

# Removal of cattle accelerates tropical dry forest succession in Northwestern Mexico

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## Abstract

Domestic livestock influence patterns of secondary succession across forest ecosystems. However, the effects of cattle on the regeneration of tropical dry forests (TDF) in Mexico are poorly understood, largely because it is difficult to locate forests that are not grazed by cattle or other livestock. We describe changes in forest composition and structure along a successional chronosequence of TDF stands with and without cattle (chronic grazing or exclusion from grazing for ~ 8 year). Forest stands were grouped into five successional stages, ranging from recently abandoned to mature forest, for a total of 2.7 ha of the sampled area. The absence of cattle increased woody plant (tree and shrub) density and species richness, particularly in mid-successional and mature forest stands. Species diversity and evenness were generally greater in sites where cattle were removed and cattle grazing in early successional stands reduced establishment and/or recruitment of new individuals and species. Removal of cattle from forest stands undergoing succession appears to facilitate a progressive and non-linear change of forest structure and compositional attributes associated with rapid recovery, while cattle browsing acts as a chronic disturbance factor that compromises the resilience and structural and functional integrity of the TDF in northwestern Mexico. These results are important for the conservation, management, and restoration of Neotropical dry forests.

## KEYWORDS

Alamos, arrested succession, chronic disturbance, chronosequence, facilitation mechanism, Reserva Ecologica Monte Mojino, Sonora

## 1 | INTRODUCTION

Tropical dry forests (TDF) are widely distributed globally and are one of the most threatened ecosystems (Ceballos et al., 2010; Miles et al., 2006). The main causes of tropical dry forest loss and degradation are agricultural expansion and intense livestock grazing within remaining forest patches (Dirzo, Young, Mooney, & Ceballos, 2011; Janzen, 1988; Jaramillo, García-Oliva, & Martínez-Yrizar, 2010; Maass et al., 2010; Portillo-Quintero, Sanchez-Azofeifa, Calvo-Alvarado, Quesada, & do Espirito Santo, M. M., 2015; Trejo, 2010).

This has resulted in reductions in species diversity and changes to the composition, structure, and functional integrity of these ecosystems (Chazdon et al., 2016; García-Oliva & Jaramillo, 2011; Poorter et al., 2016).

A long history of shifting cultivation within Neotropical TDF has resulted in forests with stands at different stages of secondary succession, each characterized by communities that differ in composition, structure, and function (Chazdon, 2014). Numerous research efforts have shown that secondary succession in the Neotropical TDF is a slow process where changes in species composition and

functional attributes are affected by multiple factors (e.g., biotic interactions, edaphic properties, and land-use history) that operate across spatiotemporal scales (Arroyo-Rodríguez et al., 2017; Chazdon, 2014; Quesada et al., 2014). These factors occasionally act synergistically, exerting a critical influence on the resilience of certain vegetation attributes along the secondary succession gradient (Chazdon, 2008a, 2014; Derroire et al., 2016; Lebrija-Trejos, Bongers, Pérez-García, & Meave, 2008; Poorter et al., 2016).

Several studies have indicated that intensive livestock grazing within TDF cause degradation of tropical ecosystems (Gill, 2006; Hester, Bergman, Iason, & Moen, 2006). Specifically for TDF, such degradation has resulted in reduced provisioning of ecosystem services such as carbon storage, freshwater, climate regulation, and soil fertility (Balvanera, Castillo, & Martínez-Harms, 2011; Davidson et al., 2017; García-Oliva & Jaramillo, 2011; Maass et al., 2005). Cattle primarily graze on grasses and herbs; however, they are generalist herbivores and also browse on woody plant leaves, stems, flowers, fruits, and meristems (Herrero-Jáuregui & Oesterheld, 2018; Hester et al., 2006; Veblen & Young, 2010).

Although some studies have shown that cattle promote seed and propagule dispersal that may facilitate forest regeneration (Bullock & Armstrong, 2000; Miceli-Méndez, Ferguson, & Ramírez-Marcial, 2008), other research indicates that livestock grazing negatively impacts forest recovery via increased soil compaction and changes to other physical and chemical properties affecting forest communities (Fleischner, 1994; Kauffman, Hughes, & Heider, 2009; Maass et al., 2010; Mehta, Sullivan, Walter, Krishnaswamy, & DeGloria, 2008). In the long-term, these negative effects may affect tree growth and structural characteristics (Breceda, Ortiz, & Scrosati, 2005) as well as vegetation structure (Stern, Quesada, & Stoner, 2002; Ribeiro, Arroyo-Rodríguez, Santos, Tabarelli, & Leal, 2015; Griscom, Griscom, & Ashton, 2009; but see Miceli-Méndez et al., 2008). Despite the well-known effects of cattle grazing on forest plant communities (Herrero-Jáuregui & Oesterheld, 2018; Hester et al., 2006; Veblen & Young, 2010; Wassie, Sterck, Teketay, & Bongers, 2009), the effects of cattle on TDF dynamics have not been extensively evaluated (but see Griscom et al., 2009; Montero-Solis, Sánchez-Velásquez, Martínez-Rivera, Moermond, & Aguirre, 2006) and may be underestimated.

In TDF, exclusion or reduction in livestock grazing has been suggested as a means to conserve biodiversity and maintain ecosystem properties (Dullinger, Dirnböck, Greimler, & Grabherr, 2003; Seifan & Kadmon, 2006). Several studies have been conducted on secondary succession in TDF (Chazdon, 2014; Piana & Marsden, 2014; Quesada et al., 2014), but more studies on the effects of cattle and/or their removal on TDF succession are necessary (see Ceccon & Hernández, 2013). The limited understanding of the role of livestock in altering forest succession and influencing forest dynamics hinders our ability to develop appropriate conservation, restoration, and management strategies within this highly threatened ecosystem.

Within the Sierra de Álamos Reserve in Northwestern Mexico (Sonora), the non-profit organization Nature and Culture International (NCI) began purchasing cattle ranches and established the Reserva Ecológica Monte Mojino (REMM) in 2008. Subsequently, livestock

production ceased and this private reserve has been managed to support biodiversity conservation and ecosystem recovery (Lopez-Toledo, Horn, & Endress, 2011). This change in land use and management provided a unique opportunity to investigate the succession of TDF and the effect of removal of chronic grazing on the compositional and structural attributes of these already-altered TDF ecosystems in Mexico.

