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The long-term effects of active management and landscape characteristics on carbon accumulation and diversity within a seasonal dry tropical ecosystem

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ABSTRACT

Reforestation is the largest natural climate solution, while potentially reversing the biodiversity crisis, especially in tropical countries. Dry tropical forests are of particular interest because they experienced greater historic loss, and offer large reforestation opportunities. This study addressed the potential of secondary forests in dry tropical systems regenerating after 60 + years in cattle pasture to accumulate carbon while increasing floristic diversity. Total carbon and woody species diversity were quantified within experimental treatments established 15 years ago. Initial active management practices included removing exotic grass with herbicide, excluding cattle by constructing live fences, and monitoring succession relative to proximity to forested riparian zones and slope position. Overall, carbon accumulated relatively slowly in this landscape (1.30 MgC Ha^{-1} Yr^{-1}). Differences were seen between management practices and landscape characteristics. Lower slope plots, adjacent to forested zones, had significantly more carbon than upper slope plots, isolated from riparian zones. The initial application of herbicide decreased total carbon. However, natural regeneration of two valuable timber species with small seeds, *Astronium graveolens* and *Cedrela odorata*, benefited from this initial treatment. Live fences that were initially planted to exclude cattle significantly increased carbon of regenerating woody species. Lianas were abundant at this successional stage. Almost half of all inventoried trees (44%) had at least one liana climbing through them, with the most common species being *Bauhinia glabra* and *Macherium microfolium*. Some valuable timber tree species found within older, protected riparian forests were not yet regenerating in any treatment, such as the wind-dispersed species, *Cieba pentandra*, and the animal dispersed species, *Hymenaea coubaril.* These species may need to be actively planted at the mid-successional stage (~15–20 years) to restore biodiversity. A trade-off between timber value, diversity, and carbon sequestration must be considered in reforestation programs and this depends on landscape characteristics and management. Passive management, even with invasive grass species, is a practical option when sites are located near forested riparian zones due to low cost and high timber value of a suite of native species that naturally regenerate. No intervention is needed other than continual protection from fire and grazing. However, low-cost management, such cutting lianas and enrichment planting at the mid-successional stage, is likely to increase carbon accumulation and diversity. More active management, such as planting drought-tolerant, higher timber value tree species, is recommended at sites isolated from forested riparian zones on upper slopes where carbon accumulation is lower. Tropical forest regeneration mechanisms in proximity to forest fragments can be surprisingly resilient if chronic human impacts are removed.

1. Introduction

Conservation, restoration, and improved forest management, particularly in the tropics, offers low cost climate-change mitigation of > 30% of greenhouse gas emissions (Griscom et al., 2017). Large scale reforestation has the potential to simultaneously increase terrestrial carbon sinks, restore biodiversity, and provide economically valuable timber (Paquette & Messier, 2010; Hall et al., 2012). Central America has a large potential to increase forest carbon sinks at low cost, a service worth hundreds of billions of dollars (Canadell and Raupach, 2008; Bonner et al., 2013). The potential across all Central American countries is 269 TgC year-1, of which 40 TgC year-1 is within Panama (Griscom et al., 2017). Throughout Central America's dry forest corridor, commercially marginal degraded cattle pasture has the potential to be restored to commercially productive forest. This would help some countries achieve their Nationally Determined Contribution (NDC)

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pledges. Most Central American countries, including Panama, have yet to identify specific actions to change terrestrial ecosystem fluxes that will contribute to their NDC. A notable exception is Honduras's ambitious pledge to restore 1 million hectares of forest by 2030.

The landscape is changing throughout Central America, creating a window of opportunity for land-based climate-change mitigation. Panama lost over 30% of its forest cover with pasture conversion in the last century (Romero et al., 1999; FAO, 2000). The Azuero peninsula was the epicenter of historic forest lost in Panama. Over the past decade, deforestation peaked in 2017 with an annual loss of 2,180 ha, which declined the following year to 1210 ha (Hansen et al., 2013, online at www.globalforestwatch.org). Degraded cattle pastureland has begun to see reforestation on a limited scale for wood production, tourism, and conservation. However, reforestation on the Azuero peninsula has yet to counterbalance forest loss, with a forest loss of 220,000 ha from 2001 to 2018 (Hansen et al., 2013, online at www.globalforestwatch.org).

Natural succession of pasture to secondary forest requires the lowest initiation cost, yet has highly variable carbon, biodiversity, and commercial outcomes compared with exotic or native species plantations. Fifteen year tropical dry forests are predicted to have 58.5 Mg ha^{-1} of above-ground biomass (AGB) with a standard deviation range of 24.5 Mg ha^{-1} to 94.5 Mg ha^{-1} (Suarez et al., 2019). Climate explains variation in AGB better than land use history at global scales (Cook-Patton et al., in press). However, biotic factors, such as remnant trees and species composition, are increasingly important in regional to local scales (Suarez et al., 2019, N'Guessan et al., 2019, Chazdon, 2014).

Proximity of abandoned pastureland to diverse riparian forests can be an important driver affecting total carbon stock and diversity. Remnant forests provide seeds and moderate edge environment for seed germination and seedling establishment (Griscom & Ashton, 2011). Many frugivorous birds and bats visit riparian forest and disperse seeds into the adjacent open pasture (Nepstad et al., 1990; Gerhardt and Hytteborn, 1992; Guevara et al., 1992; Aide, 2000; Griscom et al, 2007). Prior research from this study site in Panama found that plots associated with diverse forested riparian zones had significantly greater tree species richness and basal area than plots adjacent to deforested riparian zones after three years (Griscom et al, 2007).

