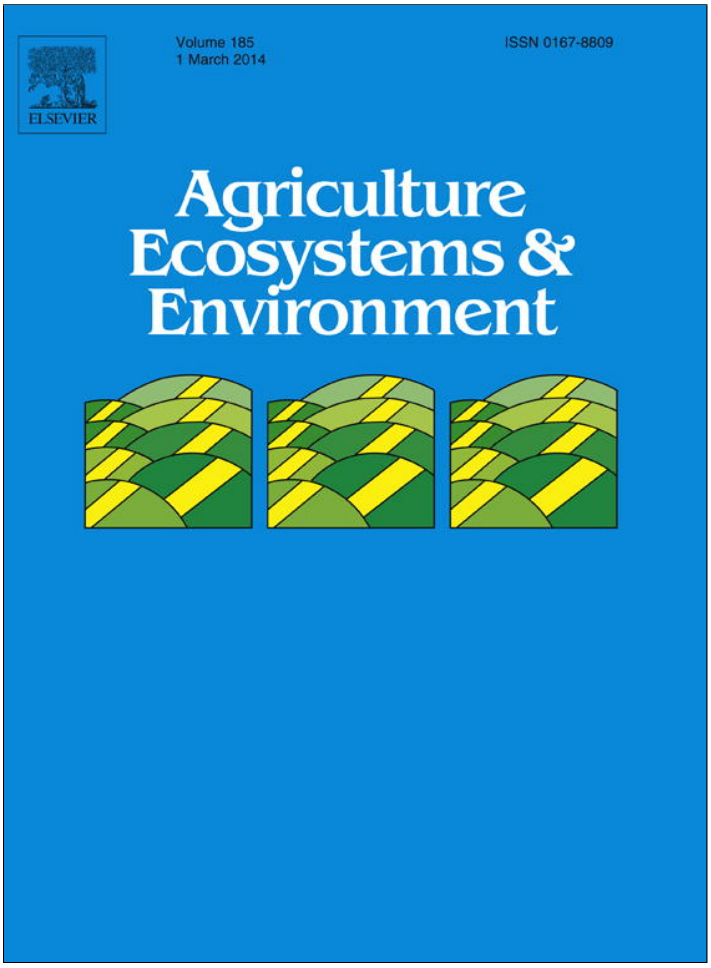

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Fire and grazing modify grass community response to environmental determinants in savannas: Implications for sustainable use

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ABSTRACT

Tropical dry forests and savannas are important repositories of plant diversity and ecosystem services in the tropics. These ecosystems are also used extensively for grazing by livestock, and represent a critical element of the rural economy of many tropical countries. Fire is considered as a part of co-evolution in these ecosystems across the globe. However, in recent decades, there has been a shift in historical fire regime. Fire has become more frequent in these landscapes, and could be further enhanced under climate change. This poses threats to existing biodiversity, ecosystem processes, and rural economy. We asked how variability in fire frequency has influenced diversity and heterogeneity in grass species composition, and richness and abundance of grass species preferred by large herbivores (referred to as grazing acceptability) in a South Indian tropical savanna forest. We assumed that an increase in fire frequency acts as the active constraint and limits an ecosystem from attaining the maximum heterogeneity, and the maximum grazing acceptability (maximum richness and abundance of grass species preferred by herbivores) in its native settings. We used MODIS active fire and burned area products to estimate fire frequency across the landscape. A nested sampling approach was used to collect information on vegetation and soil at different fire frequencies. Quantile regression analyses indicated that diversity and heterogeneity in grass species composition as well as grazing acceptability decreased with increasing fire frequencies. We found that livestock grazing intervened with the observed vegetation patterns; grass species diversity and heterogeneity, and grazing acceptability increased with grazing intensity at lower quantiles. Other measured covariates, rainfall, and soil-fertility, alone were not able to explain the observed vegetation patterns in the landscape. The results show a need to control annual fires but allow and manage intermittent fires in this landscape. A complete suppression of fire is not desirable as fire releases nutrients from burning of deeper-rooted vegetation and thus acts as a periodic nutrient pump. It also played an important role in maintaining the grass cover by reducing shrub cover. Hence, it is important to consider the complex interactions between fires–grazers–soil–vegetation to develop effective management practices. We conclude that fire frequency should be managed at low to intermediate levels (one fire in every 5–9 years, resembling the native settings), and grazing regulated, in order to sustain wild and domestic herbivores, biodiversity, and other key ecosystem processes and services over the long-term.

1. Introduction

Tropical dry forests and savannas comprise about 40% of the terrestrial landmass (Scholes and Walker, 1993). These ecosystems are important repositories of plant diversity in the tropics (Uys et al., 2004; Sankaran, 2009) and sustain large mammal herbivore assemblages, which in turn support larger carnivore species (Eisenberg and McKay, 1974; Sankaran, 2009). These landscapes generate valuable provisioning ecosystem services such as fodder for livestock, fire-wood, small timber, and medicinal plants, and represent a critical element of the rural economy of many tropical countries (Burrows et al., 1990; Augustine, 2003). They are also important determinants of local micro-climate, nutrient cycling, carbon sequestration, and storage (Lewis et al., 2009). However, tropical dry forests and savannas are under severe threat from land-cover change (Prance, 2006; Silva et al., 2006). Miles et al. (2006)

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concluded that 97% of tropical dry forests are at risk of destruction. In the remnant patches, one of the major threats to the biodiversity and ecological processes of these ecosystems is the changing fire regime, which is a result of large-scale habitat conversion, changes in fire management practices, and increasing human dependence (Ratter et al., 1997; Bond and Parr, 2010).

Fire has been an integral part in the co-evolution of tropical dry forests and savannas across the globe (Bond and Keeley, 2005; Bond et al., 2005). These ecosystems, characterized by a continuous C4-grass understory, burn often, and their floral and faunal components are believed to have evolved under a constant fire regime (Bond and Parr, 2010). However, with increasing human dependence on forest resources along with increased rate of fragmentation, the extent of burnt areas and frequency and intensity of fire in tropical landscapes have increased several folds over what they were in the past (Cochrane and Laurance, 2002; Cochrane, 2003). For example, Mouillot and Field (2005) reported a 49% increase in burnt areas from 1910 to 2000 in South Asian savannas, which increased from 25.3 Mha in 1910 to 37.7 Mha in 2000. Consequently, the fire return interval decreased from 11.2 years in 1910–1920 to 7.5 years in 1990–2000. Climate change could further exacerbate this threat in some regions (Dale et al., 2001).

In large parts of the Indian sub-continent, seasonally dry tropical forests, and savannas are the natural vegetation types (Ramankutty and Foley, 1999; Cardoso et al., 2008). Here, the majority of fires are surface fires, mainly burning the herbaceous layer, shrubs, and litter (Kodandapani et al., 2008). Kodandapani et al. (2004) have reported a threefold increase in fire frequency in South Indian tropical dry forests over the last 80 years, and the fire return interval shortened from 10, between 1909 and 1920, to 3.3, between 1989 and 2002. Thus, there has been a shift in the historical fire regime and this change is expected to have an impact on vegetation characteristics in these landscapes. However, our knowledge of the consequences of these shifts on diversity and composition of ground flora in these landscapes remains very poor.

