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Authors: Mesa-Sierra, Natalia, and Laborde, Javier

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Insights for the Conservation of Native Tree Species Gleaned From the Advance Regeneration Community in a Seasonally Dry Tropical Landscape

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Natalia Mesa-Sierra¹ and Javier Laborde¹

Abstract

The pervasive loss of primary forest in the tropics means that we need a better understanding of how transforming tropical landscapes affects plant regeneration if we wish to recover and maintain the diverse composition, structure, and function of tropical forest and landscapes. Advance regeneration (AR) is a crucial stage in forest dynamics; it includes all the immature woody plants that germinate and establish and may eventually form part of the forest as adults. In this study, we describe AR in three contiguous habitats in the tropics of central Veracruz, Mexico: a protected tropical semideciduous forest, a 17-year-old secondary forest (SF), and coastal dune scrub (DS). The community attributes of the AR were analyzed among and within the three habitats as were the relationship between its spatial variability and microenvironmental conditions and the attributes of the adult woody vegetation. In total, 3,195 individuals belonging to 95 species and 40 families were recorded in 90 quadrats of 25 m² (sampling area: 2,250 m²). *Brosimum alicastrum* (Moraceae) was the most abundant species (1,498 individuals) and occurred in all three habitats. Despite having an adult community dominated by secondary species, the AR of the SF had a high degree of similarity with the primary forest. In the DS, late successional species were rare indicating it will likely take centuries for it to become a forest. Regardless of the severe fragmentation of the area and its nutrient-poor sandy soils, our results show that the seasonally dry tropical region of central Veracruz is highly resilient.

Keywords

tropical semideciduous forest, forest regeneration, successional trajectory, seedlings, saplings, landscape dynamics, defaunation

Neotropical forests are highly dynamic owing to recurring natural disturbances, such as hurricanes and medium sized to large canopy gaps generated by tree falls. Human disturbance also plays a role with a notable recent rise in high impact activities such as cattle ranching and commercial crop cultivation (Chazdon, 2014). The extensive deforestation and resulting fragmentation of Neotropical forests are so pervasive that forest regeneration itself could be compromised, thus reducing the capability of vegetation to recover a functional and structural composition similar to the one it had prior to the disturbance (Gibson et al., 2011; Lebrija-Trejos, Meave, Poorter, Pérez-García, & Bongers, 2010a; Norden et al., 2009b; Quesada et al., 2009). An important element of forest dynamics is the advance regeneration (AR) community, which includes the immature woody plants that have germinated and established (i.e., seedlings, saplings,

and juveniles) in a given site, some of which will eventually become adults and form part of the forest (Martínez-Ramos & García-Orth, 2007; Vieira & Scariot, 2006). The floristic composition and functional traits of the AR community can be used as indicators of the success of the regeneration process and its successional trajectory. In recently disturbed sites, it can be used as a guide to indicate whether the trajectory is heading toward

¹Red de Ecología Funcional Department, Instituto de Ecología, A.C., Veracruz, Mexico

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Corresponding Author:

Javier Laborde, Red de Ecología Funcional, Instituto de Ecología, A.C., Xalapa, Carretera Antigua a Coatepec 351, Xalapa, Veracruz 91070, Mexico. Email: javier.laborde@inecol.mx



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something that resembles a mature forest or whether succession is arrested or is being delayed by secondary or invasive species (Capers, Chazdon, Redondo Brenes, & Vilchez Alvarado, 2005; Chazdon et al., 2010; Norden et al., 2009b; van Breugel, Bongers, & Martínez-Ramos, 2007).

At present, tropical landscapes in Mexico are highly heterogeneous in structure and are comprised of a mosaic of habitats with different characteristics, origins, and regeneration pathways. A clear example of this is the vegetation mosaic of the La Mancha Reserve on the coast of the Gulf of Mexico (state of Veracruz). This mosaic is made up of different types of habitats, including tropical semideciduous forest (old growth), dune scrub (DS), and secondary forest (SF) of different origins and ages, among others, that grow in close proximity to each other (Castillo-Campos & Travieso-Bello, 2006). The description of the structure and dynamics of AR in this mosaic can help us to understand the current and future capacity of such a mosaic in the conservation of biodiversity and ecosystem functions in highly fragmented seasonally dry tropical landscapes. The latter is even more urgent when we take into account the high deforestation rate in Veracruz (Castillo-Campos & Travieso-Bello, 2006) and the profusion of small patches of SF throughout the state and across the entire Neotropical region (Chazdon, 2014).

