



## Research Paper

# Can cattle grazing substitute fire for maintaining appreciated pine savannas at the frontier of a montane forest biosphere-reserve?



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## ABSTRACT

Human induced savannas in subtropical regions are often favored by small-holder farmers for livestock production and extraction of wood or non-wood products. Frequent burning and grazing are required to maintain the savanna vegetation structure. However, in conservation areas, fire suppression is promoted to avoid wild-fires; whereas domestic livestock grazing is considered a strong interfering factor for tree establishment, due to trampling and browsing. In tropical forests which were converted to savannas, competitive exotic grasses have often replaced the native grasses. Where exotic grasses are present, aboveground biomass accumulation and thus man-induced fire risk are high and potentially undermine tree recruitment. On the long-term, the savanna state may shift into a grass-dominated state with little tree cover, generating unfavorable conditions from a livelihood perspective. We examined this problem in a human-induced pine savanna in the La Sepultura Biosphere Reserve in Chiapas, Mexico. Smallholder farmers highly valued this savanna for both livestock production and resin extraction from the fire resistant pine *Pinus oocarpa*. However, fire suppression and the presence of exotic grasses are reducing the tree recruitment. The main research question was to what degree can cattle grazing replace fire in its role of biomass removal and thereby stimulate pine recruitment and maintain the desired savanna state. We determined current savanna extension in the region and interviewed farmers to reconstruct past savannization processes and expansion of exotic grasses. We related adult species-specific tree density to the herbaceous-grass cover, and pine and oak seedling and sapling densities to understory vegetation cover, canopy closure, and cattle grazing history. Finally, a field experiment was conducted to examine the effects of livestock grazing on survival and growth of planted pine saplings. The savanna currently covers 20% of the study site; it is the result of past slash-and-burn agriculture and selective logging, which have favored the expansion of several exotic grass species. In savannas where exotic grasses are abundant, sapling density was lower compared to sites with a native grass cover. While livestock grazing seemed to increase pine seedling density likely as a consequence of reduced grass cover, pine sapling survival however, was significantly reduced by livestock trampling. By seeking a balance between the livestock's benefits and adverse effects on pine recruitment, farmers may develop an integrated management system adapted to their specific biotic rangeland conditions. It should allow forage production, while controlling the negative effects of exotic grasses on pine recruitment, thus maintaining a productive pine savanna system.

## 1. Introduction

Long-term anthropogenic pressure in form of selective logging, deforestation (Veldman et al., 2009), increased fire frequency (Cochrane et al., 1999; Veldman and Putz, 2011), and drier climate may transform closed tropical forests to savanna-type ecosystems (Silverio et al., 2013). In developing countries, farmers often favor these transformed

forests for livestock production (Coppock et al., 2017; Steinfeld et al., 2006). However, since this savanna type is a highly dynamic system, it may shift back to the forest state when livestock production is removed/abandoned (Aide et al., 1996) or it may transit into an open grassland when fire frequency is high (Scholes, 2003; Silverio et al., 2013).

In induced tropical savannas, the fire regime plays a major role in

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periodic burning may be an adequate management strategy. However, in savannas with high competitive exotic grasses, burning may favor further grass expansion and undermine pine seedling establishment (Fig. 1).

Extensive cattle raising is one of the main economic activities of small-holder farmers in tropical regions (Thornton, 2010), which often leads to deforestation and soil degradation (Lambin et al., 2001; Mertens, 2002). Furthermore, ungulate trampling may cause high seedling and sapling mortality and thus reduce tree cover and favor grass expansion (Murphy and Bowman, 2012; Van Langevelde et al., 2003; Wassie et al., 2009). This direct negative effect of large herbivores on woody vegetation is well understood. However, there are also positive indirect effects of herbivores that may favor the maintenance of trees in savanna ecosystems; e.g. a) grazing generates a negative feedback on fuel load, fire intensity and frequency, and consequently reduces tree mortality (Van Langevelde et al., 2003), b) herbivory reduces tree-grass competition thereby favoring tree recruitment and growth (Werner, 2005), and c) trampling by cattle may expose mineral soil, which some species require to germinate (Archer et al., 2017; Asbjornsen et al., 2004; Posada et al., 2000).

In tropical mountainous landscapes with protection status, livestock grazing often is not compatible with conservation strategies. However, where exotic grasses are very abundant and fire is suppressed, it may be a management tool to control the dense grass cover. Negative impacts of exotic grasses in protected areas are well studied in tropical regions, but there are only a few studies that have proposed solutions to mitigate these adverse effects at a landscape scale (Brooks et al., 2004).

We addressed the following research questions: (1) what were the main historic drivers that induced the savannization process, and facilitated the expansion of exotic grass species in the original natural oak-pine forest?, (2) what current grazing and fire regimes have maintained the pine savanna system as an important land cover type, and what are the present ecological conditions that characterize this savanna?, and (3) can managed grazing substitute the role of fire in pine regeneration by reducing the competitive exotic grass cover, while controlling the negative effect of trampling on pine sapling survival?

We tested the hypothesis that extensive controlled livestock grazing in La Sepultura Biosphere Reserve, Chiapas, Mexico favors tree regeneration, reduces fire risk, and thus maintains this rather unstable but socially desirable state of pine savanna system, where exotic grasses dominate. We combined empirical and observational approaches considering three spatio-temporal scales to elucidate i) potential direct and indirect effects of livestock trampling and grass removal simulating grazing on pine seedling behavior (at local plot scale within an 18 months experimental study), ii) mid-term effects of livestock presence and 15 year fire suppression on the density of trees and pine seedling/sapling recruitment at the pine savanna community scale in micro-catchments, and iii) the regional pine savanna distribution at the SBR landscape scale.

## 2. Study area and methods

### 2.1. Study area

The study was carried out in tropical oak-pine forests under ejido tenure (a mixed private/social form of land property) belonging to the rural towns of California and Tres Picos. They are located in the designated area for sustainable development (buffer zone) of La Sepultura Biosphere Reserve (SBR) in Chiapas, Mexico (16°16'40" – 16°12'40"N and 93°37'10" – 93°32'55"W; Fig. 2). Topography is highly irregular with steep slopes. Dominant soils are regosols and cambisols over granitic rock resulting from geological processes of the Paleocene. The tropical climate of the study area is seasonally dry. Annual mean temperature ranges between 25 and 28 °C. Average annual precipitation reaches 2003 ± 484 mm (30-year average); the main rain season lasts from May to October, while 5% of the total annual precipitation

fall between November and April. (CONAGUA, 2015). The pine savanna is located between 900 and 1100 m above sea level.

Both ejidos are close to the forest frontier of one of five core protected areas of the SBR, which consists of a highly biodiverse montane cloud forest ecosystem. In the nearby buffer zone, there are pine forests, oak-pine forests, gallery forests, human-induced savannas, and tropical deciduous and sub-deciduous forests (CONANP, 2013). Exotic grasses occur throughout the buffer zone, especially in human-induced pastures, savannas, open forest stands and on roadsides. In the pine savanna, the most abundant native grass species are *Trachypogon plumosus* (Humb. & Bonpl. ex Willd.) Nees ('Llano grass') and *Muhlenbergia* spp. The most abundant exotic grass species are *Melinis minutiflora* P.Beauv. ("Gordura grass") and *Hyparrhenia rufa* D.A. Reid ("Jaragua grass"), which were all introduced to Mexico in the late 19th century for livestock production (Parsons, 1972). Low-frequency wildfires are natural disturbances of these forest ecosystem types. After humans had permanently colonized the area, the frequency of human-induced fires increased due to slash-and-burn agriculture and native grass burning. The presence of *P. oocarpa*, one of the most abundant pine species in seasonally dry forests of Central America, is directly related to natural and human-induced wildfires (Dvorak et al., 2009; Myers and Rodríguez-Trejo, 2009; Rodríguez-Trejo and Fulé, 2003). Thick bark and tall trunks without lower branches protect cones from catching fire (Keeley, 2012). Fire stimulates cone production and high temperatures produced by understory fire open the serotinous cones; besides fire eliminates pine leaf litter and competing flora and favors successful seedling establishment on bare soil (Keeley, 2012; Rodríguez-Trejo and Fulé, 2003).