The responses of herbaceous layers to increased fire frequencies in tropical savannas, across the globe, do not follow a consistent pattern and cannot be generalized to Indian savannas. For example, studies from the savannas of Cerrados and some drier parts of Africa have reported either an increase in herbaceous species diversity or no changes in diversity under recurring fire conditions (Higgins et al., 2000; Silva and Batalha, 2008); whereas, loss of diversity and abundance of herbaceous species, and changes in species composition have been reported as a response to frequent fires from other parts of the world (Cochrane and Schulze, 1999; Reich et al., 2001; Mehta et al., 2008a; Stephan et al., 2010).

In this study, we looked at the effects of recurring forest fire on herbaceous species in a South Indian tropical savanna forest, characterized by a continuous grass understory. These ecosystems play an important role in sustaining populations of both wild and domestic herbivores. The distribution and abundance of herbaceous species preferred by herbivores can determine the levels of co-existence between wild and domestic large herbivores (Fritz et al., 1996), and also the diversity and abundance of large herbivores (Olff et al., 2002; Archibald et al., 2005). Here, we focused on the effect of fire on the abundance and richness of grass species preferred by large herbivores in this landscape. Leigh and Vermeij (2002) argued that natural ecosystems are organized to support high productivity and diversity in their native settings, and any changes, such as an increase in fire frequency, tend to diminish its productivity and/or diversity in the short term. Fire by reducing the woody cover and increasing the herbaceous biomass (Sankaran et al., 2005) benefits the herbivores. However, increasing fire frequency can limit the use of a site by herbivores by encouraging a few fire tolerant but less preferred species, and thereby, limits an ecosystem from attaining the maximum diversity. We assumed that an increase in fire frequency acts as the active constraint, which limits the study ecosystem from attaining the maximum heterogeneity/diversity in species composition, and the maximum abundance and richness of preferred grass species in its native settings. We tested two specific hypotheses: (1) the diversity and heterogeneity in grass species composition decreases at high fire frequencies; (2) the abundance and richness of grass species preferred by large herbivores (henceforth, referred to as grazing acceptability) reduces at high fire frequencies. Studies have suggested abiotic factors (such as rainfall and soil-fertility) and biotic factors (such as grazing by herbivores) to have a role in shaping savanna vegetation (Polis, 1999; Bond, 2005; Augustine and McNaughton, 2006; Fuhlendorf et al., 2008; Beguin et al., 2011). Therefore, we considered the effects of both biotic and abiotic drivers, along with fire frequency in determining the vegetation patterns. We explain the observed vegetation patterns as a response to changes in fire regime and explore implications of our findings for sustainable management of these ecosystems.

2. Material and methods

2.1. Study area

Biligiri Rangaswamy Temple Wildlife Sanctuary - Male Mahadeshwara Hills and Kaveri Wildlife Sanctuary (BRT-MM HILLS-KAVERI) landscape forms a contiguous tract of tropical dry forests in South India that covers an area of approximately 3000 km^2 (Fig. 1). The elevation varies from 250 m to 1800 m asl. The forest type ranges from evergreen to dry deciduous to scrub, with large tracts of deciduous forests characterized by a sparse canopy and continuous grass undergrowth (Pascal and Ramesh, 1995). Riparian vegetation is characteristic along the river Kaveri. The annual rainfall varies from 500 to 1800 mm (Hijmans et al., 2005). For this study, we considered the drier savanna forest tracts of the landscape. Younger granites and peninsular gneiss characterizes the geology of the area. The soil type is Ustropepts with moderate to shallow gravelly-clay soils, and northern parts of the study site are characterized by rock outcrops associated with shallow gravelly-loamy soils (NBSS and LUP, 1994).

The landscape has a rich floral composition and a diverse assemblage of fauna. This has been identified as one of the most important tiger conservation landscapes (Sanderson et al., 2010). Eight ungulate species have been reported in the area. It supports the single largest population of Asian elephant (*Elephas maximus*) in the world and is one of the few strongholds for four-horned antelope (*Tetracerus quadricornis*) and grizzled giant squirrel (*Ratufa macroura*), two endemic mammals to Indian subcontinent.

Along with diverse wildlife and physiographic features, the landscape has a very high human density and a long history of human use. It has an indigenous Soliga tribal community that is dependent on forest product extraction. An estimated 1.7 million livestock reside in nearly 800 villages within and surrounding this landscape (All India Livestock Census dataset, 2007, http://dahd.nic.in/). These forested tracts play a critical role in supporting the rural economy by providing resources to a large portion of this livestock in the drier periods. Forest fire is a common feature in the savanna parts during the drier months of the year.

2.2. Identifying areas with different fire frequencies

We used moderate resolution imaging spectrometer (MODIS) Collection 5 active fire products (http://maps.geog.umd.edu) and burned area products (MCD45) (http://modis-fire.umd.edu), from January 2001 to May 2009, for identifying areas with different fire frequencies. MODIS fire products are used extensively to detect

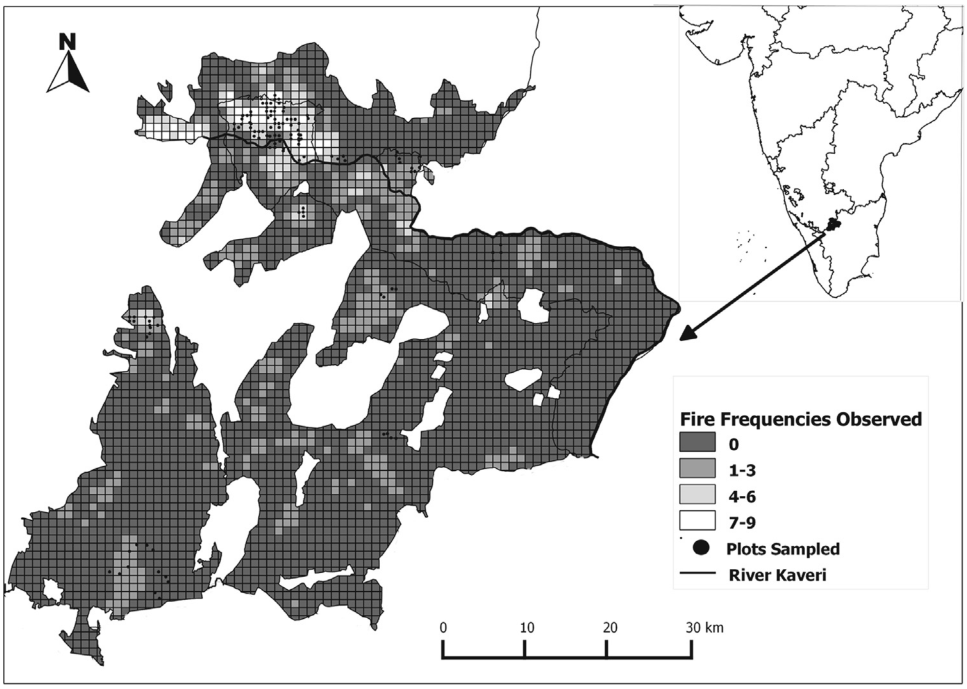

Fig. 1. The study area, BRT-MM HILLS-KAVERI landscape showing the location of sampled plots and distribution and frequency of fire. Fire is more frequent in the drier northern parts of the landscape.

and model the frequency and occurrence of fires worldwide, and have been found to be relatively accurate and reliable for open forests (Kovacs et al., 2004; Giglio et al., 2005; Devineau et al., 2010; Takahata et al., 2010). A study done in India shows that MODIS fire products perform better than other available fire information systems, such as the World Fire Atlas based on ATSR images, in detecting forest fires (Giriraj et al., 2010).