The use of active management strategies during the initial stages of succession, while increasing initiation costs, can improve the success of reforestation by natural regeneration, and forest carbon potential. Invasive exotic grasses, planted as forage for cattle, are a major barrier in reforestation efforts and the ability of forests to accumulate carbon (Nepstad et al., 1996; Holl, 1998; Hooper et al. 2002, Lamb et al., 2005). One of the most dramatic consequences of these grasses is that they perpetuate the introduced fire disturbance regime, increasing carbon emissions and slowing regeneration rates by killing fire-intolerant species (D'Antonio and Vitousek, 1992; Hooper et al. 2002). Grasses can also directly inhibit regeneration of tree species by decreasing light-levels and increasing below-ground competition for resources (Nepstad et al., 1996; Cabin et al., 2002; Hooper et al., 2002; Griscom et al., 2009; Rojas-Sandoval et al., 2012; Thaxton et al., 2012). The risk of the no-management approach in exotic grasslands that have replaced natural forest ecosystems may be an alternative stable state (Olivares and Medina, 1992; Rojas-Sandoval et al., 2012). Initial research at this study site showed conflicting results after three years; planted tree seedlings grew significantly better but natural regeneration was less where grass had been removed (Griscom et al, 2005, 2009).

In order to assess the reforestation potential by natural succession of a dry tropical forest region after extended pasture use, long-term experimental plots were designed in 2002 to quantify the effect of the following landscape attributes and management techniques on natural regeneration: (1) proximity to forested riparian zones (2) slope position (3) herbicide application to removal exotic grasses and (4) tree plantings in the form of live fences that originally excluded cattle. The overarching question was what landscape attributes and management techniques have the largest effect on carbon accumulation and species diversity of regenerating woody shrubs and trees after 15 years of succession. The prediction was that carbon biomass and woody species diversity would be greater in plots adjacent to forested riparian zones on lower slopes, surrounded by live fences. The initial herbicide application to remove exotic grass was predicted to have no long-term effect. The rationale behind these predictions was that live fences ameliorate microclimate and attract more dispersers, seed sources are limited in the open pasture, and soil moisture is more of a limiting factor on the upper slopes. This study is intended to inform management plans with better predictions of the rehabilitation potential of the landscape, as a function of passive and active management.

2. Materials and methods

2.1. Study region

The study site was located in the seasonally dry tropical forest region (Holdridge 1967; Olson et al., 2001) of Los Santos province on the Pacific side of Panama (7°25′42.2″N, 80°10′29.3″ W). The annual precipitation (1300–1700 mm), in addition to the 4 to 5 month dry season, classifies the terrestrial arc surrounding the Bay of Parita as a seasonally dry tropical forest ecosystem (Holdridge, 1967, Olson et al., 2001). The dry season is pronounced, with four to five months out of the year (December through March) receiving little rain. Rain usually begins in late April and lasts until the end of November.

The landscape is a mosaic of cattle pastures, secondary forest and plantations. In the province of Los Santos, ~ 31% of the land has tree cover (Hansen et al., 2013, online at www.globalforestwatch.org). The land was cleared for ranching approximately sixty years ago. Fire is used to clear shrubs and to facilitate grass growth for cattle production. The two most common grasses at the study site are African grasses, *Panicum maximum* and *Hyparrhenia rufa*, which were originally seeded into pastures to support grazing in previously forested areas. Both species readily burn and re-sprout. A few land-owners are currently experimenting with a mixture of native timber species (e.g, *Dalbergia retusa*) and exotic teak (*Tectona grandis*) in plantations.

Despite being a post-frontier landscape, gross forest loss rates (0.3% per year) are not much lower than the pantropical average decadal rates (0.49%) (Achard et al., 2014) in the district of Pedasi where this study site lies. There was also a net forest loss (40 ha per year) during the most recent time period where both gain (gross: 11 ha yr^{-1}) and loss (gross: 56 ha yr^{-1}) data are available (2001–2012) (Hansen et al., 2013, online at www.globalforestwatch.org).

Experiments were initially set-up in 2002 on an eighty-five hectare active cattle pasture. The pasture was grazed by a herd of 50 to 70 Brahman cattle from mid-July until mid March (~0.6 to 0.8 head per hectare) until the end of 2004 with the exception of the experimental plots where they were excluded in 2002. The experimental plots have been protected from fire since 2002.

2.2. Experimental design

Eight site locations, separated by at least 100 m, were randomly selected within the 85 ha pasture described above (Fig. 1). Moran's I test was conducted to test for spatial autocorrelation between the 8 sites (Moran's I = -0.095, p = 0.866). At each location, two sets of eight 9 × 12 m plots separated by 20 m were established. Each site had 16 plots with a replicate of each treatment (see Griscom et al., 2009 for experimental design diagram). The plots ranged in steepness from 16 to 25 degrees. A 2^3 factorial design was constructed: site location (4 levels), herbicide application (2 levels), and live fences (2 levels).

Sites were located either near forested riparian zones on upper or lower slopes or isolated from forested riparian zones on upper or lower slopes. Plot locations were initially cleared with machetes of pre-existing vegetation during the early wet season (May 2002). Live poles of

