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The propagation of disturbance in savannas through food webs

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Abstract. Savanna-grassland ecosystems are highly interactive due to effects among interconnected trophic elements. This can cause disturbance at one level in the trophic web to be propagated through that web to have effects far removed from the initial locus of disturbance. The reconstructed effects of rinderpest upon African savannas, acting directly upon susceptible grazers and browsers but indirectly upon many other ecosystem components, are used as a case history illustrating the propagation of disturbance in savanna ecosystems.

Keywords: Browsing; Grazing; Rinderpest; Serengeti.

Introduction

A disturbance to an ecosystem is some force that causes that system to depart from its normal state or course. The roles of disturbance in community and ecosystem studies have long been a concern of ecology and there is no need to review that here, beyond recognizing the contemporary rekindling of interest in disturbance and its consequences (Bormann & Likens 1979; Cairns, Dickson & Herricks 1977; Hubbell 1979; Mooney & Godron 1983; Pickett & White 1985; Sousa 1984). Much of the recent discussion has focused on the role of disturbance as a generator of patchiness (Sprugel 1976), e.g. pattern diversity (McNaughton 1983), and the degree to which disturbance prevents a steady-state from arising or, alternatively, the degree to which recurrent disturbance can create communities in steady-state under that recurrent regime (Horn 1975; Hubbell 1979).

The principal theme of this paper is that many disturbances are propagated through the food webs and environments of ecosystems so that changes at one level cascade in complex chains of cause and effect to modify process and components throughout the ecosystem (e.g. Carpenter, Kitchell & Hodgson 1985; Estes & Palmisano 1974; Paine 1980), including some that are far removed from, even seemingly divorced from, the initial specific site of action of the disturbance (Brown & Heske 1990).

Some cascades will be damped while others can be amplified as they are transmitted. Damping, or attenua-

tion, will limit the degree to which a disturbance to one ecosystem component affects others. I have elsewhere considered damping as a mechanism contributing to the stability of savanna-grassland ecosystems (McNaughton 1977a, 1984, 1985) and here concentrate upon transmission. Both transmission without damping and transmission with amplification will spread a disturbance far beyond its initial site of action; I here consider how a disturbance that initiates chains of cascading effects (Carpenter, Kitchell & Hodgson 1985) can transform an ecosystem from one state to another.

Various ecosystem processes and states may simultaneously trace quite different trajectories in response to a disturbance. For example, in northeastern USA forests, plant biomass and productive capacity may be re-established rapidly following forest destruction (Marks 1974) while species composition and trophic relationships may rarely reach a state of constancy in the intervals between disturbances (Bormann & Likens 1979). Species composition of the community may be highly unstable in response to disturbances that favor some species over others, but that very instability can serve to damp transfer of the disturbance to such ecosystem processes as energy and nutrient flow (Chapin & Shaver 1985; King & Pimm 1983; McNaughton 1968, 1977, 1985; Mellinger & McNaughton 1975; Pimm 1982, 1984).

Disturbances may be either intrinsic or extrinsic to the ecosystem. Some intrinsic disturbances are driven by the life histories of the major species whose establishment, growth, and subsequent death (Watt 1925, 1947; Sprugel 1976) can create a shifting mosaic of species composition and resultant trophic processes (McNaughton 1983; Mooney & Godron 1983; Pickett & White 1985; Sousa 1984). While any local area is in a state of constant disturbance and recovery, a patch disequilibrium, the system as a whole can be in a state of dynamic equilibrium (Watt 1964). Other intrinsic disturbances can be generated by trophic interactions that produce periodic oscillations of species abundances, productivity, and nutrient cycling (Bryant, Chapin & Klein 1983; Fox & Bryant 1984).

Alternatively, some disturbances will be driven by such extrinsic factors as windstorms (Henry & Swan 1974) and catastrophic forest fire, which are due to a particular confluence of both internal and external factors, e.g. fuel load and moisture combined with weather (e.g. Clark 1988).

Disturbances vary in duration, intensity, directionality, and recurrence. Moreover, a given change in environment for one system can constitute a severe disturbance, e.g. forest fires, while an identical factor will be no disturbance at all for another ecosystem, e.g. grassland fires (Anderson & Brown 1986).

The fundamental tasks in studying disturbance are to discriminate between those fluctuations that are extraordinary and those that are usual, and to measure the effects of the former. A hierarchical approach is required because such discrimination and measurement are scale-dependent. Grazing or browsing can be a severe disturbance to an individual plant, modifying its physiology and ecology in profound ways (Jameson 1963; McNaughton 1979a). But grazing and browsing are ordinary, characteristic processes in most savanna grasslands, excepting South America between the Pleistocene extinctions and the colonial period when livestock were introduced. In most grasslands, it is the elimination of grazing that constitutes a disturbance. Therefore, both a recognition of scale-dependence and a historical perspective are required. I consider perturbations involving Africa's indigenous fauna during historical times.

Savanna-grassland ecosystem disturbance

Geological, geographic, and historical perspectives

Savanna-grasslands and their faunas were born in the climatic disturbances that began in the Miocene and continued with varying frequency and magnitude through the Pliocene and Pleistocene epochs (McNaughton 1991; Scott 1937; Webb 1977, 1978). Those disturbances were instrumental to the origins and adaptive radiations of the *Poaceae* and large, mammalian herbivores in which the evolution of hypsodonty was diagnostic of an increasing reliance of diets upon plants with tough, abrasive tissues (Kowalevsky 1873-1874). Variations in the silicification of different plant tissues, of different plant species, and in different environments led to patterns of resource partitioning among the radiating ungulates (McNaughton & Tarrants 1983; McNaughton et al. 1985) similar to the patterns preserved in African remnants of the Pleistocene megafauna (Gwynne & Bell 1968; Jarman & Sinclair 1979; Lamprey 1963; McNaughton 1976, 1985; Sinclair & Gwynne 1972;

Talbot & Talbot 1963).

