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Livestock Herbivory Shapes Fire Regimes and Vegetation Structure Across the Global Tropics

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Abstract

Livestock grazing is the most extensive human land use and one of the key drivers of the conversion of tropical forests into grasslands. Livestock effects on vegetation structure are complex, as they can prevent tree recruitment and growth through browsing and trampling, but they can also affect vegetation indirectly through fire interactions. However, a systematic analysis of the overall effects of livestock across the global tropics is lacking. We analyzed remote sensing data on vegetation height and cover, climate, and fire as well as ground data on livestock density. We used generalized linear models and structural equation models to analyze the effects of livestock on fire regimes and vegetation structure. Across the global tropics, higher livestock densities are associated to lower fire frequency and a higher cover of shrubs and dwarf trees. This pattern occurs across continents, and is particularly pronounced at intermediate precipitation levels (1000–1500 mm y^{-1}) where fire frequency is highest. In those regions, fire frequency is on average 49% lower in areas with high versus low livestock densities. South America has much higher livestock density and lower fire frequency than Africa and Asia–Australia across the whole precipitation gradient. Our findings suggest that livestock grazing reduces fire incidence through grass consumption and favors shrubs and a sparse cover of trees in regions where forests could potentially exist. Livestock can thus be a strong modifier of the climatic effect on vegetation structure, and livestock management changes can impact the structure and functioning of savannas and grasslands throughout the global tropics.

Key words: Africa; Australia; savannas; shrub encroachment; South America; subtropical; tree cover; woody plants.

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Authors' Contributions RB conceived the original idea. All authors designed the methodology. RB and CX processed the data. All authors interpreted the results, RB and MH led the writing and all authors contributed to revising the manuscript.

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Highlights

- We analyze livestock effects on fire and vegetation patterns in the global tropics.
- Fire frequency is negatively correlated with livestock across the tropics.
- Livestock favors shrubs and low tree cover in areas which could support forests.

Introduction

Livestock grazes approximately one-third of the global land surface and about half of the world's savannas and grasslands. In the tropics, livestock ranching extends over 32 million km^2, twice the area covered by tropical moist forest (Asner and others 2004; Thornton and Herrero 2010). Despite this enormous extent, the effects of livestock management on vegetation structure have never been assessed globally. Livestock effects are hotly debated because regional- and site-level studies have described both increases and decreases in woody cover expansion with contrasting consequences for the long-term provision of ecosystem services. Grazing can promote woody encroachment (Scholes and Archer 1997; Roques and others 2001; Eldridge and others 2011) by shifting competitive interactions between herbaceous and woody plants in favor of the latter (Walter 1939; Knoop and Walker 1985; Belsky and Blumenthal 1997) or by reducing grasses that fuel fires (Bond 2008; Stevens and others 2017). On the other hand, livestock can limit woody expansion through direct browsing and trampling on tree seedlings and saplings (Huntly 1991; Prins and van der Jeugd 1993; Griscom and others 2005; Holmgren and others 2006; Chaturvedi and others 2012; Staver and Bond 2014; Bernardi and others 2016b; Etchebarne and Brazeiro 2016). Browsing can also affect tree growth by causing apical damage and activating lateral buds, which results in dwarf trees with a bushy architecture (Huntly 1991; Bond and Midgley 2001; Holmgren 2002; Archibald and Bond 2003).

The effects of grazing on fire dynamics may be particularly important for shaping the structure and functioning of tropical and subtropical terrestrial ecosystems. Fire may maintain open grasslands and savannas because trees are more susceptible than grasses to fire events. Grasses regrow fast after fire and thereby provide fuel for a subsequent fire. This creates a grass-fire positive feedback that maintains sparse tree cover. As a result of such a strong fire-filtering process, savanna ecosystems are dominated by fire-resistant woody species with traits well adapted to frequent fires (Archibald and others 2009; Hoffmann and others 2012). The grass-fire feedback has been proposed as the main mechanism explaining bimodal patterns in tropical tree cover (Hirota and others 2011; Staver and others 2011; van Nes and others 2018) and canopy height (Xu and others 2016; Xu and others 2018) in the 1000–2000 mm y^{-1} precipitation range. This implies that tropical forest and savanna can be alternative stable states separated by tipping points (Scheffer and others 2009; Hirota and others 2011). By consuming grass biomass, livestock grazing can mediate this fire feedback, thereby shaping vegetation structure in an indirect way. This effect, together with the limitation of tree recruitment and growth, could potentially lead to large-scale effects on vegetation distribution and structure.