Both ejidos were established during the 1970s by landless people (Cruz-Morales, 2014). Initially, farmers applied traditional rotational slash-and-burn practices to produce maize and beans for self-sufficiency and sale. Since the settlement, cattle raising has formed part of small-holder livelihoods (Cruz-Morales, 2014), but livestock became even more important in the late 90s, when maize prices plummeted as a result of NAFTA and the Mexican government began to subsidize cattle ranching (García-Barríos et al., 2009; García-Barríos and González-Espinosa, 2017). In 1995, the federal government designated the area as SBR and established a management plan for the reserve. Currently, the people of the study area grow maize and beans for self-supply. For monetary income, they raise livestock, grow organic coffee, and extract resin from *P. oocarpa*.

### 2.2. Methods

The research was carried out between 2014 and 2016; it included observational and experimental studies considering distinct spatial and temporal scales (Table 1). Local small-holder farmers participated throughout the research project; they helped to select the experimental sites on their rangelands considering some pre-defined criteria such as exposition, tree-cover type, and to identify representative micro-catchments within their ejido borders considering similar grazing and fire history and understory vegetation development.

#### 2.2.1. Actual spatial extent of pine savanna

To calculate pine savanna surface area in the SBR, we generated a thematic land use map with an unsupervised remote sensing technique applying GRASS GIS 6.4.3/QGIS 2.0 (GRASS Development Team, 2014; Neteler and Mitasova, 2008; QGIS Development Team, 2014). We used a SPOT 5 multispectral image (4 bands) from February 2012 with a spatial resolution of 10 m per pixel. The ten initial spectral classes were grouped into five land use types: deforested land (roads, houses, grassland, and cropland), pine savanna, oak-pine forest, montane cloud forest, and gallery forest. Finally, total cover of each vegetation class was calculated.

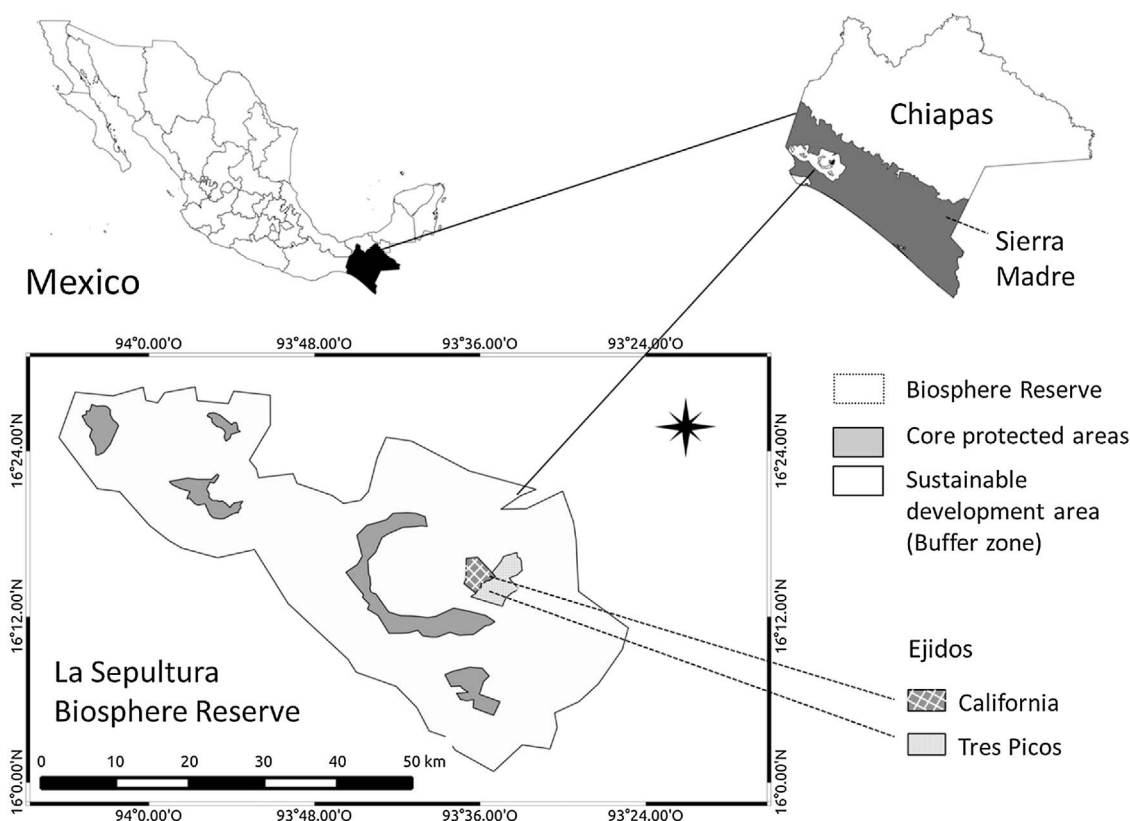


Fig. 2. Location of two rural ejidos where this study was carried out, California and Tres Picos, in La Sepultura Biosphere Reserve in the Sierra Madre mountain range of Chiapas, Mexico.

### 2.2.2. Land use history and drivers of savannization

With the snowball sampling method (Goodman, 1961), fifty-two farmers were individually interviewed to reconstruct the land use history of the pine savanna, and to learn about local knowledge of forest management practices, especially concerning cattle raising and resin production. The age of interviewed farmers ranged from 19 to 78 years; interviews focused on resin project members. The sample included 75% of all resin tapping producers, considering the total of producers of resin in 2016. We conducted a structured questionnaire composed of open- and closed-ended questions. During 40 to 60 min, farmers told us, how their forest stands and land use practices changed from early settlement to present. For later discussions and better understanding, farmers had access to photographs, maps, and drawings.

### 2.2.3. Savanna tree species composition and diameter at breast height class distribution

Based on maps, field surveys, and the help of local peasants (to clarify land use history of sites), the inventories were conducted in two micro-catchments with similar aspect – facing slopes and altitudinal range (1000–1100 m), representative for pine savannas in the two localities at the transition of oak-pine forests and pastures (Supplementary Fig. S1). To determine tree species composition, tree density, diameter at breast height (DBH) distribution and the presence of exotic grass species, we carried out inventories in 18 circular (9 in each micro-catchment) 1000 m<sup>2</sup> plots. The minimum distance between these plots was 100 m. The method used was based on the national Mexican forest inventory protocol (Olvera-Vargas et al., 1996). Within each plot, diameters of all trees from different species with a DBH > 5 cm were measured and the number of individuals counted. In the center of each plot, canopy cover was estimated using hemispherical photographs (Frazer et al., 1999), and the percentage of bare soil, leaf litter and vegetation cover of native and exotic grasses were determined with the Braun-Blanquet method (Newton, 2007).

### 2.2.4. Influence of grass type and grazing on sapling density

To determine the advanced regeneration (saplings) in the pine savanna, we established six 1-km long, 2 m wide transects with a southward orientation with three parallel transects (500 m apart from each other) in each ejido (Supplementary Fig. S1). Site selection was based on a geographic survey done with a geographic information system (vegetation cover, aspect, elevation, and slope) and farmer participation. Each sapling (max. 1 m height) was counted, and every 10 m we recorded the composition of tree canopy and grass species, measured grass height (cm), and estimated tree canopy closure and soil cover (litter, bare soil). Data were collected by the end of the dry season of 2015. With the help of land owners, we recorded current and past (ten years) grazing regimes. In all studied pine savannas, no fire had occurred for at least 12–15 years.

