Land use, fallow period and the recovery of a Caatinga forest

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ABSTRACT

Caatinga vegetation continues to be converted into mosaics of secondary forest stands, but the affect of this process on biodiversity has not yet been examined. We used 35 regenerating and old-growth stands of Caatinga to examine the recovery of plant assemblages subsequent to slash-and-burn agriculture and cattle ranching/pasture in northeastern Brazil. Plant assemblages were contrasted in terms of community structure (stem density/basal area/species richness/diversity), functional (leaf habit/reproductive traits) and taxonomic composition. Soil attributes were also examined to infer potential drivers for cross-habitat differences. As expected, plant assemblages clearly differed across a large set of community-level attributes, including all trait categories relative to leaf habit and reproduction (pollination syndrome/floral color, size, type). Overall, old-growth forest stands supported distinct and more diverse assemblages at the plot and habitat level; e.g., long-lived tree species were almost exclusively found in old-growth forest stands. For most attributes, plant assemblages subsequent to pasture exhibited intermediate values between those exhibited by old-growth forest and those of agriculture-related stands. Surprisingly, soils exhibited similar fertility-related scores across habitats. Our results indicate that: (1) sprouting/resprouting represents an important mechanism of forest regeneration; (2) assemblage-level attributes suggest recovery at distinct rates; (3) forest regeneration implies community-level changes in both vegetative and reproductive functional attributes, including directional changes; (4) Caatinga is not able to completely recover in a period of 15-yr following land abandonment; and (5) historical land use affects recovery rates and successional pathways/taxonomic trajectories. Seasonally dry tropical forests may intrinsically cover a wide range of patterns relative to successional model, recovery rates and successional pathways.

Abstract in Portuguese is available with online material.

Key words: Brazil; floral traits; forest regeneration; functional diversity; plant assemblages; pollination; reproductive traits; seasonally dry tropical forests.

HUMAN DISTURBANCES, INCLUDING SLASH-AND-BURN AGRICULTURE AND CATTLE RANCHING, represent a significant threat for tropical biodiversity (Gardner *et al.* 2009, Melo *et al.* 2013). Particularly in the case of seasonally dry tropical forests (STDF *sensu* Pennington *et al.* 2009), rural human populations will continue to convert tropical landscapes into complex mosaics consisting of agricultural fields, pasture lands, small fragments and regenerating forest patches with different ages due to cultivation-fallow cycles (Aide & Grau 2004, Sanchez-Azofeifa *et al.* 2005, Quesada *et al.* 2009). Slash-and-burn agriculture and cattle ranching are expected to threaten biodiversity persistence, ecosystem integrity and consequently some key ecosystem services such as soil and watershed protection, wildlife preservation, carbon and nutrient storage and mitigation of species extinctions (Wright & Muller-Landau 2006, Chazdon *et al.* 2009a,b). In fact, it has been argued that services provided by human-modified landscapes, including biodiversity protection, will critically depend on the potential of forest to recover (Zarin *et al.* 2005, Lawrence *et al.* 2007).

The negative effects caused by slash-and-burn agriculture/cattle ranching and the consequent ability of secondary forest patches to retain biodiversity and offer services depend on a combination of three biologically related processes: (1) disturbance regime pre- and post-land abandonment; (2) rate of forest recovery toward pre-disturbance levels (hereafter recovery rate); and (3) the successional trajectory/pathway experienced by the regenerating forest (Moran *et al.* 2000, Barlow *et al.* 2007). Accordingly, there has been an increasing interest in land use dynamics, forest regeneration mechanisms and patterns and processes relative to forest recovery rate, including the successional pathways experienced by SDTF (see Chazdon 2014). Some general observations include: (1) resprouting represents a key mechanism of forest recovery (Vieira & Scariot 2006, Pulla *et al.* 2015); (2) recovery rates vary across forest attributes, sites and biotas (Guariguata & Ostertag 2001, Chazdon 2003, Lebrija-Trejos *et al.* 2008); (3) recovery is affected/governed by a myriad of factors operating at local, landscape and regional scale (Arroyo-Rodríguez *et al.* 2015); (4) forest recovery is particularly affected by the nature of the disturbance regime during land use (size, duration and severity) and during forest recovery, *e.g.*, chronic disturbances such as firewood collection (Madeira *et al.* 2009, Griscom &

Ashton 2010, Zermeño-Hernández *et al.* 2015); (5) many successional pathways/trajectories are possible, including those leading to woody plant assemblages dominated by either invasive or ruderal flora (Ewel 1977, Burgos & Maass 2004, Colón & Lugo 2006). Despite these generalizations, uncertainties still persist as SDTFs are naturally diverse (Brown & Lugo 1990, Lebrija-Trejos *et al.* 2008), research is still concentrated in rain forests (Vieira & Scariot 2006) and several forest attributes have not been consistently examined, such as community-level functional composition (see Finegan 1996, Alvarez-Añorve *et al.* 2008, Lohbeck *et al.* 2012). This implies that recovery patterns are still relatively unknown for several forest attributes.

Caatinga vegetation consists of patches of seasonally dry tropical forest (*sensu* Pennington *et al.* 2009) and scrub vegetation covering nearly 730,000 km^2 in northeast Brazil (IBGE 1985). As do other SDTFs, the Caatinga has been frequently highlighted for having unique biota, supporting high levels of species endemism and functionally diverse plant assemblages (Machado & Lopes 2004, Leal *et al.* 2005, Machado *et al.* 2006). Slash-and-burn agriculture, cattle ranching and forestry have converted Caatinga vegetation into mosaics of regenerating forest stands with different ages continuously subjected to cultivation-fallow cycles (Sampaio *et al.* 1993). Such fallow-farming systems offer an interesting opportunity to examine patterns of land use and their effects on forest regeneration, including the functional profile of regenerating forest patches and their consequences for biodiversity conservation in human-modified landscapes, including reproductive functional diversity and its impacts on the myriad of plant attendants such as pollinators, seed dispersers and herbivores.

Here, we used 35 regenerating and old-growth stands of Caatinga to examine the recovery of plant assemblages as regeneration proceeds in human-modified landscapes. Regenerating stands are areas where shifting agriculture and pastures were abandoned about 15 yr ago. We analyzed a comprehensive set of plant assemblage attributes, including species composition and diversity of leaf habit and reproductive strategies and contrast these attributes with forest stands inhabiting former agricultural and pasture lands. We also calculated the functional diversity and functional similarity considering leaf habit and reproductive traits. As agriculture and cattle ranching result in different intensities of soil degradation (Kaschuk *et al.* 2011) and small-scale farming in the Caatinga region has been found to be highly detrimental in terms of both soil conditions and plant assemblage attributes (Pereira *et al.* 2003, Leal *et al.* 2005, Ribeiro *et al.* 2015), we test the hypotheses that: (1) land use in the Caatinga reduces species richness and diversity in pasture- and agriculture-related stands in comparison to old-growth stands; (2) land use changes the frequency of tree species and individuals within categories of leaf habit and reproductive traits and consequently changes the functional diversity of tree assemblages in regenerating the stands of Caatinga; (3) plant assemblage recovery occurs with distinct rates when comparing stands subjected to slash-and-burn agriculture and cattle ranching. Overall, we expect that: (1) forest regeneration implies directional shifts in tree assemblage attributes, which recover with distinct rates; (2) forest resilience is greater following cattle ranching; and (3) 15-yr old stands are not able to retain the biological diversity in old-growth stands (see Guariguata & Ostertag 2001, Tabarelli *et al.* 2010a, Martin *et al.* 2013).