MODIS active fire products provide information on occurrence of strong fire at a resolution of 1 km by comparing pixel values relative to the background and surrounding pixels to account for variability of surface temperature and reflection of sunlight (Giglio et al., 2003). Burned Area Products, at a resolution of 500 m, are based on spectral, temporal, and structural changes that take place in a burned area as a response to deposits of charcoal and ash, removal of vegetation, and alteration of the vegetation structure (Roy et al., 2005). Since there was about 50% gain in information on fire occurrence, we developed composite fire maps, at 500 m resolution, for each year using both the products (henceforth, referred to as fire maps).

We independently assessed the accuracy of these fire maps for the study area using high resolution (30 m) LANDSAT ETM+ imagery for the year 2003, between January 20 and March 9, mainly to evaluate their ability in estimating sizes of individual burned areas. We found that around 82% of the area under the fire maps was in moderate to high severity burn category (differenced normalized burn ratio (DNBR) 0.25–0.56, using LANDSAT images). The remaining 18% of the area under the fire maps was in the category of low severity burn to unburn (DNBR 0.09–0.2, using LANDSAT images). We estimated nearly 78% accuracy in identifying pixels in moderate to high severity burn category (DNBR 0.25–0.56) across the landscape using these fire maps. As most of the satellite imagery, including LANDSAT, were not available for the study area on a regular basis, we used MODIS fire-products, which provide data for every 24 h (Davies et al., 2009), for estimating fire frequency in the study area.

We defined fire frequency for each location as the number of years, out of nine, in which fires were detected. The inventory analysis placed a higher accuracy,>95%, in estimating the extent of moderate to high severity burned patches for the pixels where MODIS active fire and burned area products intersected. Hence, we emphasized on these pixels where both the products intersected in the fire maps while defining fire frequency. We used open source GIS software, Quantum-GIS Mimas 1.3.0 (QGIS Development Team, 2009) and Grass 6.4.0SVN (Grass Development Team, 2009), for processing the raster and vector data.

2.3. Sampling methods

2.3.1. Field sampling

We superimposed a 1 km × 1 km grid over the study area and extracted the fire frequency from the fire maps for each of these grids (Fig. 1).We used grids with known fire frequencies as basic sampling units.

Field survey was done from January to May 2010. We randomly selected a minimum of four grids in each fire frequency, except for fire frequency of eight as only three of the grids in the landscape had this frequency (we could not sample grids with a fire frequency of nine as the vegetation was already burnt during the survey). A comparison of grids with vegetation maps (Pascal and Ramesh, 1995) and soil maps (NBSS and LUP, 1994) available for the study area showed that about 75% of the sampled grids were uniform in vegetation type and about 87% of the grids were uniform in soil type. Two 20 m × 20 m plots, located within the 1 km^2 grid with a minimum distance of 500 m between them, were used to collect information on herbaceous species and soil. The plots were located randomly within a grid when the entire grid was found burnt in the fire maps for the given years. If a grid was partially burnt in the fire maps, we placed our plots randomly only in those patches that were shown as burnt in the fire maps for the given years. Additionally, the presence of burned signs from the previous years, such as burnt stems and tree scars, were taken into consideration while locating the sampling plots. We assessed vegetation characteristics in each plot using a nested sampling approach. We laid four subplots of size 5 m × 5 m, along the four sides of the 20 m × 20 m plot, such that the centre of each subplot was 2.5 m away from the midpoint of the side of the plot and 7.5 m away from the centre of the plot.

We used a modified point intercept method, where we recorded ground cover features at every 1m interval along the periphery of the plot and subplots. The ground cover features recorded include species of grass, presence of herbs, shrubs and other woody plants, seedlings, bare ground, and rock. Thus, we had 140 points for each plot, 80 points along the periphery of the 20 m × 20 m plot and 60 points along the periphery of four 5 m × 5 m subplots (each subplot shared a side with the 20 m × 20 m plot), in which we recorded the ground cover features. We classified each of the grass species as preferred or avoided by herbivores based on the available literature (Gamble, 1928; Kelkar, 2009).

We collected soil samples at the centre of each 5 m × 5 m subplot up to a depth of 15 cm. A composite soil sample was obtained for each plot. The samples were air dried before sending them to the laboratory for further analysis.

We used the same design to collect information from 30 plots with a fire frequency of zero. These plots were not burnt between 2001 and 2009, and were located in the proximity of other burned plots. The total number of plots sampled was 120, including 30 unburned plots. We sampled 15 plots each in fire frequency of one, two, and four. There were 12 plots each in fire frequency of three and seven, eight each in frequency of five and six, and five plots in fire frequency of eight.

2.3.2. Soil analysis

We analyzed soil samples from 102 plots (we could not collect soil from the rest of the plots as the soil depth was less than 5 cm), for their physical and chemical properties.

Air dried soil samples were passed through a 2 mm sieve and analyzed for their physical properties (clay, sand, and silt content) and chemical properties (cation exchange capacity (CEC); pH, organic carbon (OC); electric conductivity (EC); and N, P, and K). Soil samples were analyzed for pH (1:2 in water and 0.0 M KCl), M KCl-exchangeable acidity, and Al using NaF titration (Thomas, 1982). CEC was measured using pH 7 buffered ammonium acetate (Chapman, 1965). We analyzed soil organic carbon using modified Walkley–Black method (Allison, 1960). Texture was determined using international pipette method (Piper, 1942). We used Olson's calorimeter to extract P_2O_5. Flame photometer method was used to estimate K_2O and nitrogen was extracted using Alkaline, $KMnO_4$ method.

2.3.3. Collecting data on other variables

Rainfall-We used secondary information on rainfall in the study area due to lack of weather monitoring stations. A rainfall layer at a resolution of 1 km^2 was obtained from global climate layer available at http://www.worldclim.org (Hijmans et al., 2005).

Livestock–Our plot size was too small to capture habitat usage pattern by herbivores. Hence, we used secondary data to derive a potential grazing pressure index for livestock. We collected data on livestock population at village level for the six taluks (Chamarajanagar, Ramanagaram, Mandya, Salem, Erode, and Dharmapuri – a taluk is an administrative division comprised of several villages and a few smaller towns) surrounding the study area from All India Livestock Census dataset (2007) (http://dahd.nic.in/).