### 2.2.5. Influence of vegetation cover on seedling density

In the pine savannas, we established five parallel 25 m long, 1 m wide transects in southward orientation with distinct understory types: i) savanna dominated by native grasses, ii) savanna dominated by exotic grasses, and iii) savanna with recently burned understory. Along each transect, we recorded the number of pine seedlings (individuals up to 0.3 m tall). For each site, vegetation cover was estimated using the Braun-Blanquet method (Newton, 2007). Data were collected during the rainy season of 2015 to include new seedlings. The sites were selected with the help of local farmers and then randomly placed (Supplementary Fig. S1).

### 2.2.6. Direct and indirect effects of livestock on pine sapling growth and survival in exotic and native grass plots

To assess the effects of trampling, browsing, and aboveground biomass from native and exotic grass species on *P. oocarpa* pine sapling survival and growth, we designed a field experiment in the pine savannas with different understory vegetation, where we planted pine saplings from a nursery. The experimental plots were evenly distributed

**Table 1**  
Study design of fieldwork at different spatial scales, including methods and data analysis. Native grass species refer to *Trachypogon plumosus*, and exotic grass species to *Melinis minutiflora* and *Hyparrhenia rufa*. Please refer to questions in the main text.

Refer to Question (QN)	QN 1	QN 2	QN 2 and 3	QN 2	QN 3
Objective	Land use history and drivers of savannization	Actual spatial extent of pine savanna	Influence of grass type and grazing on sapling density	Influence of vegetation cover on seedling density	Direct and indirect effects of livestock on pine sapling growth and survival in exotic and native grass plots
Scale/Sites	Household, both ejidos	Landscape, both ejidos	Savanna on south-facing slopes, in both ejidos	Pine savanna with a) native grasses, b) exotic grasses, and in c) recently burned sites	Experimental plot scale, pine savanna dominated by one native grass and two exotic grasses, in both ejidos
Method/ Variables	Interviews 52 structured individual interviews composed of open- and closed-ended questions. Land use history, local knowledge in forest management and cattle raising	Remote sensing Thematic land use map produced from remote sensing unsupervised classification. Surface area of five land use classes, slope, aspect and elevation	Sapling census Sapling (max 1 m tall) counts along six 1000 m × 2 m transects. Sapling density and sapling height; grass species and height; percentage of vegetation in the understory, and canopy cover	Seedling census Vegetation in the understory (Braun-Blanquet method) and seedling counts along five 25 m × 1 m transects. Seedling density and percentage of bare soil in relation to vegetation cover	Grazing/pine sapling experiment Plots (9 m × 3 m) with a) grazing, b) fenced cutting and c) fenced control treatments in subplots (3 × 3 m). Pine sapling survival and growth rate; grass growth rate and final biomass; soil temperature and humidity; stocking rate and grazing period
Data analysis	Interviews were categorized based on themes and, analyzed using frequencies	Error matrix, Kappa statistics	Generalized linear model and redundancy analysis for graphical interpretation	Generalized linear model	Cox hazard model for plant survival, mixed effect and linear models for plant and grass growth

across both ejidos, using the rangelands of six landowners on south facing slopes. We established thirty 9 m × 3 m experimental plots, each with three biomass removal treatments applied to 3 × 3 m subplots (the experimental units): grazing, manual grass cutting and cattle exclusion as a control without any biomass removal (Supplementary Figs. S1 to S2). Each biomass removal treatment was applied within one of three grass cover plot types: a) native *T. plumosus*, b) exotic *H. rufa*, and c) exotic *M. minutiflora*. Each treatment combination (biomass removal by grass type) was replicated five times in each ejido (N = 90 experimental units in total). To account for potential variabilities in precipitation, soil condition, and microclimate, the factor ejido was treated as block effect (i.e. random effect). In July 2016, we planted in each of the 90 subplots 24 18-months-old pine saplings ( $33 \pm 11$  cm height) at a distance of 0.5 m between individuals; these 2160 saplings were immediately planted after they had been received from the nursery. Over the course of 18 months, sapling survival and grass height were measured monthly in all 90 experimental units.

During the active growing seasons of 2015 and 2016, aboveground grass biomass was clipped monthly to a height of 10 cm in the fenced cut plots to simulate livestock grazing without trampling. Prior to the harvest of each cut subplot, we collected aboveground grass biomass in 0.5 m × 0.5 m areas to estimate monthly grass biomass accumulation between July and November 2015. To estimate grass biomass accumulation in cut plots during the dry season (December and May), one single biomass sample was harvested in a 0.5 by 0.5 m area in each cut plot at the end of the dry season in May 2016. To determine total biomass accumulation in the fenced control plots during the rainy season, subsamples were harvested in 0.5 m by 0.5 m areas near the edge (to not influence pine sapling growth) of plots at the end of November 2015. All biomass samples were oven dried to constant weight at 65 °C and weighed in the laboratory of El Colegio de la Frontera Sur (ECOSUR). We compared total harvested biomass of the control plots with the total harvested biomass of cut plots considering the rainy season 2015. Finally, accumulated biomass of cut plots from the rainy season of 2015 was compared to the biomass of the dry season of 2016. In the case of the grazed plots, livestock stocking rate and grazing period were recorded with the help of the farmers during 18 months and related to monthly sapling survival for each of the grazed plots.

In 36 of the 90 experimental units, soil moisture was determined monthly in the top 20 cm with the gravimetric method. Soil temperature was recorded in 1h-intervals using Hobo soil temperature sensors inserted at 20 cm depth in four plots of each of the biomass removal by grass type treatment combination. With the help of local farmers, we installed a rainfall gauge in both ejidos to record each precipitation event for 18 months. At the beginning and end of the 18 months-study, basal stem diameter and height of each transplanted pine sapling were measured. The increase in plant stem volume was estimated with an allometric equation (Picard et al., 2012). At the end of the active growing seasons in 2016, a random subsample of 27 (3 replicates × 3 biomass removal treatments × 3 grass species types) saplings was excavated and separated in roots, stem, and needles; they were oven dried at 65 °C, and the increase in biomass was determined by comparing average initial biomass of 60 pine saplings of the nursery (dried and measured at the beginning of the study) with the final biomass of each sapling component. The percentage of pine canopy openness above each experimental plot was determined with hemispherical photographs (Frazer et al., 1999). Soil depth was determined with a soil drill in 30 experimental plots. For soil chemical analysis, we excavated individual soil samples (20 cm depth × 7 cm diameter) in 30 plots with the soil coring method (Robertson, 1999). The samples were analyzed in the soil laboratory of ECOSUR to determine total N, K, and P contents, as well as pH, soil organic matter (SOM) content, soil bulk density and soil texture with standard methods described in Robertson (1999).

### 2.3. Data analysis

Our land use map was tested for accuracy and validated through fieldwork and GPS data. One hundred and thirteen GPS points were analyzed using an error matrix to detect errors of commission and omission of each land cover class and proofed for significance with Kappa statistic, similar to the Chi-square test of a contingency table (Congalton and Green, 2009) using GRASS GIS 6.4.3 (GRASS Development Team, 2014).

The responses to the interview questions were organized by themes (e.g. land use history, resin production, forest, and rangeland management) and then analyzed using frequencies.

To characterize the pine savanna tree structure, the importance value index (IVI) was calculated for each species, considering the average of relative density, relative frequency and relative dominance (Newton, 2007) (for equations and calculations of these values see Supplementary Table S1). The distribution of DBH categories was analyzed considering all inventory plots with: a) exotic grass cover less than 30% (low cover), and b) exotic grass cover higher than 30% (high cover). Prior to statistical analysis, DBH was log transformed, and DBH distribution was compared between the high and low cover group using a multiple linear regression model in which factors such as canopy closure, elevation, exposure, and slope were considered as explanatory variables.