Grasslands and savannas occur in regions where the climate is characterized by spatial and temporal variability, with precipitation and resultant primary productivity varying drastically in both space and time (McNaughton 1979b, 1991). The large, mobile nomadic ungulates that came to dominate the savanna-grassland faunas dampened their exposure to the inherent climatic disturbances by evolving cursorial limbs (Hildebrand 1987) that allowed them to move rapidly in response to localized and regional patterns of precipitation (Maddock 1979; McNaughton 1979b, 1985, 1990). Normal climatic events, such as the periodic heavy rain showers that are typical of savanna-grassland climates, can serve as fatal disturbances to sedentary, small, fossorial herbivores (Senzota 1984).

Historically, savanna-grasslands have been subject to intense, recurrent human-generated disturbances of major extent. Initiation of those disturbances was concentrated in the 19th and early 20th centuries and they continue today, transforming grassland ecosystems into drastically different forms and converting native vegetation to exotic grasslands. African, Asian, and North American savanna-grasslands suffered almost total destruction of their large mammalian faunas, which were replaced by either domestic livestock with much reduced mobilities, or with cultivated agro-ecosystems. That transformation continues, but the major disturbances took place during a remarkably short time period, largely the mid- to late 19th century (Bannikov et al. 1961; Ford 1971; Haines 1975; Hornaday 1889; Huntley & Walker 1982; Roe 1951). Although there was a more recent partial restoration of the Eurasian steppe ecosystems (Bannikov et al. 1961), and small portions of the North American grasslands have been restocked with a semblance of their native fauna, the spatial restriction and lack of significant natural predator populations in those nature reserves depart markedly from precolonial conditions.

South American grasslands, which had lacked significant densities of large herbivores since the late Pleistocene (Webb 1978), were rapidly stocked with domestic livestock during the same period that North American and Eurasian grasslands were being transformed due to the replacement of wild herbivores with domesticated livestock. Though historical records of species composition are lacking, exclosure studies can leave little doubt that species composition and plant growth forms in South American grasslands were significantly affected by those changes (Sala et al. 1986).

Australian rangelands also were rapidly stocked with high densities of sheep (*Ovis aries*) near the turn of the 20th century. The accompanying provision of supplemental water and other cultural modifications, designed

to increase range carrying capacity for livestock, produced significant range expansions and density increases in some of the native *Macropodidae* (Newsome 1975). The resulting continuous, heavy stocking represented herbivore densities significantly greater than those of precolonial Australian rangelands. Range deterioration due to shrub invasion was an inevitable result.

All of these disturbances to savanna-grasslands, whether prehistoric extinction of South American large mammals, replacement of a mobile native fauna with a sedentary domesticated fauna, or expansion of the ranges and abundances of native species coupled with livestock husbandry, had major effects that drastically altered ecosystem organization. Bush encroachment, soil erosion, major shifts in species' abundances, and invasion of ranges by unpalatable plants were almost universal consequences of the changes in historic time (e.g. Skarpe 1990; Stoddart, Smith & Box 1975). Those changes all result from the propagation of disturbances through grassland food webs and environments so that an initial change had multiple effects throughout the ecosystem.

As a case history of the assertion that food webs act as media transmitting disturbances throughout ecosystems (Carpenter, Kitchell & Hodgson 1985; Estes & Palmisano 1974; Paine 1980), and thereby modifying the ecosystem's fundamental character, I consider the effects of rinderpest in Africa. This choice is based on known patterns of change in animal and human densities accompanying introduction of the disease into a susceptible ungulate community, on patterns accompanying

recovery from the disease in a specific ecosystem, and on related experimental studies in that ecosystem. Because the Serengeti has been the subject of extensive research (Sinclair & Norton-Griffiths 1979), it is a particularly suitable ecosystem for tracing disturbance cascades. Patterns in Africa described here may serve as a plausible partial model for reconstructing the effects of the 19th century extinctions of native savanna-grassland faunas and the greatly increased animal densities in localities that, like South America and Australia, did not previously support abundant grazers.

I concentrate here on the interconnections among disease, animal densities, vegetation productivity and standing crop, fire, rainfall, the balance of graminaceous and woody plants, soil nutrient budgets, and related aspects of human ecology in the Serengeti, a region encompassing the best studied natural, unmanaged ecosystem supporting an animal community representative of the megafauna with which grasses evolved and coexisted over much of the Earth until a century ago.