In this study, we addressed the following questions: (a) How do forest composition, structure, and other ecosystem properties change through secondary succession in the TDF of Álamos, Sonora?; (b) Does the removal of cattle affect structural and compositional attributes of the vegetation?; and (c) Is cattle exclusion a good management approach to promote recovery of the TDF? We expected that cattle exclusion would result in increased tree density, species richness, and basal area, which would influence additional ecosystem properties such as biomass and carbon storage. We also expected cattle exclusion to result in an increase in the evenness of the plant communities with succession compared to grazed systems.

## 2 | METHODS

### 2.1 | Study site

The Area for Protection of Flora and Fauna “Sierra de Álamos-Rio Cuchujaqui” (APFF-SARC) is a ~93,000 ha protected natural area in the state of Sonora, Mexico (Lopez-Toledo et al., 2011). The APFF-SARC forms part of a network of protected natural areas recognized by UNESCO. For this study, we selected sites within the Reserva Monte Mojino (REMM) and thirteen different private cattle ranches—all within the federally recognized APFF-SARC. REMM is a ~7000 ha private reserve in the heart of APFF-SARC where cattle have been excluded since 2008. Elevation ranges from 300 to 1,600 m asl. Mean annual precipitation is 650 mm (range 190–1,120 mm) with a pronounced eight-month dry season (November to June), which provides only 25–35 percent of the total annual precipitation. Mean annual temperature is 21.5°C, ranging between 10 and 41°C (Lopez-Toledo et al., 2011).

As with most protected areas in Mexico, activities such as extensive cattle grazing, agriculture, and forestry are practiced in the APFF-SARC. The tropical dry forest vegetation within the APFF-SARC is a mosaic of mature (37.8%) and secondary (19.2%) vegetation, as well as pine-oak forests (39.3%). Permanent pastures and agricultural fields comprise 2.3 and 1.4 percent of the area, respectively (CONANP, 2009).

Shifting cultivation is a common land-use within the area, which consists of cutting mature or secondary forest and using fire to establish crop fields that are used for 1–2 years to produce maize and other crops. Subsequently, the fields are converted to grassland-dominated meadows maintained for cattle production over a period of two or three years. After this period, sites become unproductive and are abandoned, allowing for secondary succession to begin (Álvarez-Yépez, Martínez-Yrizar, Búrquez, & Lindquist, 2008). Cattle grazing may take place in both mature and secondary

forest stands of all ages (Álvarez-Yépiz et al., 2008; CONANP, 2009). Because of the widespread and long-term practice of shifting cultivation within the TDF of the region, it is difficult or impossible to find sites free from human-induced disturbance for at least 50 years (CONANP, 2009; Lopez-Toledo et al., 2011).

## 2.2 | Data collection

We stratified observation sites across two types of land use: (1) privately owned, active ranches within APFF-SARC where cattle production has been ongoing for at least 50 years (chronic grazing), and (2) sites in the ReMM where cattle have been permanently excluded (grazing exclusion) since 2008. In both, the active ranches and the ReMM, we identified secondary forest stands across a successional gradient, representing different times since agricultural abandonment. We grouped forest stands into five successional stages: (a) 2–5 years since abandonment (Recent), (b) 5–10 years (Young), (c) 10–20 years (Intermediate), (d) 30–35 years (Late), and (e) mature old growth forest not cleared for at least ~100 years (OGF). Combined with the two cattle management regimes (cattle grazing and grazing exclusion), we evaluated 10 combinations of management and successional stage. Information on stand age and cattle production was obtained through interviews with ranch owners and forest rangers. Each treatment combination had three replicates, except for Recent and Young forests excluded from cattle. The availability of sites recently excluded from cattle in the ReMM was limited (Table S1).

We conducted vegetation sampling during the rainy season (July–October) of 2015 (~8 years after the exclusion of cattle). In each of the 27 sampling stands, we established ten 50 × 2 m (0.1-ha) transects (Gentry, 1982), for a total of 2.7 ha sampled. All woody species (trees and shrubs) of height ≥ 1.30 m and diameter at breast height (dbh) ≥ 1 cm were recorded and identified.

We calculated aboveground biomass and carbon storage for each stand using the general model developed by Chave et al. (2005) for tropical dry forests. This model converts biometric measurements of trees (dbh, height, wood density) into biomass values using empirical allometric equations (Chave et al., 2014). We obtained wood density estimates for the 38 most abundant species from Quisehuatl-Medina (2019) and García-Ramírez (2017). For the rest of the species, we obtained wood density values from the world wood density data base (Chave et al., 2009) and Ordoñez et al. (2015). We imputed an average value (0.589 g cm<sup>-3</sup>) for six species missing density data. We estimated carbon mass in the woody vegetation using a conversion factor of 0.47 g C/ g dry wood (Chave et al., 2005).

## 2.3 | Physical and chemical soil variables

To identify the effects of cattle removal and successional state on soil nutrients, we collected five soil samples in each of the 27 plots between 0 and 10 cm depth. The five soil samples were combined to make a single homogeneous sample per plot. Half of each sample

was dried and was used to measure (a) total C by coulometric detection (Nelson & Sommers, 1996), (b) total N using the micro-Kjeldahl method (Bremner, 1996) and, and (iii) P using the molybdate colorimetric method following ascorbic acid reduction (Murphy & Riley, 1962). The portion of the soil samples that remained was used to extract NH<sub>4</sub> and NO<sub>3</sub> by the phenol-hypochlorite method. Soil compaction was measured following protocols developed by Blake (1965) (For details see Appendix S1). Samples were analyzed at the Soil Laboratory of the Instituto nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP, Mexico).

## 2.4 | Statistical analysis

We compared the effects of cattle management (CM: chronic grazing or grazing exclusion), successional stage (SS: Recent, Young, Intermediate, Late, and Old Growth Forest) and their interaction on vegetation response variables, including stem density, species richness, basal area, above-ground biomass, carbon storage, and proportions of saplings (1–5 cm dbh). The proportion of saplings in a stand was used as a proxy for tree recruitment. We used generalized linear models (GLMs) for stem density, species richness and proportion of saplings and analysis of variance (ANOVA) for basal area, above-ground biomass, and carbon storage. For GLMs, we used the log and logit link for count variables (density and richness) and the proportion of saplings, respectively (Crawley, 2012; Faraway, 2004). For continuous variables (basal area, above-ground biomass and carbon storage), we first tested for normality and homogeneity of variances. For each GLM and ANOVA model, we included categorical the predictor variables of cattle management treatment (CM), successional stage (SS), and their interaction (CM:SS).