Given the widespread presence of livestock and their potential effects on fire regimes and vegetation, here we assess the interactions between livestock density, fire occurrence, and vegetation structure across the global tropics.

Methods

Global Databases

Our study region is the global tropics and subtropics between 15°N and 35°S, a region selected for consistency with previous works (Hirota and others 2011; Staal and others 2016; Xu and others 2016; van Nes and others 2018) (Figure 1). We generated a 0.1° × 0.1° fishnet with approximately 500,000 grid cells covering the study region. For each grid cell, we collected estimates of livestock density, fire frequency, tree cover, shrub cover, mean annual precipitation, and precipitation seasonality. Livestock density was obtained from the FAO Gridded Livestock of the World modeled dataset at 1 km resolution (Robinson and others 2014) and expressed in 250-kg-equivalent animal units called Tropical Livestock Units (TLU) using a scale of 0.7 for cattle, 0.5 for buffaloes and 0.1 for goats and sheep (FAO 1999). To avoid pseudoreplication of nested environmental variables that are included in the FAO model, we averaged the model values for each administrative division following Bernardi and others (2016b). We differentiated between high and low livestock densities, defined as being above and below the pantropical average value of TLU (7 TLU km^{-2}). This value is equivalent to 1750 kg km^{-2} which is very similar to the value (1500 kg km^{-2}) around which fire frequency in Africa decreases rapidly (Archibald and Hempson 2016). We performed our analysis for different precipitation ranges.

Fire frequency was derived by calculating burned frequency (burns per year) from the standard MODIS burned area product MCD45 (Roy and others 2008) for the years 2002–2010. We considered the start of each year in April and the end in March the next year, coinciding with the annual global minimum fire activity during March–April (Giglio and others 2013), to generate annual composite burned area maps.