The context: The Serengeti ecosystem

The Serengeti ecosystem (Fig. 1) is operationally defined by the movements of large herds of migratory blue wildebeest (*Connochaetes taurinus*) and plains zebra (*Equus burchelli*) over ca. 25 000 km² between 1°30' to 3° S and 34° to 35° 30' E (Watson 1967). It is bounded by natural physiographic and vegetation barriers restricting the ranges of these major large herbivores

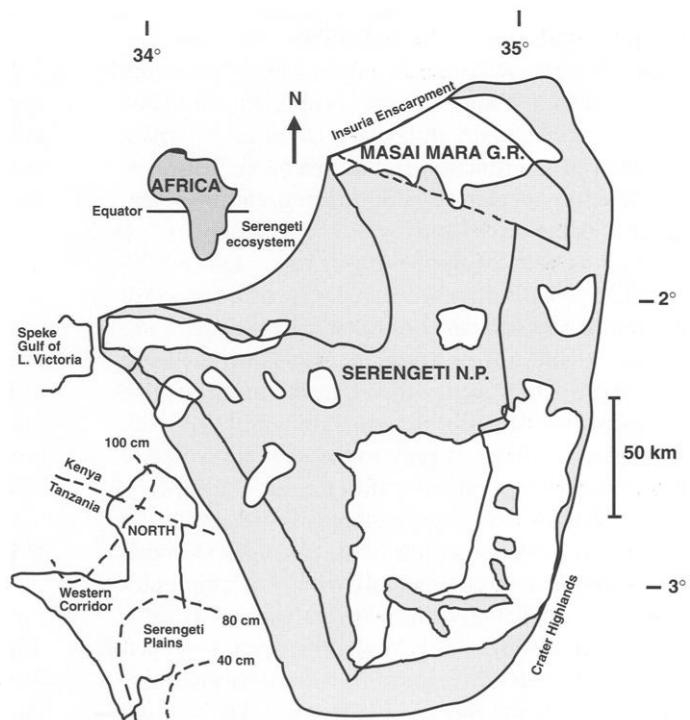


Fig. 1. The Serengeti ecosystem; the outer solid line encompasses the ranges of the major nomadic herbivore species. Stippled areas are savanna-woodland mosaics and open areas are treeless grasslands. Rainfall isohyets (cm) of the Serengeti region are shown in insert panels. From McNaughton (1985).

(McNaughton 1983, 1985; Pennycuick 1975; Schaller 1972; Watson 1967). It lies on a broad peneplain between 1100 m near Lake Victoria to 1800 m, with the Gregory Rift and the associated Crater Highlands in the east rising to near 3600 m. Those highlands create a rainshadow producing a mean annual rainfall gradient from 350 mm in the SE to 1200 mm in the NW (Norton-Griffiths, Herlocker & Pennycuick 1975). The rainfall-determined growing seasons range from less than 90 days in the SE to virtually continuous in the NW (McNaughton 1985). The nominal wet season is from November through May, and the nomadic ungulates spend much of that period on the arid Serengeti Plains in the SE. The dry-season occupancy ranges of those herds is toward Lake Victoria early in the season and across the international boundary along the Mara River basin in the NW at the peak of the dry season.

There are 1.4 million wildebeests and 250 000 zebras, as well as 450 000 Thomson's gazelles (*Gazella thomsonii*), 80 000 topis (*Damaliscus korrigum*), and 70 000 buffaloes (*Syncerus caffer*), based on aerial censuses (Campbell 1989; Grimsdell 1979; Sinclair & Norton-Griffiths 1982). Gazelles move seasonally between the Serengeti Plains in the wet season and surrounding savanna margins in the dry season; resident gazelle herds are scattered throughout the area above mean annual rainfalls of about 800 mm. Buffalo and topi are non-migratory and occur as resident herds above the 800 mm isohyet. Elephants (*Loxodonta africana*) numbered about 3500 in the mid-1970s, first appearing in historical time in 1955 (Lamprey et al. 1967), but have now been reduced to less than 400 by serious poaching that began in the late 1970s. They are presumed to have occupied the area during the 19th century based on ivory-trading evidence (Fosbrooke 1968) and are now, like the black rhinoceros (*Diceros bicornis*), threatened with extinction in the Serengeti. There are over 20 other species of large grazing and browsing mammals in the ecosystem.

Large sections of the Serengeti ecosystem are located on exposed portions of an old, degraded section of the Precambrian African Shield that has long been comparatively stable, but the landscape also shows evidence of vulcanism, rifting, continental warping, and lacustrine sedimentation followed by erosional stripping (Epp 1980; McNaughton 1983). Orogeny to the west beginning in the Miocene and continuing into the late Pleistocene produced Lake Victoria as a tectonically-induced backwater on the western margins of the Serengeti (Kendall 1969). It has its own convergence front that contributes to higher rainfall in the north and west (Norton-Griffiths, Herlocker & Pennycuick 1975). The open Serengeti Plains lay on deep ash deposits from massive eruptions of Kermasi Volcano about 150 000 yr ago. The volcano

Oldoinyo Lengai, has erupted several times this century.

The Serengeti ecosystem has been a locus of evolution of both humans (Leakey et al. 1976) and a well-described paleofauna with clear phyletic relationships to the extant animal community (Gentry & Gentry 1977, 1978). So, by inference, grassland-savanna vegetation not unlike the current vegetation has long occupied the area, with the balances between grasses and trees shifting with climatic oscillations (Kendall 1969). Present vegetation ranges from open grasslands to uncommon closed canopy woodland (Herlocker 1975; Herlocker & Dirschl 1972; McNaughton 1983; Schmidt 1975a, 1975b). Much of the region is occupied by a mosaic of grasslands and deciduous to semi-deciduous thorn tree savanna with an *Acacia* or *Commiphora* overstory.

Although explorers searching for the origins of the Nile passed near the Serengeti, the region was first viewed by Europeans when Baumann (1894) traversed the southern Serengeti. The present configurations of reserves include about 13 250 km² in Tanzania's Serengeti National Park, the eastern portions of the system in Ngorongoro Conservation Area and Loliondo Game Control Area, and ca. 2300 km² in Kenya's Masai Mara Game Reserve, portions of which were degazetted twice in the past two decades. The range of the major wildebeest and zebra herds occurs in these reserves and surrounding areas in Tanzania. Hunting, now formally poaching, by surrounding human populations has become so prevalent as to denude western border areas of buffalo and much other game (Campbell 1989).