2.4. Data analysis

2.4.1. Vegetation indices

We developed two different vegetation indices, index of heterogeneity and index of grazing acceptability, by using Bray–Curtis dissimilarity measures (Bray and Curtis, 1957) and appropriate reference compositions.

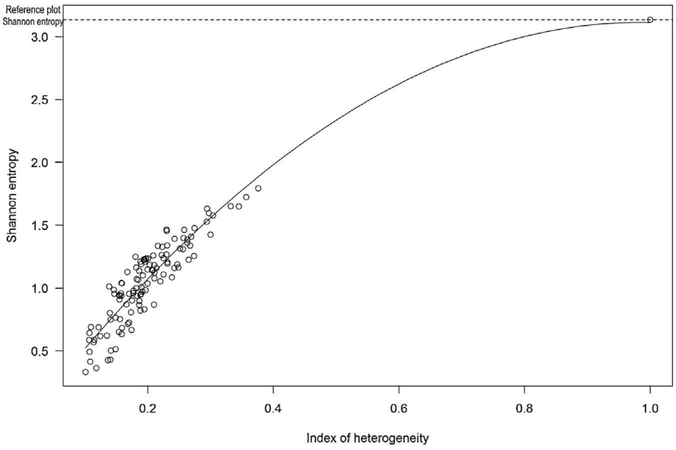

Fig. 2. Relationship between the index of heterogeneity, developed for sampled plots, and Shannon entropy. The graph shows a quadratic relationship, $r^2 = 0.86$, between the developed index of heterogeneity and Shannon entropy estimated for the same plots. The dotted line indicates the horizontal asymptote at reference plot Shannon entropy.

Index of heterogeneity–We considered both species richness and relative abundance in each of the plots for deriving the index of heterogeneity. We developed a composition for the reference plot by considering all species in the landscape to be present at equal frequency in the plot. Hence, the reference plot has maximum species richness and maximum evenness, and thus represents the hypothetical most diverse and the most heterogeneous plot in the study area. We calculated Bray–Curtis dissimilarities in richness and abundance of grass species composition between this reference plot and each of the sampled plots. If the Bray–Curtis dissimilarity or compositional distance of a plot to this reference plot is higher, the less diverse and more homogeneous is that plot. We subtracted dissimilarity values from 1 to get similarity values, which we referred to as the index of heterogeneity. This index ranged from zero to one. The diversity at a plot as well as heterogeneity in grass species composition increases with the index of heterogeneity. We observed a quadratic relationship, $r^2 = 0.86$, between the developed index of heterogeneity and Shannon entropy estimated for the same plots (Fig. 2).

Index of grazing acceptability–We considered both the richness and relative abundance of grass species preferred by large herbivores in each of the plots to develop index of grazing acceptability. The values for grass species avoided by herbivores were considered as zero in the reference plot. We converted the maximum frequency values observed for each of the preferred grass species across all the plots to percentage relative abundances, and set this as the composition for the reference plot. Thus, the reference plot has the maximum richness and abundance of preferred grass species and represents the hypothetical most preferred grass species composition by herbivores in the landscape. We calculated Bray–Curtis dissimilarities in richness and percentage relative abundance (calculated from frequency) of preferred grass species between this reference plot and each of the sampled plots. With an increase in Bray–Curtis dissimilarity of a plot to the reference plot, the richness and abundance of preferred grass species decrease in that particular plot. We subtracted the dissimilarity values, which ranged from 0–1, from 1 to get an index of grazing acceptability. Thus, the grazing acceptability in a plot increases with the index of grazing acceptability.

2.4.2. Soil index

A Euclidean distance between reference plot and each sampled plot was calculated to derive an index for soil fertility. We considered six soil properties, clay, organic carbon (OC), cation exchange capacity (CEC), nitrogen (N), phosphorus (P), and potassium (K), which determine soil fertility, to develop the reference plot. The maximum value of each of these soil properties across all the plots was set as the reference plot. Thus, the reference plot represents hypothetically the most fertile plot in the study area. The greater the distance value of a plot to the reference plot the lesser the soil fertility of the plot. We divided each value with the maximum dissimilarity value to get a continuous range between 0 and 1. These values were then subtracted from 1 to get an index of similarity, which is referred as the index of soil fertility.

All distance matrices were built by using Ecodist library of R 2.12.1 software (Goslee and Urban, 2007).

2.4.3. Grazing index

We developed an interpolation layer, indicating the potential grazing pressure at each of the plots, using inverse distance weighting (IDW) method (Shepard, 1968). As livestock was the dominant herbivore species in the landscape, we used the numbers of livestock at each of the villages and distances of each of the plots to the surrounding villages as the two attribute values to derive this layer. If the plot to a village is nearer and the livestock number in the nearest village greater, the weight forthat plot is higher. We referred this as the index of grazing. The potential grazing pressure at a site increases with the index of grazing. The IDW interpolation layer was created using interpolation plug-in of open source GIS software- Quantum-GIS Mimas 1.3.0, with a distance coefficient value of 2.

2.4.4. Quantile regression

We did not use traditional parametric regression methods because of pronounced non-constant variance of the response variable with respect to the covariate (heteroscedasticity), as well as lack of normality (Shapiro–Wilk normality test: heterogeneity $W = 0.96$, $P = < 0.01$). We assumed that an increase in fire frequency acts as the active constraint and limits the study site from attaining the maximum heterogeneity/diversity, and grazing acceptability (i.e., maximum richness and abundance of species preferred by herbivores) in its native settings. As many other measured and unmeasured variables could influence vegetation response along with fire frequency, a lot of vertical scatter in the measured response is expected at a given fire frequency. Therefore, the effect of the limiting constraint, i.e., fire frequency, will be more detectable at upper bounds of response variable distribution rather than at the mean response, which is what linear regression models assume (Cade et al., 1999; Cade and Noon, 2003). Quantile regression helps in testing this hypothesis by allowing analysis in the upper limits of the response variables (Cade et al., 1999). We created the estimates of the regression slope and intercept at 25th, 50th, 75th, and 90th percentile. The 90% confidence intervals were obtained for the same. We used square root transformed values of fire frequency for the regression analysis. We constructed quantile regression models for each of the covariates- rainfall, index of soil fertility and index of grazing, independently, to determine whether they influence the observed vegetation patterns. These models were then compared with the models with fire frequency as the variable. We also constructed multiple regression models by adding each of the covariates individually to the fire frequency model.

The quantile regression was performed using quantreg library of R 2.12.1 software (Koenker, 2011).

3. Results

The existing variability in diversity and heterogeneity in grass species composition and index of grazing acceptability across the landscape was well explained by fire frequency. The results of the effect of fire on various vegetation characteristics are presented below.