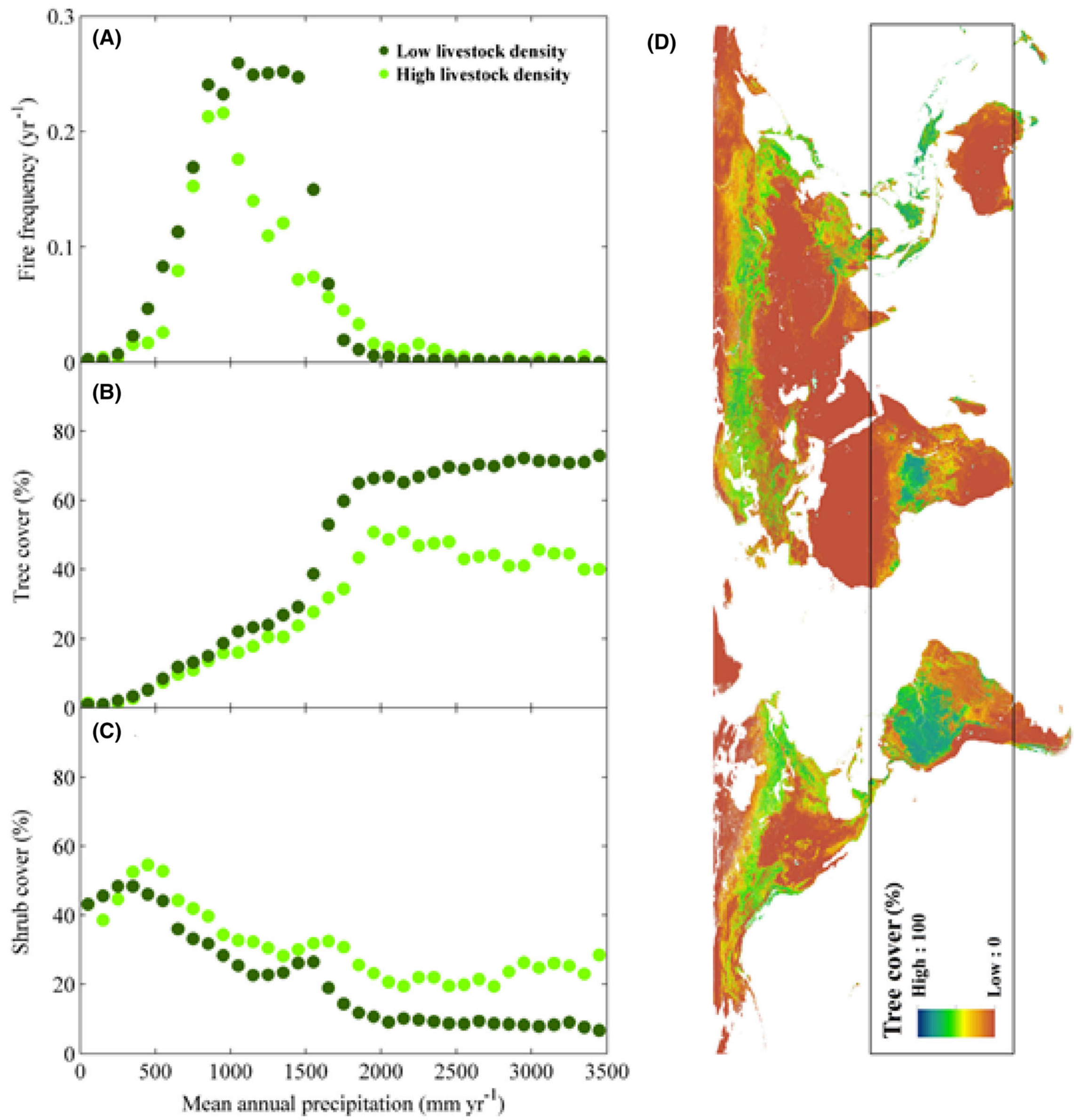

Figure 1. Differences in fire frequency, tree cover and shrub cover associated with tropical livestock density. **A** Mean fire frequency averaged in 100 mm mean annual precipitation bins for sites with above-average (TLU ≥ 7 units km^{-2}, light dots) versus below-average (TLU < 7 units km^{-2}, dark dots) livestock densities, **B** tree cover (%), **C** cover of shrubs and dwarf trees (%), **D** region of analysis.

Tree cover data were extracted from the MODIS Vegetation Continuous Field (VCF) Collection 5 dataset for the year 2009 (DiMiceli and others 2011). The MODIS VCF product estimates tree cover as the woody cover taller than 5 m. To estimate woody cover below this 5 m lower limit (including dwarf trees and shrubs, hereafter referred to as shrub cover for simplification), we used a remote sensing dataset (LiDAR) of global vegetation height (Los and others 2012). The 5 m threshold between trees and shrubs coincides with standard life forms definitions (Pérez-Harguindeguy and others 2016) and is supported by observed distributions of global vegetation height for trees and shrubs (Scheffer and others 2014; Xu and others 2016). The LiDAR dataset of vegetation height was assembled using measurements (''footprints'') collected by the Geoscience Laser Altimeter System (GLAS) on the Ice, Cloud and land Elevation Satellite (ICESat) during the years 2003–2009. It gives the vegetation height distribution between 0–70 m in 0.5 m intervals per 0.5° × 0.5°

grid cell. The shrub cover was calculated as the percent of LiDAR footprints falling in the 1–5 m range over the total footprints for each cell. We tested for the robustness of our estimates using a different canopy height range (0.5–1.5 m for the lower height) to define dwarf trees and shrubs, but this did not yield significantly different results.