To evaluate whether cattle grazing exclusion affects species richness, we conducted an analysis of covariance (ANCOVA), with plot-wise species richness as the dependent variable and the number of individuals and the cattle management treatment as explanatory variables. We tested differences among slopes of the regression lines between cattle management schemes (CM, chronic grazing and grazing exclusion).

We compared the species richness and evenness between cattle management and successional stages using two methods, rarefaction curves and rank-abundance curves. We constructed rarefaction curves using EstimateS 9.1.0 (Colwell, 2013). We computed curves based on individuals for each treatment, using all registered trees and the extrapolation method to the fifteen units sampled. In this analysis, we excluded the "Recent" forest stages given the low number of individuals. Rank-abundance curves (McGill et al., 2007) for both CM schemes were plotted for each successional stage. Rank-abundance curves express density of individuals of each species as a function of the range of abundance of species (Magurran, 2004; Mueller-Dombois & Ellenberg, 1974). Linear models (in the form:  $y = mx + b$ ) were fitted for rank-abundance curves. To fulfill all the assumptions of the linear model (normality and homoscedasticity), the abundance data were logarithmically transformed (Crawley, 2012).

We tested differences between slope of cattle management treatments (CM) and successional stages (SS) using ANCOVA. The slopes of the straight-line equation are considered indicative of dominance and/or evenness in the treatments (Magurran, 2004); curves with steeper slope correspond to dominance by only a few species and flatter curves indicate greater evenness (Gotelli & Colwell, 2001). We conducted these statistical analyses using R 3.1.2 (R Core Team, 2019). Additionally, we calculated the expected species richness per site using the non-parametric estimators ACE and Chao 1 (Colwell, 2013). Finally, we compared the relative density of the most abundant species in the different CM x SS to evaluate species' affinity for a given successional stage (Figure S1).

We conducted non-metric multidimensional scaling (NMS) using PC-ORD Version 7.00 (McCune & Mefford, 2015) to extract the dominant community composition gradients from our dataset. We only included saplings (1–5 cm dbh) in this analysis to increase our ability to detect a relationship between cattle grazing, tree recruitment, and community composition. We excluded large trees because we did not expect trees that established prior to cattle exclusion (8 years prior to sampling) to be substantially impacted by changes in cattle management over the duration of this study. We used a Sorensen's distance measure, Kruskal's strategy 2 for penalization for ties in the distance matrix, and the "slow and thorough" NMS autopilot setting (McCune & Mefford, 2015). We represented woody species abundance for ordination analyses with the non-transformed importance value (IV; Magurran, 1988), which is a combination of relative abundance and relative basal area for a species in each plot. We did not include relative frequency in our calculations of importance values because species abundance was assessed at the plot scale. We produced two-dimensional ordinations with a random starting configuration and a maximum of 500 iterations. The instability criterion (standard deviation in stress over the preceding 10 iterations; 0.0000001) was met before the maximum of 500 iterations were reached. We used a randomization test to evaluate whether the observed minimum stress was smaller than expected by chance (McCune & Mefford, 2015). We explored linear relationships between community variation (ordination Axes) and individual species abundance (IV), biological factors (basal area, density, and richness) of small-sized individuals, above-ground biomass, and CG scheme using joint plots. The ordination including all stands revealed that much of the species composition variation was explained by differences between the Recent and other stands (Figure S3). Axis 1 (explaining 40% of variation) was strongly related to time since abandonment, and Axis 2 (explaining 34% of variation) was most strongly related to separation between the recent stands from the other stands in species space, which was driven primarily by high abundances of *Brogniartia alamosana* and *Malva spp.* in the recent stands (Figure S2). To reduce noise introduced by the Recent stands and to enhance our ability to detect relationships between cattle grazing and species composition variation, we constructed a second NMS ordination with the Recent plots removed for analyses and interpretation.

Finally, we used a canonical correlation analysis (CCA) to analyze the effect of soil variables on the distribution species and to identify the historical influence of cattle through the successional gradient. We compared the differences in each physical and chemical variable of the soil between cattle management and among successional stages using a non-parametric test of permutations (PERMANOVA), which uses distance matrices to analyze multivariate variance (Anderson, 2001). We  $\log_{10}$  transformed ( $N + 1$ ) the abundance of the species matrix to homogenize the effect of the presence of very abundant species. For this analysis, we used 33 species with abundance > 5 individuals.

### 3 | RESULTS

We recorded a total of 6,396 individual trees and shrubs, belonging to 62 species and 23 families (Table S2) across the 27 sampled sites (total area of 2.7 ha). We identified 91 percent of individuals to species or genus level. A relatively small fraction (six taxa) of the total could not be identified taxonomically. Of the species recorded, 66, 31, and 3 percent corresponded to trees, shrubs, and arborescent columnar cacti, respectively. Overall, sites with chronic grazing had 46 percent of all registered individuals, while grazing exclusion sites had 54 percent. Of the 62 species registered, 42 (68%) were found at the chronic grazing sites and 57 (92%) in the cattle-excluded sites. Fifteen species were only found in plots where cattle had been excluded, while there were no species exclusively found in grazed sites.

#### 3.1 | Community attributes and regeneration

Significant differences in stem density and species richness were found among cattle management regimes and forest successional stages (Table 1). In general, both stem density and richness increased as forest age increased. Forest stands with cattle excluded generally had greater stem density and species richness (Figure 1a,b). The rarefaction curves followed the same tendency (Figure 1c), exhibiting greater species richness in sites with cattle exclusion at each successional stage. The curves indicated that for the minimum sample size of 2,700 individuals, species richness varied from ~ 23 to ~ 36 species in sites with cattle grazing (dotted line, Figure 1c) and from ~ 33 to ~ 47 species in sites with cattle excluded. In the latter case, the intermediate successional stages had the lowest species richness and the OGF had the highest species richness. Similarly, the non-parametric estimators of expected species richness indicated that species richness per site was higher than expected based on sampling effort (Chao =  $3 \pm 1.4$  and ACE =  $5 \pm 1.1$ ) in plots where cattle were excluded.