There are two main potential limitations to the regeneration of vegetation in a landscape: one is seed dispersal (dispersal limitation) and the other, the conditions required for plant establishment (niche-based limitation; Larson & Funk, 2016; Norden et al., 2009a, 2009b; Powers, Becknell, Irving, & Perez-Aviles, 2009). Plants may be absent from a given site because their seeds have not been able to reach the site or because unfavorable conditions at the site prevent germination and establishment. In central Veracruz, a strong limitation is imposed by climate, which takes the form of an extended dry season (4–6 months) that represents a significant obstacle to seed germination and seedling establishment. Woody plants that form part of the AR in a given forest have germinated and established as seedlings or saplings, and in the seasonally dry tropics, they have also survived at least one dry season. Some time must pass before they are successfully recruited as adults, and they must face several hazards, even though these plants have already surmounted some of the most stringent limitations to forest regeneration in the dry tropics (Quesada et al., 2009; Vieira & Scariot, 2006).

The aim of this study was to characterize the attributes of the AR community in three contiguous habitats in the seasonally dry tropics of central Veracruz: a protected semideciduous tropical forest, a 17-year-old SF, and DS on semistabilized sand dunes. We determined the structure, floristic composition, and the dispersal syndromes

and growth forms of the AR, analyzing its spatial variation within and among the three habitats as well as the relationship of AR with local microenvironmental conditions and the structural attributes of the adult woody vegetation present in each habitat. We expect this approach to help us learn whether the AR of the SF and the DS provides any evidence that the species composition is moving toward a semideciduous forest or whether the current adult vegetation will undergo no turnover or successional change. This information is needed to increase our understanding of forest dynamics in this vegetation mosaic and can help improve management and conservation strategies.

Methods

Study Area

This study was conducted at the La Mancha Coastal Research Centre (CICOLMA, from its name in Spanish: *Centro de Investigaciones Costeras La Mancha*) located in the state of Veracruz, Mexico (19°35'50" N; 96°22'45" W; Figure 1). Climate is AW₂ with a mean annual temperature of 25.6°C and a mean annual precipitation of 1,286 mm/year. There are two seasons based on the precipitation regime: a rainy season from June to September when 78% of the annual precipitation falls and a dry season from October to May, within which, from November to February there is a relatively humid and cold period characterized by strong northeasterly winds, locally known as *nortes* (Castillo-Campos & Travieso-Bello, 2006).

For this study, we selected three locations (Figure 1) that correspond to distinct types of habitats or landscape units (hereafter called “sites”) that differ in their physiognomy and floristic composition. All three are located in CICOLMA, which is a protected area (70 ha): (a) a protected tropical semideciduous forest (PF; protected forest); (b) a SF, and (c) coastal DS. The semideciduous forest (*selva mediana subcaducifolia*, sensu Miranda & Hernandez, 1963) is a type of seasonally dry tropical forest (sensu Pennington, Lavin, & Oliveira-Filho, 2009), in this case an old-growth forest that is more than 200 years old and has been protected since 1977 (Castillo-Campos & Travieso-Bello, 2006). The SF used to be a man-made pasture 5.9 ha in area that was abandoned at the end of 1995, when it was incorporated into CICOLMA. This pasture was used as a single management unit (i.e., never subdivided), where the African grass *Panicum maximum* Jacq. was planted to raise cattle for at least 20 years before it was abandoned. After 17 years of succession, this SF has a closed canopy that is 10 to 15 m tall (Guerrero-Reyna, 2016). Within CICOLMA, an area of 24.5 ha is covered by a sand dune system with coastal scrub vegetation. Cover is predominantly grasses with