For tree sapling density along the six 1 km long transects, we analyzed data separately for pine and oak saplings with univariate statistics. For each species, we applied a generalized linear model as recommended for count data (Crawley, 2013). We used sapling density as a response variable, which was correlated with the explanatory variables grass species cover, soil cover (bare soil and litter), canopy cover, and grazing (past and present livestock presence in the rangeland). To simplify the model and to fit the explanatory variables to the model a stepwise multiple regression technique was applied (Crawley, 2013). To visualize and interpret these data, multivariate descriptive statistics was used. Hence, all variables were numerically categorized and square root transformed, and separated into a matrix of response variables (pine and oak saplings) and a matrix of explanatory variables. Then we used redundancy analysis (RDA) to show positive and negative correlations among response and explanatory variables.

To analyze the spatial distribution of exotic grasses at the landscape scale, in a separate RDA, landscape characteristics such as aspect, slope, and elevation (determined using GIS) as explanatory variables were correlated with exotic and native grass cover as response variables. The data were categorized, square root transformed and separated in a matrix of response and a matrix of explanatory variables. For both analyses, a permutation test was applied to evaluate the significance of the constraint axes of the RDA (Legendre et al., 2011).

With a generalized linear model for count data (Crawley, 2013), we correlated the density of pine seedlings with the percentage of bare soil as the explanatory variable for three vegetation cover types: i) savanna with native grasses, ii) savanna with exotic grasses, and iii) recently burned savanna.

To examine the survival rate of transplanted pine saplings in monthly intervals, a time step model of the nonparametric Cox proportional hazards model was applied (Crawley, 2013). The model's significance and H-ratios were calculated for the biomass removal treatment (grazed, fenced cut, fenced control), grass species type (*T. plumosus*, *H. rufa*, and *M. minutiflora*) and livestock presence (yes, no). The H-ratio is defined as the instantaneous risk of death over time (Fox, 2002). H-ratio > 1 implies higher risk; H-ratio < 1 lower risk; while a value close to 1 implies no difference among treatment levels of a factor.

The effect of biomass removal treatment on grass height of each grass species and the difference in biomass accumulation between cut and control plots of each grass species were analyzed with linear models. To reach linearity, normality of residuals, and homogeneity of

variance, grass height and biomass increment were square root transformed (Crawley, 2013). The growth rate of pine saplings was analyzed with a mixed model with biomass removal treatment and grass species type as fixed effects and experimental plots nested within the two ejidos were random effects. To reach normality of the residuals, pine sapling height and volume increment were square root transformed (Crawley, 2013). All data were analyzed using R software, 3.13 version (R Core Team, 2015).

### 3. Results

#### 3.1. Current spatial extent of pine savanna

California and Tres Picos have a total surface area of 1110 ha and 2222 ha, respectively, with open pine savanna covering 26% of the total land area in California, and 16% in Tres Picos. In California, 53% of the total land area is closed forest, and 21% have been deforested for pasture, crops, and housing. In Tres Picos, closed forest makes up 71% of the total land area, and deforested areas only account for 13% (Supplementary Fig. S3). The kappa statistic for the map as a whole is 0.71 suggesting a high level of accuracy.

#### 3.2. Land use history and drivers of savannization

When peasants formed the ejidos Tres Picos and California in the 1970s, they deforested dense valley-bottom oak stands for agriculture, as these were the most fertile areas. To prepare these areas for cultivation and maintain them in a treeless state, they applied loosely controlled annual burnings. In steeper areas, farmers extracted pine trees for timber to build their houses and furniture and oak trees for fuel wood use. In both ejidos, agricultural burnings frequently triggered forest fires and led to high mortality of both saplings and adult trees. Deforestation, selective logging, cattle ranching and annual forest fires favored the invasion of exotic grasses in the understory. Both exotic grass species, *H. rufa* and *M. minutiflora* had been present in open sites before farmers arrived, as they had been introduced by previous large landowners. In the late 90s, when livestock grazing increased, farmers intentionally seeded these forage grasses, and seed dispersal was favored by cows together leading to a rapid expansion of these exotic grasses. Farmers prefer these exotic grass species over the native grass *T. plumosus*, because the former are more drought resistant and produce more aboveground biomass. After annual burnings were suspended in 1998, an increase in tree sapling density was observed by farmers in forest understories covered by the native grass *T. plumosus*. A nearly 20-year fire-free phase after the last burnings (the last fire induced pine cone opening, seed germination, and seedling establishment) favored pine sapling survival. However, in forests with dense exotic grass covers in the understory, no pine seedlings recruited. Since the implementation of the resin project in 2012, farmers have avoided fire and actively protected existing pine and oak saplings (Fig. 3).

Interviewed small-holder farmers considered the sale of resin has been contributing significantly to their livelihoods ever since 2012. Thus, they were highly interested in restoring treeless areas with pine plants to secure future resin extraction. As the main limitation for natural forest regeneration, farmers identified low seed tree density followed by accumulation of pine-needle litter, the presence of exotic grasses, and insufficient livestock grazing to maintain an open understory (Supplementary Fig. S4a). They also pointed out that risk of fire is very high when grazing is absent. Although local peasants recognized browsing and trampling to have an adverse effect on tree establishment, they considered regulated grazing a potential mechanism to reduce the risk of fire and to improve soil surface conditions for the natural regeneration of resin-producing pines (Supplementary Fig. S4b).

#### 3.3. Savanna tree species composition and DBH class distribution

Seven tree species were recorded in the pine savannas. The importance value index for all inventory plots changed in the following declining order: *Pinus oocarpa*, *Quercus acutifolia*, *Q. sapotifolia*, *Q. pedunculata*, *Agarista mexicana*, *Q. segoviensis*, and *Byrsonima crassifolia*. The importance value index did not differ in forest stands dominated by exotic and native grass species (Supplementary Table S1). However, DBH class distribution was significantly different considering pine savannas with exotic and native grass understory ( $P < 0.001$ ). In savannas dominated by exotic grasses, all tree DBH diameter classes were equally abundant, while in savannas with native grasses lower diameter classes were more frequent than higher diameter classes (Fig. 4a, b). Canopy openness and elevation did not differently affect exotic and native grass abundance in the respective savannas ( $P > 0.4$ ).

#### 3.4. Influence of grass type and grazing on sapling density

A total of 98 pine saplings and 104 oak saplings were recorded along six 1-km transects in the pine savanna. A positive relationship was observed between grazing and presence of pine saplings (GLM regression coefficient  $R^2 = 0.23 \pm 0.07$ ;  $P < 0.001$ ), and between the presence of pine sapling and presence of the native grass *T. plumosus* ( $R^2 = 0.22 \pm 0.09$ ;  $P = 0.01$ ). A negative relationship between pine sapling number and the exotic *M. minutiflora* grass was found ( $R^2 = -0.27 \pm 0.08$ ;  $P = 0.001$ ). Oak sapling number increased under a more closed canopy cover ( $R^2 = 0.51 \pm 0.07$ ;  $P < 0.001$ ) and in the presence of livestock grazing ( $R^2 = 0.40 \pm 0.07$ ,  $P < 0.001$ ) (Fig. 4c). At the landscape scale, exotic grasses were most abundant in pine savannas covering 65% of the total area, while native grasses covered only 35% (Fig. 4d). Native grass cover was positively correlated with elevation and tree canopy cover, while exotic *H. rufa* was more abundant in valley bottoms and under relatively open tree canopies; in contrast, *M. minutiflora* was more abundant on steep slopes (Supplementary Fig. S5).