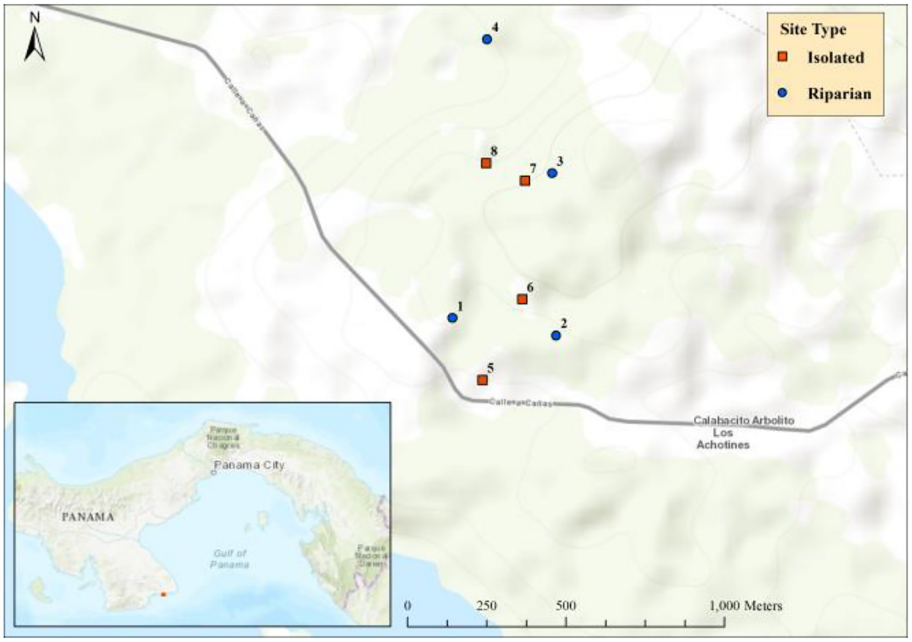

Fig. 1. Location of eight experimental sites within a 15 year secondary forest on the Azuero Peninsula, Panama.

Spondias mombin, Bursera simaruba and *Cordia alliodora* were placed around all plots in June 2002 (at a cost of ~ $80 per 100 m). Plots without cattle also had barbed wire between the poles to prevent cattle entry. However, the poles without barbed wire did not last through time. This resulted in a long-term effect of live fences on 4 sides of the plots (42 m) where cattle had been initially excluded. Plots exposed to cattle had live fences on 1 or 2 sides of the plots (9 m or 21 m) that bordered plots excluding cattle. Roundup® herbicide (Glyphosate) was applied evenly to designated plots in July and September 2002. Plots were protected from fire every year during the dry season by constructing fire breaks.

Natural regeneration was re-inventoried 15 years after the experiment began. All species > 5 cm diameter at breast height (dbh) were measured and identified in the plots (108 m^2). All lianas of any size were identified and lianas > 2.0 cm in diameter were measured. All seedlings (> 10 cm in height; < 1 m in height) and saplings (< 5 cm dbh, > 1 m in height) were counted and identified.

Diversity was estimated with the on-line version of SpadeR (Chao & Shen, 2010), with the estimates of Hill numbers of order *q1* (Chao and Jost, 2015). Total biomass for each species was calculated using a dry tropical forest allometric equation for above and below ground biomass (Chave et al., 2014, Mokany et al., 2006) and the global wood density database, which provides species specific wood densities (Chave et al., 2009, Zanne et al., 2009). Equations for biomass were as follows from Model 7 in Chave et al., 2014:

$$\textbf{Aboveground biomass}(\textbf{AGB})_{\textbf{est}} = \exp[-1.803 - 0.976E + 0.976\ln(r) + 2.673\ln(D) - 0.0299[(\ln(D)]^2]$$

where E = measure of environmental stress at the site location (0.112324), ρ = species specific wood density (g cm^{-3}), D = diameter (cm) and ln = log base e

$$\textbf{Belowground biomass}(\textbf{BGB})\textbf{est} = 0.489x^{890}$$

where × = AGB est

Total biomass was multiplied by the conversion factor of 0.47 to estimate total carbon stock.

Data was analyzed using SPSS software (Version 22) as an unbalanced, multifactor analysis of variance. A three-way ANOVA using a univariate GLM (general linear model) was performed with the main effects of location, herbicide and live fence and all possible interactions. Total carbon and diversity of woody species > 5 cm dbh as well as abundance of woody seedlings and saplings < 5 cm dbh were transformed by natural log to normalize the data. Significant differences in measured variables between location treatments were analyzed using Tukey's comparison of means test.

3. Results

3.1. Vegetation characteristics through time

Total carbon stock increased at a linear rate of 1.3 MgC Ha^{-1} Yr^{-1} (excluding live fences) . This is a conservative estimate since live fences occupied growing space. Including live fences increased the rate to 2.56 MgC Ha^{-1} Yr^{-1}. After 15 years of forest regeneration, carbon stock (19.9 MgC Ha^{-1}) was ~ two-thirds less than the carbon stock within riparian forest zones in active pasture (67.4 MgC Ha^{-1}) and ~ three-fourths less than the carbon stock within 80 + year old secondary forest (93.0 MgC Ha^{-1}). Total carbon stock, including live fences, was almost doubled the about of carbon to 38.7 MgC per ha. Of the trees naturally regenerating, *Albizia adenocephela* had the greatest average carbon gain of 16.01 Kg C yr^{-1} $stem^{-1}$ followed by *Cedrela odorata*, a valuable timber species, with an average of 7.57 Kg C yr^{-1} $stem^{-1}$ (Table 1).

Stems > 5 cm dbh increased three-fold after the first three years (from 354 to 1039 stems ha^{-1} in 15 years), slightly more than the density found within old secondary forest (900 stems ha^{-1}). Sixty-nine percent of the stems were < 10 cm in dbh. The largest trees (30–35 cm dbh) were *Cocolospermum vitifolium* and *Sapium gladulosum* (Fig. 2). Approximately 27% of the total stems counted, representing 11 different species (Table 2), are valued for their timber on the international market (Gerard et al., 2017).

Species richness followed the predicted trend of a greater number of species found at the mid-successional stage because pioneer, mid-successional, and late-successional species were all represented. A total of 47 woody species > 5 cm dbh were found after 15 years, four times the number of species inventoried at 3 years in the same plots. Species diversity estimates with Hill numbers (Chao and Jost, 2015) of stems > 5 cm dbh was much higher in the 15 year old secondary forest (^1D = 21.25) compared to 3 year old secondary forest (^1D = 5.38) within the same 8 sites.

Table 1
Average diameter growth rates and carbon gain Kg yr^{-1} of individual species measured in 2005 (3 years after abandonment) and 2017 (15 years after abandonment) on the Azuero Peninsula of Panama. Bolded species are considered timber species (Gerard et al., 2017). Species are ordered from greatest to least average carbon gain.

