The influence of fire frequency on the abundance of *Maerua subcordata* in the Serengeti National Park, Tanzania

Ayron M. Strauch[1],* *and Stephanie Eby*[2,3]

[1] *Department of Biology, Tufts University, 163 Packard Avenue, Medford, MA 02155, USA*
[2] *Department of Ecology and Evolutionary Biology, 106A Guyot Hall, Princeton University, Princeton, NJ 08544, USA*
[3] *Present address: Department of Ecology and Evolutionary Biology, Yale University, PO Box 208106, 165 Prospect Street, New Haven, CT 06520-8106, USA.*
*Correspondence address. Department of Natural Resources and Environmental Management, University of Hawai'i at Manoa, 1910 East-West Road, Sherman 101, Honolulu, HI 96822, USA. Tel: +1-808-933-8121; fax: +1-808-933-8120; E-mail: astrauch@hawaii.edu

Abstract

Aims

Invasive species alter the composition and function of communities, threatening the conservation of important ecosystems worldwide. In savanna ecosystems, fire plays a key role by modifying biogeochemical cycles and shaping the composition and structure of vegetation communities. Although many studies have examined the long-term effects of fire frequency on grassland communities, few studies have examined the relationship between fire regime and woody species invasions.

Methods

The Serengeti ecosystem is an ecologically and economically valuable natural resource in East Africa whose conservation is currently threatened by a variety of factors, including invasive species. We determined the abundance of *Maerua subcordata*, a noxious woody shrub, in three different regions of the Serengeti National Park, Tanzania. We then examined the influence of fire frequency, developed through the use of 7 years of Moderate Resolution Imaging Spectroradiometer (MODIS) imagery, on *M. subcordata* abundance.

Important Findings

In all regions, burned transects had significantly greater abundances of *M. subcordata* compared to unburned transects. Furthermore, the number of times each transect burned from 2000 to 2006 had a significant positive effect on the abundance of *M. subcordata* and the number of years since a transect last burned had a significant negative relationship with abundance. These results are particularly important as this species provides little forage value and is potentially toxic to wildlife and cattle. Additional studies are needed to determine the ecological consequences of increasing *M. subcordata* abundance, as the potential expansion of noxious shrubs into protected areas of important conservation status is of serious concern.

Keywords: Serengeti • fire • savanna • *Maerua subcordata* • MODIS

Received: 29 January 2012 Accepted: 22 February 2012

INTRODUCTION

Fire has long played an important role as a disturbance mechanism shaping semi-arid ecosystems and maintaining landscape heterogeneity (Fuhlendorf and Engle 2001; Keane *et al.* 2008; Turner *et al.* 1994). Periodic fires are essential for the maintenance and function of grassland communities (Axelrod 1985), altering the availability of resources by converting unusable biomass into more usable forms and increasing the nutritive quality of forage (Anderson *et al.* 2007). Fire is a naturally occurring process that influences the structure, composition and dynamics of vegetation (Bond and Keeley 2005; Bond *et al.* 2005; van Wilgen 2009) and increases grass productivity while decreasing the growth of woody species (Bragg and Hulbert 1976; Hoch *et al.* 2002; van Langeveld *et al.* 2003). As a management tool in African savannas, prescribed burns have been shown to increase landscape heterogeneity, primary productivity and structural diversity (van Wilgen *et al.* 2003). In East Africa, prescribed burns are also used to stimulate new vegetation growth for grazing, reduce tick load and prevent large catastrophic fires (Butz 2009).

Fire history—the frequency, intensity and extent of burning—is an important factor in understanding the influence of fire in ecological systems. Frequent burning provides a reoccurring disturbance that alters the dynamic relationship between soils, vegetation and wildlife (Nkwabi *et al.* 2011). By keeping the growth of dominant grass or forb species in check and preventing the recruitment of woody species, frequent burning provides an opportunity for other species to thrive—particularly fast-growing versatile species (MacDougall *et al.* 2009; Valery *et al.* 2008). In a long-term study, Masocha *et al.* (2011) demonstrated that frequent burning increases grass and shrub species richness but promotes the establishment of alien plant species. Repeated burning of grasslands can also increase fire adapted less nutritious species (Anderson *et al.* 2007) as well as increase grazing intensity, resulting in the survival and dominance of pioneer or unpalatable species due to overgrazing (Trollope *et al.* 1995).