#### 3.5. Influence of vegetation cover on seedling density

Pine seedling density was highest in the recently burned site, where 50% of all seedlings were recorded ( $N = 56$ ); 30% and 14% of seedlings occurred in sites with native and exotic grasses, respectively ( $P = 0.033$ ). Seedling presence was positively correlated with the percentage of bare soil ( $P = 0.036$ ) (Supplementary Fig. S6a). The percentage of bare soil in the burned area was 56%, in savannas with native grasses 33%, and in savannas with exotic grasses 16% (Supplementary Fig. S6b).

#### 3.6. Direct and indirect effects of livestock on pine sapling growth and survival in exotic and native grass plots

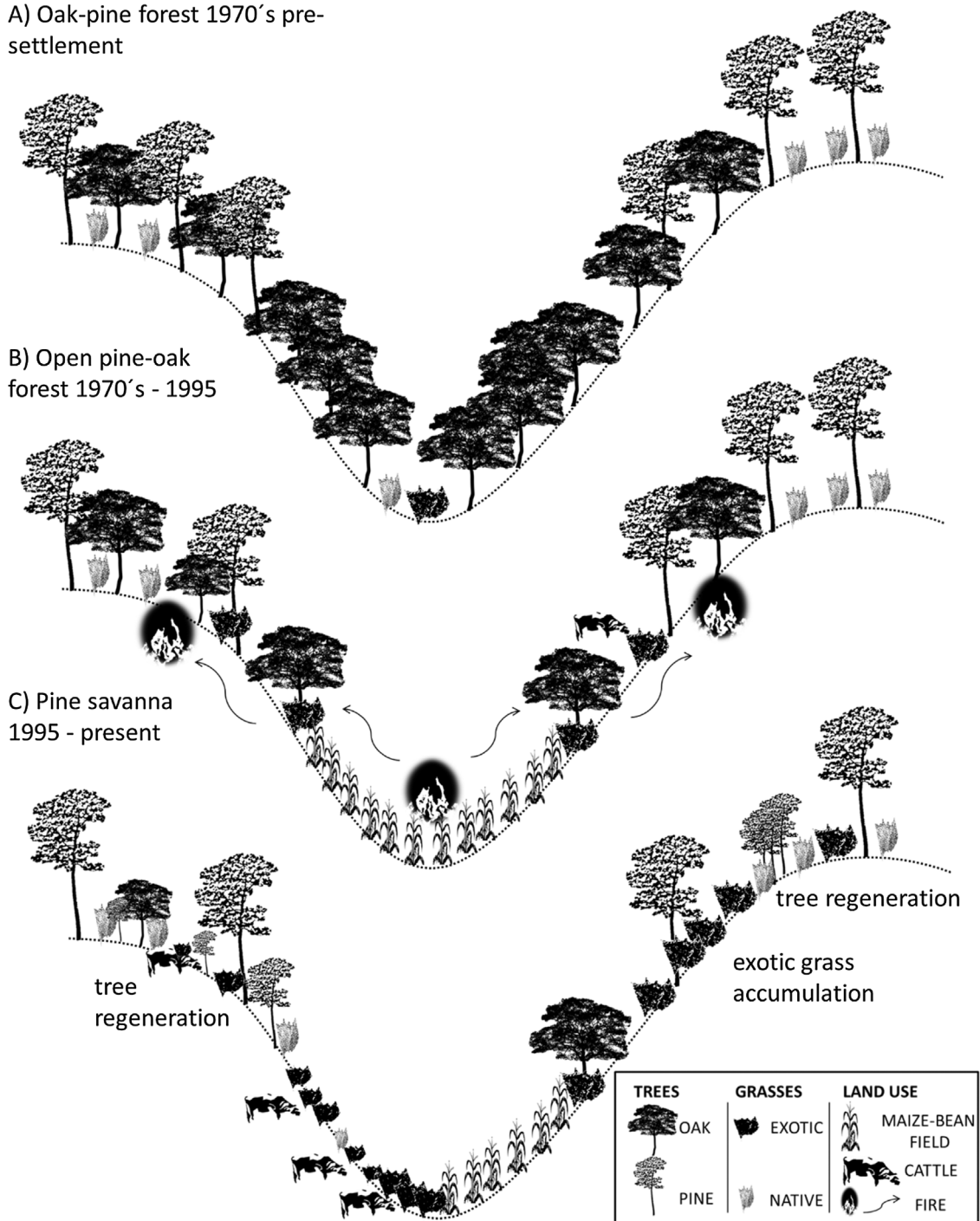
##### 3.6.1. Soil conditions, soil temperature and soil humidity in the experimental plots

Average soil depth of experimental plots was  $37 \pm 6$  cm, with an A horizon of 4 cm depth. Soil physical and chemical properties were characterized by relatively low content of SOM ( $3.1 \pm 0.16\%$ ), total N ( $0.16 \pm 0.008\%$ ), potassium ( $89 \pm 4.62$  mg kg<sup>-1</sup>) and phosphorus ( $7.8 \pm 0.75$  mg kg<sup>-1</sup>), a pH value of  $5.18 \pm 0.06$ , and soil bulk density of  $1.1 \pm 0.02$  g cm<sup>-3</sup>. No significant differences in these soil properties were detected among savannas with different grass species ( $P > 0.1$ ). Soil temperature was significantly higher in native than exotic grass plots, and it was significantly lower in control plots without biomass removal than in grazed and cut plots ( $P < 0.001$ ). Soil humidity did not differ significantly among the three biomass removal treatments ( $P = 0.07$ ). However, soil humidity was overall higher in plots with *H. rufa* ( $P < 0.001$ ) than in those with *M. minutiflora* and *T. plumosus* (Supplementary Fig. S7).

A) Oak-pine forest 1970's pre-settlement

B) Open pine-oak forest 1970's - 1995

C) Pine savanna 1995 - present



**Fig. 3.** Land use history of the two ejidos: A) at time of pre-settlement, when farmers arrived, an oak-pine forest dominated by native grasses in the understory; B) savannization process: after the colonization by small-holder farmers massive deforestation by slash-and-burn agriculture in dense oak stands in valley-bottom and selective logging in the steeper parts. Uncontrolled forest fires were common during this phase and favored the expansion of exotic grass species into the open oak-pine forest; C) establishment of the La Sepultura Biosphere Reserve, Chiapas, Mexico: increase in livestock production, maize and bean production only for self-supply, oak extraction for fuel wood and fence posts. Fire suppression management, and since 2012, resin extraction project using *Pinus oocarpa*.