The disturbance: rinderpest

Rinderpest, or cattle plague, is an acute disease of the *Artiodactyla* that is caused by an RNA virus closely related to canine distemper and primate measles viruses, with immunological and morphological similarities to paramyxoviruses (Andrewes & Pereira 1967; DeLay et al. 1965; Fenner et al. 1974; Plowright 1963, 1968; Tajima & Ushijima 1971). It was first recognized during a major epizootic of 376 to 386 A.D. due to its devastating effects on the cattle (*Bos taurus*) population of Europe. It is presumed to be enzootic on the steppes of Eurasia and to have been carried into Europe by invaders from the East. Many, perhaps most, species of wild ungulates in Africa proved susceptible to the disease (Plowright 1968).

Primary effects

Pathological manifestations of rinderpest in susceptible ungulates are many (Andrewes & Pereira 1967; Tajima & Ushijima 1971) and death ensues in 3-6 days. Transmission is through direct contact and presence of the virus in nasal discharges, dung, and urine. The virus

is rapidly destroyed by desiccation in natural environments so residual pathogenicity is short-lived. The principal species in the Serengeti fauna that are acutely sensitive are wildebeest, buffalo, and giraffe (*Giraffa camelopardalis*). Cattle can act as carriers (Atang & Plowright 1969), but wild ungulates apparently either develop immunity or die. Suckling calves are protected through the milk so the disease usually manifests itself at weaning (Plowright & McCulloch 1967; Taylor & Watson 1967). Studies of ungulates in the Serengeti ecosystem during the late 1950s described a 'yearling disease' that almost certainly was rinderpest (Talbot & Talbot 1963). Repeated passages of the virus through some host species may reduce virulence toward other species (Plowright 1968) and some wild ungulate populations may maintain attenuated strains of low transmissibility and pathogenicity (Provost 1981; Rossiter et al. 1983). Whether there are also host strains of varying susceptibility is unknown.

Rinderpest in Africa: a severe disturbance

Probably, rinderpest was introduced into Africa with Indian cattle during the 1889 Italian military campaign to conquer Somaliland and Ethiopia (Branagan & Hammond 1965; Plowright 1968). It was in East Africa within a year, reached Lake Nyasa by 1892, and swept into South Africa's Cape Province by 1897. It was one of the great pandemics of history (Ford 1971). Although there were no formal historical records to document the destruction, informal observers suggested that 95% of the cattle, buffalo, and wildebeest in East Africa died (Lydekker 1908).

The people, and particularly the pastoralists, were plunged precipitously into abject poverty. Famine, smallpox, and endemic diseases ravaged Africa's indigenous human populations (Ford 1971). Tsetse fly (*Glossina*) probably declined at first but underwent a resurgence due to bush encroachment and partial recovery of the game populations. The resultant incidence of both human and cow trypanosomiasis rendered land reclamation untenable and little was attempted under the colonial governments until the 1930s. So, just before European discovery of the Serengeti region (Baumann 1894), and two decades before it became widely known (White 1914), rinderpest swept through the region, destroying pastoralists exploiting the open grasslands of the Serengeti Plains, driving the pastoralist-cultivator and hunting populations of the west into enclaves along the shores of Lake Victoria, leading to the maintenance of only small cleared agricultural areas separated by expanses of tsetse-infested bush, and reducing wildebeest, buffalo, giraffe, and other susceptible game animal populations to fractions of their previous levels (Ford 1971; Sinclair 1977, 1979). Severe rinderpest outbreaks re-

occurred repeatedly until extensive cattle inoculation programs with attenuated viruses brought the disease under control in the mid-1960s (Atang & Plowright 1969; Plowright & McCulloch 1967; Taylor & Watson 1967). Nevertheless, neutralizing antibodies to rinderpest virus continue to be widespread in many wild animal species and a major fatal outbreak affected buffalo in the Serengeti National Park in 1982 (Rossiter et al. 1983).

Propagation of a disturbance through food webs

There were neither scientists nor historians to quantify the consequences of rinderpest in ecosystems at the time that it scourged Africa, beyond the general records outlined above. In fact, since much of the affected area lay outside the spheres of influence of colonial governments, effects in many areas went completely unrecorded. The reconstruction of recovery from rinderpest that follows depends upon two principal direct sources: (1) data from research by scientists of the Serengeti Research Institute (Sinclair & Norton-Griffiths 1979), and (2) reasonable inferences from what research has revealed about the functioning of grassland-savanna ecosystems (e.g. Huntley & Walker 1982). The assumption of this reconstruction is that there was no major functional or structural hysteresis of the ecosystem, so changes over the last 25 yr approximated, although of opposite direction, the changes accompanying the appearance of rinderpest. In fact, the slight hysteresis manifested in the slower rate of recovery than of decimation of the animal populations may have allowed some changes to be more readily observed during recovery than upon appearance of the disease. Since the vegetation, for example, changes rapidly in both species composition and genotypic structure of species when protected from the animals (McNaughton 1979b, 1983, 1985), trends can be traced more clearly during recovery than likely would have been possible during almost instantaneous near-extirminations of game, livestock, and human populations at the onset of the plague.