The consequences of prescribed burning are of particular concern for the management of protected areas in Eastern, Central and Southern Africa. Parks, game reserves and conservation areas (referred to hereafter as parks) have historically been managed to preserve the biological and environmental diversity of habitats (Mentis and Bailey 1990). However, the expansion of exotic and invasive species is threatening the ecological integrity of African ecosystems (Foxcroft *et al.* 2011; Mirijam *et al.* 2011). Frequent prescribed burning to maintain savanna ecosystems remains popular, despite evidence that burning may negatively influence species composition or open niches for invasive species (Ford and McPherson 1996; Masocha *et al.* 2011). In the Serengeti ecosystem, fire has long played an important role in shaping the vegetation community (Owen 1971). In the 1930s, there was low fire activity in the Serengeti, most likely due to low human population (Sinclair 2004). However, by the 1960s, up to 90% of the park was burned annually due to an increase in human population and thus anthropogenic ignition events and a relatively low wildebeest density that resulted in high fuel loads (Mduma *et al.* 1999; Owen 1971). It was not until the 1970s, following the elimination of rinderpest and the subsequent increase in the wildebeest population, that fire declined within the central regions of the park due to reduced biomass from increased grazing (Holdo *et al.* 2009b; McNaughton 1992; Mduma *et al.* 1999; Norton-Griffiths 1979). In recent years, as part of a policy of early burning by the park management, over 30% of the park has burned annually (Dempewolf *et al.* 2007). The repeated application of fire has limited the survival of woody seedlings and altered the age-structure of Serengeti forests (Norton-Griffiths 1979; Dublin *et al.* 1990).

Given the multitude of threats that protected areas now face (population growth, poaching, disease, invasive species and climate change), there is a need for a more detailed understanding of species-specific responses to fire management to give managers a clearer idea of the effects of their policies (van Wilgen *et al.* 2003). In this study, our objective was to measure the abundance of *Maerua subcordata* (Gilg.) DeWolf, a small blue–green shrub, in the Serengeti National Park (SNP) and determine if abundance is influenced by fire frequency. Fire frequency was obtained from burn maps created through use of Moderate Resolution Imaging Spectroradiometer (MODIS) imagery with an algorithm developed by Dempewolf *et al.* (2007). We hypothesized that an increase in fire frequency was positively related to the abundance of *M. subcordata* and that abundance was negatively related to the length of time since a transect last burned.

MATERIALS AND METHODS

Maerua subcordata is a native woody shrub in the Capparaceae family that commonly occurs in the understory of forests in East Africa, especially along riverine habitats (Maingi and Marsh 2006). It grows up to 2 m tall and produces elliptical- or oval-shaped blue–green leaves and single yellow flowers. In the Serengeti ecosystem, the shrub is usually <60 cm in height and can be found in the uplands and slopes as well as the floodplains on a variety of soils (personal observations). *Maerua subcordata* usually flowers 2–4 months after the wet season (June–August) and the shrub is easily identified in both burned and unburned regions.

Previous accounts of *M. subcordata* have identified a variety of human uses. *M. subcordata* fruit is edible and consumed during times of food scarcity as well as plenty in Ethiopia (Teklehaymanot and Giday 2010) and Kenya (Morgan 1981). Kenyan farmers also utilize *M. subcordata* as a traditional medicine for treating helminthic infections (Gakuya 2001; Githiori *et al.* 2005) and extracts may have anti-fungal properties (Tegegne *et al.* 2007). In addition to its potential in ethnomedicine, the juice of *M. subcordata* is frequently used as a traditional flocculating agent that aides in the settling of sediments in water, improving its drinkability (Mavura *et al.* 2008).