METHODS

Study site.—This study was carried out at an experimental station and in an adjacent farm named Fazenda Caldeirão (latitude 7°59′00″ S, longitude 38°19′16″ W), both located in Pernambuco State, northeast Brazil. The IPA (Instituto Agronômico de Pernambuco) Experimental Station (3200 ha) comprises a mosaic of Caatinga vegetation, including old-growth and regenerating forest stands (A. Silva, pers. obs.). The IPA station is situated on 450–650 m plateaus with a predominance of Alfisols and Inceptisols (Machado *et al.* 1997); annual rainfall is around 700 mm, with a 7-mo dry season (data from INMET). The vegetation is typical for the Caatinga, with a predominance of Leguminosae, Euphorbiaceae, Anacardiaceae shrub and tree species (see Ferraz *et al.* 1998).

Habitat classification and plant survey.—We inventoried all woody plants with stems ≥3 cm in diameter at soil level (DSL) (except lianas and columnar cacti due to their low abundance in the studied area) into three habitat types: (1) old-growth or mature forest stands, (2) regenerating forest stands following pasture abandonment, and (3) stands following the abandonment of patches devoted to subsistence agriculture (slash-and-burn). Secondary-forest or regenerating stands were about 15-yr old and covered patches that were devoted to pasture/agriculture for decades. Prior to agriculture, slash-and-burn patches were subjected to forest clearing, including stump removal to limit stem sprouting. Plant surveys were based on 100 m^2 plots (50 m × 2 m) distributed across the three habitats as follow: (1) 14 spatially independent plots in old-growth/mature forest stands, (2) seven plots in stands regenerating following cattle ranching or pasture (hereafter pasture-related stands), and (3) 14 plots in stands regenerating after slash-and-burn agriculture or shifting cultivation (hereafter agriculture-related stands) (Table S1). Plots were 30–5500 m apart and immersed in a typical human-modified landscape, in which the matrix consists of Caatinga vegetation (dry forest and scrub vegetation patches). Sampling effort, plot size and number and spatial distribution were constrained by the presence of large vegetation patches and the availability of regenerating stands meeting two basic pre-requisites: forest protection since land abandonment and presence of historical records relative to land use. We conducted plant surveys between 2006 and 2009, in which we recorded a total of 1726 stems and assigned them into 69 woody plants species. Plant vouchers were deposited in two Herbaria in Brazil: Federal University of Pernambuco (UFP) and Instituto Agronômico de Pernambuco (IPA).

Vegetative and reproductive plant traits.—We assigned all plant species into four categorical functional traits: (1) vegetative phenology (leaf habit = leafing pattern *sensu* Frankie *et al.* 1974,

Morellato *et al.* 2000, and Tabarelli *et al.* 2010b), (2) floral biology, (3) sexual systems (following Girão *et al.* 2007 and Lopes *et al.* 2009), and (4) pollination syndromes, summing up 38 traits. In each category, traits were mutually exclusive (Table 1). Species assignment was based on: (1) floras and botanical monographs (e.g., Andrade-Lima 1989, and Lorenzi 2002a,b), (2) web searches, including published and referenced data, (3) field observations and a survey of specimens from the UFP and IPA Herbaria, and (4) our personal knowledge and other published observations (see Machado & Lopes 2003, 2004, Machado *et al.* 2006 for a review). The few species (7.2%) that were not assigned to any trait categories were excluded from statistical analyses. Prior to the data analysis (described below), percentages of species and individuals within each trait (dependent variables) were arcsine-transformed (Sokal & Rohlf 1995, Gotelli & Ellison 2004).

We adopted pollination- and flower-related traits because: (1) flowers represent a wide spectrum of resources for plant attendants including a myriad of pollinator and herbivore groups, ranging from diverse small insects (DSI) to endemic hummingbirds in the Caatinga; (2) changes in the functional profile of plant assemblages, including functional diversity of reproductive traits, are likely to cascade over population, community and ecosystem level processes; (3) plant assemblages in the Caatinga have long been recognized as extremely diverse in terms of reproductive traits (Machado & Lopes 2004, Machado *et al.* 2006), including several species bearing specialized flowers and strategies; and (4) pollination- and flower-related traits, syndromes and strategies are much more diverse than other traits related to plant life history such as dispersal syndrome (most Caatinga species bear abiotically dispersed seeds). Accordingly, pollination- and flower-related traits represent key indicators to address community-level functional recovery, and as they represent a unique component of Caatinga biodiversity, should be protected from threats brought about by land-use changes.

FUNCTIONAL DIVERSITY.—Here, a functional group was defined as a set of tree species within the same category of phenological and reproductive traits, *i.e.*, a set of species sharing a life-history trait as previously adopted elsewhere (see Mayfield *et al.* 2005, Girão *et al.* 2007, Lopes *et al.* 2009). Therefore, functional composition is used in the text to refer to the percentage of species and individuals within these trait-related or functional groups. Evenness-based indices for estimating the functional diversity have been frequently recommended (see Petchey & Gaston 2002, Petchey *et al.* 2004, and Ricotta 2005). The functional diversity of vegetative phenology (leaf habit), pollination syndromes and floral biology traits (size, type, color) in old-growth and regenerating stands was therefore calculated on the basis of Shannon's (log base 2) and Simpson's indices (Krebs 1989), according to Girão *et al.* (2007) and Lopes *et al.* (2009) and described as follows. We used these two metrics to evaluate the contribution of richness and evenness to the diversity scores. Considering trait categories as equivalent to species, we calculated these indices twice for each of the 35 plots: first using the number of species within each category as an equivalent of individuals; and second by using the number of individuals assigned to each category (see Girão *et al.* 2007 and Lopes *et al.* 2009 for details).