Climate data were obtained from the Climate Research Unit (CRU) database at 0.5° resolution for the period 1951–2002 (Jones and Harris 2013), from which we derived mean annual precipitation (MAP) and precipitation seasonality. As measure of seasonality, we used Markham's Seasonality Index (MSI) (Markham 1970).

We excluded from all datasets the areas covered by croplands, water or bare ground, as defined as categories [11–30 and 190–230] in the 2009 European Space Agency (ESA) Globcover dataset at 300 m resolution. Analyses were performed using ArcGIS 10.0 and R 3.2.3.

Data Analyses

We used Generalized Linear Models (GLM) to correlate fire frequency (number of burns), tree cover and shrub cover (%) with explanatory variables. Explanatory variables were mean annual precipitation (MAP), Markham's Seasonality Index (MSI), fire frequency (F) and livestock density (LD). The analysis included the whole tropics and subtropics between 15°N and 35°S. We used a Poisson distribution for fire frequency and used ordinary least square models for the tree and shrub cover models. We applied an arcsine-square root transformation for tree cover, following Hirota and others (2011). Variables were scaled. We used a random subsample of 1% of the points and selected the best models with the bestglm function based on the Akaike Information Criterion (AIC). Spatial autocorrelation in the model residuals was assessed using Moran's I. We found weak spatial autocorrelation indicated by rather low Moran's I values (Table S1 in Supporting Information). We also detected weak multicollinearity among the explanatory variables (Pearson's $\rho < 0.45$ in all cases). The statistical analyses were performed in R 3.2.3 with the packages bestglm (McLeod and Xu 2011) and geoR (Ribeiro Jr and Diggle 2001).

To facilitate a comprehensive understanding on how the focal factors interact with each other, we developed a conceptual model based on the observed relationships between variables for the whole area of study area. We constructed a piecewise structural equation model (SEM) to test this network of relationships using the piecewiseSEM package (Lefcheck 2016) in R 3.2.3. Although there may be complex causal relationships among livestock, fire, and vegetation, the SEM allows us to propose a ''minimal model'' (van Nes and Scheffer 2005) and to statistically test for predicted relationships between the main variables. We performed bootstrapping with 1000 repetitions, using randomly selected 1000 points per run. The observed relationships based on bootstrapping are highly consistent with those based on all data points, indicating that our results are not biased by the repeated sampling of coarse-grained data.

Results

Across the tropics, high livestock density correlates with lower fire frequency ($p < 0.001$; Table S1). Fire frequency is highest at intermediate precipitation levels (Figure 1A). However, at which level it peaks depends on livestock density. At low livestock density, fire frequency remains high up to 1500 mm annual precipitation whereas at high livestock density, fire frequency declines sharply after 1000 mm y^{-1}. Within this 1000–1500 mm y^{-1} range, fire frequency is on average 49% lower at high livestock density. We also find differences in vegetation structure between sites with low and high livestock densities. High livestock density correlates with lower tree cover (Figure 1B; $p < 0.001$) and higher shrub cover (Figure 1C; $p < 0.001$), especially at precipitation levels above 1500 mm y^{-1}.

We synthesized these relationships among livestock density, fire frequency and vegetation structure into a conceptual model (Figure 2) and assessed them using structural equation models (SEMs). We found that livestock has significant negative effects on fire frequency and tree cover ($p < 0.001$), and an indirect positive effect on shrub cover through suppressing tree cover (Figure 3). Based on the patterns reflected in Figure 1, we also developed SEMs for three different subsets of mean annual precipitation (MAP): dry areas (MAP < 1000 mm y^{-1}), intermediate precipitation areas (1000 ≤ MAP < 1500 mm y^{-1}) and wet areas (MAP ≥ 1500 mm y^{-1}). We found that the negative effects of livestock on fire only become significant above 1000 mm y^{-1} precipitation (Figure S1).