Study area

Data were collected in the SNP of Northern Tanzania. The ecosystem is characterized by the migration of large herbivores, such as wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*) and Thomson gazelle (*Gazella thomsonii*) that follow seasonal and regional patterns driven by climate and forage (Holdo *et al.* 2009a). The SNP is a 14 763 km^2 protected area surrounded by various game reserves, conservation areas and game controlled areas (Fig. 1). Climate in the region is divided into distinct wet (November–April) and dry (May–October) seasons, although the onset and conclusion of the rainy season vary from year to year. Mean annual rainfall in the southern part of the ecosystem is 400 mm and in the north is 1200 mm, resulting in regionally variable habitat composition. Soil composition is driven by differential weathering from rainfall and ash inputs from Ol Doninyo Lengai, an active volcano in the Rift Valley (Anderson and Talbot 1965). The southern
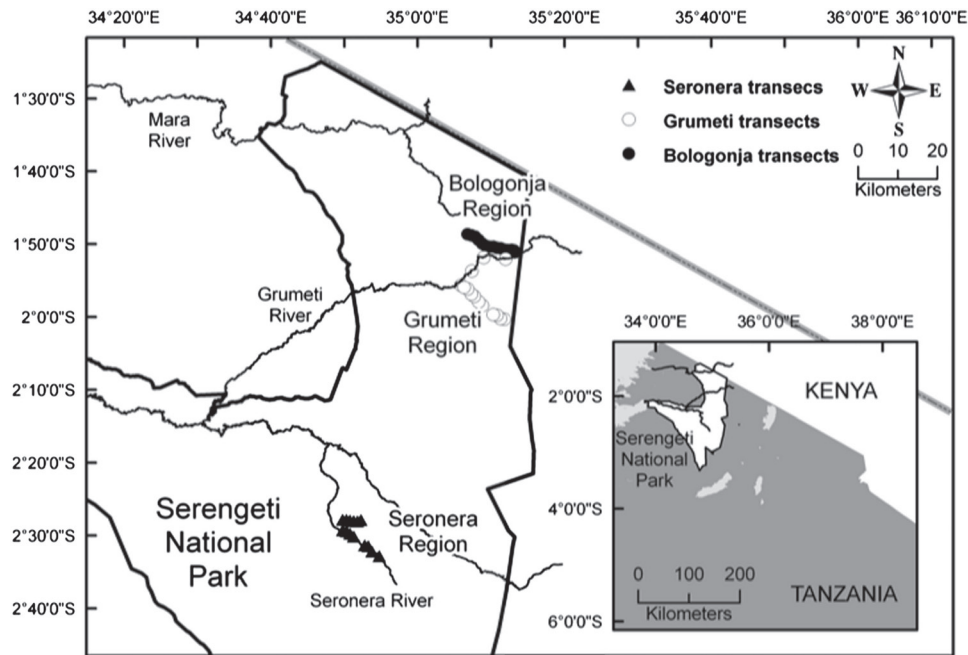
Figure 1: map of the SNP and surrounding conservation zones in Northern Tanzania and Southern Kenya. The southern-most points for each transect in the three different regions are indicated by the symbols.

landscape is composed of smooth short-grass plains with occasional rock outcroppings, while savanna forests are interspersed with tall grasslands on gently undulating hills in the north.

M. subcordata survey

To capture some of the environmental heterogeneity in the SNP, vegetation was sampled in three regions: 15 transects near the Bologonja River, 15 transects near the Grumeti River and 21 transects near the Seronera River (Fig. 1). The Bologonja transects were located from 35° to 35°15′E and 1°50′ to 1°52′S, the Grumeti transects were located South of the Grumeti River from 35° to 35°15′E and 1°52′ to 2°S and the Seronera transects were located North of the Seronera River from 34°45′ to 35°E and 2°25′ to 2°35′S. The Bologonja and Grumeti regions are located in the northern savanna, while the Seronera region is on the edge of the grasslands. Transects were oriented in the North–South direction with a minimum East–West distance of 500 m established between transects. Each transect was 100 m long and the abundance of *M. subcordata* within 1 m of each transect (200 m² total) was quantified.

Fire history

During transect sampling, the current state of the vegetation was recorded as burned if the understory vegetation appeared charred within the last few months or unburned if there was no charcoal. For each transect, fire history was established using fire maps created from MODIS images at a 250-m² resolution and processed with an algorithm developed by

Dempewolf *et al.* (2007). The starting point for each transect was marked by a Geographic Positioning System (GPS) location and mapped using a WGS 1984 projection in ArcMap (ESRI, San Diego, CA). A transect was categorized as either burned or unburned based on the burn status of the MODIS pixel the GPS location fell upon for each burn year from 2000 to 2006. A burn year begins on 1 May and runs to 30 April of the following year because most burning occurs in the dry season. More than 500 m separated transects, which was greater than the MODIS pixel resolution, guaranteeing the independence of each MODIS datum.

Rainfall sampling

To explore the effect of rainfall, differences in seasonal precipitation across regions were determined from 2000 to 2006 by comparing 5-month seasonal rainfall totals measured using nearby rainfall gages (December-April, wet season; June–October, dry season).