Regarding the analysis of species recruitment as a function of individuals, we found that as more individuals were recorded, the species richness increased. This relationship, calculated for the interval of the minimum-maximum number of individuals (12–420 ind), differed between CM regimes, resulting in significantly different

**TABLE 1** Effect of cattle management and succession on community attributes of the woody plant species of the TDF at Alamos, Sonora. Factors included cattle management (CM), Successional stages (SS), and their interaction (CM:SS). ANOVA was used to test for differences in ACE, Chao1, basal area, carbon storage, and GLMs used to test differences in stem density, species richness, and the proportion of saplings.  $F/\chi^2$  statistics,  $df$ , and  $p$ -values are provided for ANOVA and GLM analyses, respectively. Significant terms are indicated in bold

	Cattle management (CM)			Successional stage (SS)			CM:SS		
	$F/\chi^2$	$df$	$p$	$F/\chi^2$	$gl$	$p$	$F/\chi^2$	$df$	$p$
Density of individuals (Ind/0.1 per ha)	3.93	1	.04	60	4	<.001	4.39	4	.35
Density of species (Sobs/0.1 ha)	4.03	1	.02	20.35	4	<.001	3.70	4	.31
Chao 1	4.51	1, 29	<.001	7.36	4, 29	<.001	1.72	4, 29	.27
ACE	6.61	1, 29	<.001	12.52	4, 29	<.001	4.71	4, 29	.04
Proportion of saplings ( $\leq 5$ cm dbh)	4.55	1	.03	27.29	4	<.001	13.89	4	<.01
Basal area (m <sup>2</sup> /ha)	0.10	1, 29	.75	4.36	4, 29	.01	0.94	4, 29	.46
Aboveground biomass (Mg/ha)	0.61	1, 29	.44	5.84	4, 29	<.01	0.81	4, 29	.53
Carbon storage (Mg C/ha)	0.61	1, 29	.44	5.84	4, 29	<.01	0.81	4, 29	.53

slopes (chronic grazing,  $m = 0.02$ ; grazing exclusion,  $m = 0.05$ ), which indicates greater number of species in stands where cattle were excluded (S-CM:  $F_{1,23} = 58, p < .001$ ; Figure 1d).

The proportion of individuals in forest stands that were saplings, an estimate of recruitment, was also higher in sites with cattle exclusion (Figure 2). Analysis indicated differences among CM schemes, successional stages, and their interactions (Table 1). Specifically, the early successional stages (Recent and Young) contained about 70 and 60 percent of saplings, in contrast to more advanced successional stands.

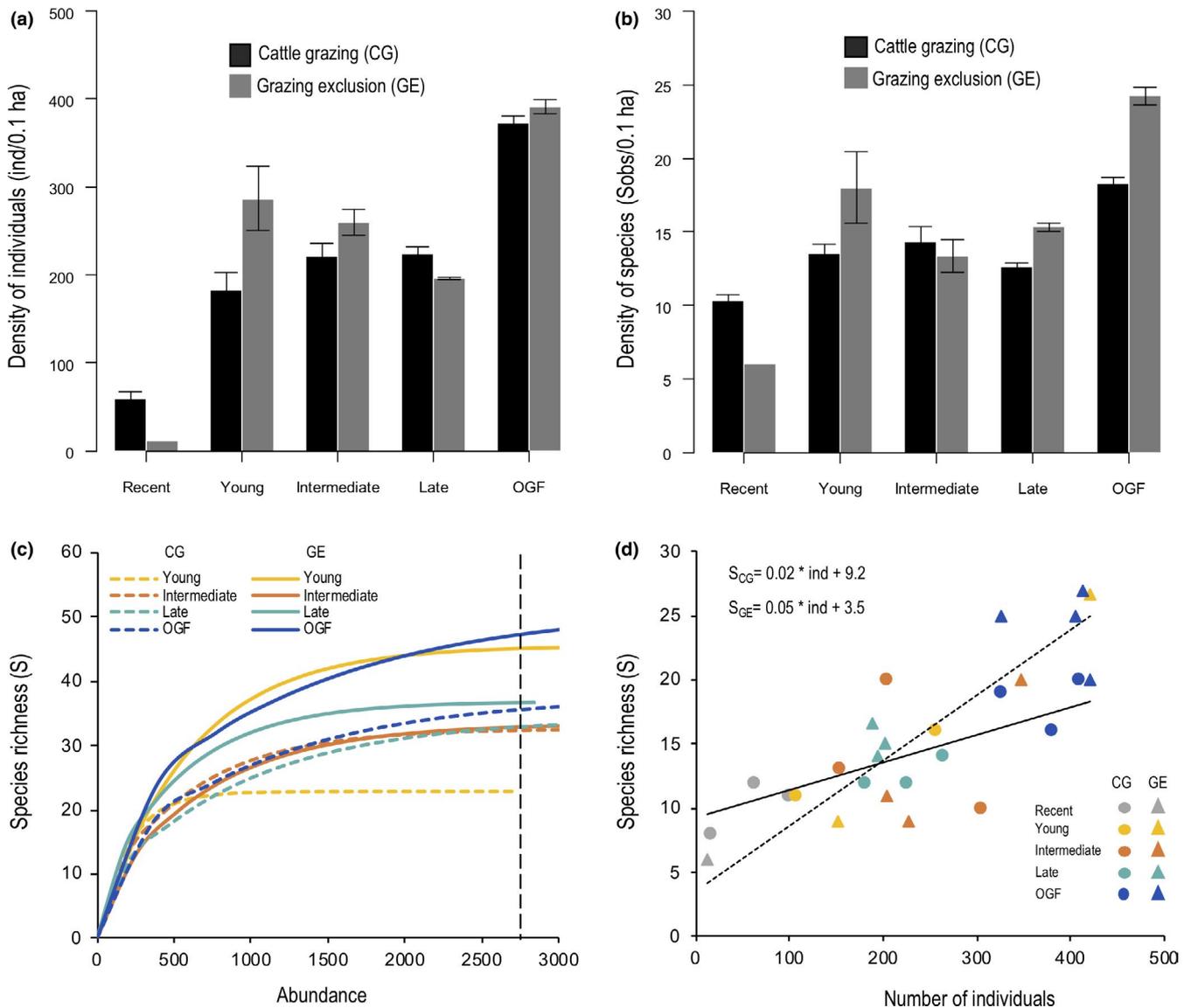
The slopes of the rank-abundance curves differed significantly across cattle management schemes (CM,  $F_{1,215} = 29.5, p < .001$ ), successional stages (SS,  $F_{4,215} = 122.8, p < .001$ ), and their interactions (CM-SS,  $F_{4,215} = 4.35, p < .01$ ; Figure 3). The greatest evenness was reached in the OGF sites with cattle excluded (Figure 3). The most pronounced slope of the rank-abundance curves corresponded to the Recent sites with no cattle ( $m = -0.40$ ), while the least pronounced was for OGF sites with no cattle ( $m = -0.14$ ). In general, sites with chronic cattle grazing had similar slopes along the chronosequence, while sites with cattle grazing exclusion varied along the chronosequence, ranging from  $m = -0.40$  to  $-0.14$  (Figure 3).