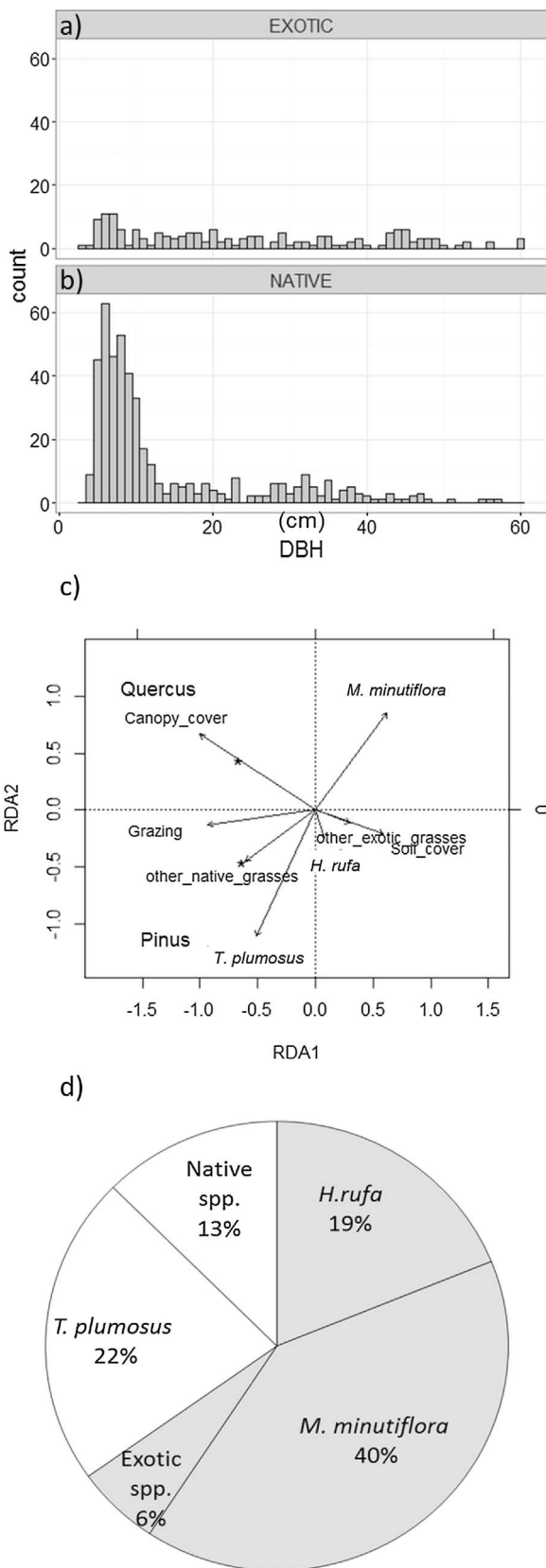
3.6.2. Grass growth and aboveground biomass production

After the first year of our study (July 2015 to June 2016), grass height was significantly greater ( $P < 0.001$ ) in control plots than in grazed plots for all grass species, while between grazed plots and cut plots no differences were detected ( $P > 0.5$ ). Grass height of the native *T. plumosus* was significantly lower ( $P < 0.001$ ) than that of the exotic *M. minutiflora* and *H. rufa* in control plots (Fig. 5a) (grass species x grass removal interaction;  $P = 0.006$ ).

Total aboveground grass biomass production differed significantly

between the two exotic grass species and the native grass species ( $P < 0.001$ ) (Fig. 5b). During the rainy season of 2015, in the cut plots total accumulated biomass was higher for the exotic grass *H. rufa* than for *T. plumosus*. No differences were found between *H. rufa* and *M. minutiflora*, and between *T. plumosus* and *M. minutiflora*. For all three grass species, the increase in biomass in control plots was twice as high as that of the cut plots ( $P < 0.001$ ). During the dry season, the increase in biomass was significantly lower than during the rainy season in the cut and control plots for all grasses ( $P < 0.001$ ; Fig. 5b). There was a





**Fig. 4.** a) Number of adult pine trees in different distribution classes of tree diameter at breast height (DBH; cm) for exotic grass dominated savannas with 49% covered by exotic grasses, and b) native grass dominated savannas with 10% covered by exotic grasses. Average tree canopy openness was 55% for both groups. c) Redundancy analysis for tree sapling density from six 1000 m × 2 m long transects, as well as relationship among frequency of pine (N = 98) and oak (N = 104) saplings, with grass species, grazing presence, soil vegetation cover, and canopy cover; permutation test global  $P < 0.001$ ; the proportion of inertia for the constrained and unconstrained axes was 0.08 and 0.92, respectively; d) percentage of recorded grass species along the six transects.

significant interaction between grass species and biomass removal for the variable increase in biomass ( $P = 0.0065$ ).

**3.6.3. Survival of pine saplings in response to biomass removal treatments and grass species**

At the end of the 18-months study, total pine sapling survival was 41%. It differed significantly between the grazed subplots (31%) and the cattle exclusion subplots (46% for cut and 47% for control) ( $P < 0.001$ ). Corresponding H-ratios for grazed subplots were  $H = 1.57$  and for cut subplots  $H = 1.05$ , compared with the fenced control subplots (Fig. 5c). Mortality was significantly higher in grazed subplots ( $P < 0.001$ ) compared to exclusion subplots. Pine sapling survival rate during 18-months was significantly lower in plots of native grasses ( $H = 1.59$ ;  $P < 0.001$ ) than in plots with the two exotic grass species (Fig. 5d). A significant interaction between grass removal and grass species type was observed for the variable sapling survival ( $P = 0.003$ ; Supplementary Fig. S8a, b, c). Grazing had a stronger effect on the native grass *T. plumosus* than on the exotic grass *H. rufa* ( $P < 0.001$ ), while no significant differences were observed between *H. rufa* and *M. minutiflora*, and between *T. plumosus* and *M. minutiflora*. Comparing sapling survival between grazed and cut plots considering grass species, clear differences were shown for *T. plumosus* ( $P < 0.001$ ) and *M. minutiflora* ( $P < 0.001$ ). No significant differences between the cut and control treatments for all three species of grass were observed (Supplementary Fig. S8d).

Monthly variations in soil temperature and soil humidity did not influence pine sapling survival ( $P > 0.1$ ). However, sapling mortality was significantly lower during the rainy season of 2015 (432 deaths) than during the following dry season of 2016 (708 deaths) ( $P < 0.001$ ). In the rainy season of 2016, only 125 saplings died. Precipitation during the 2015 rainy season was 650 mm, during the dry season 2016, 161 mm, and for the rainy season 2016, 934 mm.

Monthly stocking rate and rotation frequency varied with each farmer. However, total cattle density per hectare in the rangeland plots was quite similar in the 2015 and 2016 rainy seasons, while in the 2016 dry season it was lower (Supplementary Fig. S8e).

**3.6.4. Growth of pine saplings in experimental plots**

The increase in pine sapling stem volume differed significantly among the grass removal treatments ( $P = 0.03$ ), while grass species type did not have any influence ( $P = 0.8$ ) (Fig. 5e). The increase in height of pine saplings was significantly lower in cut ( $P = 0.001$ ) and grazed plots ( $P < 0.001$ ), when compared to control plots, while sapling height was not significantly different among grass species ( $P < 0.7$ ) (Fig. 5f). There was no significant biomass removal by grass species interaction for stem volume ( $P = 0.35$ ) and pine height increment ( $P > 0.10$ ).

Total average biomass increment of 27 harvested pine saplings compared with initial sapling biomass was 19.9 g (48% needles, 35% stem, and 18% root). Total and specific biomass increase did not differ among biomass removal treatments ( $P = 0.45$ ); however, pine root biomass was significantly higher in *H. rufa* grass plots compared to *M. minutiflora* plots ( $P = 0.04$ ) and *T. plumosus* plots ( $P = 0.02$ ; Supplementary Fig. S9). There was no significant biomass removal by grass species interaction for the variable total pine biomass increase ( $P = 0.3$ ).