Data analysis

Abundances of *M. subcordata* per 200 m² were compared by region. For subsequent analyses, data were Log_{10} $(x + 1)$ transformed to eliminate skew and abnormally distributed residuals. A two-way analysis of variance (ANOVA) was used to examine the effect of region (three regions) and the 2006 burned status (burned or unburned). For the 7 years of fire history, the proportion of transects that burned in each region was calculated and mean differences between regions for all years was determined using a one-way ANOVA and a Tukey multiple comparisons test. Bivariate plots were then used to

examine how fire frequency and time since each transect last burned influenced the abundance of *M. subcordata*. To test for linear correlations between abundance and fire history, we used a student's *t*-test and a Pearson product–moment correlation coefficient (reported as adjusted r^2) based on least-squares regression. To examine the influence of regional differences in rainfall, mean wet season and dry season rainfall between regions were analyzed using a one-way ANOVA with a Tukey multiple comparisons test. All analyses were conducted using JMP statistical software (version 5.0.1.2, SAS Institute Inc.).

RESULTS

In each of the three regions, there was a greater abundance of *M. subcordata* in transects that burned during 2006 than in the unburned transects (Fig. 2). Additionally, the Bologonja and Grumeti regions had greater abundances of *M. subcordata* than the Seronera region for both burned and unburned transects. The whole model found a significant effect of region and 2006 burn status on abundance (two-way ANOVA: $F = 23.5$, df = 5,45, $P < 0.001$), which explained a substantial proportion of the variability in the data ($r^2 = 0.69$). The individual effect of burn status was larger than the individual effect of region and there was a significant interaction effect (Table 1). The Grumeti region had the greatest density of *M. subcordata*, with a mean ($\pm$SE) of 17.5 ($\pm$3.09) per 200 m^2 in burned areas compared to 1.57 ($\pm$0.72) per 200 m^2 in unburned areas, supporting the hypothesis that burning has a positive effect on *M. subcordata* abundance. Similar patterns were observed in the Seronera and Bologonja regions (Fig. 2).

The 7 years of fire history showed that fewer transects in the Seronera region burned each year than in either the Bologonja or the Grumeti regions (Table 2). Only one transect in the
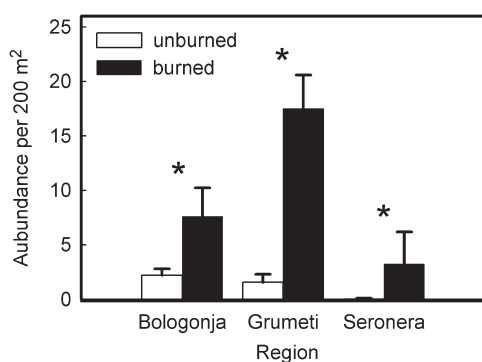
Seronera region burned more than once over the 7 years, while 10 of 15 transects from the Bologonja and 9 of 15 transects from the Grumeti region burned two or more times. Across the three regions, there was a significant difference in the mean number of burn years per transect ($F = 9.94$, df = 2,48, $P < 0.001$), with the Bologonja region (mean $\pm$ SE) (1.67 $\pm$ 0.32 burned years per transect) and the Grumeti region (1.93 $\pm$ 0.34 burned years per transect) significantly greater ($P < 0.05$) than that in the Seronera region (0.43 $\pm$ 0.16 burned years per transect).

There was a significant ($t = 44.8$, df = 49, $P < 0.001$) negative relationship between the abundance of *M. subcordata* and the number of years since a transect last burned that explained almost half of the variability in the data ($r^2 = 0.46$; Fig. 3a). There was also a significant ($t = 21.2$, df = 49, $P < 0.001$) positive relationship between the abundance of *M. subcordata* and the total number of times a transect burned (fire frequency) between 2000 and 2006, which explained much of the variability in the data ($r^2 = 0.29$; Fig. 3b).

From 2000 to 2006, there was no significant difference in wet season rainfall between the three regions ($F = 0.14$, df = 2,18, $P = 0.86$), although there was a significant difference in dry season rainfall ($F = 3.87$, df = 2,18, $P = 0.04$), with the Bologonja region (mean $\pm$ SE) receiving significantly ($P < 0.05$) more rainfall (196 $\pm$ 15 mm/year) than the Grumeti (131 $\pm$ 35 mm/year) or Seronera (106 $\pm$ 15 mm/year) regions.

DISCUSSION

These results support the hypothesis that the occurrence of fire has a positive effect on the abundance of *M. subcordata*. In all

Figure 2: mean ($\pm$SE) 2006 abundance of *Maerua subcordata* in burned (areas burned in 2006) and unburned (areas not burned in 2006) transects (200 m^2) in three regions of the SNP, Tanzania. Stars represent significant differences ($P < 0.001$) between treatments within regions based on a Tukey post hoc analysis following a significant two-way ANOVA. Bologonja: $n = 10$ unburned, $n = 5$ burned; Grumeti: $n = 7$ unburned, $n = 8$ burned; Seronera: $n = 17$ unburned, $n = 4$ burned.