Recovery

Initial point of action

The inoculation of cattle in the mid-1950s in areas surrounding the Park was accompanied by the rapid and complete disappearance of neutralizing antibodies to rinderpest virus in blood samples from both buffalo (from 100% - 0 in 8 yr) and wildebeest (from over 80% to 0 in 6 yr). Populations of both game species began to increase immediately, the buffalo population eventually reaching an apparently stable size around 60 000 and the wildebeest stabilizing near 1.4 million by the late 1970s

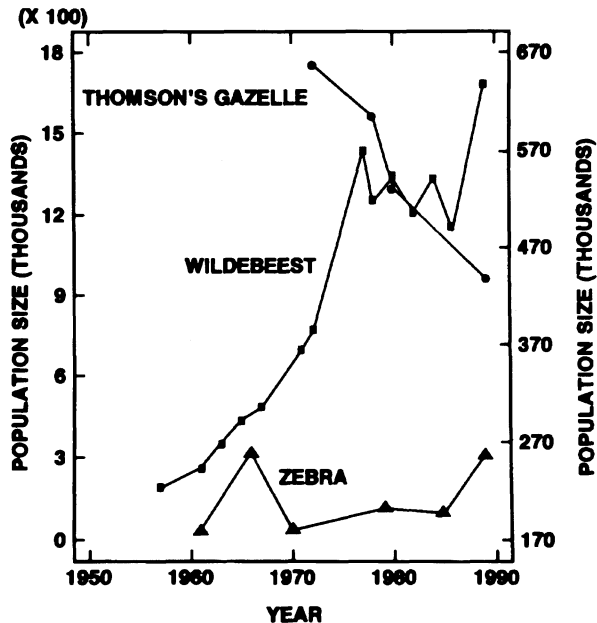


Fig. 2. Temporal trends of population sizes of wildebeest (left hand scale) and zebra and Thomson's gazelle (right hand scale). Data from Sinclair (1977, 1979), Sinclair & Norton-Griffiths (1982), and Campbell (1989).

(Fig. 2). Recovery began with an immediate increase in the recruitment of yearlings into the populations. Yearling wildebeest made up only about 8% of the pre-inoculation herd (Talbot & Talbot 1963), but rapidly increased to ca. 15% (Sinclair 1979). Impala (*Aepyceros melampus*), topi, and giraffe all increased markedly, although fewer censuses are available (Campbell 1989; Grimsdell 1979). Although also infrequently and imprecisely sampled, populations of the rinderpest insensitive zebra and less sensitive Thomson's gazelle were little changed over the recovery period (Fig. 2).

Secondary actions

Aerial surveys through the year of movements of the major nomadic herds (Grzimek & Grzimek 1960b) before rinderpest control, showed that the herds moved over a comparatively restricted range between the base of the Crater Highlands and the mid-grass savanna areas of the central Serengeti (Fig. 3). Subsequent studies (Talbot & Talbot 1960; Watson 1967) culminated in the development of a system of monthly survey flights on a standard grid system (Norton-Griffiths 1972). The fundamentals of long-term ecological research and ecological monitoring were established in studies at the Serengeti Research Institute (McNaughton & Campbell 1991), much of it directed toward the region's unique, large-scale animal migrations, which have been obliterated throughout much of the rest of Africa (McNaughton & Georgiadis 1986).

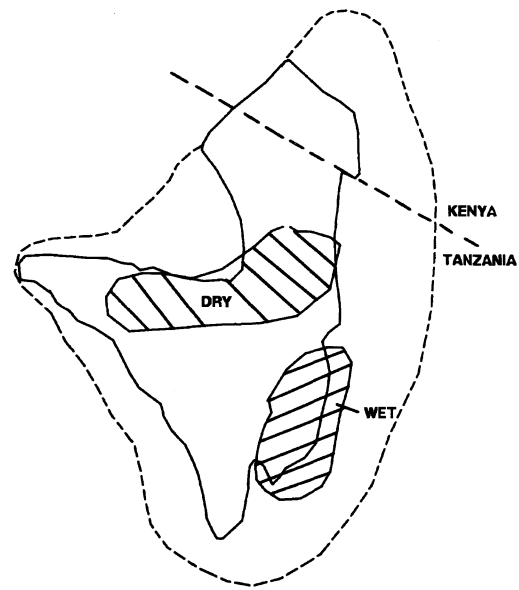


Fig. 3. Seasonal ranges of wildebeest and zebra during the period before rinderpest control. Following recovery, the migratory ungulates ranged into Kenya during the dry season and were unable to use the Serengeti Plains for the entire wet season. Redrawn from Grzimek & Grzimek (1960a), Pennycuik (1977) and Maddock (1979).

The range utilized by the nomadic herds expanded progressively (Maddock 1979; Pennycuik 1975) as the populations increased.

In the early years of recovery, the animals moved mainly from the Serengeti Plains in the wet season to the Western Corridor in the dry season, with a small proportion of the animals going to the North. As the population expanded, the number of animals traveling north into the Mara River basin increased steadily. Although early observations indicate that the wildebeest, zebra, and gazelle herds spent the majority of the wet season on the Serengeti Plains, and the wildebeests' major calving period was there, in recent years the herds have been able to utilize the Plains for only limited portions of the wet season, and wildebeest have sometimes calved in other areas (McNaughton 1983, 1985).

Therefore, the survey flights and censuses indicate that a secondary action of the rinderpest disturbance was to modify the ranges of the major nomadic species. Wildebeest, gazelle, and zebra herds moved less extensively when the population of wildebeest was much reduced. Although neither zebra nor gazelle population sizes changed, the expansion of the wildebeest population during recovery from rinderpest drove the other species into expanded ranges due to competition for food (Sinclair 1977; Sinclair & Norton-Griffiths 1982).