3.1. Fire frequency, rainfall, and grazing index across the landscape

About 45% of the area (1377 grids out of 3082 grids) experienced fire, at least once, between 2001 and 2009. Fire was more frequent in the northern drier savanna parts of the landscape (Fig. 1). Grids with fire frequency of one and two accounted for 84% of total number of burned grids, with a count of 861 and 293 grids, respectively. Only three of the grids had burned every year, 18 grids had burned eight times, and 22 grids had burned seven times between 2001 and 2009. An analysis of MODIS active fire data for the given period suggests that 98% of these fires occurred between December and May months (*c* 90% of them occurred between January and March, $n = 1331$ fire incidences) in the study landscape.

The mean annual rainfall across the sampled plots ranged from 590 mm to 940 mm. The median was at 692 mm with more than 75% of plots falling within a range of 600–750 mm.

The values for grazing index for the plots ranged from 0.46 to 2.75 with a median at 1.34. Fifty percent of the plots had a grazing index between 1 and 1.5, suggesting a moderate potential grazing pressure in these plots. Only two plots had a grazing index of less than 0.5 and 13 plots had an index of more than 2.0.

3.2. Herbaceous species composition

3.2.1. Response in grass species richness, diversity, and heterogeneity

We identified 23 species of grasses from the landscape. All 120 plots sampled had grass species, and the number of species seen per plot varied from two to nine, with the maximum number observed in an un-burned plot. *Heteropogon contortus* and *Cymbopogon flexuosus*, the two grass species avoided by herbivores, accounted for around 75% of the total grass abundance in the landscape.

The index of heterogeneity ranged from 0.10 to 0.38, with a median of 0.19, indicating a lower diversity and heterogeneity in grass species composition across the landscape (Fig. 2). Quantile regression estimates showed a negative linear relationship between index of heterogeneity and fire frequency (Table 1, Fig. 3a). The 90th quantile estimate provided the strongest negative linear relationship, with a 90% CI that excluded zero. A near doubling in slope estimates was observed between the 75th and 90th quantiles, $\beta(0.75) = -0.025$ to $\beta(0.90) = -0.047$; whereas, the difference between estimates from the 25th to 75th quantile was very little (Table 1). This suggests that the most of the decreasing variation in diversity and heterogeneity in grass composition as a function of fire frequency occurred above the 75th quantile. We did not find any influence of rainfall and soil fertility on index of heterogeneity, as neither of these terms differed substantially from zero ($P > 0.05$), and 90% CI overlapped zero for all the regression quantiles. This suggests that these covariates alone did not explain the observed diversity and heterogeneity in the landscape. The estimates for fire frequency for all the quantiles were consistent across the additive models with rainfall and index of fertility as covariates, and did not change the sign. We observed an increasing variation in index of heterogeneity as a function of index of grazing at lower quantiles, 25th and 50th (Table 1). However, at higher quantiles, 75th and 90th, grazing index was not different from zero ($P > 0.10$), which suggests that at higher quantiles factors other than potential grazing pressure act as limiting constraints. In the additive model, where both fire frequency and grazing index were included, for regression quantiles > 50th grazing index was not different from zero ($P > 0.05$) while fire frequency had

Table 1
Summary of quantile regression results with index of heterogeneity as response variable and fire frequency and grazing index as two individual predictor variables. Tau represents different quantiles. Table legend: FF- fire frequency – refers to the number of years, out of nine (between January 2001 and May 2009), in which fires were detected in a particular area based on fire maps. Fire frequency ranges from 0–9; GI- grazing index – a derived index of grazing which indicates the potential grazing pressure at a particular site. Higher the index higher the potential grazing pressure at a particular site.

Tau	Coefficient		SE		CI 90%		*P*	
	FF	GI	FF	GI	FF	GI	FF	GI
0.25	−0.0156	0.0518	0.0073	0.0149	−0.0206 to −0.0004	0.0006 to 0.0719	0.0355	0.0007
0.50	−0.0104	0.0302	0.0061	0.0102	−0.0219 to −0.0043	0.0068 to 0.0539	0.0910	0.0037
0.75	−0.0248	0.0292	0.0082	0.0229	−0.0304 to −0.0147	0.0214 to 0.0504	0.0030	0.2055
0.90	−0.0446	0.0434	0.0120	0.0405	−0.0541 to −0.0058	−0.0029 to 0.0662	0.0003	0.2868

significant negative influence ($P < 0.05$), suggesting the role of fire frequency as a limiting constraint on diversity and heterogeneity in grass species composition at higher quantiles. The negative relationship observed between index of heterogeneity and fire frequency at higher quantiles across all the models, supports our hypothesis 1.

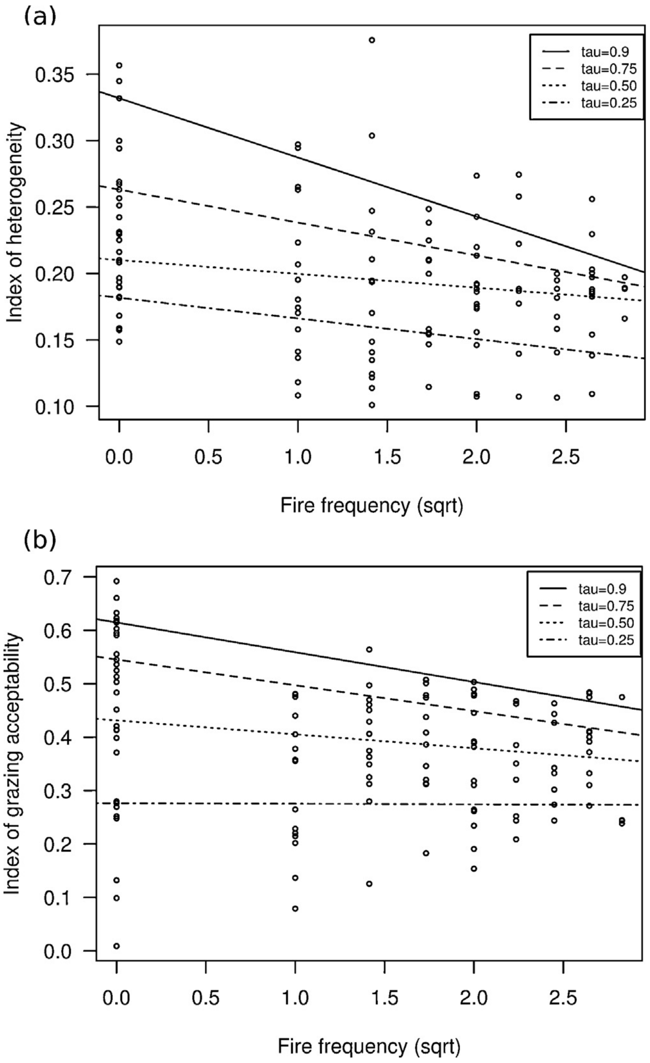

Fig. 3. Effect of fire frequency on vegetation characteristics. (a) Response of index of heterogeneity (diversity and heterogeneity in grass species composition) to increasing fire frequency; (b) Response of index of grazing acceptability (expressed in terms of richness and abundance of grass species preferred by herbivores) to increasing fire frequency. Square root transformed values of fire frequency (fire frequency ranges from 0 to 8) are used for the regression analysis. Quantile lines represent 25th, 50th, 75th, and 90th percentiles.

