth (consumption) and yet assures the persistence of the renewable resource over an infinite time horizon (i.e., renewable resource sustainability), and the competitive solution results where pastoralists pursue self-interest goals with $\lambda_1 \rightarrow 0$ as $\delta \rightarrow \infty$ resulting in overexploitation of the resource.

Bioeconomic Effects of Reducing Trypanosomiasis Risk

Ecosocial Data. The trypanosomiasis program at Luke, Ethiopia, was initiated in 1995, and by 2005, tsetse populations were very low, and the prevalence of trypanosomiasis fell from 29% to 10% (23, 26). The prevalence of disease would have been lower had infected cattle not been continually introduced from outside the suppression zone and trypanosomiasis not been endemic in wildlife. Cattle numbers including oxen increased 5-fold, calving rates 8.2-fold, milk production 13-fold, per-capita income doubled, and human populations increased 40%. Increases in highly susceptible oxen allowed cultivated land to increase from 12 ha in 1995 to 506 ha in 2005. Increased revenues enabled the building of a school and allowed the villagers to continue the tsetse/trypanosomiasis suppression program. The latter 2 items are measures of economic consumption as well as indicators of the Luke community's readiness to adopt change and reacted to new opportunities. Studies undertaken in Africa under different cultural and ecological conditions have also shown fast economic responses to tsetse control operations (28).

Predictions of the Bioeconomic Model. The dynamics of the bioeconomic model can be reduced mathematically to the zero isoclines for the shadow prices for cattle (λ_1) and cattle populations (M_2) at different levels of trypanosomiasis risk (δ_{trypt}) (see appendix in ref. 17). As observed, the model predicts that a dramatic reduction in risk ($\delta_{\text{trypt}} \rightarrow 0$) and increased productivity (θ_2) lead to increased cattle (M_2) and human (M_3) populations, and to increases in the marginal value (λ_1) of cattle. Some of the dynamics are summarized in the $(\lambda_1, M_2, \theta_2)$ phase space (Fig. 4) where positive changes in λ_1, M_2 and θ_2 along the optimal path (point A to B) are measures of increasing economic health. All of the points along the optimal path are saddle points. In contrast, $M_{2,c}$ on the abscissa and points along the trace from it ($\lambda_1 = 0, M_2, \theta_2$) is the path of the competitive solution. Point $M_{2,e}$ on the abscissa is a hypothetical level where the system collapses (17, 18).

As δ_{trypt} decreases from an initial high level (Fig. 4, point A), the optimal trajectory (λ_1^*, M_2^*) increases on θ_2 to the point of maximal societal benefit (point B). However, overgrazing beyond B reduces natural capital (M_1 and soil fertility) resulting in a reversal of θ_2 with the optimal path of λ_1^*, M_2^* (the dashed line) declining in the direction of system collapse (i.e., $M_{2,e}$; point C). The rate of change of the optimal trajectory from A to C may be relatively fast, whereas the reversal or remediation from C back to the "maximum optimal societal benefit" at B is slow commensurate with the time required to rebuild soil structure and function. This illustrates the effects of fast and slow variables in the system (5, 7).

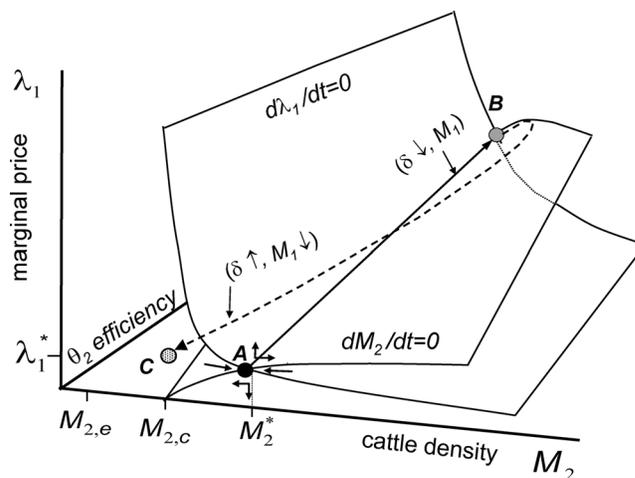


Fig. 4. The (λ_1, M_2) phase plane on increasing θ_2 for an East African agropastoral system (see text).