SOIL FEATURES.—To infer the factors affecting forest recovery, we examined the soil attributes across the three habitats as follows. We took soil samples randomly within each 100 m^2 plot by extracting soil cores of 6 cm in diameter and 20 cm in depth. We removed litter and coarse woody debris (>2 cm in diameter) prior to soil sampling. All soil samples were ground, sieved (2 mm mesh), air-dried in the lab and then oven-dried at 40°C. Total soil organic carbon (C) was determined by wet oxidation, total nitrogen (N) was determined using Kjeldahl extraction, phosphorus (P) was determined using the phosphomolybdic acid method recommended for soils with low phosphorus concentrations, and effective cation exchange capacity (CEC) was measured. Carbon and nitrogen were determined by a specialized commercial agronomic laboratory (AGROLAB – Análises Ambientais Ltda., Casa Forte, Recife, PE, Brazil); phosphorous content and soil physical attributes were measured by the Instituto Agronômico de Pernambuco (IPA). All procedures followed the recommendations of the Brazilian Ministry of Agriculture for soil fertility analyses (EMBRAPA, 1997).

DATA ANALYSIS.—We used analysis of variance to compare the three habitats in terms of stem density, proportion of individuals

TABLE 1. *Major classes of vegetative phenology (leaf habit) and reproductive traits with their respective categories observed in this study.*

Traits	Trait categories
1 Leaf habit[1]	1. deciduous and 2. evergreen
2 Floral biology	
Color[2]	1. orange, 2. yellow, 3. white, 4. green (including beige and cream), 5. lilac/purple (including blue), 6. pink, and 7. red
Size[2]	1. very small (≤4 mm), 2. small (>4 ≤ 10 mm), 3. medium (>10 ≤ 20 mm), 4. large (>20 ≤ 30 mm), and 5. very large (>30 mm)
Type[3]	1. open, 2. camera, 3. bell (including funnel), 4. flag, 5. gullet, 6. inconspicuous (INC), 7. brush, and 8. Tube
Reward	1. nectar, 2. pollen, 3. brood or mating places/floral tissues (BMFT), and 4. Oil
3 Pollination syndromes[4]	1. cantharophily (hereafter beetles), 2. sphingophily (hereafter sphingids/hawkmoths), 3. melittophily (hereafter bees, including wasps), 4. myophily (flies), 5. ornitophily (birds), 6. psychophily (butterflies), 7. chiropterophily (bats), and 8. pollination by diverse small insects (DSI).
4 Sexual system (morphological expression)	1. hermaphrodites, 2. dioecious (including all subtypes), 3. monoecious, and 4. andromonoecious

[1]Frankie *et al.* (1974) and Morellato *et al.* (2000); [2]*sensu* Machado and Lopes (2004); [3]modified from Faegri and van der Pijl (1979); [4]*sensu* Faegri and van der Pijl (1979).

with regrowth, basal area, plant species richness, species diversity, functional composition (proportion of species within each functional group) and functional diversity. For species richness and number of individuals (stem density), we used square-root transformations, whereas for the proportion of individuals with regrowth, we adopted the arcsin transformation (Gotelli &

Ellison 2004). Species richness per habitat was assessed with species-individual accumulation curves after 1000 randomizations (following Gotelli & Colwell 2001) in the vegan package in R (Oksanen *et al.* 2015). To document levels of taxonomic and functional similarities between habitats, we performed a non-metric multidimensional scaling (NMDS) ordination of all 35

TABLE 2. *Frequency (mean ± SE) of species and individuals within categories of leaf habit and reproductive traits (color, size, floral type, and reward), which occur in habitats of Caatinga with different land use histories: old-growth = core forest areas of Caatinga (areas of mature forest without history of anthropogenic disturbance during the last four decades); pasture = regenerating stands, 15-yr old areas following the abandonment of cattle ranching/pastures; and agriculture = regenerating stands, 15-yr old areas following the abandonment of shifting-agriculture. Significant differences in Tukey post-hoc comparisons between-habitat types are indicated by different letters in the same row. Bold values indicate significant differences (P<0.05).*

Traits/Categories	Old-growth % species	Pasture % species	Agriculture % species	ANOVA F	P	Old-growth % individuals	Pasture % individuals	Agriculture % individuals	ANOVA F	P
Leaf habit (N = 51 spp.)										
Deciduous	1.28 ± 0.04 a	1.49 ± 0.04 b	1.49 ± 0.04 b	**7.31**	**0.0028**	1.35 ± 0.04 a	1.53 ± 0.02 b	1.54 ± 0.01 b	**10.87**	**0.0004**
Evergreen	0.28 ± 0.04 a	0.07 ± 0.04 b	0.07 ± 0.04 b	**7.31**	**0.0028**	0.21 ± 0.04 a	0.03 ± 0.02 b	0.03 ± 0.01 b	**10.97**	**0.0004**
Color (N = 60 spp.)										
Orange	0.00	0.00	0.05 ± 0.03	1.58	0.21	0.00	0.00	0.02 ± 0.01	1.57	0.22
Yellow	0.23 ± 0.03 a	0.40 ± 0.04 b	0.44 ± 0.04 b	**8.00**	**0.0018**	0.21 ± 0.03 a	0.32 ± 0.06 ab	0.40 ± 0.06 b	**3.32**	**0.04**
White	0.69 ± 0.01 a	0.78 ± 0.06 ab	0.82 ± 0.03 b	**4.90**	**0.01**	0.62 ± 0.02 a	0.93 ± 0.11 b	1.04 ± 0.06 b	**16.41**	**<0.0001**
Green	0.67 ± 0.01 a	0.50 ± 0.09 a	0.24 ± 0.07 b	**15.13**	**<0.0001**	0.75 ± 0.02 a	0.40 ± 0.09 b	0.10 ± 0.03 c	**66.59**	**<0.0001**
Lilac	0.05 ± 0.02	0.04 ± 0.04	0.00	1.56	0.22	0.07 ± 0.03	0.02 ± 0.02	0.00	1.97	0.15
Pink	0.05 ± 0.02	0.03 ± 0.03	0.02 ± 0.02	0.25	0.77	0.07 ± 0.04	0.03 ± 0.03	0.01 ± 0.01	0.88	0.57
Red	0.30 ± 0.03	0.18 ± 0.06	0.28 ± 0.05	1.20	0.31	0.24 ± 0.03	0.16 ± 0.05	0.17 ± 0.03	1.23	0.31
Size (mm) (N = 56 spp.)										
Very small (≤4)	0.58 ± 0.02 a	0.46 ± 0.02 a	0.24 ± 0.06 b	**15.31**	**<0.0001**	0.59 ± 0.02 a	0.27 ± 0.03 b	0.14 ± 0.04 b	**45.65**	**<0.0001**
Small (>4 ≤ 10)	0.58 ± 0.02 a	0.57 ± 0.03 a	0.73 ± 0.04 b	**6.72**	**0.0033**	0.63 ± 0.03 a	0.66 ± 0.10 ab	0.83 ± 0.04 b	**5.67**	**0.0079**
Medium (>10 ≤ 20)	0.31 ± 0.04	0.44 ± 0.03	0.29 ± 0.04	2.27	0.11	0.28 ± 0.04	0.33 ± 0.07	0.33 ± 0.07	0.16	0.84
Large (>20 ≤ 30)	0.26 ± 0.03	0.27 ± 0.07	0.31 ± 0.04	0.38	0.68	0.22 ± 0.03	0.23 ± 0.07	0.19 ± 0.03	0.23	0.79
Very large (>30)	0.42 ± 0.03	0.45 ± 0.01	0.42 ± 0.06	0.10	0.9	0.39 ± 0.03	0.58 ± 0.06	0.39 ± 0.07	2.32	0.11
Floral type (N = 60 spp.)										
INC[a]	0.57 ± 0.02 a	0.46 ± 0.02 a	0.24 ± 0.06 b	**14.53**	**0.0001**	0.58 ± 0.02 a	0.27 ± 0.03 b	0.14 ± 0.04 b	**44.53**	**<0.0001**
Open	0.44 ± 0.03	0.50 ± 0.03	0.54 ± 0.02	2.82	0.07	0.51 ± 0.04	0.62 ± 0.05	0.66 ± 0.06	1.98	0.15
Flag	0.35 ± 0.03 a	0.54 ± 0.04 b	0.51 ± 0.02 b	**9.81**	**0.0007**	0.39 ± 0.04 a	0.64 ± 0.08 b	0.61 ± 0.05 b	**6.53**	**0.004**
Brush	0.45 ± 0.02	0.38 ± 0.02	0.42 ± 0.04	0.73	0.50	0.34 ± 0.03	0.30 ± 0.05	0.30 ± 0.05	0.25	0.78
Tube	0.35 ± 0.02	0.24 ± 0.06	0.35 ± 0.05	1.20	0.31	0.29 ± 0.03	0.16 ± 0.05	0.22 ± 0.05	1.66	0.20
Camera	0.05 ± 0.02	0.03 ± 0.03	0.00	1.64	0.20	0.07 ± 0.04	0.03 ± 0.03	0.00	1.46	0.24
Bell	0.03 ± 0.02	0.14 ± 0.07	0.10 ± 0.04	1.33	0.27	0.02 ± 0.01	0.11 ± 0.06	0.06 ± 0.03	1.71	0.19
Gullet	0.07 ± 0.03 a	0.00 ab	0.00 b	**3.76**	**0.03**	0.06 ± 0.03 a	0.00 a	0.00 a	**3.43**	**0.04**
Reward (N = 59 spp.)										
Nectar	1.41 ± 0.04	1.44 ± 0.06	1.33 ± 0.05	0.87	0.57	1.42 ± 0.05	1.47 ± 0.04	1.45 ± 0.03	0.33	0.72
Oil	0.01 ± 0.01	0.04 ± 1.19	0.00	1.03	0.36	0.01 ± 0.01	0.03 ± 0.03	0.00	0.96	0.60
Pollen	0.07 ± 0.03 a	0.07 ± 0.04 a	0.23 ± 0.05 a	**3.50**	**0.04**	0.06 ± 0.03	0.04 ± 0.02	0.11 ± 0.03	1.18	0.32
BMFT[b]	0.09 ± 0.03 a	0.03 ± 0.03 ab	0.00 b	**3.65**	**0.03**	0.09 ± 0.04	0.03 ± 0.03	0.00	2.73	0.07