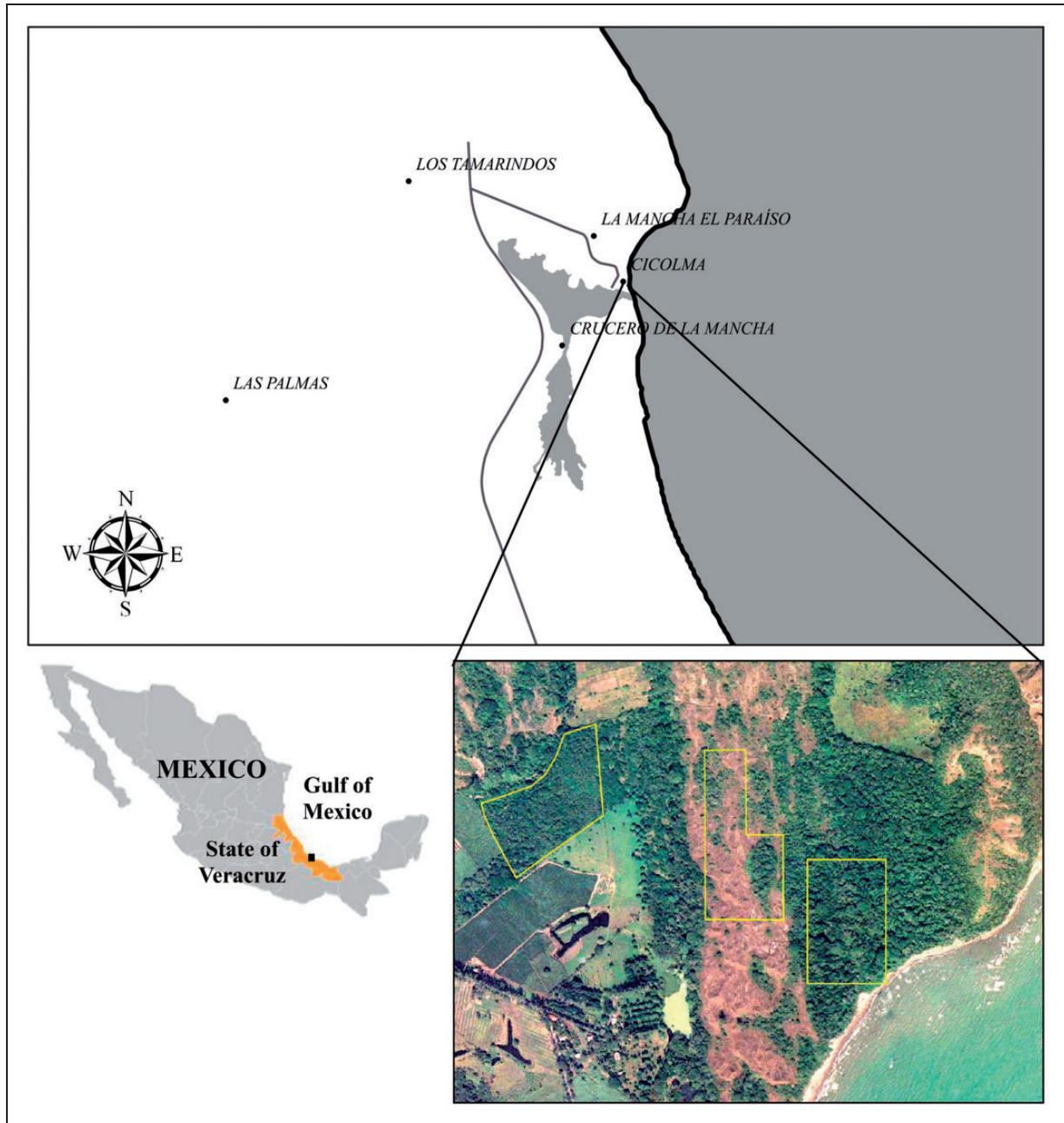


Figure 1. Sampling plot location in Centro de Investigaciones Costeras La Mancha, municipality of Actopan, Veracruz, Mexico. The figure shows the polygons for each site sampled: secondary forest, dune scrub, and protected forest.

small, scattered patches of shrubs and trees growing in the dune slacks (Moreno-Casasola & Travieso-Bello, 2006).