Our data identified well-differentiated groups of species associated with different forest stand ages along the successional gradient. *Acacia cochliacantha* and *Guazuma ulmifolia* were common species during early successional stages and their abundance diminished gradually in older forest stands. Another group of species, including *Mimosa palmeri*, *Mimosa aculeaticarpa*, and *Brogniartia alamosana*, were common in intermediate stages, while species such as *Haematoxylum brasiletto*, *Croton flavescens*, *Bursera laxiflora*, *Jatropha cordata*, *Jatropha malacophylla*, *Pachycereus pecten-aboriginum*, *Stenocereus thurberi*, *Karwinskia humboldtiana*, and *Randia echinocarpa* were associated with later stages of forest succession.

However, not all species showed clear trends in abundance along the successional sequence (e.g., *Senna pallida* and *Lysiloma divaricatum*; Figure S1).

Multivariate analyses of saplings provided additional insight into the role of cattle effects on forest regeneration. A two-dimensional NMS ordination (Final stress = 12.2, randomization test,  $p = .004$ , Figure 4) yielded a stable solution and explained 88% of the variation in composition of the sapling class species. Axis 1 (representing 67% of variation in the distance matrix) was most strongly related ( $r = .69$ ) to time since abandonment. Younger stands were located to the left along Axis 1 and later secondary successional stands were to the right along Axis 1 (Figure 4). Axis 2 (representing 21% of variation in the distance matrix) was most strongly related to cattle grazing ( $r = -.41$ ; Figure 4, Table S3). The presence of cattle management (0 = grazing exclusion; 1 = cattle grazing) increased with decreasing Axis 2 scores. Basal area ( $r = .18$ ), density ( $r = .28$ ), richness ( $r = .42$ ) were positively associated with Axis 2, indicating that these metrics increased—particularly species richness—with cattle exclusion (Figure 4 and Table S3). Above-ground biomass at the plot level and basal area, density, and richness of saplings all increased with time since abandonment (Figure S2, Figure 4; Table S2 and S4). Basal area, density, and richness of saplings, aboveground biomass, and carbon storage were lowest in the most recently abandoned stands (Figure S2; Table S3 and S4).

Sapling species showed varied relationships within the ordination space (all plots included). Later successional species including *Croton flavescens*, *Jatropha cordata*, and *Randia echinocarpa* had moderate-to-strong positive correlations with Axis 1 (Figure S2; Table S4). Early to mid-successional species (*Acacia cochliacantha* and *Mimosa palmeri*) were negatively associated ( $r = -0.62$  and  $r = -0.45$  respectively) with Axis 1. *B. alamosana* and *Malva* spp. were negatively associated with Axis 2 indicating greater establishment in recently



**FIGURE 1** Community attributes of woody species of the TDF at Alamos, Sonora, Mexico, under different cattle grazing scenarios along a succession chronosequence. (a) density of stems (ind 0.1 per ha); (b) species richness (S); (c) rarefaction curves to evaluate the accumulation of species as a function of the number of individuals for each of the ten treatments, and (d) relationship between species richness and number of individuals between cattle management schemes. Bars indicate mean value, and vertical lines represent  $\pm 1$  standard error

abandoned stands (Figure S2). Most species including *L. divaricatum*, *D. bicornutus*, and *G. ulmifolia* were positively related to Axis 2 when Recent plots were removed from the analyses, indicating increased abundance of these species in plots that were excluded from cattle grazing (Figure 4; Table S3). Only a few species including *M. palmeri*, *C. flavescens*, and *M. aculeaticarpa* had weak negative correlations with Axis 2 indicating higher abundances in plots with cattle grazing.

The first two CCA were significant ( $F_{1,20} = 3.25, p = .008$ ) and explained 70.7% of total variance in the distance matrix. Time since abandonment was positively correlated with Axis 1 ( $r = 0.95, p = .0001$ ; Figure S4), while soil compaction had the strongest negative relationship to Axis 2 ( $r = -0.91, p = .01$ ). The rest of the variables were not significantly correlated with the first canonical axes ( $NO_3: F_{1,20} = 0.85, p = .54$ ;  $C: F_{1,20} = 1.19, p = .29$ ;  $P: F_{1,20} = 0.38, p = .94$ ). Two of five variables were strongly related to variation

in woody species composition ( $F_{5,20} = 1.41, p \leq .0001$ ; Figure S4). We observed different CCA values between successional stages ( $F_{4,21} = 104.8, p < .0001$ ;  $F_{4,21} = 4.84, p = .006$ , Axis 1 and 2, respectively), but not for cattle management ( $F_{1,24} = 0.58, p = .45$ ;  $F_{1,24} = 2.68, p = .11$ , Axes 1 and 2, respectively). The ANOVA also provided additional information on changes in nutrient availability along the successional gradient (Table 2 and Table S4). N and C varied by stand age, but were similar between cattle management schemes (Table 2). The effect of cattle management on  $NO_3$  and  $NH_4$  differed by successional stage and P varied independently of cattle management or successional stage. Finally, soil compaction differed across cattle management regimes and across successional stages (Table 2).