[a]INC, inconspicuous.

[b]BMFT, brood or mating places/floral tissues.

plots based on the Chao-Sorensen abundance-based similarity index (Chao *et al.* 2005). The advantage of using this index is that it is not biased by abundant species and performs well in cases of unequal sampling, contrary to the classical indices Morisita–Horn and Sorensen (Chao *et al.* 2005, 2006). This analysis was performed in the 'fossil' package in R (Vavrek 2011).

To analyze differences between regenerating and old-growth plots concerning functional similarity, we used the index proposed by Pavoine and Ricotta (2014):

$$S_{\text{Sørensen}} = \frac{\sum_{ij} x_i z_j \sigma_{ij}}{\frac{1}{2} \sum_{ij} x_i x_j \sigma_{ij} + \frac{1}{2} \sum_{ij} z_i z_j \sigma_{ij}}$$

where x and z are the relative abundances of the species found in community A and B, respectively, and σ is the Gower distance among traits. The use of the Gower distance is recommended by Pavoine and Ricotta (2014) for categorical variables, which are standardized before calculation. $S_{\text{Sørensen}}$ is an extension of the Rao Quadratic Entropy index and is bounded between 0 and 1, from total dissimilarity to total similarity between plots, respectively (Pavoine & Ricotta 2014). $S_{\text{Sørensen}}$ is associated with other functional similarity indices, such as: S_{st}, $S_{\text{Sokal-Sneath}}$, S_{Jaccard} and S_{Ochiai}. In fact, we calculated all the indices proposed by Pavoine and Ricotta (2014) and we found the same results. For simplicity, we only present here the results of $S_{\text{Sørensen}}$. The analyses were performed in R using the function 'dsimcom' provided by Pavoine and Ricotta (2014) and we used the traits showed in Table 2.

An analysis of similarity (ANOSIM) test was performed to examine the effect of habitat type on the taxonomic and functional similarities between plots (Clarke & Gorley 2001). The functional similarity was correlated with taxonomic similarity using a Mantel test after 1000 randomizations.

RESULTS

Stem density exhibited similar scores across the three Caatinga habitats: 47.07 ± 2.8 (stem/plot; mean $\pm$ SE) in old-growth forest stands, 55.7 ± 5.5 in pasture-related stands, and 48.3 ± 5.5 in agriculture-related stands ($F_{32,2} = 13.45$, $P = 0.49$). Although stumps were reported to have been removed as part of slash-and-burn operations (in agriculture-related stands), habitats differed in terms of stem regrowth or number of multitrunk individuals, since $17.3 \pm 2.8\%$ of all plant individuals sampled in old-growth stands were regrowth or multitrunk individuals, while this value reached $43.1 \pm 4.2\%$ across pasture- and $41.2 \pm 3.9\%$ in agriculture-related stands ($F_{32,2 \, v} = 16.25$, $P < 0.001$). Basal area also differed between habitats, with old-growth stands presenting the highest scores: 56.81 ± 9.05 m^2/ha, vs. 24.85 ± 2.78 m^2/ha in pasture- and 14.74 ± 1.24 m^2/ha in agriculture-related stands (ANOVA, $F_{32,2} = 13.44$, $P < 0.001$). In addition, plant assemblages exhibited consistent differences in terms of species richness and diversity as well as functional diversity. Species richness was significantly higher in old-growth (15.7 ± 0.8 species/100 m^2) than pasture- (11.7 ± 1.7) and agriculture-related (7.5 ± 0.6) stands ($F_{32,2} = 21.71$, $P < 0.0001$). Species richness also differed at habitat scale as indicated by rarefaction curves: old-growth stands had a similar number of species when compared to pasture-related stands, whereas these habitats supported higher numbers of species as compared to agriculture-related stands (Fig. 1). Species diversity was also higher in old-growth stands (H' = 2.4 ± 0.06) as compared to either pasture- (1.86 ± 0.17) or agriculture-related stands (1.41 ± 0.07; $F_{32,2} = 34.2$, $P < 0.0001$). Interestingly, agriculture-related stands reached between 26.2 percent (basal area) and 58.7 percent (species diversity) of the scores presented by old-growth stands. Furthermore, long-lived trees (*e.g.*, *Licania rigida* Benth., *Spondias tuberosa* Arruda, *Tabebuia impetiginosa* (Mart. ex DC.) Standl., *Cordia trichotoma* (Vell.) Arrâb. ex Steud., *Hymenaea courbaril* L.) were almost exclusively found in old-growth stands.