The scrub site is part of a large and relatively recent parabolic semistabilized sand dune, with an estimated age of no more than a few centuries (Kellman & Roulet, 1990). It is 10 to 15 m and up to 20 m higher in elevation than the surrounding areas, where the other two sampling sites (SF and PF) are located. The SF and PF are located on an ancient dune system that is much older as it is late glacial in origin, and they have more fertile soils with

a higher organic matter content. The soil is 80% sand, while the younger and the poorer soils of the DS are >90% sand. However, in the deepest dune slacks of the DS where there are dense woody patches, the soil properties are more similar to those of the PF and SF than to those of the surrounding dune slopes and crests (Suárez, Campos, & Cruz, 2015). Several authors (see review by Moreno-Casasola & Travieso-Bello, 2006) have proposed that the DS is undergoing a long-term primary succession process; based on their review, the current patches of scrub vegetation would be expected to expand

by nucleation and ultimately become a semideciduous tropical forest.

Vegetation Sampling

A 6 ha plot (200 × 300 m) was delimited in each of the three sites, and within each of these plots, thirty 5 × 5 m quadrats were placed randomly. All woody plants rooted within the quadrats with a stem diameter < 5.0 cm and a height ≥ 20 cm were recorded. Don David Díaz, a local eco-guide, has worked with plant ecologists and botanists at CICOLMA for many years and assisted with the species identification of seedlings and saplings in the field. Collected specimens were also shown to botanists at the XAL herbarium, including Dr. Gonzalo Castillo-Campos, head of the Flora of Veracruz project (Instituto de Ecología, A.C. [INECOL], 2016), who is an expert on the local woody flora. Taxonomic nomenclature follows *The Plant List* (2013).

The percentage of tree canopy cover and leaf area index (LAI) above each quadrat was estimated using the Digital Plant Canopy Imager CI-110 (<http://www.cid-inc.com/ci-110.php>), which takes hemispherical photos and processes each digital image with specialized software. For each 25 m² quadrat, the slope of the terrain was measured with an inclinometer and percentage ground cover was visually estimated for grasses, dicotyledonous herbs, leaf litter, and bare ground. Additionally, a 10 × 10 m quadrat with the 5 × 5 m quadrat at its center was set up to record, identify, and measure the diameter at breast height (DBH) (cm) of all rooted woody plants with a DBH ≥ 5 cm, which we regarded as adults (see Norden et al., 2009b). These were classified as local variables in further analyses and are considered proxies for the microenvironmental conditions in each quadrat that could affect the AR.

Data Analysis

Total species richness and abundance per site and their respective means per quadrat were estimated. We compared richness and abundance per quadrat among sites using generalized linear models, with a negative binomial error type because of the overly dispersed nature of our data. Then, when significant differences were found, a post hoc contrast test (Tukey) was used to determine which sites were different. This analysis was run in the statistical programming language R (version 2.14.10; R Development Core Team, 2015). The diversity of both the AR and adult communities in each site was analyzed by way of diversity profiles, estimating Hill numbers for observed richness ($q=0$), for typical diversity ($q=1$), and for the diversity of the most abundant species ($q=2$), using the R software package iNEXT (Hsieh et al., 2016).

The floristic composition of the AR and its variation within and among sites was analyzed with a principal components analysis (PCA) ordination run in PC-ORD, version 6 (McCune & Grace, 2002). For each species, abundance data per quadrat was also log-transformed ($\log + 1$). Quadrats with no woody plants inside (12 from the DS) were excluded from the ordination. The option “variance/covariance” in PC-ORD was used to emphasize variation in species composition. The species ordination (PCA) was complemented with a correlation analysis of the PCA scores on each axis and the local variables of each quadrat mentioned earlier. A cutoff value of $r^2 > .2$ was used to decide which local variables to include in the ordination graph or biplot. The PCA ordination of samples and important (i.e., $r^2 > .2$) local variables are shown on the same figure, drawing local variables as vectors, following McCune and Grace (2002) and Peck (2010). Also, a variance partitioning analysis of the AR species composition was run using the local variables grouped into four categories as explanatory matrices: topography (slope), adults (richness, abundance, and biomass), canopy (cover and LAI), and ground cover (percentages of grass, herbs, litter, and bare ground). This analysis was run in R with the Vegan library (*varpart* function; Oksanen et al., 2017) for the three sites and for each one independently. Additionally, the Jaccard similarity index was used to compare both the adult and AR communities among the three sampling sites.