Species	Average diameter growth rate(cm yr^{-1})	Average carbon biomass gain (Kg C yr^{-1} $stem^{-1}$)	Max carbon biomass gain(Kg C yr^{-1} $stem^{-1}$)	Number of individuals measured	Standard Deviation
Albizia adenocephala	1.40	16.07	28.2	5	10.1
Cedrela odorata	1.47	7.57	19.68	6	6.01
Maclura tinctoria	0.84	5.9	6.09	2	0.23
Cecropia peltata	1.07	5.62	12.06	8	3.81
Sapium glandulosum	1.10	4.79	4.49	1	NA
Tabebuia rosea	0.40	4.16	7.6	3	3.18
Cocolospermum vitifolium	1.24	4.21	12.85	11	4.03
Hura crepitans	0.97	4.05	14.58	8	4.66
Enterolobium cyclocarpum	0.87	2.6	2.6	1	NA
Bursera simaruba	1.20	2.54	4.4	11	1.58
Astronium graveolens	0.48	2.21	6.9	7	2.2
Cordia alliodora	0.58	1.87	9.58	24	1.78
Guazuma ulmifolia	0.52	1.64	4.4	24	1.25
Cordia panamensis	0.49	1.5	2.36	10	0.86
Calycophyllum candidissimum	0.49	1.33	4.0	5	1.57
Tabebuia ochracea	0.40	1.12	3.59	21	0.94
Genipa americana	0.54	0.99	1.76	5	0.56
Acacia collinsii	0.38	0.73	1.47	5	0.49

Dominant species by stem count changed through time (Table 2). *Guazuma ulmifolia*, a short-statured tree often left in pastures, comprised 60% of regenerating species > 5 cm dbh at 3 years followed by *Trema micranthra* (11% of total stems). By 15 years, *Trema micranthra* had been completely replaced by other species and *Guazuma ulmifolia*, although still the most common species, decreased in importance to 19% of total stems. *Cordia alliodora* (12%) and *Bauhinia ungulata* (7%) were the other two species that comprised > 5% of total stems at 15 years. Some species showed poor regeneration (none or very few found > 5 cm), relative to their representation in the surrounding landscape. This suite of mid to late successional species included the following: *Anacardium excelsum, Andira inermis, Brosimum alicastrum, Ceiba pentandra, Enterolobium cyclocarpum, Manilkara zapota, Pseudobombax septenatum,* and *Tabebuia rosea* (Table 2). However, some of these species were found in the seedling layer in considerable numbers, most notably the timber species, *Tabebuia rosea* (34 seedlings in 1.35 ha). In addition, > 10 seedlings of *Andira inermis, Pseduobombax septenatum* and *Enterolobium cyclocarpum* were recorded in all plots combined (1.35 ha) (Table 3).

Of the woody species > 5 cm in dbh, half of the identified species had biotic dispersal modes and the other half of the identified species had abiotic dispersal modes (Croat, 1978, Janzen 1984, Griscom & Ashton 2011) (Table 2). By stem count (> 5 cm dbh), 53% were abiotically dispersed , 47% were biotically dispersed. However, abiotic and biotic dispersal modes were not equally represented in the seedling and sapling layer. Of the total number of woody species < 5 cm dbh, 70% were abiotically dispersed and 30% were biotically dispersed; 20 of the species were biotically dispersed and 18 species were abiotically

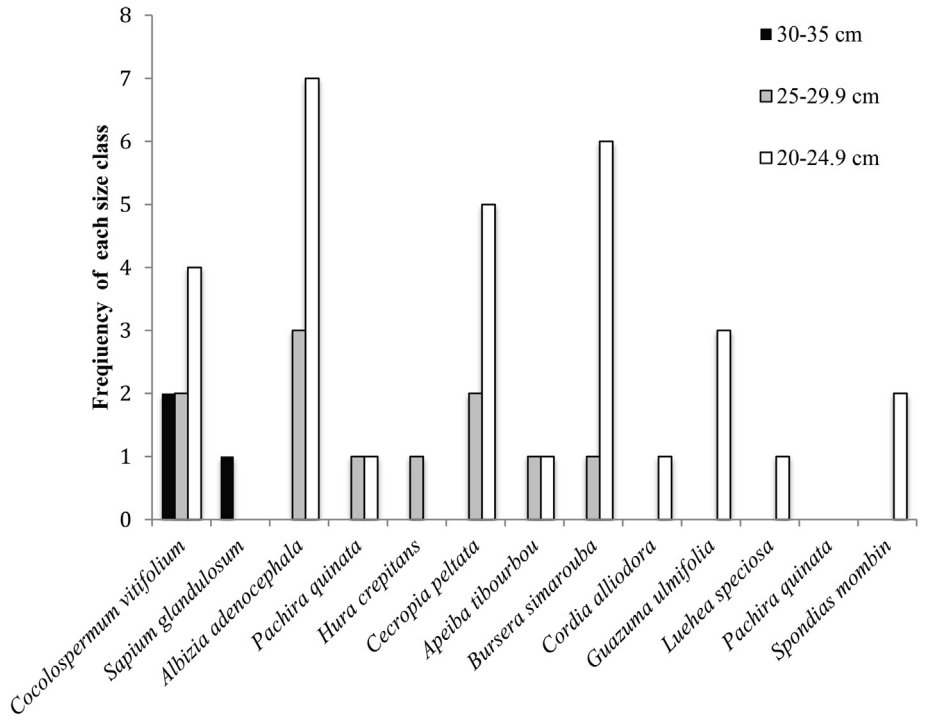

Fig. 2. Size class distribution of tree species greater than or equal to 20.0 cm dbh within all experimental plots.