Plant assemblages were dominated by hermaphroditic species bearing small (4–10 mm), white and inconspicuous flowers (over one-third of all species and individuals), which offer nectar as a resource for pollinators (Table 2). This general pattern differed in terms of the relative abundance of species and individuals within several trait categories (i.e., contrasting functional profiles) by comparing mature vs. regenerating stands or contrasting regenerating stands emerging from pasture vs. agriculture. Briefly, mature forest stands exhibited a higher proportion of species/individuals bearing inconspicuous/small, white/green
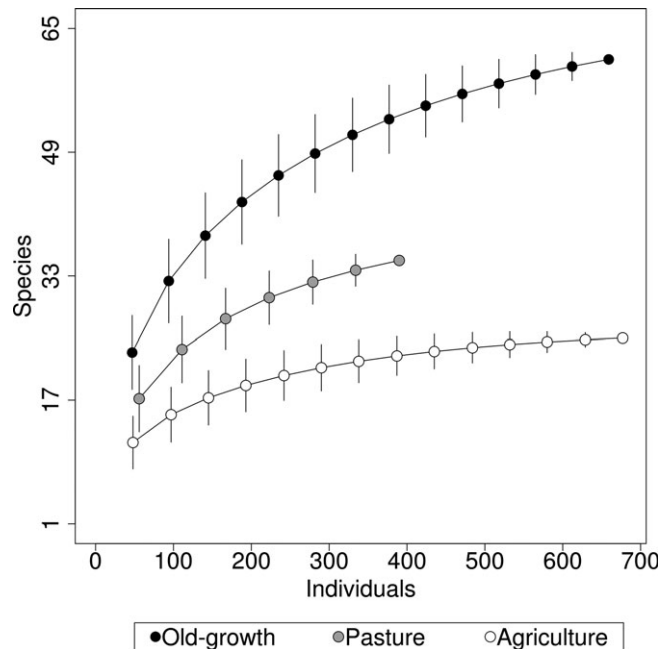

FIGURE 1. Accumulation curves of species per individual (S_{obs} mean $\pm$ 95% confidence limits) in three habitats of Caatinga, from regenerating to mature forest: (1) core forest areas (old-growth areas of forest without history of anthropogenic disturbance during the last four decades), (2) pasture (regenerating stands, 15-yr old areas following the abandonment of cattle ranching/pastures), and (3) agriculture (regenerating stands, 15-yr old areas following the abandonment of shifting-agriculture).

flowers, whereas regenerating forest stands exhibited a higher frequency of white/yellow, small and flag/open type flowers. In addition, species with more specialized strategies (*e.g.*, offering oil and brood or mating places/floral tissues [BMFT]) were not found among agriculture-related regenerating stands. Species with syndromes suggesting pollination by diverse small insects (DSI) and bees dominated all plant assemblages across all habitat types, but regenerating stands following agriculture diverged more clearly from mature forest stands; *i.e.*, they supported a higher frequency of species pollinated by bees and a complete absence of species pollinated by beetles, birds and vertebrates (chiropterophily + ornithophily) (Fig. 2), in addition to a lower frequency of dioecious species and individuals (Fig. 3). Finally, disturbed habitats showed a higher proportion of deciduous species (97.9 ± 1.31% and 97.4 ± 1.44%, for pasture- and agriculture-related stands, respectively) and individuals (99.4 ± 0.34%, for pasture, 99.5 ± 0.24%, for agriculture) than mature forest stands (89–93%; $F_{32,2} = 6.7$, $P = 0.004$; $F_{32,2} = 7.1$, $P = 0.003$). By contrast, evergreen species and

individuals were much more frequent in mature forest stands (6–10% of all individuals and species) than across regenerating stands (ca. 2.5%; $F_{32,2} = 6.7$, $P = 0.004$ in terms of species, and ca. 0.5%; $F_{32,2} = 7.1$, $P = 0.003$, in terms of individuals) (Table 2). Regenerating stands following pastures, in almost all functional attributes, exhibited intermediate scores as compared to other habitats. In summary, habitats differed in 46.1 percent of the 39 categories of leaf habit and reproductive traits analyzed (considering species richness), and in 30.8 percent of the categories considering species abundance. On the other hand, 100 percent of the analyzed categories of traits relative to leaf habit and reproductive traits (pollination syndrome, floral color, size, and type) differed between habitats either in terms of species richness or abundance (Table 3).

Overall, functional diversity relative to leaf habit, floral size, and type was higher in old-growth forest than in regenerating stands following the abandonment of agricultural fields, regardless of the metric used to estimate them (Shannon or Simpson). Such a trend emerged by considering trait categories
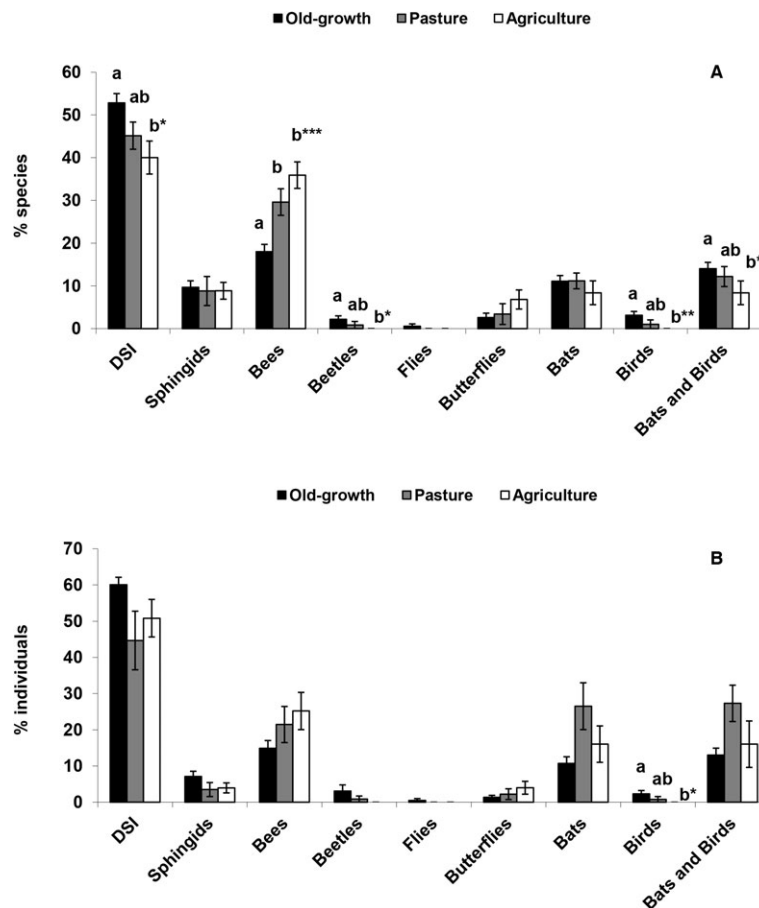