For every species recorded in this study, its dispersal syndrome was determined based on fruit and seed morphology and an extensive review of the published literature (mainly INECOL, 2016, Castillo-Campos & Travieso-Bello, 2006). There were only three categories: endozoochory (species with fleshy fruit dispersed by vertebrate frugivores, mainly birds and bats), anemochory (species dispersed by wind), and other types of dispersal (including: barochory, dispersal by ungulate herbivores—mainly domestic animals, and unknown dispersal methods). Growth form was also assessed based mainly on the maximum height attained by each species and fell into four categories: (a) tall trees (adults taller than 15 m); (b) medium-sized trees (taller than 8 m but shorter than 15 m in height); (c) small trees, treelets, and shrubs (adults less than 8 m in height, regardless of their branching pattern); and (d) lianas. For simplicity, palm species were regarded as trees. We compared the variation in the percentage of growth forms and dispersal syndromes among sites for both the AR and adult communities in terms of richness and abundance.

Results

A total of 3,195 individuals belonging to 95 morphospecies and 40 families were recorded as part of the AR stage

in the 90 quadrats sampled (total area 2,250 m²). The richest families in the PF were Rubiaceae, Celastraceae, Flacourtiaceae, and Verbenaceae; in SF the richest were Fabaceae, Flacourtiaceae, Celastraceae, and Rubiaceae; and in the DS, Rubiaceae, Celastraceae, Myrtaceae, and Bignoniaceae. Overall, the most abundant species in the AR was *Brosimum alicastrum* (Moraceae) with 1,438 individuals. This species also had the greatest basal area and was recorded in all three sites, although 96% of its individuals were recorded in the PF. The most abundant and frequent species recorded in each site were in the PF, *B. alicastrum*, *Nectandra salicifolia*, *Crossopetalum uragoga*, and *Psychotria erythrocarpa*; in the SF, *Casearia corymbosa*, *C. uragoga*, and *Bonellia macrocarpa*; and in DS, *Randia laetevirens*, *C. uragoga*, and *P. erythrocarpa* (online Appendix A).

Richness, Density, and Composition of the Advanced Regeneration

The site with the richest AR community was the SF with 67 morphospecies, followed by the PF with 55, and then the DS with only 27 species. Mean species richness (χ^2 test, $p < .001$) and mean abundance per quadrat (χ^2 test, $p < .001$) were significantly different among sites. The post hoc test (Tukey test, $p < .05$) confirmed that the three sites were significantly different in both variables (Table 1); richness was highest in SF followed by PF and then DS, while abundance was highest in PF, followed by SF and then DS.

The PCA ordination explained 65% of the total variance in floristic composition (36% along Axis 1 and 29% along Axis 2). Axis 1 separates the quadrats of the PF (highest values on the right) from those of the SF and the DS (Figure 2). The species whose presence and abundance per quadrat were most highly correlated (Pearson's correlation) with the ordination scores for Axis 1 were *B. alicastrum* ($r = .94$), *N. salicifolia* (.71), *Leucaena leucocephala* ($-.32$), and *C. corymbosa* ($-.33$). The first two species had higher abundances and were recorded in more quadrats within the PF, while the other two were more abundant in the DS and the SF.

Along Axis 2, the SF quadrats had the highest variation in ordination scores. Most of the PF quadrats are in the middle of this axis, while the DS quadrats are located at the bottom (Figure 2). The species with the highest correlations along Axis 2 were *B. macrocarpa* (.70), *C. corymbosa* (.69), *C. uragoga* (.71), and *P. erythrocarpa* (.70). Of all our local variables (i.e., environmental proxies and adult vegetation attributes) recorded per quadrat, only three were significantly correlated with the PCA scores from the species ordination: grass cover (%), litter ground cover per quadrat (%), and woody plant canopy cover (%) above each quadrat. Grass cover was negatively correlated with PCA scores along both ordination axes. Most of the DS quadrats and some SF quadrats had the highest values of grass cover (lower left corner of the plot). The woody canopy cover above each quadrat was positively correlated with PCA scores on both axes (upper right in the ordination plot; Figure 2).