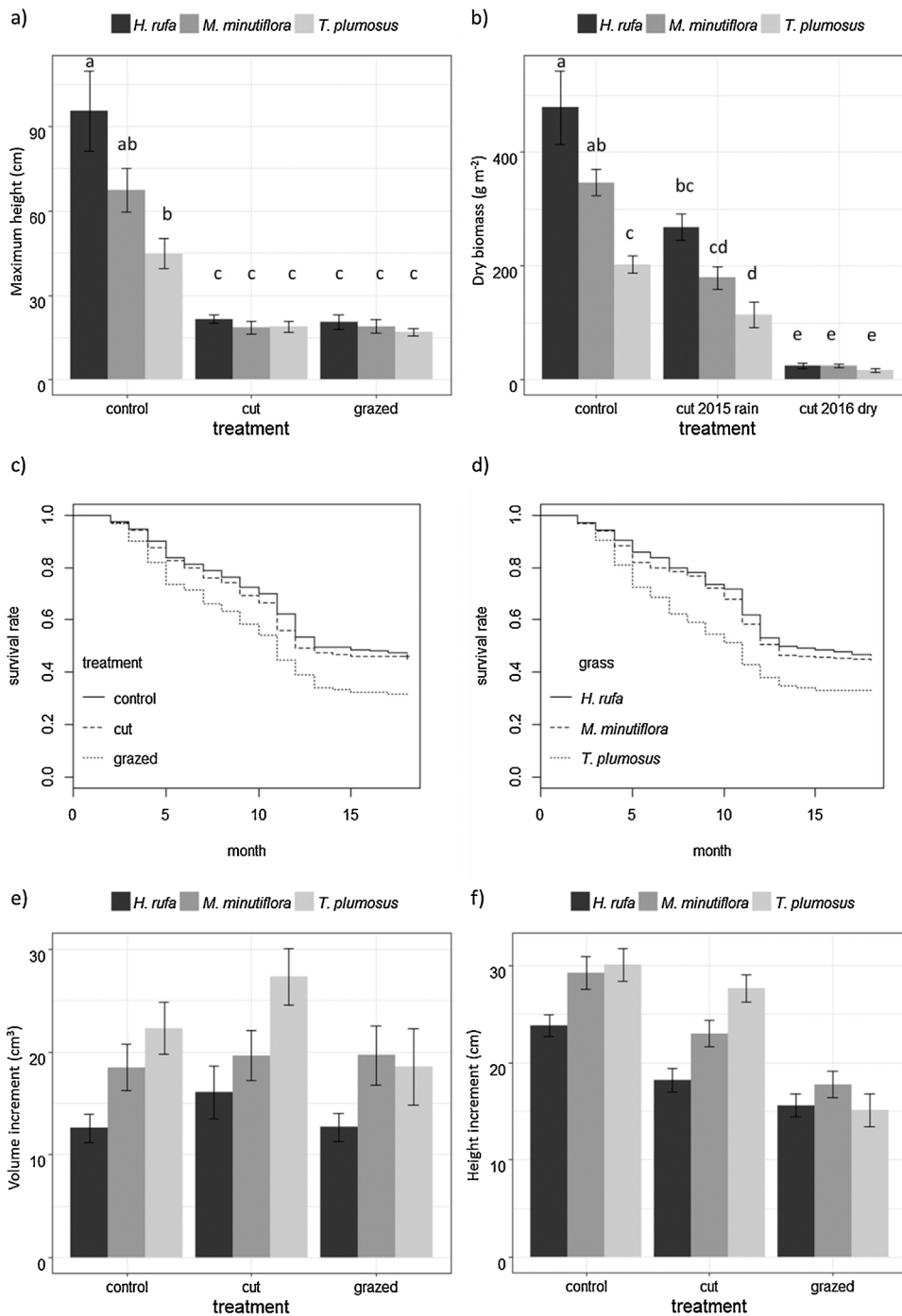


Fig. 5. a) Grass height measured after the 2015–2016 growing season in June 2016 by grass species (*Hyparrhenia rufa*, *Melinis minutiflora*, and *Trachypogon plumosus*) and biomass removal treatment (mean  $\pm$  1 SE). b) Total biomass accumulation in control plots during the 2015 growing season, total harvested grass biomass by grass species during the 2015 rainy season and the 2016 dry season in the cut plot (mean  $\pm$  1 SE). Same letters over bars indicate no significant difference according to the Tukey multiple mean comparisons test ( $\alpha = 0.05$ ). Biomass accumulation in the grazed plot is not reported, because it was removed by cattle. c) Kaplan Mayer survival curve over the course of the 18-months study for the three biomass removal treatments (grazing, livestock exclusion with grass harvesting (cut), and exclusion control). The sapling survival curve for the grazing treatment is significantly different compared to the curves for the two exclusion treatments ( $P < 0.001$ ), d) Kaplan Mayer survival curve for the three grass species: *H. rufa*, *M. minutiflora* and *T. plumosus*. The sapling survival rate for the native grass *T. plumosus* is significantly different compared to the two exotic grass species ( $P < 0.001$ ). e) Increase in pine-stem volume for biomass removal treatment and grass species type, and f) increase in pine height (cm) for biomass removal treatment and grass species type over the course of the experiment (mean  $\pm$  1 SE).

#### 4. Discussion

In the SBR, savannization and exotic grass invasion have been caused by the same set of drivers as in other tropical forests around the world. Light-demanding savanna grasses invaded the forest as a consequence of selective logging, deforestation, overgrazing, and frequent fires (D’Antonio and Vitousek, 1992; Silverio et al., 2013; Veldman and Putz, 2011; (Fig. 3). Pine savannas cover 20% of the study site and they are highly valued for resin and livestock production. Savanna understorey grass vegetation is dominated by exotic grasses, which currently cover close to 65% of these open ecosystems. In sites where exotic grasses are abundant, adult tree diameter distribution is homogeneous (Fig. 4a) suggesting these trees belong to one age class cohort that established likely prior to the invasion of exotic grasses, while later

potential establishment was not successful. In pine savanna with native grass cover, tree recovery is observed, while in exotic grass-dominated sites the accumulation of old senescent grass biomass inhibits the regeneration of *P. oocarpa*. On the other hand, livestock grazing in exotic grass-dominated sites favored sapling density (Fig. 4c) as it seemed to have opened the dense grass canopy (Fig. 1). Archer et al. (2017) described non-excessive browsing as a disturbance-based control to maintain savanna structure, where large herbivores remove the competitive effect of a dense grass cover allowing tree establishment and growth. Posada et al. (2000) reported the same effect of livestock grazing in a Colombian tropical forest invaded by *M. minutiflora*. Furthermore, lower grass biomass reduces wildfire risk, and fire intensity and frequency, which eventually increases tree sapling survival on the long-term as a synergistic indirect effect of grazing and low fire (Van

Langevelde et al., 2003; Fig. 1). On the long-term, however, tree density may not be high enough for a closed forest canopy to develop, because livestock trampling and browsing may cause a relatively high sapling mortality (Jimenez et al., 2005; Wassie et al., 2009; Werner, 2005). This trade-off between lower fire risk and reduction in plant competition as an indirect positive grazing effect and tree mortality by trampling as a direct negative grazing effect on pine establishment (Fig. 1) is shown in our grazing experiment. There, sapling survival was approximately 15% lower in the grazed than in the cut subplots (Fig. 5c), which confirms the adverse effects of trampling, as also reported by small-holder farmers in our study site (Supplementary Fig. S4b). This results in savanna systems with a typically lower tree cover that favors grass establishment and periodic wildfires as a consequence of higher understory grass biomass, compared to closed forests (Hoffmann et al., 2012). This trade-off between a relatively lower pine tree density and moderate grazing, allows forage production to maintain livestock and pine seedling survival for long-term resin production, and simultaneously reduces, but not eliminates, fire risk (Van Langevelde et al., 2003).

In natural protected areas (NPAs) like the SBR, the local conservation agency and other actors often show keen interest in preserving or restoring forest ecosystems according to historical records (CONANP, 2013). However, mountainous tropical lands, such as those encompassed by the SBR, also support important livelihoods for a relatively large smallholder farmer population, who owns this land and has the right to use it. In the SBR, human-induced savannas provide more income from resin extraction from pine trees and cattle raising than from closed oak-pine forests. Often, residents are willing to engage in forest conservation guaranteed they benefit from such conservation programs, or at least are not negatively affected by them (Durigan et al., 2013). Within this framework an increasing farmers' interest in conserving trees and restoring open sites can be understood. Such an interest has arisen in that resin can potentially be extracted from those trees as a source of income.