Tertiary actions

Fire is a characteristic, chronic phenomenon in African savannas, and in grasslands generally (Rundel 1981). The spatial extent of burning during the dry season in the Serengeti is positively correlated with wet season rainfall (Fig. 4). The greater the wet season rainfall, the greater the accumulation of tinder, and the greater the extent of fires during the dry season.

During the period of ecosystem recovery from the cascading effects of rinderpest, the prevalence of fire declined in every Serengeti landscape region (Fig. 5). The proportion of the grasslands in the North that burned declined from 100 to about 25% during the recovery period. The proportion of the Serengeti Plains that were burned, on average, declined from 50%/yr to near zero. While fires during the pre-recovery period used to burn regularly to within 5 km of the southeastern Park borders, there have been no fires in that area since the early 1970s (records of the Serengeti Ecological Monitoring Program).

Therefore, an important tertiary consequence of recovery from rinderpest was a reduction of the importance of fire in the ecosystem. The relationship between the extent of fire and wildebeest population size suggests that there is a transition between 600 000 and 800 000 head leading to large-scale fire suppression. Below this transition density, much of the region was burned every year; above that density, little of the region burned. When wildebeest leave the Serengeti Plains at the end of the wet season, they move into the surrounding grasslands as large herds, removing up to 90% of the initial standing crop before it dies to become tinder (McNaughton 1976, 1985). Since grazing is not evenly spread across the landscape because the animals concentrate in certain vegetation types and avoid others (McNaughton 1976, 1983, 1985; Sinclair 1977), their grazing produces extensive firebreaks throughout their early dry season range, creating a mosaic inimical to widespread grass fires during the period of maximum fire frequency.

Quaternary actions

Depopulation of humans in the Lake Victoria basin, followed by resistance to recolonization due to trypanosomiasis (Ford 1971), appears to have led to a shift of elephants to moister habitats west of the Park (Lamprey et al. 1967; Watson & Bell 1969). Humans and elephants are incompatible (Matzke 1975) and the expansion of human populations and associated bush clearing west of the Park (Kurji 1976) during recovery of the ecosystem from the effects of rinderpest led to the phenomenon referred to as 'compression', the forcing of animals into restricted, often marginal, habitats, now almost solely in national parks and game reserves (Laws,

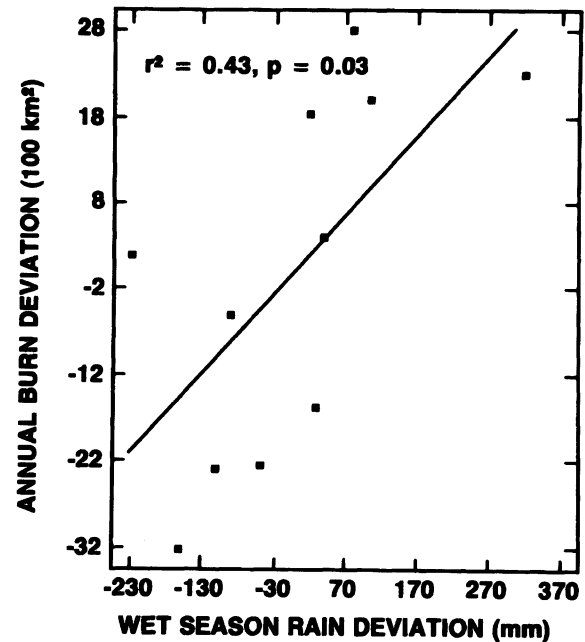


Fig. 4. Departure of annual dry season burning from detrended temporal patterns in relation to departure of rainfall from the long-term means of rainfall in the previous wet season. Redrawn after Norton-Griffiths (1979).

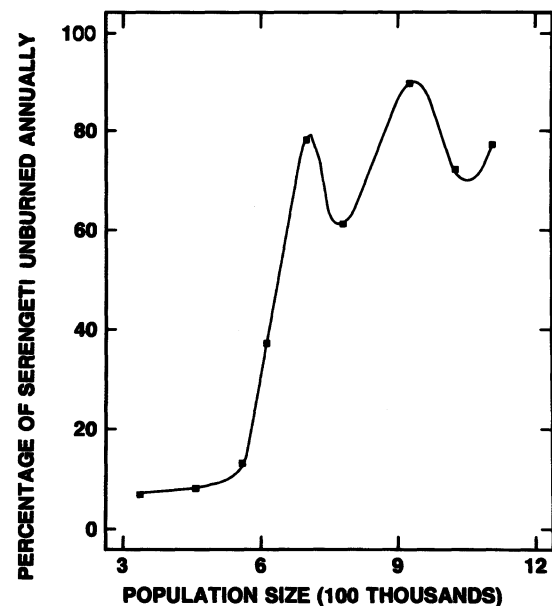


Fig. 5. Relationship between the proportion of the area of the Serengeti National Park unburned each year and the estimated size of the wildebeest population in that year. Data from the Serengeti Research Institute.

Parker & Johnstone 1975). Wholesale elephant poaching in the Park has now pushed the few remaining herds into the far east.

Compression of elephants into the Park during recovery from the rinderpest disturbance led to drastic declines in tree cover, with some areas going from closed canopy woodlands to essentially open grasslands in less than two decades (Norton-Griffiths 1972). On an average basis, tree cover in the northern woodlands declined from 1962 to 1972 at a rate of 0.9 %/yr in the far north to 0.3 %/yr in the central area (Norton-Griffiths 1972). As percentages of tree cover present at the start of the decade, those relative declines represented 26% of the total in the northern part and 7% in the central area. Therefore, one of the cascading effects of recovery from rinderpest has been a change in the distribution of elephants, with the population forced into the Park and a resultant decline in tree cover. Drastic elephant poaching in the 1980s reduced that population to ca. 10% of its peak level.