3.2.2. *Response in grazing acceptability*

The maximum value observed for index of grazing acceptability was 0.69, with a median of 0.39. Regression quantile estimates showed a negative linear relationship between acceptability index and fire frequency for the quantiles > 50th (Table 2, Fig. 3b). The 90th quantile estimate provided the strongest negative linear relationship, with a 90% CI that excluded zero. The most of the decreasing variation in richness and abundance of grass species preferred by large herbivores as a function of fire frequency occurred above the 50th quantile, as there was a near doubling in the slope estimates between 50th and 90th quantiles, $\beta(0.50) = -0.026$ to $\beta(0.90) = -0.056$. We did not find any influence of rainfall and soil fertility on richness and abundance of preferred grass species as neither of these terms differed substantially from zero ($P > 0.05$), and 90% CI overlapped zero for all the regression quantiles. The rate of change values for fire frequency for all the quantiles were consistent across the additive models, with rainfall and soil fertility as covariates, and did not change the sign. We observed an increasing variation in index of grazing acceptability as a function of index of grazing from 25th to 75th quantiles (Table 2). The strongest positive linear relationship was observed for 25th quantile, which decreased gradually across until the 75th quantile and the relationship was not significant at 90th quantile ($P > 0.05$). This suggests the role of factors other than potential grazing pressure in limiting the index of grazing acceptability at higher quantiles. In the additive model, where both fire frequency and grazing index were included, fire frequency remained significant at the higher quantiles ($P < 0.05$), whereas grazing index was not different from zero for regression quantiles > 50th ($P > 0.05$). This suggests the role of fire frequency as a limiting constraint on the richness and abundance of grass species preferred by large herbivores at higher quantiles. The negative relationship observed between the grazing acceptability and fire frequency at higher quantiles across all the models, supports our hypothesis 2.

3.2.3. *Response in relative abundance of shrubs*

Fire frequency had considerable effect on co-occurrence of shrub cover and grass cover in the landscape. The shrub cover decreased with an increase in fire frequency; whereas, grass cover increased with increasing fire frequency (Fig. 4).

3.3. *Soil properties*

The surficial soil was light textured, with majority being sandy loams (60%). The mean organic carbon (OC) was 1.29% (range 0.29–2.69) with a co-efficient of variance (CV) as high as 41%. Cation exchange capacity ranged from 7.2 to 22.6 cmol kg^{-1} with a mean of 14.39 cmol kg^{-1} and a CV of 26%. Nitrogen content across the plots ranged from 0.005% to 0.023%, with a mean value of 0.011%. The concentrations of P_2O_5 and K_2O ranged between 0.7 to 6.0 g m^{-2} (mean = 1.1 g m^{-2}) and 24 to 119 g m^{-2} (mean = 55 g m^{-2}) respectively.

Table 2
Summary of quantile regression results with index of grazing acceptability as response variable and fire frequency and grazing index as two individual predictor variables. Tau represents different quantiles. Table legend: FF–fire frequency – refers to the number of years, out of nine (between January 2001 and May 2009), in which fires were detected in a particular area based on fire maps. Fire frequency ranges from 0–9; GI–grazing index – a derived index of grazing which indicates the potential livestock grazing pressure at a particular site. Higher the index higher the potential grazing pressure at a particular site.

Tau	Coefficient		SE		CI 90%		*P*	
	FF	GI	FF	GI	FF	GI	FF	GI
0.25	−0.0009	0.1092	0.0265	0.0205	−0.0397 to 0.0347	−0.0716 to 0.2114	0.9715	0.0000
0.50	−0.0261	0.0711	0.0191	0.0354	−0.0711 to −0.0064	0.0372 to 0.1856	0.1758	0.0468
0.75	−0.0483	0.0839	0.0147	0.0325	−0.0726 to −0.0227	0.0365 to 0.1046	0.0013	0.0110
0.90	−0.0557	0.0830	0.0111	0.0531	−0.0719 to −0.0447	0.0571 to 0.1406	0.0000	0.1205

The index of soil fertility across the sampled plots ranged from 0 to 0.833 with a median value of 0.35, showing that majority of plots sampled had a medium range of soil fertility. The exploratory data analysis showed a strong positive relationship between index of soil fertility and fire frequency. The index of soil fertility increased with increasing fire frequency suggesting a positive feedback between soil properties and fire (Fig. 5).

4. Discussion

The effects of frequent forest fires on fragmented tropical dry forests and savannas of India, needs attention as their sustainable use and management has implications for the largest populations of wild ungulates in South Asia and for co-management of the landscape for biodiversity and ecosystem services. In this study, we asked specific questions pertaining to the effects of recurring forest fires on grass species diversity and heterogeneity, and grazing acceptability. Our results suggest that increasing fire frequency acts as an active constraint resulting in a decrease in grass species diversity and heterogeneity, and richness and abundance of grass species preferred by herbivores in the landscape. Although the limiting effects of fire frequency on vegetation patterns was evident at higher quantiles, we found that at lower quantiles grazing by livestock intervened with these observed patterns. A reduction in shrub cover and an increase in herbaceous cover with fire frequency were also evident from the study. Furthermore, fire frequency increased soil fertility. Thus, the key processes influencing composition of grass species preferred by herbivores, species abundance and diversity in these ecosystems were fire, grazing, soil nutrient cycling, and their interactions along the rainfall gradient (Fig. 6).

4.1. *Grass species diversity and heterogeneity decreased with fire frequency*

Several studies have shown a decrease in plant species diversity and heterogeneity with frequent fires. Studying the vegetation dynamics in African savannas Archibald et al. (2005), it has been found that the systems with frequent fires become dominated by a few tall and fast growing grasses that are fire tolerant. A study done in tropical forests of Cerrados suggested a loss of floral species in areas with high fire frequencies. However, the same study found a unique assemblage of fire tolerant vegetation in annually burned sites and proposed maintaining areas with different fire frequencies in the landscape to achieve higher beta diversity (Silva and Batalha, 2008). In our study, two fire tolerant species, *Cymbopogon flexuosus* and *Heteropogon contortus*, were abundant at high fire frequencies. However, they were not restricted to these sites and found across all the fire frequencies. This suggests that in areas with a long fire history, maintaining a few sites with higher fire frequencies may not result in increased beta diversity. The increase in heterogeneity at low fire frequencies indeed suggest that a longer duration between two successive fires is important to maintain a higher diversity.