FIGURE 2. Frequency of species (A) and individuals (B) in the categories of pollination syndromes ($N = 62$ spp.), occurring in habitats of Caatinga with different land use histories: old-growth = core forest areas of Caatinga (areas of mature forest without history of anthropogenic disturbance during the last four decades); pasture = regenerating stands, 15-yr old areas following the abandonment of cattle ranching/pastures; and agriculture = regenerating stands, 15-yr old areas following the abandonment of shifting-agriculture. Bars = frequency in each of the three habitats; letters illustrate the statistical difference among them; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; DSI = pollination by diverse small insects.
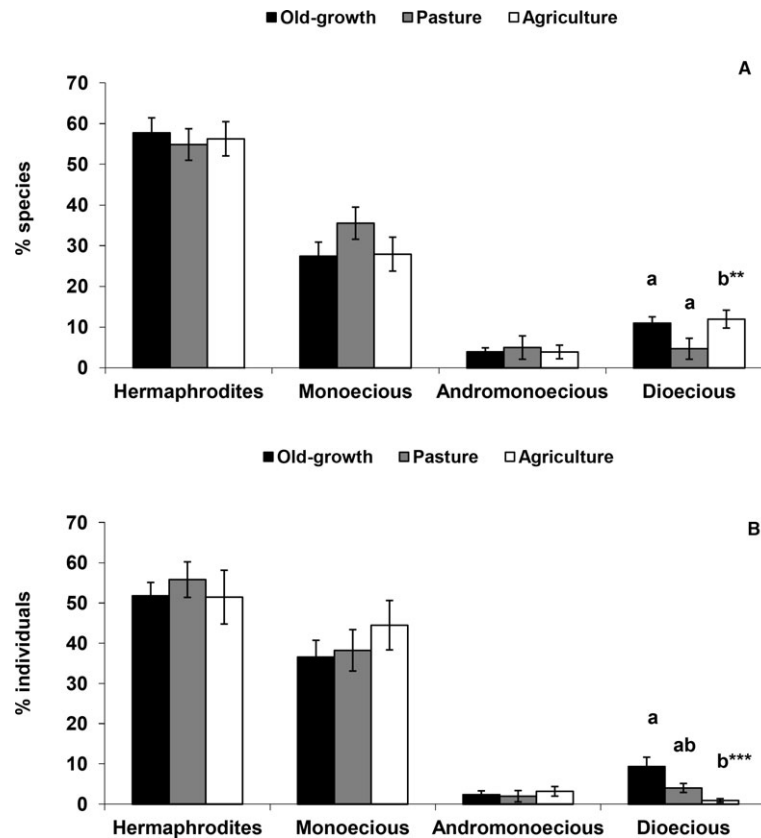
FIGURE 3. Frequency of species (A) and individuals (B) in the categories of sexual systems ($N = 64$ spp.), occurring in habitats of Caatinga with different land use histories: old-growth = core forest areas of Caatinga (areas of mature forest without history of anthropogenic disturbance during the last four decades); pasture = regenerating stands, 15-yr old areas following the abandonment of cattle ranching/pastures; and agriculture = regenerating stands, 15-yr old areas following the abandonment of shifting-agriculture. Bars = frequency in each of the three habitats; letters illustrate the statistical difference among them; $**P < 0.01$; $***P < 0.001$.

among either species or individuals (Table 3), and in many cases regenerating stands reached just a fraction of the old-growth scores (e.g., leaf habit diversity). Other traits, such as pollination syndrome, also had higher frequencies in mature when compared to regenerating stands when considering species abundance and some other cross-habitat differences; e.g., floral color (Table 3). Considering composition, the NMDS ordinations of tree plots based on taxonomic similarity segregated agriculture-related from old-growth forest plots, while pasture-related stands exhibited intermediate scores (Fig. 4A). Agriculture- and pasture-related stands formed a different group to old-growth forests for functional similarity (Fig. 4B). These patterns were supported by ANOSIM ($R = 0.15$; $P < 0.05$ for taxonomic similarity and $R = 0.72$; $P < 0.05$ for functional similarity; Fig. 4). A Mantel test confirmed that taxonomic and functional similarities were correlated ($r = 0.39$; $P < 0.05$). Finally, soils across old-growth forest and regenerating stands presented similar scores. The exceptions were percentage of clay, which was higher in agriculture-related, followed by pasture-related and old-growth stands, and coarse sand, which was higher in old-growth, followed by pasture-related and agriculture-related stands (Table 4).

DISCUSSION

Overall, most of our initial expectations were confirmed and our whole set of findings permit six interesting conclusions about the nature of the regeneration process in the Caatinga vegetation following shifting agriculture and cattle ranching (i.e., secondary succession). First, sprouting or resprouting represents an important mechanism for forest regeneration, although stumps are frequently removed in agriculture-related stands. Second, assemblage-level attributes suggest recovery at distinct rates—rapidly in the case of stem density but slower regarding species richness and functional diversity. Third, forest regeneration implies community-level changes (i.e., successional trends) in both vegetative and reproductive functional attributes, including changes correlated with land use (agriculture vs. pasture). For instance, agriculture-related stands supported a reduced number or no species or individuals at all that bear more specialized reproductive traits (e.g., floral types other than inconspicuous/open flowers, offering resources that were at least partly concealed, or specialized resources such as oil), pollinated by specialist vectors (e.g., flying vertebrates, sensu Kang & Bawa 2003), and phenological strategies related to old-growth species, such as foliage persistence (Tabar-

TABLE 3. *Functional diversity (mean ± SE) of species and individuals within categories of leaf habit, pollination syndrome, color, size and floral type, which occur in habitats of Caatinga with different land use histories: old-growth = core forest areas of Caatinga (areas of mature forest without history of anthropogenic disturbance during the last four decades); pasture = regeneration stands, 15-yr old areas following the abandonment of cattle ranching/pastures; and agriculture = regeneration stands, 15-yr old areas following the abandonment of shifting-agriculture. Significant differences in Tukey post-hoc comparisons between-habitat types are indicated by different letters in the same column. Bold values indicate significant differences (P<0.05).*