Table 2
Percent of each tree species > 5 cm dbh inventoried within experimental plots at 5 years and 15 years and within remnant riparian forest. Bolded species are considered timber species (Gerard et al., 2017). Species dispersal mode is also given (Croat, 1978, Janzen 1984, Griscom & Ashton 2011).

Species (> 5 cm)	5 years	15 years	Remnant Riparian forest	Dispersal Mode
Acacia collinsii		2.0		Ants
Albizia adinocephala		3.0	1.0	Wind
Allophylus racemosus		0.4		Birds
Amphilophium paniculatum		0.1		Water
Anacardium excelsum			1.0	Bats
Andira inermis			1.0	Bats
Annona purpurea	4.0	1.0	1.0	Mammals, Birds
Apeiba tibourbou		0.4		Wind
Astronium graveolens		4.0	3.0	Wind
Bauhinia ungulata		7.0		Wind
Brosimum alicastrum			1.0	Mammals, Birds
Bunchosia odorata		0.4		Mammals, Birds
Bursera simaruba		5.0	4.0	Birds, Monkeys
Byrsonima crassifolia		1.0		Birds
Calycophllum candidissimum	1.0	3.0	4.0	Wind
Casearia aculeata		0.3		Birds
Cecropia peltata	6.0	2.0	7.0	Birds, Bats
Cedrela odorata		2.0	3.0	Wind
Ceiba pentandra			1.0	Wind
Chomelia spinosa		4.0		Birds
Calycophyllum candidissimum	1.0	0.3		Wind
Cochlospermum vitifolium	2.0	4.0	3.0	Wind
Combretum decandrum		0.1		Wind
Cordia alliodora	2.0	12.0	6.0	Wind
Cordia collococca	1.0	0.5		Mammals, Birds
Cordia panamensis		2.0	3.0	Mammals, Birds
Coursertia ferruginea		3.0		Wind
Dalbergia retusa		0.3	1.0	Wind
Diphysa americana		2.0	1.0	Wind
Enterolobium cyclocarpum		0.7	4.0	Ungulates, Rodents
Eugenia hiraeifolia		0.9	1.0	Mammals, Birds
Genipa america		3.0	3.0	Mammals, Birds
Guazuma ulmifolia	60	19.0	22.0	Ungulats, Bats
Hamelia patens		0.4		Birds
Hura crepitans	1.0	1.0	8.0	Wind
Lantana trifolia		0.2		Mammals, Birds
Licania arborea		0.1		Bats
Lippia americana	1.0	0.2		Unknown
Lonchocarpus velutinus		0.3	1.0	Wind
Luehea speciosa	2.0	0.6		Wind
Machaerium biovulatum		0.1		Wind
Machaerium microfolium	1.0	1.0		Wing
Macherium pittieri		0.7		Wind
Maclura tinctoria		0.3	3.0	Bats
Manilkara achras			1.0	Mammals
Muntingia calabura	1.0			Birds, Bats
Pachira quinata		0.4	1.0	Wind
Pithecellobium lanceolatum		0.1		Birds
Platymiscium pinnatum		0.4		Wind
Pouteria campechiana	1.0	0.1	2.0	Monkeys
Pseudobombax septenatum			1.0	Wind
Pseudosamanea guachapele		0.1	1.0	Wind
Psidium guineense		0.4		Mammals, Birds
Sapium glandulosum		0.5	4.0	Birds
Sciadodendron excelsum		0.4	4.0	Birds
Securidaca diversifolia		0.1		Wind
Senna dariensis		0.1		Mechanical
Spondias mombin		0.6	4.0	Monkeys, Bats
Stemmadenia grandiflora		2.0		Monkeys
Sterculia apetala			1.0	Monkeys, Gravity
Swartia simplex			1.0	Birds
Tabebuia ochracea		4.0		Wind
Tabebuia rosea		0.5	3.0	Wind
Trema micranthra	1.0			Birds
Trophis racemosa		0.1		Birds, Monkeys
Vernonanthura patens	6.0			Wind

Table 3
Total number of seedlings (> 10 cm in height; < 1 m in height) encountered in experimental plots after 15 years. Bolded species are considered timber species (Gerard et al., 2017).

Species	Total number (1.35 ha)	Percent of total
Astronium graveolens	1024	27.33
Acacia collinsii	716	19.11
Bursera simarouba	417	11.13
Cedrela odorata	362	9.66
Hura crepitans	225	6.00
Diphysa americana	140	3.74
Genipa america	128	3.42
Tabebuia ochracea	113	3.02
Calycophyllum candidissimum	91	2.43
Byrsonima crassifolia	79	2.11
Cordia alliodora	66	1.76
Licania arborea	51	1.36
Guazuma ulmifolia	40	1.07
Lonchocarpus velutinus	35	0.93
Maclura tinctoria	34	0.91
Tabebuia rosea	34	0.91
Eugenia hiraeifolia	26	0.69
Albizia adenochephala	17	0.45
Pouteria campechiana	17	0.45
Cordia panamensis	15	0.40
Andira inermis	13	0.35
Enterolobium cyclocarpum	13	0.35
Luehea speciosa	12	0.32
Pseudobombax septenatum	12	0.32
Cocoloba caracasana	11	0.29
Cocolospermum vitifolium	10	0.27
Cordia collococca	8	0.21
Sapium glandulosum	8	0.21
Spondias mombin	8	0.21
Anacardium excelsum	6	0.16
Apeiba tiborou	5	0.13
Brosimum alicastrum	5	0.13
Manilkara achras	2	0.05
Dalbergia retusa	1	0.03
Pachira quinata	1	0.03
Platymiscium pinnatum	1	0.03
Sterculia apetala	1	0.03

dispersed. This may either indicate a shift to wind-dominated species through time or a higher survival rate of animal-dispersed species after they reach 5 cm dbh.