South America has much higher livestock density and lower fire frequency than Africa and Asia–Australia across the whole precipitation gradient (Figure 4). Despite these differences in magnitude, we find that fire frequency peaks between 1000–

1500 mm y^{-1} of precipitation across all continents (Figure 4). This is also the precipitation range where the effect of livestock on fire is largest for all continents. As done for the global tropics, we developed SEMs for each continent at the same three levels of MAP (Figure S2). In Africa, livestock has a negative effect on fire across climates, whereas in Asia–Australia this is the case only at intermediate and high precipitation, and in South America only at intermediate precipitation (Figure S8). Curiously, the effect of livestock on fire turns weakly positive in the wet regions of South America.

Discussion

Our results suggest that livestock reduces fire frequency across the global tropics (Figures 1, 3; Table S1). This is in line with local and regional studies showing that grazing limits fire occurrence by either reducing the availability of grass fuel (Bond 2008), or by forming grazing lawns that act as barriers for fire spread (Leonard and others 2010; Hempson and others 2015b).

Sites with higher livestock densities have sparser tree cover (Figures 1B, S3) but a denser cover of low-statured woody plants (dwarf trees and shrubs) (Figures 1C, S4). This is likely the net result of conflicting effects of livestock on trees and shrubs. Livestock includes grazers and mixed feeders that differ in foraging behavior and preferences for herbaceous and woody plants (Shipley 1999). On the one hand, regenerating trees and shrubs may benefit from fire suppression in grazed lands,

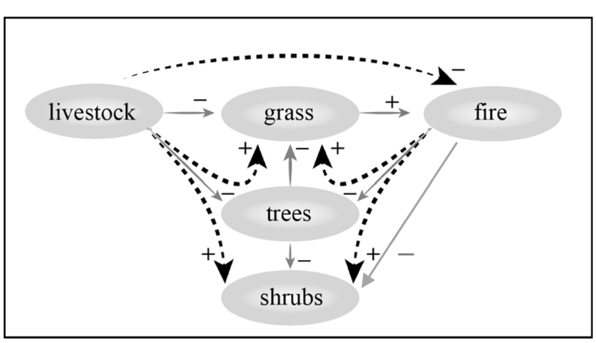

Figure 2. Conceptual model of the relationships between livestock, grass cover, fire frequency and tree and shrub cover. Positive effects are indicated by pluses and negative effects by minuses; dashed lines indicate indirect effects. Livestock grazing reduces grass cover and thereby fuel for fire, favoring woody expansion; however, livestock grazing also limits tree growth, favoring shrubs and dwarf trees which are highly susceptible to fire.

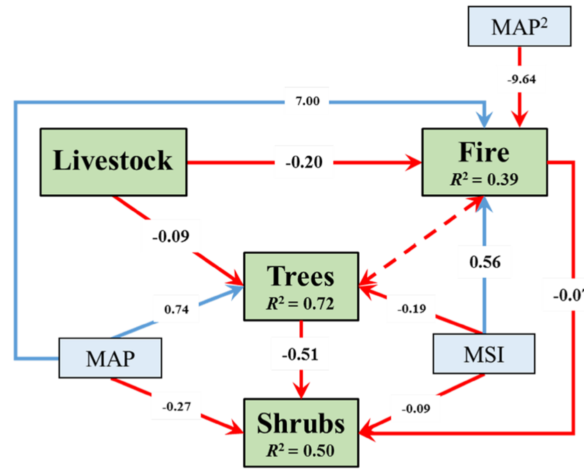

Figure 3. Piecewise structural equation model. Positive relations in blue arrows, negative in red. Dashed arrows indicate a strong mutual effect. All tested relationships have p values < 0.001. Numbers indicate coefficient estimates of relationships. The light-blue boxes indicate climatic variables (MAP, mean annual precipitation; MAP^2, quadratic term of MAP; MSI, Markham's Precipitation Seasonality Index), the green boxes represent ecosystem variables (Livestock, livestock density; Fire, fire frequency; Trees, tree cover; Shrubs, cover of shrubs and dwarf trees). R^2s for component models are shown in the boxes of response variables. The Fire model is fitted using generalized linear model with Poisson distribution, the Trees and Shrubs models are fitted using ordinary least square models (Color figure online).