It is generally conceded that elephants alone cannot accomplish widespread woodland destruction (McNaughton & Sabuni 1988). Models of tree, fire, elephant, and browser interactions suggest that all must act in concert to reduce woodlands to savannas or, at the extreme, to open grasslands (Norton-Griffiths 1979).

Fire acts to kill seedlings and burn saplings back to ground level. Browsers keep seedlings and saplings within the fire zone. The resurgence of giraffe, the major browser, due to rinderpest control, appears to have been an important factor in woodland disappearance by preventing recruitment into the adult canopy zone which is generally impervious to fire. The interactions between fire and the biota may be responsible for maintaining savannas and preventing closure of the tree canopy in many African ecosystems (Werger 1978). Repeated, intense fire in grasslands, on the other hand, can open the grass canopy and reduce the vigor of the grasses sufficiently to allow rapid increases in fire-resistant bush (Trollope 1982). It seems likely that there soon will be widespread increases of the tree canopy in the Serengeti due to the combined effects of elephant poaching and fire suppression.

Little is known of the relationship between overstory tree density and productivity of the grass layer in the Serengeti (McNaughton 1985), but studies of bush clearing in Zimbabwe suggest that an arborescent cover can suppress primary productivity of the underlying grasses (Dye & Spear 1982). The most dramatic effect of bush clearing was in low-altitude arid lands at a rainfall level below the median for the Serengeti. The higher evaporative stress and lower rainfall may create severe competition for soil water due to little drainage into deep soil layers where much of the tree root lies (Walker

et al. 1981). Over rainfall ranges similar to the Serengeti ecosystem, bush removal had an additive effect on grassland productivity, but the slope of yield on rainfall remained constant (Dye & Spear 1982). These results suggest that the destruction of woody plants due to the combined effects of elephants, browsers, and fire would increase grassland productivity additively, but without altering the overall relationship between productivity and rainfall.

Alternatively, grass and forb standing crop in the Serengeti is often conspicuously higher under trees (McNaughton 1983), due to the combined effects of shading reducing evaporative stress, nutrient enrichment from deep soil layers due to tree leaf fall, and congregation of animals in the shade with resultant dung and urine accumulation. Research in a much drier and hotter savanna than the Serengeti, the Turkana District of Kenya, found peak herbaceous biomasses of 220 g/m² under trees, only 95 g/m² between trees (Weltzin & Coughenour 1990). Water relations, temperature, and soil nutrients were implicated as causative factors. Effects on grass-layer productivity of woody cover reductions associated with ecosystem recovery from rinderpest are likely to have been highly complex.

The spacing of trees in many savannas is not due to the combined effects of browsers and fire, but is caused by competition between trees (Skarpe 1991; Smith & Grant 1987; Smith & Walker 1983); removal of neighbors produced a large growth increment in survivors (Smith & Grant 1987; Smith & Walker 1983). Whether competition is for water or nutrients is unknown. Since trees and grasses draw upon nutrients from substantially different soil levels (Walker et al. 1981), seedlings and young saplings may compete with the grasses for light, nutrients, and water, but their escape from the ground layer by vertical growth may depend upon their roots penetrating soil zones not exploited by grasses. If there is a large population of saplings that have escaped the ground layer but are arrested by competition with the canopy trees, a major effect of tree destruction in the absence of fire will be to create dense bush as those saplings overtop the grass layer and develop into a closed canopy of small trees that then go through the process of self-thinning, leading ultimately to an open canopy of widely spaced adults (Skarpe 1991; Smith & Grant 1987; Smith & Walker 1983). The Serengeti has patches that appear to represent this entire spectrum and many of the grasslands are dotted with small saplings no taller than the ungrazed grass canopy.

Another cascading consequence of rinderpest for which there are no historical records, but which can be inferred from recent patterns of increase in the Serengeti's predators (Hanby & Bygott 1979), was a likely decline of those predators during the plague's prevalence

An additional modification of ecosystem trophic relationships due to the drastic changes in African ecosystems during the period of rinderpest prevalence can

Running time backwards

The recovery patterns described above allow a plausible reconstruction of the network of interconnected chains of cause and effect caused by the rinderpest-driven perturbation of African ecosystems (Fig. 6). Rapid, severe reductions in game animal, livestock, and human populations produced an immediate increase in the tinder available for fires as grasslands grew up in the absence of grazing. Subsequent recurrent fires during the dry season, whether due to lightning or to the remaining humans seeking to facilitate hunting by creating grass regrowth (McNaughton 1985; Sinclair 1977), initially destroyed tree size classes capable of recruitment into the canopy layer. The intensity and extent of