Forty-four percent of trees had vines climbing through their canopy, and almost half of these vines were > 2 cm dbh. The most common vines were *Bauhinia glabra* (62%) and *Macherium microfolium* (21%), which could achieve diameters > 5 cm dbh and often affected multiple trees simultaneously (Fig. 3). Interestingly, species that are described as shrubs (e.g., *Lippia americana, Pithecellobium lanceolatum*) showed liana traits of crushing new seedlings and expanding laterally. They were included in the liana category.

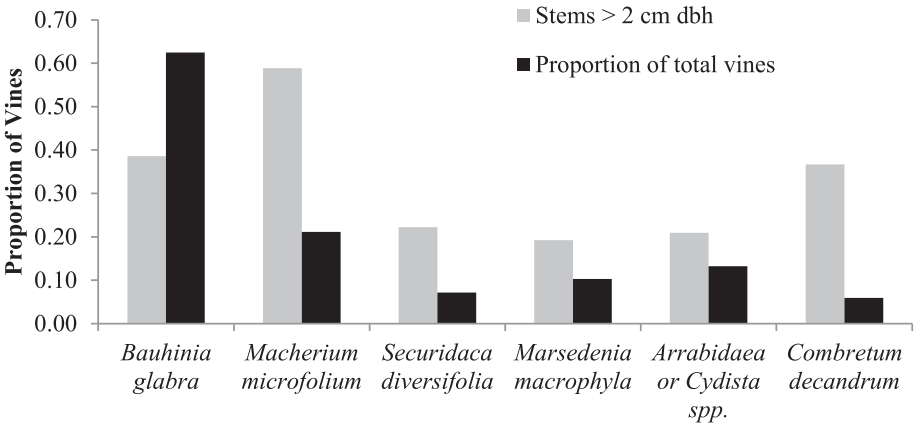

Fig. 3. Most common vine species by proportion of total vines on trees and proportion of individuals for each vine species that were > 2 cm dbh within experimental plots.

3.2. Treatment effects

Site location had a significant effect on total carbon ($F_{3, 122} = 3.94$; $p = 0.010$). Lower riparian slope plots had significantly more carbon than upper slope plots ($p = 0.045$). Upper slope plots isolated from forested riparian zones had a much smaller range of carbon (0.00–0.24 MgC per 108 m^2). In contrast, the other three site locations had upper bounds exceeding 0.32 MgC per 108 m^2 of carbon (Fig. 4).

Lower slope plots, adjacent to forested riparian zones had significantly more seedlings than the other three site locations ($F_{3, 122} = 4.6$; $p = 0.006$) (Fig. 5).

The initial application of herbicide had a lasting effect on natural regeneration. Plots applied with herbicide in 2002, overall had significantly lower total carbon compared to plots where herbicide was not applied ($F_{1, 122} = 5.67$; $p = 0.019$). The herbicide treatment did not affect tree species diversity, although some small-seeded, wind-dispersed species were more abundant where herbicide had been applied. Sixty-four percent of encountered stems of *Cedrela odorata* and 80% of *Astronium graveolens*, were found in herbicided plots, both of which are considered timber species (Fig. 6).

Live fences made up on average 16% of the total carbon in plots originally excluding cattle and 7% in plots that initially allowed cattle.

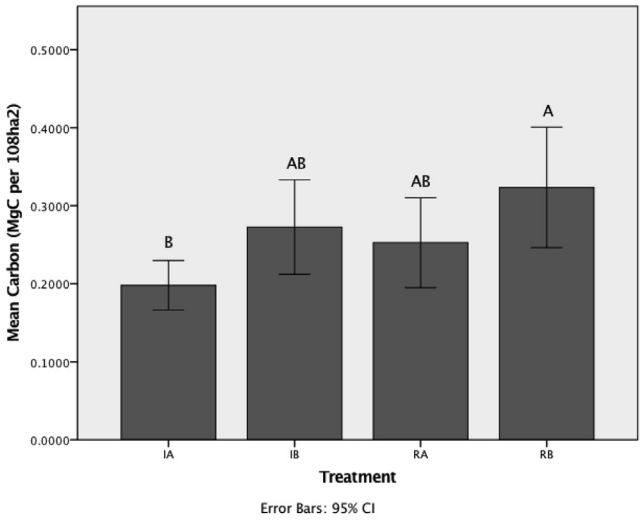

Fig. 4. The effect of site location on total carbon (above + below biomass * 0.47) (Mg C per 108 m^2) of natural regeneration > 5 cm dbh after 15 years in a dry tropical forest of Panama. Significance is displayed with upper case letters where A is significantly greater than B and AB is not significantly different from either treatment.

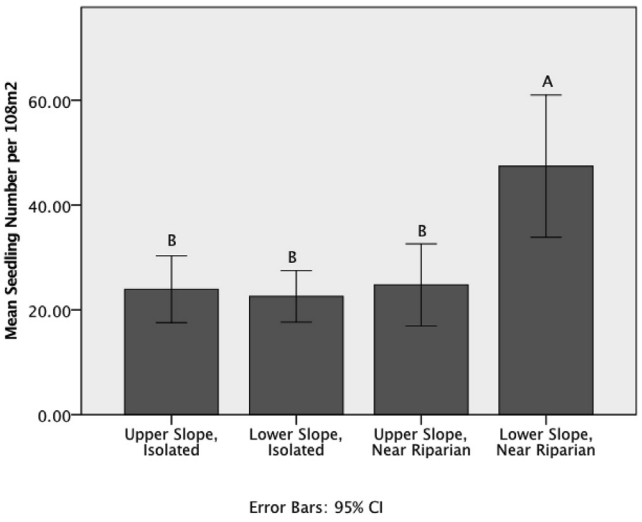

Fig. 5. The effect of site location on seedling number (> 10 cm in height; < 1 m in height) after 15 years in a dry tropical forest of Panama. Significance is displayed with upper case letters. A is significantly greater than B.