Currently, pine savanna ecosystems in SBR have a sufficiently high adult tree density as seed source; however, natural mortality of adult trees may increase by pest infestations, windfall, increasing droughts or other extreme meteorological events associated with climate change (Allen et al., 2010) and thereby seed dispersal can be reduced. On the other hand, strict fire suppression policies have led to a great accumulation of fuel in the form of leaf/needle litter and dry/senescent grass biomass over the past 20 years; this may trigger catastrophic wildfires potentially affecting both pine savannas and the adjacent montane forests in the core conservation zone of SBR. Although localized prescribed burning is currently allowed, fire suppression is now preferred in both ejidos; this has become typical in Mexican rural areas close to pine forests (Rodríguez-Trejo and Fulé, 2003). Fire suppression combined with the presence of exotic grasses undermines the regeneration of *P. oocarpa*, and over time, the savanna tree component will decline (Myers and Rodríguez-Trejo, 2009). In some Mexican Biosphere Reserves, conservation strategies include economic incentives such as payments for environmental services, by which rural people receive money as compensation for restricting land use, for example by restraining fire use for agriculture, hunting, and extensive cattle raising (Cortina-Villar et al., 2012). However, such passive conservation strategies do not fully solve problems of land degradation caused by exotic grass invasion. Sometimes, active strategies such as planting or fostering natural regeneration are required, as is the case in our study area.

To overcome the problem of exotic grass expansion, controlled burning may not automatically induce forest recovery. Twenty years ago, before fire was systematically suppressed in the SBR, human-induced forest fires were common, and proliferation of pines could have been promoted (CONANP, 2013; Huffman, 2010). However, for many years two processes interrupted tree recovery in our study sites; firstly, human pressure types in form of selective logging for fence posts, cutting saplings to control shrub and tree encroachment in pastures of

exotic grasses, and overgrazing, which all have been reported in other Mexican pine forests in the state of Chiapas (Ramírez-Marcial, 2003). Secondly, although *P. oocarpa* is fire resistant, this species also requires a fire-free period for uninterrupted growth in height and bark thickness to protect the trees from fire (Huffman, 2010; Keeley, 2012). If burning were practiced annually or high fuel accumulation by exotic grasses induced frequent burning, nearly all saplings would burn, and the ecosystem would never reach the fire suppression threshold, i.e. a more closed canopy structure that limits grass establishment, high microclimatic humidity and thus reduced fire risk (Hoffmann et al., 2012; Kennedy and Horn, 2008).

So, can livestock grazing substitute fire for maintaining this valued pine savanna? Regulated or moderate grazing may be a suitable mechanism to open up the dense grass canopy and, thereby, facilitate natural tree regeneration. However, as noted by Smit et al. (2006a,b) and Wassie et al. (2009), overgrazing should be avoided in these sites, because under heavy grazing no or little regeneration is possible, because, it increases the risk of mortality by trampling and browsing, and the savanna system may shift to a grassland.

In native grass dominated savannas, the grazing pressure should be held lower than in exotic grass dominated savannas, because, in the current study, the lowest pine sapling survival rate was recorded in the native *T. plumosus* plots in the first five months after transplantation (Fig. 5d). This result may be explained by a relative lower biomass production of this species (Fig. 5b), which may lead cattle to move and trample more standing biomass in search for fodder than in sites with higher biomass accumulation. Also, lower forage availability may imply higher browsing rates on young trees, especially on young buds (Smit et al., 2006a,b).

To reduce sapling mortality by trampling, an adequate cattle management plan is needed, which includes regular rotation as well as temporary livestock exclusion as recommended by McEvoy et al. (2006), and Smit et al. (2006a,b), or lower stocking rate. However, on the long-term fire suppression also inhibits seedling establishment, because pine needles accumulate and shrubs or other species that are avoided by livestock may invade (Ager et al., 2013). Hence, occasional prescribed fire may help reduce this problem for *P. oocarpa* (Rodríguez-Trejo and Fulé, 2003). Improved pine savanna management includes a combination of controlled fire and grazing regime in a spatial and temporal context. Fuhlendorf et al. (2009), called this pyric herbivory and recommended this spatiotemporal interaction of biomass removal and vegetation rejuvenation a suitable management strategy to maintain rangelands without a significant reduction in livestock load, as it stimulates growth and increases the quality of cattle forage (Limb et al., 2011).

In the current study, plant survival during the first year – from July 2015 to June 2016 – was 46%, a lower percentage compared to other studies examining pine survival, such as Jimenez et al. (2005), who reported 70% plant survival. However, in the second year, mortality did not increase and survival rates were similar in all treatments (Fig. 5c, d). We hold higher mortality during the first year due to the strong El Niño Southern Oscillation event in 2015 (NOAA, 2016), with an annual precipitation 35% lower than the 30-year average. Furthermore, during the rainy season 2015 two drought periods occurred in June and August.

Our study focused on analyzing the positive and negative effects of livestock grazing on pine recruitment in human-induced pine savanna with native and exotic grass cover in the understory. However, livestock grazing in forest ecosystems may affect a broad spectrum of environmental services (Trilleras et al., 2015) including floristic species composition (Stern et al., 2002) and overall biodiversity. This study focused on two provisioning ecosystem services forage production and resin production, this combined interest supports the interest of local farmers to maintain this unstable pine savanna ecosystem and in particular to conserve the pine tree component to secure future resin extraction. As has been demonstrated for the SBR, farmers quickly respond to

emerging markets of new commodities such as pine resin, however, in parallel they try to maintain livestock production. As livestock production interferes with futures resin production, considering the critical stage of pine seedling or sapling survival, farmers are required of adaptive learning in livestock management. If resin production decreases in the future or resin prices drop, farmers who are currently preserving the savanna system may quickly switch back to pure livestock raising, which may favor the expansion of open pastures or the production of new cash crops, which would require new land clearing (García-Barrios et al., 2009).

## 5. Conclusions

In this work, we analyzed the history of the transition of a tropical oak-pine forest to a human-induced pine savanna, as well as the possibility to prevent a shift into a state of treeless pasture of exotic grasses, because of low natural pine tree recruitment. Areas degraded by highly competitive non-native grasses are often remarkably resilient and may persist in that state for a long time. This condition is considered to be a landscape trap. Although open pastures can be profitable if they are used for livestock grazing, a mixed silvopastoral use is preferable on such land, not only concerning ecological benefits, but also because it allows farmers to diversify their income in the face of market uncertainties. Furthermore, if farmers establish a resin-harvesting silvopastoral project, they have a vested interest in increasing and controlling tree density.

Our observations and experiment in the field show clear evidence that cattle can partly substitute the role of fire in controlling grass biomass increase and in favoring pine trees in savannas, where fire suppression management is practiced. In grazed sites, pine tree recruitment was significantly higher than in ungrazed sites dominated by exotic grasses, because of an indirect beneficial effect of grazing on seedling establishment. Lower aboveground grass biomass may reduce light and water competition between tree seedlings and exotic grasses. Our results also show a trade-off of livestock grazing in that higher sapling mortality occurred when stocking rate was high in the rangelands; hence moderate livestock grazing may greatly enhance the survival and growth of pine saplings. At appropriate livestock rates, pine survival may be sufficiently high to maintain the required balance of tree and grass cover in this savanna silvopastoral system. Evidently, more detailed experiments referring to functional biodiversity, soil conditions and continuous monitoring of pine recruitment are needed to identify best management practice in the long-term.

Furthermore, there is a need for a paradigm shift from traditional conservation management to a more adaptive system, where forest use and tree recovery are promoted simultaneously through controlled livestock raising. This adaptive form of management will favor human-induced pine savannas and protect the highly biodiverse forest frontier from wildfires, where the agricultural use of fire has been prohibited. In the mid-term, cattle can substitute fire; however, on a long-term prescribed burnings are needed in natural and exotic grass-dominated sites to remove excess biomass that is not consumed by livestock.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2017.08.033>.

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