				Floral Biology		
Functional diversity	Habitats	Leaf habit	Pollination syndrome	Color	Size	Type
Categories and species						
Shannon's (H')	Old-growth	0.12 ± 0.02 a	0.56 ± 0.02	0.51 ± 0.01	0.61 ± 0.01 a	0.68 ± 0.01 a
	Pasture	0.03 ± 0.02 b	0.53 ± 0.02	0.47 ± 0.05	0.65 ± 0.02 a	0.67 ± 0.02 ab
	Agriculture	0.03 ± 0.01 b	0.49 ± 0.02	0.45 ± 0.02	0.52 ± 0.03 b	0.62 ± 0.02 b
ANOVA	F	**7.21**	2.95	2.15	**6.86**	**3.70**
	P	**0.0029**	0.0651	0.1311	**0.0036**	**0.0348**
Simpson's (1–D)	Old-growth	0.17 ± 0.03 a	0.65 ± 0.02	0.65 ± 0.01	0.73 ± 0.01 a	0.76 ± 0.01
	Pasture	0.03 ± 0.02 b	0.66 ± 0.02	0.61 ± 0.05	0.76 ± 0.01 a	0.77 ± 0.01
	Agriculture	0.04 ± 0.02 b	0.64 ± 0.02	0.59 ± 0.02	0.65 ± 0.02 b	0.75 ± 0.01
ANOVA	F	**6.97**	0.22	2.06	**7.50**	1.02
	P	**0.0034**	0.8022	0.1417	**0.0025**	0.3716
Categories and individuals						
Shannon's (H')	Old-growth	0.08 ± 0.02 a	0.49 ± 0.01 a	0.49 ± 0.01 a	0.57 ± 0.01 a	0.63 ± 0.01 a
	Pasture	0.01 ± 0.007 b	0.48 ± 0.04 ab	0.38 ± 0.08 ab	0.51 ± 0.04 a	0.55 ± 0.04 b
	Agriculture	0.009 ± 0.005 b	0.41 ± 0.02 b	0.29 ± 0.03 b	0.42 ± 0.02 b	0.48 ± 0.02 b
ANOVA	F	**10.13**	**4.24**	**9.88**	**12.79**	**18.60**
	P	**0.0006**	**0.0226**	**0.0007**	**0.0002**	**<0.0001**
Simpson's (1–D)	Old-growth	0.11 ± 0.03 a	0.57 ± 0.02	0.63 ± 0.01 a	0.70 ± 0.01 a	0.74 ± 0.01 a
	Pasture	0.01 ± 0.006 b	0.60 ± 0.05	0.47 ± 0.10 ab	0.62 ± 0.05 ab	0.65 ± 0.03 b
	Agriculture	0.008 ± 0.004 b	0.54 ± 0.03	0.36 ± 0.05 b	0.54 ± 0.03 b	0.59 ± 0.02 b
ANOVA	F	**8.22**	0.94	**9.11**	**11.76**	**16.57**
	P	**0.0016**	0.5974	**0.0010**	**0.0003**	**<0.0001**

elli *et al.* 2010b). Fourth, our results support the idea that forest regeneration implies deterministic or directional changes in community-level attributes, such as species richness, functional attributes, and taxonomic composition (*e.g.*, the lack of long-lived tree species across regenerating stands). We shall briefly mention the occurrence of species/individuals bearing evergreen foliage, yellow, white, and green flowers, very small, small, and inconspicuous flowers, were concomitant with species bearing yellow, white, and green flowers, very small and inconspicuous flowers in addition to shifts associated with pollination by DSI, bees, and birds, which exhibited either an increment or decrease as compared to old-growth stands.

Such findings for the Caatinga vegetation reinforce the notion that in some SDTF forests, regeneration implies on the establishment of structurally, taxonomically, and functionally distinct woody plant assemblages (as compared to old-growth stands), with community-level changes occurring at different rates and involving directional replacement of species and plant trait attributes as regeneration proceeds (Lebrija-Trejos *et al.* 2008, 2010, Alvarez-Añorve *et al.* 2012). It has been frequently reported that structural attributes (*e.g.*, stem density, basal area, canopy cover) recover first, followed by species richness and

diversity, with taxonomic and functional composition requiring longer periods of time to reach predisturbance levels (Brown & Lugo 1990, Quesada *et al.* 2009, Maza-Villalobos *et al.* 2011, Alvarez-Añorve *et al.* 2012). In addition, some taxonomic and ecological groups have been documented to be replaced or appear sequentially along the regeneration trajectory (Lebrija-Trejos *et al.* 2008, 2010). Such directional replacements indicate the occurrence of a regeneration process that is more complex than the 'initial floristic composition' (*sensu* Egler 1954), which has been advocated to represent a general successional model or pathway experienced by SDFT (see Ewel 1980, Murphy & Lugo 1986, Vieira *et al.* 2006, Sampaio *et al.* 2007).

Fifth, our results suggest that Caatinga vegetation is not able to recover completely in a period of 15 yr following land abandonment. Although SDTF intrinsically differ in terms of recovery rate or resilience (*sensu* Lebrija-Trejos *et al.* 2008), most woody plant assemblage attributes of SDTF are likely to be recovered 20–70 yr after land abandonment in the absence of intense habitat degradation or disturbance (Kennard 2002, Chazdon 2003, Colón & Lugo 2006, Lebrija-Trejos *et al.* 2008, 2010, Maza-Villalobos *et al.* 2011). Caatinga biota apparently fits somewhere into this wide range, but the scores for some attributes
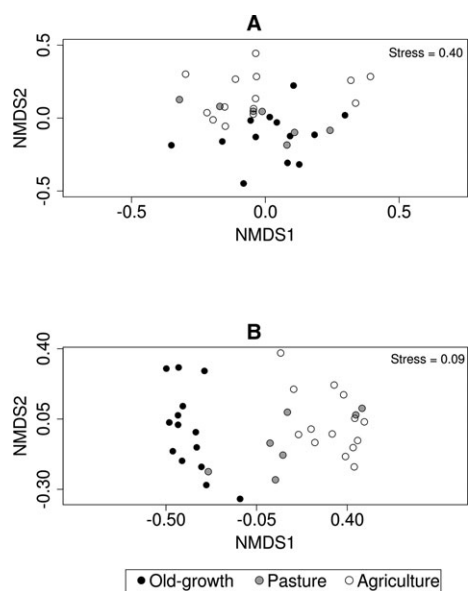
FIGURE 4. Non-metric multidimensional scaling ordination of 35 plots based on their similarity in floristic (A) and reproductive traits (B) in habitats of Caatinga with different land use histories: old-growth = core forest areas of Caatinga (areas of mature forest without history of anthropogenic disturbance during the last four decades); pasture = regenerating stands, 15-yr old areas following the abandonment of cattle ranching/pastures; and agriculture = regenerating stands, 15-yr old areas following the abandonment of shifting-agriculture. Black, grey, and white dots represent plots in old-growth (N = 14), pasture (N = 7), and agriculture (N = 14) stands, respectively.