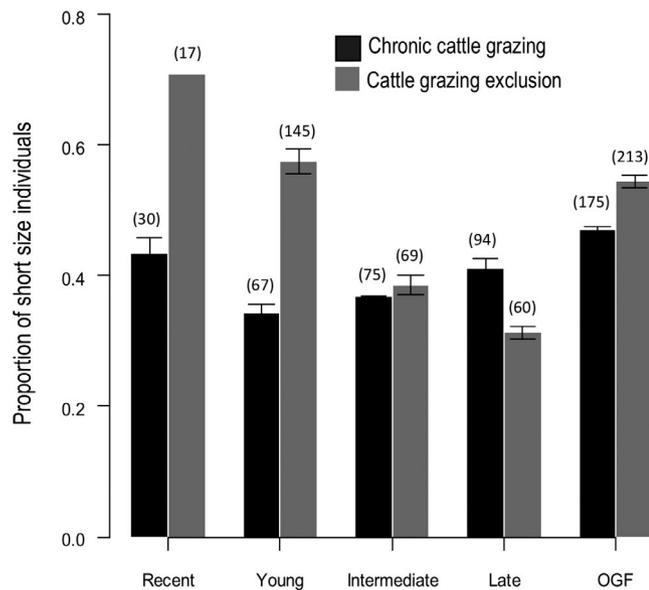
Species negatively associated with CCA Axis 1 were abundant in sites in early stages of succession (e.g., *B. alamosana* and *D. bicornutus*, Table S6). These sites also had higher  $NO_3$ . By contrast, species such as

*J. malacophylla* and *R. thurberi* were associated with later successional stands. The stands with highest values of C were OGFs (placed at the top of CCA Axis 2). The main species associated with high C and OGFs were *C. flavescens* and *B. laxiflora* (Table S6). Sites with high soil compaction were most associated with the Recent stage stands and species such as *Malva* spp. and *Mimosa palmeri* (Table S6).

### 3.2 | Aboveground biomass resilience

Total basal area differed among successional stages (Table 1). On average, the lowest values were reported in Recent stands ( $8.94 \pm 3.7$

$m^2$  ha), while the highest values were reported in the intermediate stages and were up to 8.2 times greater than the Recent stand estimates ( $73.1 \pm 11.1 m^2$  ha). Aboveground biomass followed a similar trend, with highest values ( $229.7 \pm 38.9$  Mg ha) in intermediate-aged stands. As with basal area, aboveground biomass differed among successional stages, but no significant differences were found between cattle management schemes or the interaction with successional stage (Table 1; Figure S3a,b). This may be expected given the fact that grazing likely does not affect the large trees that comprise the overstory, which strongly influence basal area and biomass estimates. With respect to aboveground carbon content, no effects of cattle management were found, but differences were found between successional stages (Table 1). Surprisingly, the highest average aboveground biomass was found in the intermediate stages ( $107.9 \pm 18.3$  Mg C ha) and was 1.4 and 1.9 times higher than in the OGF and Recent sites, respectively (Figure S3c).



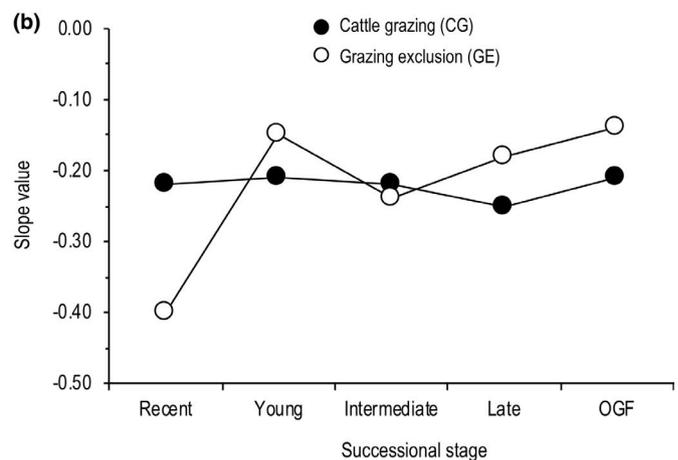
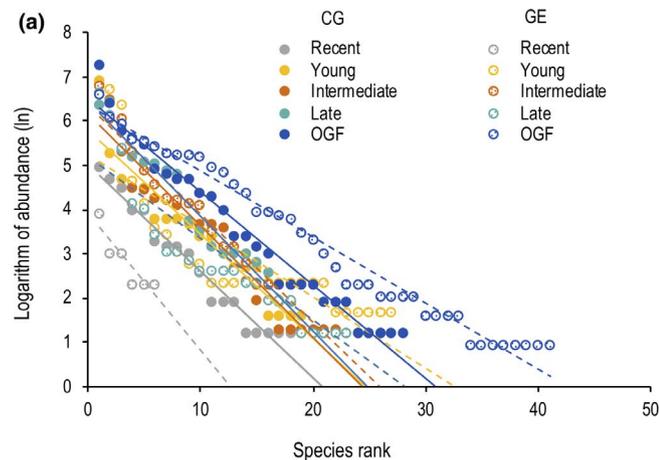
**FIGURE 2** Changes in the mean ( $\pm$  SE) proportion of small size individual (1–5 cm dbh) in woody species of the TDF at Alamos, Sonora, to evaluate the effects of cattle management schemes and successional stages. Figures above the bars indicate the mean number of individuals recorded per treatment

## 4 | DISCUSSION

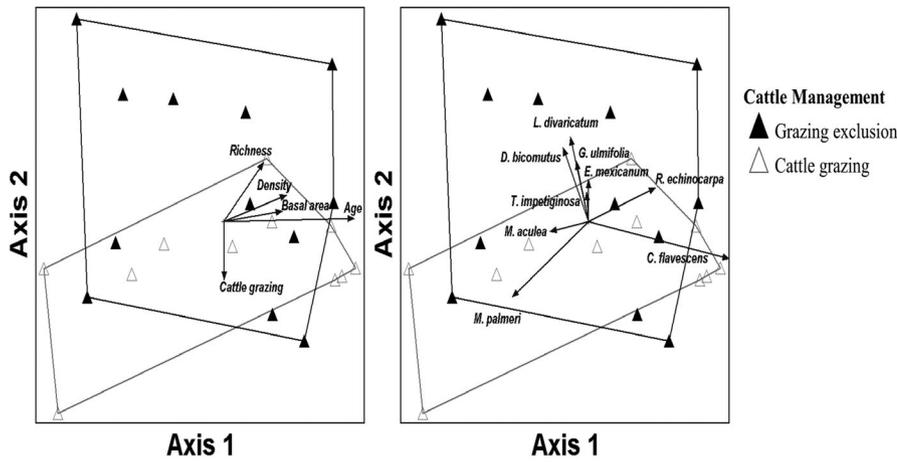
This study highlights how livestock affect stand structural attributes and successional trajectories of TDF through suppression and facilitation. Activities of cattle such as trampling, soil compaction, and browsing are considered chronic disturbance factors that may play an important role in the successional trajectories (Fleischner, 1994; Stern et al., 2002). In many cases, this type of disturbance compromises the resilience of these ecosystems (Chazdon, 2003, 2014; Derroire et al., 2016; Lebrija-Trejos et al., 2008).