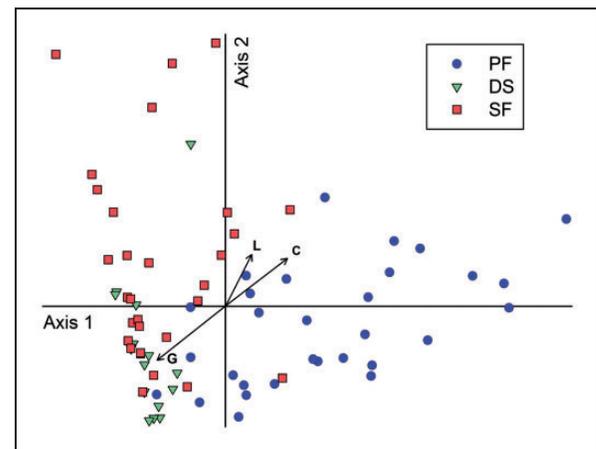


Figure 2. Principal components analysis (PCA) ordination of sample units from each site (PF = protected forest; DS = dune scrub; SF = secondary forest) and local variables shown as vectors that had the highest correlation with PCA scores ($r^2 > .2$ with at least one of the axes, following Peck, 2010); G = grass cover; L = leaf litter cover; C = canopy cover above quadrat tree (see Methods section).

Table 1. Species Richness and Abundance per Quadrat (25 m²) in the Advance Regeneration Stage for Each Site.

	Richness in 25 m ² (n = 30)				Abundance in 25 m ² (n = 30)			
	Mean (\pm SD)	Med.	Range	(outl.)	Mean (\pm SD)	Med.	Range	(outl.)
PF	6.9 \pm 3.2 ^b	6	2–14		68.4 \pm 132.3 ^a	26	8–72	(159, 162, 237, 713)
SF	10.3 \pm 4.9 ^a	9	2–21	(23)	31.9 \pm 21.2 ^b	25	7–84	
DS	2.8 \pm 3.5 ^c	2	0–8	(12)	7.6 \pm 12.6 ^c	1	0–22	

Note. Mean values (\pm SD) with different superscript letters are statistically different (Tukey test $p < .05$). Median values (Med.) are also shown. Range values are shown without outliers, whose values are given separately (outl.). PF = protected forest; SF = secondary forest; DS = dune scrub.

Regarding the variance partition analysis of AR composition among and within sites, we found that the variation explained by all of the local variables together was highest for the DS (.821), followed by PF (.343; see online Appendix B). For the SF, the variables combined as adult attributes and those combined as ground cover type accounted for most of the variation, although with relatively low explanatory power (.210). For the PF, the combination of topography, adults, and canopy were the most explanatory (.322); and in the DS, it was the combination of adults, canopy, and cover type (.813).

Comparison of Adult Vegetation and AR

Adult vegetation was richest in the PF (53 spp.) followed by the SF (40 spp.) and the DS, which had less than one third of the species (13 spp.) recorded in the first two sites. In the SF, adult vegetation had the highest density (890.0 ind./ha) and basal area (23.3 m²/ha), with similar but lower values in the PF (670.0 ind./ha and 20.9 m²/ha) and much lower values in the DS (173.3 ind./ha and 4.4 m²/ha), where nearly 60% of its area (6 ha) was covered by grasses and forbs with no woody plant cover.

Plant diversity was much lower in the DS for both the AR and the adult vegetation in comparison with the PF and the SF (Figure 3). Species accumulation curves show that the AR of the 17-year-old SF had a slightly higher richness than the PF did (Figure 3(a)), while the opposite was true when comparing the community of adults (i.e., plants with DBH \geq 5 cm) between the two sites (Figure 3(c)). However, the estimated 95% confidence intervals (CI) of these curves as well as the diversity profiles (Hill numbers) suggest that there was no statistical difference in the observed richness ($q_0 \pm 95\%$ CI) between these sites for either the AR or adult vegetation (Figure 3(b) and (d)). Nevertheless, the numbers of typical (q_1) and very abundant (q_2) species in the AR were higher in the SF (Figure 3(b); $q_1 = 43.2 \text{ spp.} \pm 4.1$, CI 95%; $q_2 = 31.7 \pm 3.8$) than in the PF ($q_1 = 29.7 \pm 4.4$; $q_2 = 17.7 \pm 2.5$), where just two species, *B. alicastrum* and *N. salicifolia*, were notoriously abundant (70.5% and 11.4% of AR abundance, respectively). In the adult vegetation, diversity was very similar between the SF and the PF, with around 30 typical species (q_1) and around 21 very abundant species (q_2) in both sites (Figure 3(d)).