especially when grazers control grass growth (Belsky and Blumenthal 1997; Scholes and Archer 1997; Roques and others 2001; Asner and others 2009; D'Odorico and others 2012). On the other hand, by browsing and trampling on young seedlings and saplings, livestock can also limit tree recruitment, resulting in a reduction in tree cover after a few decades of foraging. Also, browsing at early growth stages can favor multi-stemmed, shorter-sprouted trees which can contribute to the increased shrub cover detection in areas with high livestock density. Cultural views of livestock managers can also contribute to removing regenerating trees (Holmgren and Scheffer 2017) despite their potential positive effects on forage productivity (Bernardi and others 2016a). Therefore, trees need time and favorable growth conditions to escape from the control imposed by herbivory and people (Holmgren and others 2006; Bond 2008; Scheffer and others 2008; Hoffmann and others 2012).

The apparent effects of livestock on fire and vegetation structure have important implications for our interpretation of the biogeographic distri-

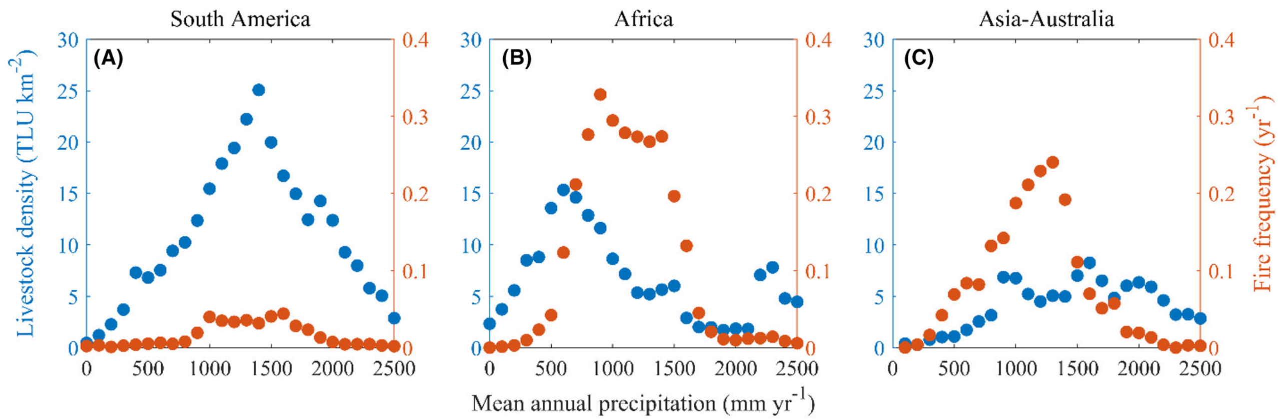

Figure 4. Livestock density (blue circles) and fire frequency (brown circles) as a function of precipitation for **A** South America, **B** Africa, and **C** Australia. Values averaged over 100 mm bins of mean annual precipitation (Color figure online).

butions of forests and savannas. Remote sensing studies suggest that savannas and forests can be alternative stable states (Hirota and others 2011; Xu and others 2016), maintained by a grass-fire feedback (Staver and others 2011; Hoffmann and others 2012; Murphy and Bowman 2012; van Nes and others 2018). Also, local- and regional-scale studies using empirical (Archibald and others 2005; Archibald and Hempson 2016; Dantas and others 2016) and modeling approaches (van Langevelde and others 2003; Suding and others 2004; Staal and others 2018) indicate that herbivory can replace fire as main disturbance generating alternative tree cover states. Our analysis shows that livestock can control tree recruitment despite the reduction in fire frequency. In these regions, livestock likely promotes sparse woody vegetation with a shrubby architecture that can persist in the absence of fire.