Table 1: whole model, individual effects and interaction effect results from the two-way ANOVA examining the effects of region and burn status on *Maerua subcordata* abundance

	Sum of squares	df	*F* value
Whole model	8.65	5,45	23.5***
Region	2.43	2	16.6***
Burn status	3.07	1	41.9***
Interaction	0.66	2	4.5*

Abbreviation: df = degrees of freedom.
*$P < 0.05$, ***$P < 0.001$.

Table 2: proportion of transects that burned for each region during the given burn year

	2000	2001	2002	2003	2004	2005	2006
Bologonja	0.53	0.20	0.53	0.07	0	0	0.33
Grumeti	0.60	0.20	0.47	0.13	0	0	0.53
Seronera	0.10	0	0.10	0.05	0	0	0.19

Burn years run from May 1 of the stated year to April 30 of the following year.
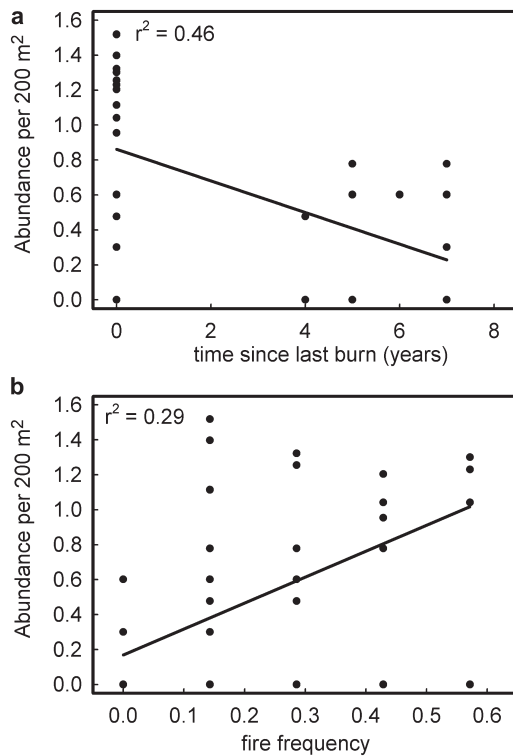
Figure 3: bivariate plots of Log_{10} $(x + 1)$-transformed abundances of *Maerua subcordata* versus (**a**) the time since last burning before 2006 ($r^2 = 0.46$, $t = 44.8$, df = 49, $P < 0.001$) and (**b**) the fire frequency between 2000 and 2006 ($r^2 = 0.29$, $t = 21.2$, df = 49, $P < 0.001$). Lines represent the least-squares regression line.

three regions, we found greater abundances in burned transects compared to unburned transects. Furthermore, both increased fire frequency and decreased time since last burning resulted in greater abundances. The significant interaction effect between region and 2006 burn status is likely the result of the significantly lower fire frequency in the Seronera region compared to the other two regions resulting in the lower abundance of *M. subcordata* in both burned and unburned transects of the Seronera region. Despite this interaction, the abundance pattern still held up: there were greater abundances in burned transects than unburned transects (Fig. 2). During the study period, wet season rainfall did not differ substantially between regions whereas dry season rainfall was significantly greater in the Bologonja region. However, *M. subcordata* abundance was not greatest in the Bologonja region. Based on these results, we conclude that soil moisture alone, driven by rainfall, would not produce these patterns in *M. subcordata* abundance. The two regions in the northern part of the park did receive greater annual rainfall and greater dry season rainfall compared to the Seronera region, which may have led to a greater standing biomass, increased fuel load, more intense fires and increased fire frequency. There may be a positive feedback effect on the abundance of *M. subcordata* if increased rainfall and increased fire frequency result in increased growth and reduced compe-

tition for *M. subcordata*. Such feedbacks are not uncommon in grassland systems, although an increase in fire frequency is not usually associated with the expansion of non-grass species (van Auken 2000). Increased standing biomass does not necessarily lead to increased fire frequency but prescribed fires are less likely to burn themselves out in conditions with higher fuel loads. Furthermore, fires set by poachers around the park boundary are more likely to spread into the park if high standing biomass makes conditions more favorable.