The higher density live fence (262 stems per ha) treatment had a significant effect on increasing total carbon compared to plots with a lower density of live fences (69 stems per ha), after excluding live fences themselves assigned to this treatment ($F_{1, 122} = 18.04$; $p = 0.00004$). This was true for all sites except for sites isolated from forested riparian zones on upper slopes. This was not due to lack of live fences on upper slopes adjacent to forested riparian zones as the amount of live fence carbon was similar to the other sites. Life fences did not affect tree species diversity, although some species such as *Bursera simaruba* (74% of encountered *B. simaruba* stems) and *Astronium graveolens* (82% of encountered *A. graveolens* stems) were much more common in the higher density live fence plots.

4. Discussion

Forest succession is proceeding slowly in this landscape compared to other young secondary forests in tropical dry forests. Total carbon stock (excluding live fences) has been accumulating at a rate of 1.30 MgC Ha^{-1} Yr^{-1} (2.56 MgC Ha^{-1} Yr^{-1} with life fences) with an average of 19.9 MgC per ha (36.9 Mg Ha^{-1} ABG) without including live fences (38.7 MgC per ha including live fences) after 15 years. At this rate, the forest will have similar total carbon (80 MgC Ha^{-1}) as old remnant secondary forest in another 46 years without using live stakes and 16 years with live stakes initially planted (~262 stakes per ha). Rates

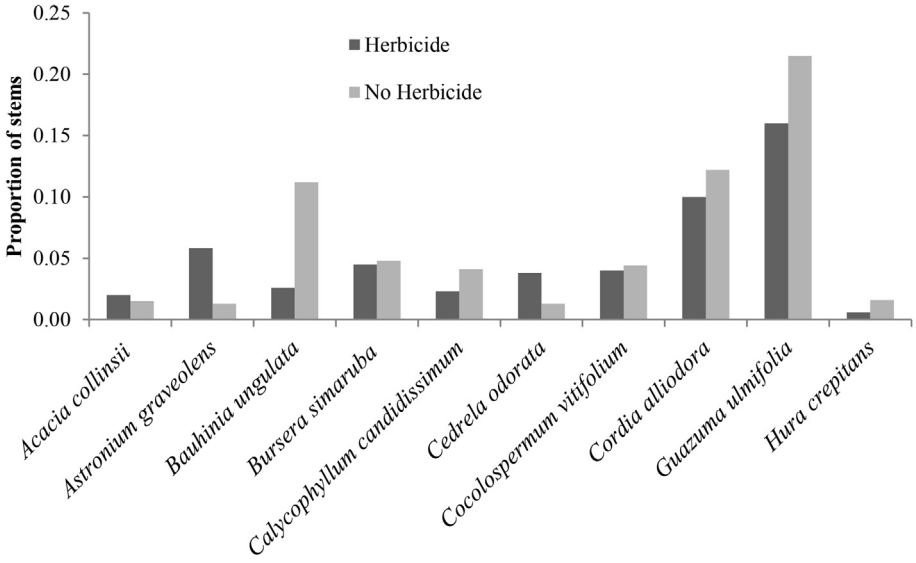

Fig. 6. Common tree species (> 5 cm dbh) in herbicided and non-herbicided experimental plots in Panama after 15 years.

and total carbon from this study site are lower compared to predicted values from other studies. Based upon refined IPCC default rates drawn from a wide review of published field data, tropical dry secondary forests (inclusive of this study site) at 15 years are expected to have a AGB of 58.5 Mg C per ha assuming a linear increase in AGB (Suarez et al., 2019). This is 37% more than the AGB quantified in this study.

The lower rates at this study site may be a consequence of extended period of pasture use (> 60 years) and steep topography, which combined with cattle ranching leads to pronounced soil erosion. These factors could greatly decrease sequestration rates in the first five years. Total soil nitrogen and carbon on lands converted to pasture in the tropics decline 20% to 60% (Johnson and Wedin, 1997; Ellingson et al., 2000; Garcia-Oliva et al., 2006; Sandoval-Perez et al., 2009). The soil compaction from cattle also reduces subsurface soil water availability (Martinez and Zinck, 2004; Zimmerman et al., 2006; Germer et al., 2010). The decline in soil productivity may explain the slower carbon accumulation rates in this system. A recent study found that edaphic factors and initial conditions explained up to 45% in the variation of successional trajectories at this same site (Estrada-Villegras et al., 2019).

Woody species diversity (^{1}D) increased three-fold between 3 and 15 years. Species dominance was expected to shift from the initial years of forest succession to more common species found in forest fragments, such as *Tabebuia* spp. and *Calycophyllum candissimum*, following the relay floristics model. After 3 years, *Guazuma ulmifolia* was the dominant tree species (60% of total stems) regenerating from stump (Griscom et al., 2009). This was still true after 15 years but its dominance had decreased to 19% of total stems (a similar percentage as the more common species found in forest fragments). This species also dominated early succession in Costa Rica, where it represented 18% of the total individuals > 5 cm dbh (Kalacska et al., 2004). *Guazuma ulmifolia* is often left in pastures because it provides food and shade for cattle and is resilient to fire because of its ability to stump sprout repeatedly (Griscom & Ashton, 2011). The forested riparian zones with the lowest number of species were almost entirely composed of *Guazuma ulmifolia*. The prevalence of *G. ulmifolia* in the landscape is likely to decline further as taller trees shade out this low stature, low branching species.