### 4.1 | Grazing exclusion, succession on the TDF, and ecosystem services

Our results suggest that cattle grazing within TDF alters successional trajectories and slows forest recovery. When cattle were



**FIGURE 3** (a) Rank-abundance curves for woody species at stands of TDF at Alamos, Sonora, Mexico. (b) Slope values of regression lines among treatments of cattle management and successional stages, as indicative of the dominance/evenness of the community. Circles and triangles represent stands with cattle grazing and grazing exclusion, respectively



**FIGURE 4** NMS joint plots of forest stands varying in successional stage (minus the recent successional stands) in woody species community. Linear relationships between biological disturbance, species abundance, and the ordination space are indicated. Richness, density, and basal area correspond to small-sized individuals only. The chronic cattle grazing vector is represented by a binomial (0/1) response, and therefore, the vector points in the direction of increased density of plots grazed by cattle

excluded from forest stands, we detected an increase in stem density, species richness, and evenness across most of the suc-

**TABLE 2** Results of the statistical analysis for the physical and chemical variables of soil samples compared between livestock management and successional stages of the TDF at Alamos, Sonora. Mean values ± standard error for each variable at each treatment are found at Table S5. Significant terms are indicated in bold

Nutrients	Cattle management (CM)		Successional stages (SS)		CM:SS	
	<i>F</i> <sub>1,17</sub>	<i>p</i>	<i>F</i> <sub>4,17</sub>	<i>p</i>	<i>F</i> <sub>4,17</sub>	<i>p</i>
N	0.19	.66	4.84	<b>&lt;.01</b>	1.37	.28
C	0.34	.56	5.19	<b>&lt;.01</b>	1.63	.21
P	0.25	.62	0.76	.56	1.59	.22
NO <sub>3</sub>	1.83	.19	3.09	<b>&lt;.05</b>	4.47	<b>&lt;.05</b>
NH <sub>4</sub>	2.51	.13	1.75	.18	2.80	<b>.05</b>
Soil compaction	23.5	<b>&lt;.001</b>	4.18	<b>&lt;.05</b>	0.36	.82

cessional stages. Thus, livestock production with TDF seems to limit the recruitment of new individuals and consequently affect TDF structure and composition. This was particularly evident when considering small trees (which potentially represent new recruitment), being more abundant in sites where cattle have been permanently excluded. This effect was strongest in younger forest stands where competitive pressure for space and resources is lower compared to the more advanced stages of succession (Huston & Smith, 1987; Lebrija-Trejos, Meave, Poorter, Pérez-García, & Bongers, 2010). If we consider the general patterns of diversity based on rarefaction curves (Figure 1d), grazing, and trampling by cattle due to livestock production appears to substantially affect the establishment and/recruitment of new species, resulting in increased dominance of a few species and the loss or substantial reduction in abundance of others.

Various studies in TDF have documented the high resilience of structural attributes such as tree abundance, species richness, basal

area, and/or diversity, with estimates remaining comparable to those of the OGF during the first decades following a disturbance (Derroire et al., 2016; Kennard, Gould, Putz, Fredericksen, & Morales, 2002; Lebrija-Trejos et al., 2008; Letcher & Chazdon, 2009). We observed similar patterns across our chronosequence. Attributes such as basal area, aboveground biomass (see Poorter et al., 2016), and carbon storage gradually and positively increased with age of abandonment, rapidly reaching values close to those of the OGF in just 20 years. In OGF sites with chronic cattle grazing, basal area averaged 61.7 (±18.9) m<sup>2</sup>/ha, while basal area averaged 69.2 (±10.7) m<sup>2</sup>/ha in sites with grazing exclusion. This observed increase in basal area was concomitant with increases in stem density and species richness. The present study also shows much higher values of basal area than those reported in other studies from Mexico and other Neotropical TDFs (Álvarez-Yépiz et al., 2008; Dupuy et al., 2012; Gentry, 1995; Martínez-Yrizar, Búrquez, & Maass, 2000; Trejo, 1998), yet similar to those reported elsewhere (Marín-Spiotta, Cusack, Ostergag, & Silver, 2008).

The trends in carbon storage patterns among successional stages were similar to those of basal area. Interestingly, the highest values of carbon storage were reported in intermediate secondary stage forests. Some studies have reported similar values in wet forest in the Neotropics (Marín-Spiotta et al., 2008); however, these are the highest values reported in a TDF in Mexico. One important mechanism that could contribute to the apparent rapid recovery of basal area and aboveground biomass within successional stands was the high capacity for resprouting found in several common species (e.g., *Acacia cochliacantha* and *Guazuma ulmifolia*), as well as the presence of remnant vegetation (post-clearing) in early and intermediate stages of succession (e.g., *Haematoxylum brasiletto*, *Pachycereus pecten-aboriginum*, and *Stenocereus thurberi*). It is likely that the high number of individuals and multi-stemmed trees in intermediate and advanced stages could give secondary forest the capacity for carbon storage equivalent to that of the OGF.

In recent years, role of secondary forests in the Neotropics has been examined not only in terms of their benefits for biodiversity but also for the provisioning of multiple ecosystem services, providing an incentive for climate change mitigation (Chazdon, 2014; Chazdon

et al., 2016, 2011). The TDF, given its wide distribution in Mexico and throughout the Neotropics, acts as an important repository of carbon, both above and belowground. The accelerated conversion to pasture, farmland, and other land uses produces significant emissions of carbon to the atmosphere (Balvanera et al., 2011; García-Oliva & Jaramillo, 2011). Recent estimates suggest that processes such as the deforestation and degradation of tropical forests contribute between 6–17 percent and 8–15 percent of global anthropogenic carbon emissions per year, respectively (Houghton, Byers, & Nassikas, 2015; van der Werf et al., 2009). Unfortunately, these rates appear to be increasing dramatically (FAO, 2016) and emissions in Mexico are following global trends (Dirzo et al., 2011; Masera, Ordóñez, & Dirzo, 1997). Livestock production in Mexico has been cataloged as one of the main causes of forest disturbance (Maass et al., 2010; Masera et al., 1997). This causes the reduction of organic matter and carbon content in the soil, diminishing the capacity of the ecosystem for carbon storage, and increasing the flow of CO<sub>2</sub> to the atmosphere (Balvanera et al., 2011; Jaramillo, Martínez-Yrizar, & Sanford, 2011). Safeguarding natural regeneration and assisting the regeneration of secondary forests represent an effective instrument for climate change mitigation (Chazdon et al., 2016), which will help to reduce the impacts of livestock production on tropical dry forests and their ecosystem services.