The application of early season prescribed fire (cool burns) in order to decrease fuel loads and reduce the occurrence of late season wildfires (hot burns) has a long history of effective practice in savanna ecosystems (Brynard 1971). However, fire intensity, frequency and extent can influence the distribution (Laurance 2003) and composition (diversity and abundance) of vegetation communities (Anderson *et al.* 2007; Harrison *et al.* 2003). Fire has been shown to result in an increase in the abundance of invasive and native shrubs by reducing competition with dominant grass species (Heisler *et al.* 2004; Masocha *et al.* 2011). In the SNP, *M. subcordata* survives wildfires, while grasses and seedlings combust. Furthermore, *M. subcordata* blooms in the dry season, which is usually after the period when cool burns are ignited, and thus, its flowers may face reduced competition for pollinators and nutrients following a burn. This may provide a mechanism for their increased abundance in regions with higher fire frequency and shorter time since last burning.

These results demonstrate that fire enhances the distribution of *M. subcordata*, which may lead to long-term reductions in habitat quality for grazers. Although recently burned grasslands usually attract grazers from unburned patches where they preferentially feed on the younger more-nutritious vegetation growth (Archibald *et al.* 2005; Hobbs *et al.* 1991), wildlife avoid consuming *M. subcordata*, possibly because it is mildly poisonous (Verdcourt and Trump 1969). Cattle also avoid *M. subcordata*, although goats and sheep have been observed eating this plant (Morgan 1981). The large migration of ungulates in the Serengeti spends the majority of the dry season in the northern part of the ecosystem, where they graze on new grass shoots growing in burned patches, and it is likely that *M. subcordata* gains additional benefits through reduced competition caused by the preferential grazing of more palatable species. Similarly, Archibald *et al.* (2005) demonstrated that periodic burning to promote forage availability in South Africa actually limited the extent of grazer-preferred habitat. Thus managers of parks need to consider how burning may cause potential increases in the abundance of noxious shrubs that may result in a reduction in habitat quality. We suggest managers reevaluate justifications for frequent repeated burning of particular regions in light of the affect fire frequency has on grassland communities and possibly establish a maximum fire frequency for any one region. If frequent prescribed fires are expected to continue, then an additional management protocol to limit *M. subcordata* may need to be imposed. Alternatively, outside protected areas, if cultivation of *M. subcordata* is desirable, it is

important for farmers to understand the potentially beneficial role that fire has on the abundance of this species.

Fire has played an important role in shaping the ecological community of the Serengeti, yet only in the last several decades has the frequency of fires increased due to growing human disturbance. In some savanna systems, fire frequency has no significant effect on tree density (Higgins et al. 2007) or woody species composition and richness (van Wilgen et al. 2007), but here we demonstrate that fire frequency may affect the abundance of small woody species. By altering the magnitude, frequency and duration of natural disturbances, current fire management protocols could be leaving ecosystems vulnerable to the growth of fire-tolerant species, including exotic or invasive species (Folke *et al.* 2004). As population pressures continue to increase around conservation areas in Africa, there is concern that changes to historic patterns of fire—through fire suppression in ecosystems that frequently burn or through fire ignition in ecosystems that infrequently burn—will irreversibly alter ecosystems (Keane *et al.* 2008). Monitoring changes in abundance of invasive species is important for maintaining habitat quality and evaluating fire management protocols. This is particularly true for regions of important conservation status, such as the Serengeti, where many rare or endangered species, as well as economically important species, are dependent on successful management. The utilization of remotely derived data products, such as those provided by MODIS, can be a powerful tool to analyze landscape characteristics across time scales.

FUNDING

ACKNOWLEDGEMENTS

REFERENCES

Anderson GD, Talbot LM (1965) Soil factors affecting the distribution of the grassland types and their utilization by wild animals on the Serengeti plains, Tanganyika. *Ecology* **53**:33–56.

Anderson TM, Richie ME, Mayemba E, *et al.* (2007) Forage nutritive quality in the Serengeti ecosystem: the roles of fire and herbivory. *Am Nat* **170**:343–57.

Archibald S, Bond WJ, Stock WD, *et al.* (2005) Shaping the landscape: fire-grazer interactions in an African savanna. *Ecol Appl* **15**:96–109.

Axelrod DI (1985) Rise of the grassland biome, central North America. *Bot Rev* **51**:163–201.

Bond WJ, Keeley JE (2005) Fire as a global ''herbivore'': the ecology and evolution of flammable ecosystems. *Trends Ecol Evol* **20**:387–94.

Bond WJ, Woodward FI, Midgley GF (2005) The global distribution of ecosystems in a world without fire. *New Phytol* **165**:525–38.