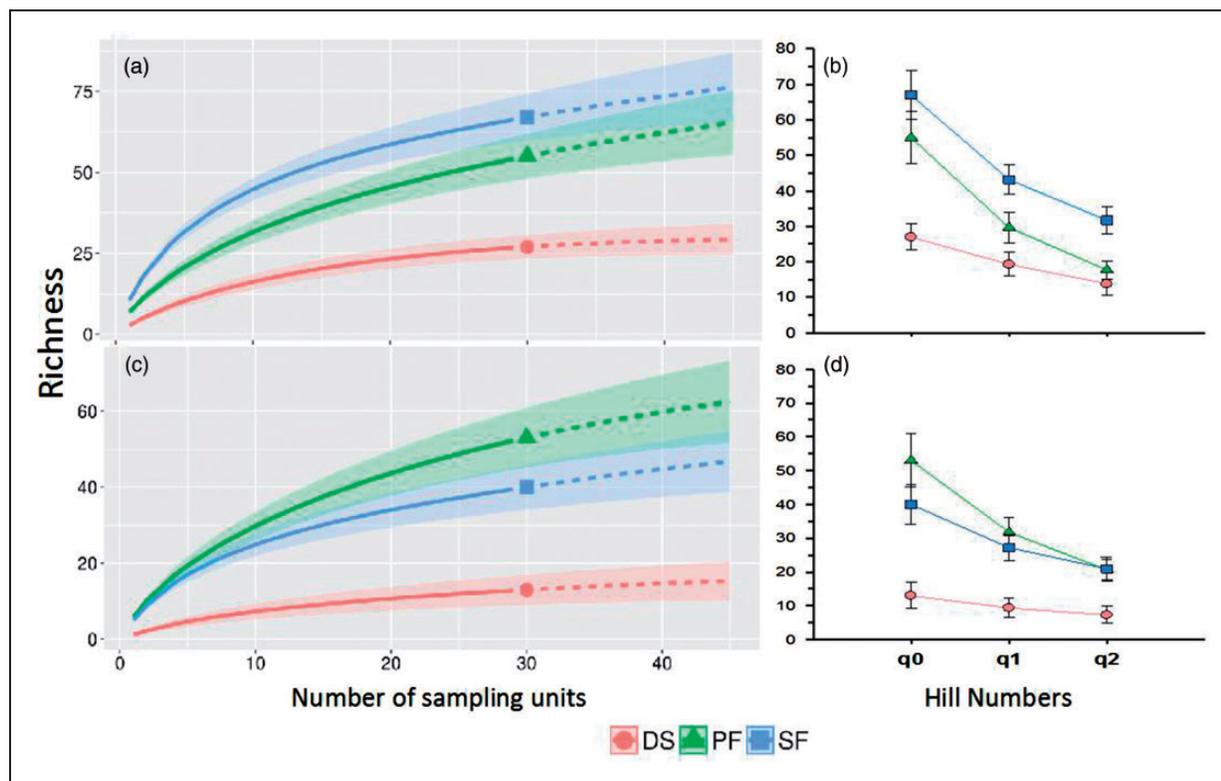


Figure 3. Species accumulation curves for the advance regeneration (a) and the adult community (c) in each of the sites sampled: dune scrub (DS), protected forest (PF), and secondary forest (SF) in Centro de Investigaciones Costeras La Mancha, Veracruz, Mexico, and their diversity profiles (b and d, respectively) showing Hill's numbers (q_0 = observed richness, q_1 = number of typical species, q_2 = dominant species) and their 95% confidence intervals.

Table 2. Similarity Between Advance Regeneration and Adult Communities Within and Among the Three Habitats Sampled.