Abiotic dispersed species were predicted to be more commonly represented than biotic dispersed species in all treatments across the landscape. Loss of large tracts of forest combined with low tree diversity decreases seed dispersers (Cleary et al., 2016; de la Pena-Cuellar et al., 2015, Avila-Cabadilla et al., 2009), which in turn, decreases animal-dispersed species. Live fences help mitigate loss of fragments, serving as important wildlife corridors and habitat within the agricultural landscape (Leon and Harvey 2006; Harvey et al., 2005). Animal-dispersed species were just as common as wind-dispersed species after 15 years, by both species number and total stem count in all treatments. This is due, in part, to relic, fleshy-fruited tree species (such as *Guazuma ulmifolia*) regenerating from stump. If this species is removed from the analysis, animal-dispersed species represented 34% of all individuals counted. *Bursera simaruba*, a bird dispersed species and a common species in live fences, was the most successful tree species regenerating by seed in this landscape. Many different species of birds forage on this species during the dry season and disperse the fruit (Griscom et al., 2007). Animal-dispersed shrubs and small trees, such as *Chomelia spinulosa* and *Genipa americana*, were also common, which will attract more animals into the regenerating landscape. For example, white-capuchin monkeys (*Cebus capuchinus*), forage on *Genipa americana* and they were observed several times within the plots, which was never observed 15 years ago.

The effect of applied treatments within the landscape on total carbon changed after 15 years. Most notably, the effect of site location changed after 15 years. Initially, tree basal area was only affected by proximity to forested riparian zones and not by topography (Griscom et al., 2009). In the current inventory at a later stage in succession, lower slopes, either near or isolated from riparian zones had significantly more total carbon than upper slopes isolated from riparian zones. Lower potential maximums of carbon stock at these sites is likely due to lower soil moisture and nutrients as well as decreased seed inputs. Water run-off leaches and transports base cations from the upper slopes to the lower slopes (Scatena & Lugo 1995). Initial plantings of drought-tolerant species is expected to have the biggest impact in increasing carbon accumulation on upper slopes isolated from forested riparian zones.

Site location also determined the number of encountered seedlings. Significantly more seedlings were recorded on lower slopes adjacent to riparian zones. This may be due to forested riparian zones serving as a major source of seeds and animal seed dispersers in a landscape devoid of large forest fragments (Nepstad et al.1990, Gerhardt & Hytteborn 1992, Guevara et al. 1992, Aide 2000). However, most of these seedlings are unlikely to progress to the sapling stage due to intense competition and the presence of both herbaceous and woody lianas.

The effect of an active management treatment used to decrease the dominance of exotic grasses did not change over 15 years. After three years of succession, herbicide application, while increasing species

richness, reduced the density of regenerating stems because pre-existing root systems were killed by glycophosphate at the beginning of the experiment. This was still true after 15 years, with herbicided plots having significantly less total carbon than non-herbicided plots. However, some species benefited from this removal treatment. After three years, the small-seeded, *Trema micrantha*, was most competitive in these plots. Interestingly, *Trema micrantha* (generally lasting 30 years) had disappeared by 15 years. After 15 years, *Astronium graveolens,* a valuable timber species*,* benefited the most from the herbicided treatments (79% of all *A. graveolens* stems were encountered in this treatment). This suggests that a mixed management approach for grass removal may be optimal for increasing species richness and favoring small-seeded, timber species.

Live fences, which initially excluded cattle, also changed the pattern of regeneration. Increasing the number of live fences (~262 stems per ha) increased total carbon of natural regeneration compared to plots with less live fence trees. This could be due to either initially excluding cattle (2002–2004) and/or ameliorating effects of the live fences themselves. Previous studies have found that pasture trees improve microclimate conditions by reducing solar radiation, lowering air and soil temperature and reducing soil water evaporation (Uhl et al., 1982; Somarriba, 1988; Guevara et al., 1992; Callaway and Pugnaire, 1999; Padilla and Pugnaire, 2006; Santiago-Garcia et al., 2008, Hooper et al., 2004). These facilitation factors likely outweigh the negative effect of plant competition from live fences at this stage.

Management recommendations for reforestation are dependent on site. In areas close to diverse riparian zones (< 100 m) or on lower slopes, passive management is recommended, allowing natural regeneration to take its course with little input. Annual liana cutting where liana loads are heavy, requires little additional input, has been found to improve growth rates by 20% (Lai et al., 2017). Enrichment planting of late successional species with high timber value, such as *Andira inermis* and *Hymanea coubaril*, on isolated lower slopes will likely be successful and increase resources for animals as well as economic value of the land. Grass removal recommendations are more complex. After three years, a combination of grass removal treatments was recommended to accelerate forest succession (Griscom et al., 2009). This is still the recommendation after quantifying 15 year data. Both seed and stump-spouting modes of regeneration should be leveraged. Small seeded trees, such as *Astronium graveolens* (a fast-growing, timber species), do best when grass competition is eliminated and may be appropriate to use where stump-sprouters are more rare and tree seedlings are planted. If stump-sprouting tree species are abundant, then broad-spectrum systemic herbicide should be avoided, unless managing for specific small seeded timber species. Upper slopes isolated from forested riparian zones will require more intensive management, such as planting drought-tolerant species (e.g., *Brysonima crassifolia* (NTFP), *Sterculia apetala* (timber species)) if accelerated forest succession is a priority.

This study addressed tree regeneration after 15 years in long-term experimental plots within one landscape setting. Reforestation with either passive management or management with some intervention has the potential to increase terrestrial carbon sinks while providing economically valuable timber (~27% of the tree species in one hectare without enrichment planting). The findings from this study are both consistent with the conclusions of Holl and Brancalion (2020), and further indicate that not only is planting not necessary, but other forms of assisting natural regeneration may not be necessary for carbon sequestration even in degraded lands experiencing intensive competition from exotic grasses. Tropical forest regeneration mechanisms in reasonable proximity to forest fragments can be surprisingly resilient, if chronic human impacts (in this case fire and grazing) are removed. Next steps in experimental research on native forest regeneration should include investigations on (1) impact of lianas on tree growth and (2) effect of enrichment planting of late successional, timber species (such as *Ceiba pentandra, Hymanea coubaril*) at the mid-successional stage to increase diversity.

Declaration of Competing Interest

The authors declared that there is no conflict of interest.

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