Bragg TB, Hulbert LC (1976) Woody plant invasions of unburned Kansas bluestem prairie. *J Range Manag* **29**:19–23.

Brynard AM (1971) Controlled burning in the Kruger National Park: history and development of a veld burning policy. In *Tall Timbers Fire Ecology Conference Proceedings*, Vol. 11. 219–31. Tall Timbers Research Station, Tallahassee, FL.

Butz RJ (2009) Traditional fire management: historical fire regimes and land use change in pastoral East Africa. *Int J Wildland Fire* **18**:442–50.

Dempewolf J, Trigg S, DeFries RS, *et al.* (2007). MODIS derived burned area mapping of the Serengeti-Mara region. IEEE **4**:312–6.

Dublin HT, Sinclair ARE, McGlade J (1990) Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *J Anim Ecol* **59**:1147–64.

Folke C, Carpenter S, Walker B, *et al.* (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annu Rev Ecol Evol* **S35**:557–81.

Ford PL, McPherson GR (1996) Ecology of fire in shortgrass prairie of the southern Great Plains. In: Finch DM (ed). *Ecosystem Disturbance and Wildlife Conservation in Western Grasslands: A Symposium Proceedings. General Technical Report RM-GTR-285*. Fort Collins, CO: USDA Forest Service, Rocky Mountain Experiment Station.

Foxcroft LC, Jarošík V, Pyšek P, *et al.* (2011) Protected-area boundaries as filters of plant invasions. *Conserv Biol* **25**:400–5.

Fuhlendorf SD, Engle DM (2001) Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. BioScience **51:**625–32.

Gakuya DW (2001) Pharmacological and clinical evaluation of anthelmintic activity of *Albizia anthelminica* Brogn, *Maerua edulis* De Wolf, and *Maerua subcordata* De Wolf plant extracts in sheep and mice. *Ph.D. Thesis.* Nairobi, Kenya: University of Nairobi, Department of Veterinary Clinical Studies.

Githiori JB, Höglund J, Waller PJ (2005) Ethnoveterinary plant preparations as livestock dewormers: practices, popular beliefs, pitfalls and prospects for the future. *Anim Health Res Rev* **6**:91–103.

Harrison S, Inouye BD, Safford HD (2003) Ecological heterogeneity in the effects of grazing and fire on grassland diversity. *Conserv Biol* **17**:837–45.

Heisler JL, Briggs JM, Knapp AK, *et al.* (2004) Direct and indirect effects of fire on shrub density and aboveground productivity in a mesic grassland. *Ecology* **85**:2245–57.

Higgins SI, Bond WJ, February EC, *et al.* (2007) Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology* **88**:1119–25.

Hobbs NT, Schimel DS, Owensby CE, *et al.* (1991) Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. *Ecology* **72**:1374–82.

Hoch GA, Briggs JM, Johnson LC (2002) Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. *Ecosystems* **5**:578–86.

Holdo RM, Holt RD, Fryxell JM (2009*a*) Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. *Am Nat* **173**:431–45.

Holdo RM, Sinclair ARE, Metzger KL, *et al.* (2009*b*) A disease-mediated trophic cascade in the Serengeti and its implications for ecosystem C. *PLoS Biol* **7**:e1000210.

Keane RE, Agee JK, Fule P, *et al.* (2008) Ecological effects of large fires on US landscapes: benefit or catastrophe. *Int J Wildland Fire* **17**:696–712.

Laurance WF (2003) Slow burn: the insidious effects of surface fires on tropical forests. *Trends Ecol Evol* **18**:209–12.

MacDougall AS, Gilbert B, Levin JM (2009) Plant invasions and the niche. *J Ecol* **97**:609–15.

Maingi JK, Marsh SE (2006) Composition, structure, and regeneration patterns in a gallery forest along the Tana River near Bura, Kenya. *For Ecol Manag* **236**:211–28.

Masocha M, Skidmore AK, Poshiwa X, *et al.* (2011) Frequent burning promotes invasions of alien plants into a mesic African savanna. *Biol Invasions* **13**:1641–8.

Mavura WJ, Chemelil MC, Saenyi WW, *et al.* (2008) Investigation of chemical and biochemical properties of *Maerua subcordata* plant extract: a local water clarification agent. *Bull Chem Soc Ethiop* **22**:143–8.

McNaughton SJ (1992) The propagation of disturbance in savannas through food webs. *J Veg Sci* **3**:301–14.