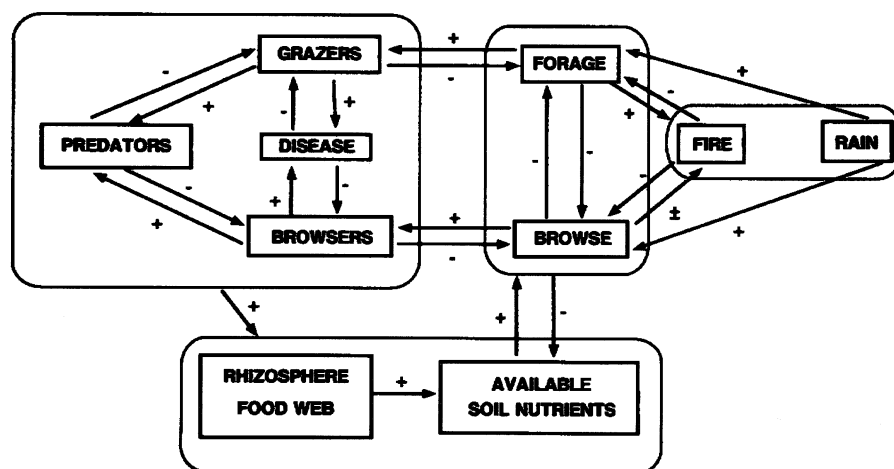


Fig. 6. Model of the organization of the major consolidated trophic web and environmental components in a generalized African savanna ecosystem with the sign of effect indicated on the arrows connecting causes and effects. Disease, specifically rinderpest, has a negative effect upon the susceptible grazer (major species: wildebeest) and browser (major species: giraffe) communities, but these can be propagated through the trophic web and environment to have effects elsewhere. The nature of the effect of modification of any one component upon any other can be obtained by the algebraic product of signs along any connecting pathway.

such fires depended upon rainfall during the preceding wet season, having major effects during wet years and less prevalent effects during dry years. Repeated burning caused a deterioration of the grass canopy leading to bush encroachment (Trollope 1982). Reduction of the abundance of rinderpest-sensitive browsers allowed tree saplings to rapidly escape from the fire zone. Competition between the developing saplings resulted in self-thinning, and an open, savanna canopy in more arid areas (Smith & Grant 1987; Smith & Walker 1983), but allowing a more closed woodland in wetter areas as elephants moved into surrounding, even wetter areas abandoned by dwindling human populations. The increase of arborescent cover provided shade, and a modest recovery of game populations as the survivors developed immunity, led to a resurgence of tsetse flies (Ford 1971), tending to further reduce utilization by both humans and their domestic livestock that survived the plague. Grassland productivity declined during initial bush encroachment and then increased again where the tree canopy was opened by competition. Predator populations, after a short period of prosperity associated with vastly increased herbivore mortality, slid into population declines due to diminished prey abundance. Scavenger populations, however, such as the Serengeti's abundant vulture avifauna (Houston 1974) remained at comparatively high levels due to recurrent death of calves as they were weaned, lost their acquired immunity, and succumbed to the plague.

Eventually, the Serengeti ecosystem came to the state that was described from its discovery, just post-rinderpest, until control of the disease. The open Serengeti Plains served as the continuous wet season range of the migratory animals. There were wildebeest in seemingly great numbers, but they actually were far below pre-rinderpest levels. Populations of zebras and gazelles equalled and exceeded, respectively, wildebeest numbers. Slightly less arid areas came to equilibrium as open savannas that were the principal dry season foraging area of the nomadic ungulates. Large areas of the ecosystem were only lightly exploited by herbivores and fires burned regularly through these areas, but the well developed tree canopy was immune to the effects of such fires. Much of the northern part was dense bush and closed canopy woodland, rarely visited by the migratory herds. Elephants were absent, predator populations were sparse (comparatively), although wild dogs were more abundant than now, nutrients were recycled through fire or litterfall over large areas, and ecosystem state, therefore, departed drastically from the state before rinderpest appeared, and after it had been controlled.

Conclusion

A significant part of the above discussion is inferential in character, although the historical trends and much data from the Serengeti ecosystem provide strong evidence that the rinderpest disturbance radically changed the character of African savanna-grassland-woodland ecosystems. The propagation of disturbances through food webs can produce changes in the total state and dynamics of the ecosystem, modifying them through unexpected pathways and with unanticipated amplification to completely reorganize both structure and function. Disturbances that have such cascading effects may be more likely due to exotic, novel factors than to factors intrinsic to the system. The development of food-web structures based on specific, evolved and coevolved traits will tend to damp fluctuations in response to the normal bound of disturbance within which the organisms evolved. Food web structures based on specific inter-connections that arise through evolutionary time may be resistant to perturbations commonly encountered through ecological time.

I have shown that many functional traits of the Serengeti ecosystem are buffered against those fluctuations commonly encountered, and adaptive traits of the organisms are an important component of the mechanisms accomplishing that buffering (McNaughton 1977, 1984, 1985). The occurrence of exotic disturbances, however, may be propagated through ecosystems by the very interactions that damp perturbations to fluctuations commonly encountered. There can be little doubt that grasses and grazers co-evolved (Kowalevsky 1873-1874; McNaughton & Tarrants 1983; McNaughton et al. 1985; Stebbins 1981) in the strictest definition of that process (Ehrlich & Raven 1964; Janzen 1980). I believe the information available indicates that the exotic disturbance, rinderpest, had effects far beyond its primary site of action, the susceptible native herbivores. Such cascading pathways of alternating cause and effect (Carpenter & Kitchell 1984; Carpenter, Kitchell & Hodgson 1985), where effect becomes cause and vice versa, can completely alter the fundamental dynamics of ecosystem processes. Hutchinson (1948) referred to such pathways as circular causal systems, coupled by feedback through the food web and the physical environment.

Modifications of processes will, in turn, be manifested by changes in state. Understanding precisely how the links of recognized direct effects are translated into indirect effects, and how those links are, therefore, organized and coupled to processes in natural ecosystems resulting from long periods of evolution, coexistence, coevolution, and interaction is, I believe, an important goal for ecosystem science. Disturbance does not take place in a vacuum, therefore its effects can be propagated

far from the obvious site of action. Is it a general principle that the most severe disturbances are caused by exotic agents with which a flora and fauna have not evolved, while fluctuating conditions under which they have evolved are not disturbances, no matter how pronounced the fluctuations?

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