(e.g., species richness, taxonomic composition, and functional diversity) across regenerating stands prevent the recovery of the Caatinga being classified as a rapid process (see Lebrija-Trejos et al. 2008, Mora et al. 2015). Finally, our results reinforce the notion that historical land use or disturbance regime (sensu Zermeño-Hernández et al. 2015) affects recovery rate and successional pathways/taxonomic trajectories. More precisely, forest recovery proceeded more slowly following shifting cultivation

than traditional cattle ranching as regenerating stands following agriculture supported relative to old-growth: (1) impoverished plant assemblages at plot and habitat spatial scales (e.g., evergreen and long-lived tree species); (2) lower scores of functional diversity; and (3) a distinct composition even as compared with pasture-related stands.

In fact, land use is intrinsically associated with the nature of disturbance regimes, which directly affect soil conditions (Fleischner 1994, Belsky & Blumenthal 1997, Kaschuk et al. 2011), and thus the main regeneration mechanisms (e.g., soil seed bank, sprouts, and seedlings from dispersed seeds) and, consequently, the speed of forest recovery (Kennard 2002, Powers et al. 2009), and successional trajectories (Burgos & Maass 2004, Colón & Lugo 2006). Agriculture and cattle ranching, for instance, differ in terms of fire use, weeding, fertilization, and biocide application, in addition to soil compacting due to trampling and browsing pressure (Miller & Kauffman 1998, Moran et al. 2000, Dupouey et al. 2002, Stern et al. 2002). The presence of stumps and sprouts, for example, has long been interpreted as the main regeneration mechanism exhibited by SDTF (Ewel 1977, Perkulis et al. 1997, Miller & Kauffman 1998, Ceccon et al. 2002, 2004), and their high frequency as a signal of less intensive agricultural practices, particularly the limited use of fire (Sampaio et al. 1993, Miller & Kauffman 1998).

Here, the mechanisms directly controlling Caatinga regeneration were not addressed, and since both types of regenerating stands exhibited similar soil attributes and abundance of sprouts, we can only briefly speculate on the potential processes leading to slower recovery rates in former agricultural stands. It is reasonable to expect that pasture-related stands experience increasing levels of plant invasion before abandonment, including by native tree species, in response to: (1) selective grazing by cows, goats, and sheep (Pereira et al. 2003); and (2) a lack of regular weeding operations. There are at least a dozen native shrub and tree species that are usually avoided by livestock but frequently occur across Caatinga regenerating stands, including Jatropha mollissima (Pohl) Baill. and Caesalpinia pyramidalis Tul. (see Pereira et al. 2003, Moreira et al.

TABLE 4. Soil attributes across undisturbed and regenerating stands of Caatinga vegetation in northeastern Brazil. Significant differences in Tukey post-hoc comparisons between-habitat types are indicated by different letters in the same column. Significant differences (P < 0.05) are in bold.

Physical and chemical components	Old-growth (mean ± SD)	Pasture (mean ± SD)	Agriculture (mean ± SD)	ANOVA	
				F	P
Al (cmolc/dm^3)	0	0	0.01 ± 0.02	1	0.3985
Ca (cmolc/dm^3)	6.1 ± 1.71	5.64 ± 1.76	8.62 ± 2.14	3.64	0.0572
CTC (cmolc/dm^3)	10.6 ± 1.85	10.66 ± 3.56	14.24 ± 1.66	3.45	0.0644
K (cmolc/dm^3)	0.54 ± 0.12	0.55 ± 0.21	0.48 ± 0.09	0.32	0.7358
P (mg/dm^3)	4.2 ± 1.79	7.2 ± 5.31	5.6 ± 3.05	0.83	0.5373
pH (H$_2$O)	6.32 ± 0.19	6.02 ± 0.32	6.06 ± 0.45	1.16	0.346
Clay (%)	15.40 ± 2.07 a	14.6 ± 1.67 a	23.2 ± 4.15 b	**13.93**	**0.001**
Coarse sand (%)	44.2 ± 3.11 a	40.60 ± 3.21 ab	37.8 ± 1.92 b	**6.51**	**0.0121**
Real density (g/cm^3)	2.52 ± 0.05	2.5 ± 0.01	2.53 ± 0.03	0.91	0.5675
Residual moisture (%)	2.33 ± 0.41	1.83 ± 0.37	1.96 ± 0.41	2.11	0.1629

2006, Santana *et al.* 2011). Conversely, crop stands are expected to remain free of forest invasion due to regular weeding before land abandonment. In other words, agricultural practices and plant susceptibility to grazing (in addition to potential differences in soil degradation) may explain differential forest recovery associated with land use (see also Griscom *et al.* 2005, 2009, Sampaio *et al.* 2007) as documented across our regenerating stands of Caatinga vegetation. These variables have been considered as a 'basic basket' of inseparable forces affecting vegetation dynamic across human-modified landscapes (Powers *et al.* 2009, Laliberté *et al.* 2012).

From an applied perspective (*i.e.*, biodiversity conservation in human-modified landscapes), it is clear that fallow periods of around 15 yr are not enough for regenerating stands to recover the community-level scores presented by old-growth stands, even in the presence of sources of regeneration, such as sprouts. This includes functional diversity, which has been considered to affect ecosystem productivity, persistence of biodiversity, and ecological services (Isbell *et al.* 2011). Unfortunately, the information available on land use in the Caatinga region indicates the predominance of fallows shorter than 15–20 yr (Kauffman *et al.* 1993), including the stand management for fuelwood (Brasil 2008). We argue that short fallows represent a key driver for the observed contemporary biomass collapse and biological impoverishment experienced by the Caatinga vegetation at multiple spatial scales (Leal *et al.* 2005), including long-lived and evergreen tree species (see also Ribeiro *et al.* 2015).

In synthesis, tropical forest regeneration persists as a key research topic due to a combination of both theoretical and applied issues. The Caatinga regeneration reinforces an emerging notion that the regeneration of SDTF may intrinsically cover a wide range of patterns relative to successional model, recovery rates, and successional pathway (see also Arroyo-Rodríguez *et al.* 2015). In this context, the variation observed across a comprehensive set of functional attributes in the Caatinga vegetation (including functional diversity) indicates that regeneration may be not as simple and rapid as observed in other SDTF biotas. In addition, SDTF regeneration is affected by historical land use, including the structural, taxonomic, and functional profile of woody plant assemblages involved in regeneration (see Martin *et al.* 2004, Lawrence *et al.* 2007). Accordingly, cultivation-fallow cycles or the length of fallow periods should be compatible with forest recovery rates, thus permitting regenerating stands to approach old-growth status (*i.e.*, adaptive management). In many STDFs, it may be a condition that is essential for secondary forests to serve as biodiversity repositories, particularly in SDTF exhibiting more complex patterns of recovery.

ACKNOWLEDGMENTS

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

TABLE S1. *Descriptive information about land use for the 21 regenerating stands of Caatinga vegetation in northeastern Brazil.*

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