Mduma SAR, Sinclair ARE, Hilborn R (1999) Food regulates the Serengeti wildebeest: a 40-year record. *J Anim Ecol* **68**:1101–22.

Mentis MT, Bailey AW (1990) Changing perceptions of fire management in savanna parks. *J Grassl Soc S Afr* **7**:81–5.

Mirijam G, Richardson DM, Privett SDJ (2011) Effects of alien plants on ecosystem structure and functioning and implications for restoration: insights from three degraded sites in South African fynbos. *Environ Manag* **48**:57–69.

Morgan WTW (1981) Ethnobotany of the Turkana: use of plants by a pastoral people and their livestock in Kenya. *Econ Bot* **35**:96–130.

Nkwabi AK, Sinclair ARE, Metzger KL, *et al.* (2011) Disturbance, species loss and compensation: wildfire and grazing effects on the avian community and its food supply in the Serengeti Ecosystem, Tanzania. *Austral Ecol* **36**:403–12.

Norton-Griffiths M (1979) The influence of grazing, browsing, and fire on the vegetation dynamics of the Serengeti. In: Sinclair ARE, Norton-GriffithsM (eds). *Serengeti: Dynamics of an Ecosystem*. Chicago, IL: University of Chicago Press, 310–52.

Owen JS (1971) Fire management in the Tanzania National Parks. In *Tall Timbers Fire Ecology Conference Proceedings*, Vol. 11. 233–41. Tall Timbers Research Station, Tallahassee, FL.

Ribeiro A, Romeiras MM, Tavares J, *et al.* (2010) Ethnobotanical survey in Canhane village of Massingir, Mozambique: medicinal plants and traditional knowledge. *J Ethnobiol Ethnomed* **6**:33.

Sinclair ARE (1979) The Serengeti environment. In: Sinclair ARE, Norton-GriffithsM (eds). *Serengeti: Dynamics of an Ecosystem*. Chicago, IL: University of Chicago Press.

Sinclair ARE (2004) History of fire management in the Serengeti National Park. In *Proceedings Workshop I: Fire Management Plan for the Serengeti National Park*. Tanzania Wildlife Research Institute, Seronera, Tanzania (in press).

Sinclair ARE, Norton-Griffiths M (1979) *Serengeti: Dynamics of an Ecosystem*. Chicago, IL: University of Chicago Press.

Tegegne G, Johan AE, Pretorius C (2007) In vitro and in vivo antifungal activity of crude extracts and powdered dry material from Ethiopian wild plants against economically important plant pathogen. *Biocontrol* **52**:877–88.

Teklehaymanot T, Giday M (2010) Ethnobotanical study of wild edible plants of Kara and Kwego semi-pastoralist people in lower Omo River Valley, Debub Omo Zone, SNNPR, Ethiopia. *J Ethnobiol Ethnomed* **6**:23.

Trollope WSW, Biggs HC, Potgieter ALF, *et al.* (1995) A structured vs. a wilderness approach to burning in Kruger in South Africa. In *Proceedings of the Fifth International Rangeland Congress, Salt Lake City, UT*. Denver, CO: Society for Rangeland Management, 574–5.

Turner MG, Hargrove WW, Gardner RH, *et al.* (1994) Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. *J Veg Sci* **5**:731–42.

Valery L, Fritz H, Lefeuvre JC, *et al.* (2008) In search of a real definition of the biological invasion phenomenon itself. *Biol Invasions* **10**:1345–51.

van Auken OW (2000) Shrub invasions of North American semiarid grasslands. *Annu Rev Ecol Syst* **31**:197–215.

van Langeveld F, Van de Vijver CADM, Kumar L, *et al.* (2003) Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**:337–50.

van Wilgen BW (2009) The evolution of fire management practices in savanna protected areas in South Africa. *S Afr J Sci* **105**:343–9.

van Wilgen BW, Govender N, Biggs HC (2007) The contribution of fire research to fire management: a critical review of long-term experiment in the Kruger National Park, South Africa. *Int J Wildland Fire* **16**:519–30.

van Wilgen BW, Trollope WSW, Biggs HC, *et al.* (2003) Fire as a driver of ecosystem variability. In: du Toit JT, Rogers KH, Biggs HC (eds). *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Washington, DC: Island Press, 149–70.

Verdcourt B, Trump EC (1969) *Common Poisonous Plants of East Africa*. London, England: Collins Press.

Whitlock C, Higuera PE, McWethy DB, *et al.* (2010) Paleoecological perspectives on fire ecology: revisiting the fire-regime concept. *Open Ecol J* **3**:6–23.