Fire acts as an effective selection pressure by removing succulent fire intolerant species and encouraging the growth of fire

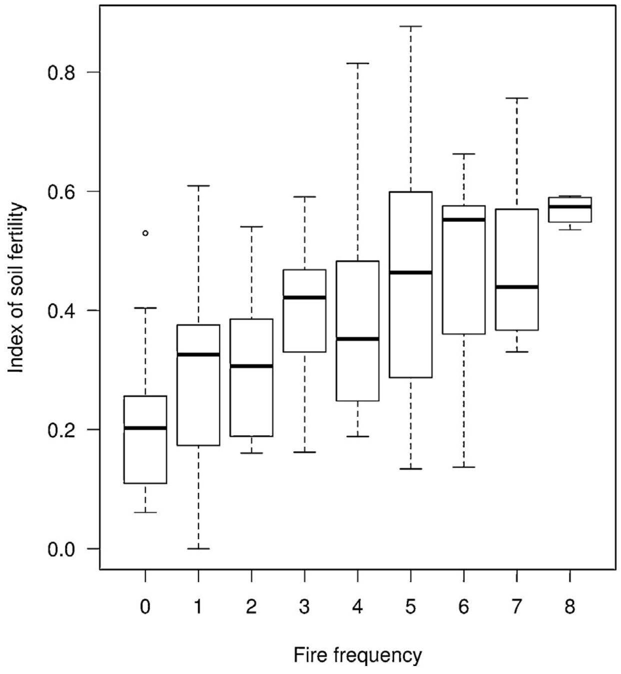

Fig. 4. Effect of increasing fire frequency on relative abundance of woody vegetation, defined as shrub: grass cover ratio.

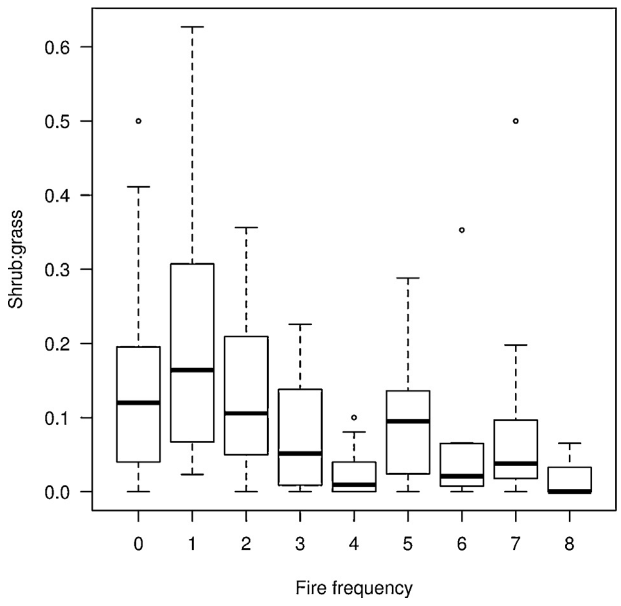

Fig. 5. Effect of fire frequency on surficial soil fertility index. Surficial soil fertility increases with the index of fertility.

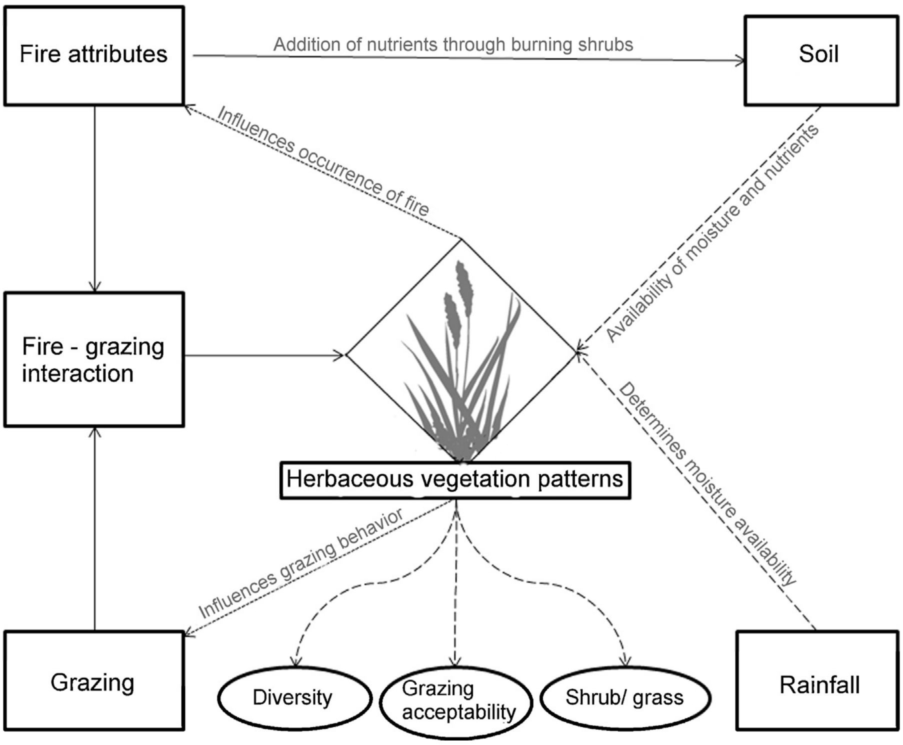

Fig. 6. Diagrammatic representation of the conceptual interaction that occurs between fire and other biotic and abiotic variables and vegetation. Rainfall determines the potential vegetation type along with soil properties, soil properties are greatly modified by frequent fires, frequent fires interact with grazing in determining the vegetation, and vegetation characteristics in turn influence fire and grazing behavior.

tolerant species. The competitive superiority of these fire tolerant species can result in less variation in vegetation patterns (Bond and Midgley, 1995; Rogers and Hartnett, 2001) and this could have attributed to the observed homogeneity in grass composition with fire frequency in the landscape. A longer duration between two successive fires allows colonization of areas with both fire intolerant and fire tolerant flora, which might contribute towards an increase in diversity at low fire frequencies.

4.2. *Grazing acceptability reduced with fire frequency*

Similar to our findings, studies in Africa have suggested a decrease in richness and abundance of grasses preferred by herbivores with increasing fire frequency. A high fire frequency is shown to decrease the spread of lawn grasses, which are highly preferred by herbivores, in the savanna ecosystems (Archibald et al., 2005; Archibald, 2008). A general belief in the tropics behind burning grasslands is that fire induces growth of tender and more palatable grasses. Although, the immediate new flush that follows fire is nutritious and highly preferred by herbivores, the results show that the long-term influences of repeated fires on grazing acceptability in terms of richness and abundance of grass species preferred by herbivores is negative.

The decrease in richness and abundance of grass species preferred by herbivores could be a consequence of selective pressure for fire tolerant species in frequently burned areas. Fire tolerant species are less palatable due to the very same reasons that make them fire tolerant, fast growing with high lignin content (Bond and Midgley, 1995). Furthermore, losses of nitrogen with increased fire frequencies may increase the advantages of chemical defense in plants against herbivory and thus increase abundance of species generally avoided by herbivores (Augustine and McNaughton, 1998).