#### 4.2 | The effect of chronic cattle grazing on species dominance during succession

Despite the fact that various species were common across forest successional states, no single dominant species was found, indicating a replacement of species through time as succession advanced. We observed marked differences groups of species and their relative abundances among cattle management schemes and successional stages. However, some species showed a marked dominance throughout succession, such as *Acacia cochliacantha* (Fabaceae). This is consistent with other studies in TDF that document the establishment of near-monospecific communities in abandoned fields (Gei et al., 2018); mainly consisting of species of the family Fabaceae (Álvarez-Yépiz et al., 2008; Martín et al., 1998; Tinoco-Ojanguren, Díaz, Martínez, & Molina-Freaner, 2013; Van Devender, Sanders, Wilson, & Meyer, 2000) such as *Acacia* and/or *Mimosa* in Jalisco (Burgos & Maass, 2004; Ortiz, 2001) and Oaxaca (Lebrija-Trejos et al., 2008).

It is also important to consider the mechanisms that may influence the establishment and colonization of a few species over the course of succession (e.g., cattle management, resprouting of remnant vegetation). Various studies have shown that livestock can facilitate the germination, dispersion, and subsequent establishment of seeds of the genus *Acacia* (Bodmer & Ward, 2006; Miller, 1995; Or & Ward, 2003; Razanamandranto, Tigabu, Neya, & Odén, 2004; Rohner & Ward, 1999; Tjelele, Ward, & Dziba, 2014, 2015). These studies highlight the fact that the passage of *Acacia* seeds through the digestive tract of ruminant livestock has a positive effect on

their germination via scarification and that large herbivores such as cattle play an essential role in the long-distance dispersion of seeds (Miceli-Méndez et al., 2008). It is likely that the affinity of livestock for species of the genus *Acacia* is linked to the fact that these species produce seed pods with high protein contents (close to 35%) (Bodmer & Ward, 2006). The findings from our study support the premise that cattle grazing affects species differently, favoring the establishment and development of some species through selective herbivory (competitive-release; Dumont et al., 2011; Ojeda, Obispo, Canelones, & Muñoz, 2012) and/or facilitation of establishment (Miceli-Méndez et al., 2008). Livestock also influence physical–chemical characteristics of the soil through compaction and the continuous deposition of nutrients (NO<sub>3</sub>) in early stages of development, which may also compromise natural trajectories of forest succession by altering species performance and competitive interactions among species.

It is important to consider that in the sites within the private reserve (ReMM), extensive livestock production had been in place previously for decades (~50 years), and it is therefore possible that this management history explains the observed patterns of diversity, such as the dominance of *A. cochliacantha* in many stands. Our study examined the effects of cattle grazing on successional trajectories in the tropical dry forest, measuring structural attributes and composition. Chronic cattle grazing can prolong the presence of some species resulting in an apparently arrested stage of succession. The influence of grazing is evident in the different slopes of the range-abundance curves, which are inversely proportional to the evenness of the species. Slopes from sites with cattle grazing did not vary by forest age, while slopes for sites with cattle exclusion varied along a successional gradient. For this reason, it could be argued that chronic cattle grazing directly affects species evenness, promoting and maintaining the dominance of a certain few species over the course of secondary succession. Our study suggests that, in Neotropical dry forests, cattle management constitutes a deterministic force that directly affects vegetation communities. Given the widespread and long-standing presence of cattle in the region, ecological costs may be severe (Balvanera et al., 2011; Chazdon, 2003; Jaramillo et al., 2011).

In this study, we did not directly analyze successional habitat specialization, or the association of plant lineages with particular points on the gradient of succession (Letcher et al., 2015). In general, it has been suggested that successional habitat specialization is lower in tropical dry forests compared to their counterparts in humid regions (Letcher et al., 2015). Theoretically, this assumption would allow for the rapid colonization and permanence of late species in early stages of succession, contributing to the resilience of these ecosystems in terms of composition (Chazdon, 2014; Derroire et al., 2016; Lebrija-Trejos et al., 2010; Letcher et al., 2015). However, if these species arrive during the influence of a chronic disturbance such as cattle grazing, such recovery is less probable, since this is a slow process that can take more than 50 years (Chazdon, 2008b; Derroire et al., 2016). If we consider that the initial composition and abundance of species that colonize after abandonment critically determine the successional trajectories for decades or perhaps centuries (Chazdon,

2014), then a direct and recurring disturbance, such as livestock production, can alter and/or slow secondary succession, especially if this acts in early stages of development.

We finally cannot rule out the possibility that differences in the observed patterns of community structure along the chronosequence are instead the result of possible differences in environmental conditions, land-use histories, or landscape characteristics (Chazdon, 2014). The confounding influence of these variables may invalidate inference based on chronosequences (Johnson & Miyanishi, 2008). However, many complementary studies of chronosequences and successional dynamics in TDFs have shown that space-for-time substitution is a valuable and appropriate approach to document and describe successional trajectories of these ecosystems (Lebrija-Trejos et al., 2010).

## 5 | CONCLUSION

Forest community attributes of the TDF of Álamos, Northwestern Mexico, vary as a function of cattle grazing and successional stage. Cattle grazing influenced the community of woody plants within TDF along the successional gradient, including species richness, species evenness, stem density, and species composition. It is likely that: (a) selective herbivory against specific taxa and (b) facilitation of the establishment of some species (i.e., *A. cochliacantha*) may consolidate near-monospecific communities, promoting alternative states of development and the arrest and/or slowing down of succession. Thus, cattle grazing exclusion can allow recovery of vegetation attributes favoring successional development. Furthermore, we found evidence that community composition and vegetative structure varied across stages of succession in the TDF of Álamos, Sonora (Lebrija-Trejos et al., 2010; Letcher et al., 2015). Future studies should examine the relationship between succession and functional groups (Ferreira-Nunes et al., 2014; Ward, 2006). In addition, it is important to design dynamic studies of woody vegetation that measure direct change in the vegetation attributes over time. Our results show that strategies of conservation which exclude livestock production, favor the maintenance, and long-term continuity of these highly threatened ecosystems, safeguarding not only their biodiversity but also the ecosystem services they support.

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## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.5mkkwh71z> (Quisehuatl-Medina, Averett, Endress, & Lopez-Toledo, 2019) and at the Mendeley Data under the name "Data for removal of cattle accelerates tropical dry forests succession in Northwestern Mexico."

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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