The reduction of fire frequency at higher livestock densities becomes significant across the tropics above 1000 mm of mean annual precipitation, as productivity increases. It is particularly significant at intermediate precipitation (1000–1500 mm y^{-1}) where tropical flammability is highest (Figure S1). Effects of livestock density on shrub cover become stronger with precipitation (Figures 1, S1), as the overall probability of closed canopies increases (Hirota and others 2011; Staal and others 2016).

Significant differences exist among continents in the structure and composition of vegetation. Separate evolutionary histories leading to different functional and architectural traits may explain some of these differences, and how they are shaped by the interplay of climate, soils and disturbances (Lehmann and others 2014). However, the precise mechanisms are still not fully understood. We propose that livestock distribution could partially account for differences in fire frequency and woody vegetation across the tropics. Our remote sensing analyses pave the road for building a holistic picture on the role of livestock in those complex ecological interactions. Only through detailed field observations and experiments will we be able to disentangle which mechanisms drive continental differences.

The openness of South American landscapes has puzzled naturalists and ecologists for centuries (Darwin 1890). These landscapes are found in regions with relatively high precipitation and low fire frequency conditions that generally favor tree establishment. Yet tree cover is low. Our results indicate that high livestock densities in South America play a fundamental role in maintaining these open landscapes. These results agree with findings for southeastern South America (Bernardi and others 2016b). Interestingly, we also find that high livestock density is associated with an increase in fire frequency in the wettest regions. This increase in fire frequency could be explained by grazing management practices in these areas with very high productivity, where grazing alone would be insufficient to maintain open landscapes. Here, rangers use fire as a tool to clear vegetation and prevent regrowth of closed forests (Uhl and Buschbacher 1985; Fearnside 1990; Mistry 1998).

Herbivory is known to reduce fire frequency in large regions of Africa (Archibald and Hempson 2016). At present, livestock is the dominant herbivore, and the distribution of livestock in Africa is similar to the natural herbivore distribution (Archibald and Hempson 2016; Hempson and others 2017). Unlike South America, where livestock densities are high across the precipitation spectrum, in wetter regions of Africa, fire is the main consumer of grass biomass and livestock densities are lower (Figure 4). This could be the case in regions with leached, poor-nutrient soils (Hempson and others 2015a). In those regions, recurring fires can maintain tall grasses with low palatability and therefore can impose a dietary constraint especially for mesoherbivores (Waldram and others 2008; Archibald and Hempson 2016). However, intense grazing by, for example, large herds of wildebeest, can overcome this limitation and reduce fire occurrence (McNaughton 1984). A relevant question is whether a potential expansion of livestock into wetter areas in Africa could lead to significant reductions in the occurrence of fire (Venter and others 2017) and to significant changes in ecosystem structure (Bucini and Hanan 2007; Hempson and others 2017; Venter and others 2017).

We observed no significant relationship between livestock and fire below 1000 mm y^{-1} for South America and Asia–Australia (Figure S2). This may be explained by lower herbivore densities in these dry regions or be related to the predominance of large widespread fires (Hantson and others 2017) regardless of livestock densities.

In conclusion, our results suggest that in tropical regions where wild large herbivores are no longer dominant, livestock management may shape the structure of savannas and grasslands by maintaining sparse tree cover, reducing fire frequency and favoring the expansion of shrubs and dwarf trees. Therefore, changes in current livestock management regimes can impact fire frequency and may result in structural vegetation changes and woody-cover transitions.

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Data accessibility Data used in this paper can be found in the following databases: Livestock: http://www.fao.org/ag/againfo/resources/en/glw/home.html. MODIS tree cover: http://glcf.umd.edu/data/vcf/. Lidar tree height: http://icesat.gsfc.nasa.gov/icesat/glas.php. MODIS fire data: http://modis-fire.umd.edu/pages/BurnedArea.php.

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