4.3. *Relative abundance of shrubs reduced with fire frequency*

A reduction in shrub cover and an increase in herbaceous growth are evident from several studies in the tropics (Sankaran et al., 2005; Higgins et al., 2007). One of the reasons for decrease in woody cover and increase in grass cover could be that, in an increased surficial soil environment (Fig. 5), the shallow, fibrous root system of grasses is better able to extract surface moisture and nutrients when compared to their woody counterparts (Bond and Midgley, 1995; Rogers and Hartnett, 2001). In addition, frequent burning does not allow woody vegetation to grow beyond the stage at which they are more susceptible to herbivory, and the shade produced by fast growing grasses affects the establishment of shade intolerant savanna shrubs and other woody vegetation (Bond, 2008).

The results suggest that in order to prevent the complete succession of these grassland ecosystems by woody-components, it is important to maintain some level of fire. Intermittent fire can convert the deeper-rooted shrubs to flushes of nutrients for the shallow rooted grasses. However, in long-term, frequent fires may result in a complete removal of deeper-rooted plants from savannas, which is likely to disrupt the "nutrient pump" that adds nutrients to the surficial soil periodically.

4.4. *Increase in surficial soil nutrients at periodic intervals*

Although, over longer time-scales, the overall nutrient pool is likely to be depleted due to frequent fires and subsequent leaching and oxidation losses, the plant available nutrients are available to the shallow rooted grasses at the surface, periodically, mainly because of fire (Certini, 2005). Several studies have shown similar short-term increases in nutrient status of soil due to fire (Reich et al., 2001; Certini, 2005; Silva and Batalha, 2008). As stated earlier, one of the key mechanisms behind increased surficial soil fertility is that fire effectively transfers nutrients from deeper soil horizons to the surface by burning deeper-rooted shrubs (Johnson and Curtis, 2001). In these weathered soils, fire can enhance soil-pH and generate additional cation exchange capacity on the organic matter (Krishnaswamy and Richter, 2002; Mehta et al., 2008b). It also results in increases in organic matter in surficial soils by stimulating plant growth on the surface through periodic nutrient pulses, even though there may be losses in the overall soil organic matter pool and nutrients in the deeper soil profile in the long-term, especially in highly weathered nutrient poor sites.

4.5. *Effects of livestock grazing on vegetation patterns*

In the study landscape, we found potential livestock grazing pressure to be an important variable, which intervened with the effects of fire frequency in determining the vegetation patterns at lower quantiles. At lower quantiles, grass species diversity and heterogeneity, and compositional abundance of grasses preferred by herbivores increased with increasing livestock grazing pressure. Studies on lawn grasses in Africa suggest grazing by wild ungulates as the key factor in maintaining the palatable lawn grasses in the landscape (Augustine and McNaughton, 1998; Archibald, 2008). Increase in richness and diversity of grass species have been observed in areas with natural population of large grazing herbivores (McNaughton, 1985; Noy-Meir, 1995; Olff and Ritchie, 1998). Similar results were found when livestock were managed at low stocking rates (Wieren, 1995). Presently, livestock are the dominant grazers in the landscape and the spread of grazing index suggests that the potential livestock grazing pressure at the sampled plots is moderate and not heavy. This may be one of the reasons for the observed higher heterogeneity and abundance of grasses preferred by herbivores in the landscape. However, the derived grazing index is a rough measure of the livestock grazing pressure and the results need to be interpreted with caution.

Moderate grazing by herbivores is known to stimulate grass growth and nutrient cycling (Augustine, 2003), and tends to increase easily available nutrients from urine and dung (Augustine and McNaughton, 2006). This may be one of the reasons for increased grazing acceptability as well as greater heterogeneity at lower quantiles. At landscape level, the ecological interaction between fire and grazers plays a major role in determining the vegetation composition and structure in many ecosystems (Archibald et al., 2005; Augustine and McNaughton, 2006; Fuhlendorf et al., 2008). Herbivores, by removing the grass cover and preventing the vegetation escaping into the unpalatable and flammable state, markedly reduce fire potential and influences the distribution and extent of fire (Bond, 2008; Leonard et al., 2010). A reduced grass cover and subsequent low fire frequency in grazed areas may promote fire sensitive, grazing-tolerant, nutritious species of grasses in the landscape, and thus result in greater diversity and grazing acceptability (Collins et al., 1998; Olff and Ritchie, 1998; van Langevelde et al., 2003).

The interaction between fire and grazing further suggests a feedback system that occurs between vegetation properties and fire, and grazing behavior. The fire tolerant species which are also highly inflammable determine the occurrence and extent of fire (D”Antonio and Vitousek, 1992; Bond and Midgley, 1995); the new growth in the burned areas influences herbivore habitat use patterns; and the removal of biomass by grazers determines the fire potential (Fig. 6).

4.6. *The role of gradients in rainfall and soil properties*

Rainfall and soil are two climatic variables that determine the distribution of savannas and dry forests at larger biome scales. Rainfall, by influencing the amount of available moisture, influences the diversity of plants, and relative abundance of shrubs and grasses. The availability of moisture to plants is largely influenced by soil properties, which also determine the amount of available nutrients (Scholes, 1990). Our study suggests that, at landscape level, fire frequency may over turn, to some extent, the influence of rainfall and pre-fire soil fertility gradients on vegetation composition in savannas. Furthermore, periodic fires change surficial soil properties and nutrient availability (section 4.4). Our study suggests there is a complex interaction between fire and other biotic and abiotic factors, and vegetation. Rainfall determines the potential vegetation type along with soil properties, soil properties are greatly modified by fires, fires interact with grazing in determining the vegetation, and vegetation characteristics in turn influence fire and grazing behavior (Fig. 6).

5. Conclusions

A shift in historical fire regime can have a severe impact on herbaceous species patterns in savanna forests. In spite of having a long fire history, the recent increase in fire frequency and predicted increase under climate change can act as a limiting constraint on grass diversity and richness, and abundance of grasses preferred by herbivores in these ecosystems. As revealed by the study, grazing, by both wild and domestic herbivores, can counteract to some extent the negative effects of high fire frequency on grass species composition and grazing acceptability. Results suggest that in landscapes, such as savanna-woodlands of South Asia, where livestock have replaced natural herbivores, grass species highly preferred by herbivores can recover only under management regimes with low fire frequency and some intermediate levels of livestock grazing, unless natural population of wild herbivores is restored. Hence, it is important to consider the complex interaction between fires–grazers–vegetation to develop effective management practices in these landscapes.

The presence of fire tolerant species throughout the landscape suggests the co-evolution of these systems with some level of intermittent fires. Furthermore, fire plays a major role in regulating surficial soil nutrient pool and preventing succession of these grasslands by woody vegetation. Hence, a complete suppression of fires is not desirable in these ecosystems; fires with longer return intervals (low fire frequencies) can increase surficial soil-fertility and grass cover. Nearly 45% of the landscape had experienced at least one fire between 2001 and 2009 and 84% of these fires had a longer return interval (fire frequency of 1 and 2), which could be representing the native settings. We, therefore, conclude that fire frequency should be managed at low to intermediate levels (one fire every 5–9 years) in order to sustain wild and domestic herbivores, biodiversity, and other key ecosystem processes, and services over the long-term.

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