	Advance regeneration (AR)			Adults		
	PF	SF	DS	PF	SF	DS
AR						
PF	55	0.341	0.242	0.217	0.133	0.081
SF	31	67	0.306	0.270	0.277	0.145
DS	16	22	27	0.177	0.179	0.258
Adults						
PF	18	24	11	53	0.250	0.137
SF	11	23	10	17	40	0.159
DS	5	10	8	7	7	13

Note. Jaccard similarity index values are shown upper right, the number of shared species are lower left (light gray background), and the total number of species per sampling site are in the diagonal (dark gray boxes). PF = protected forest, SF = secondary forest; DS = dune scrub.

Overall, pairwise comparisons between sites for both of the stages sampled (AR and adult) had low similarity values, with the highest recorded for the AR between the SF and the PF (.341), which had the highest number of shared species (31) between them (Table 2), representing almost half of the total number of species recorded in the SF and more than half of those recorded in the PF. The latter was followed closely by the similarity between the AR of the SF and that of the DS (.306). The similarity of the AR to the adults of the SF (.277) and the adults of the PF (.270) was also comparatively high. The least similar samples were the AR of the PF and the adults of the DS, which only shared five species. It is noteworthy that similarities among sites were generally higher for AR than for adults and that the AR of a given site was less similar to the adults growing in the same site than with the AR of the other two sites.

Regarding dispersal syndrome, the most prevalent type of dispersal in the three sites and for both the AR and the adult vegetation was endozoochorous, followed by anemochorous dispersal (Figure 4). A relatively high proportion of adult plants was anemochorous in the SF and the DS; while in the AR of both of these sites, there was a much higher abundance of endozoochorous seedlings and saplings. Regarding the growth form of the woody plants, the absence of lianas in the DS is notable, but they were recorded in the SF and PF as adults, saplings, and seedlings, although their richness and abundance were low in both sites. Small trees (treelets) and shrubs, which in this study were grouped into a single growth form category (see Methods section), were the most prevalent type of species in the three sites for both AR and adults and accounted for a greater proportion of species in AR than in the adults. In the adult vegetation of the PF and the SF, the most abundant growth form was medium-sized trees, followed closely by tall trees in

the PF and by shrubs and treelets in the SF. In the AR of the SF and the DS, shrubs and treelets were the most abundant growth form (Figure 4(d)); while in the PF, tall trees were by far the most abundant, mainly due to the high abundance of *B. alicastrum* seedlings in this site.

Discussion

Plant regeneration is a process that allows for the recovery of the structure and function of a habitat after a given disturbance; however, regeneration can be limited or facilitated by several biotic and abiotic factors that usually interact in highly complex ways (Hoper, 2008; Larson & Funk, 2016; Powers et al., 2009). We need a better understanding of the factors that prevent and those that favor the processes of forest regeneration because of the dramatic rise in the deforestation and fragmentation of tropical landscapes. The highly heterogeneous vegetation mosaics and disturbance regimes prevailing in anthropogenic landscapes could be unfavorable for the regeneration of many species of native woody plants. Thus, the long-term regeneration of remnant forest patches as well as the restoration of forest in deforested areas could be in jeopardy (Lebrija-Trejos et al., 2010a; Norden et al., 2009b; Quesada et al., 2009). In the heterogeneous vegetation mosaic of CICOLMA, we detected large differences in the density, richness, and composition of the AR community between contiguous habitats, showing that the process of forest regeneration can differ greatly over short distances. This could be related to the high degree of heterogeneity of the local conditions at each site or habitat exerting a differential effect on each AR.

Successional Trajectories Deduced From the AR Stage

The analysis of species accumulation curves suggests that differences in the observed richness of adult woody plants (DBH ≥ 5 cm in this study) were not statistically significant between the secondary and the preserved forests. Nevertheless, diversity profiles show that the AR in the SF was more diverse than it was in the preserved forest. This is a remarkable result, since the SF site was used continuously for raising cattle 20 years prior to its abandonment, yet 17 years after the exclusion of cattle, not only is its richness in adults comparable to that of the preserved forest but its AR is also more diverse than that of the preserved forest owing to the mixture of early, mid- and late successional species in the site. The main difference between the SF and the preserved forest was their floristic composition, most notably in the dominant species of adult plants.

It has been pointed out that forest recovery within seasonally dry tropical regions should be much slower

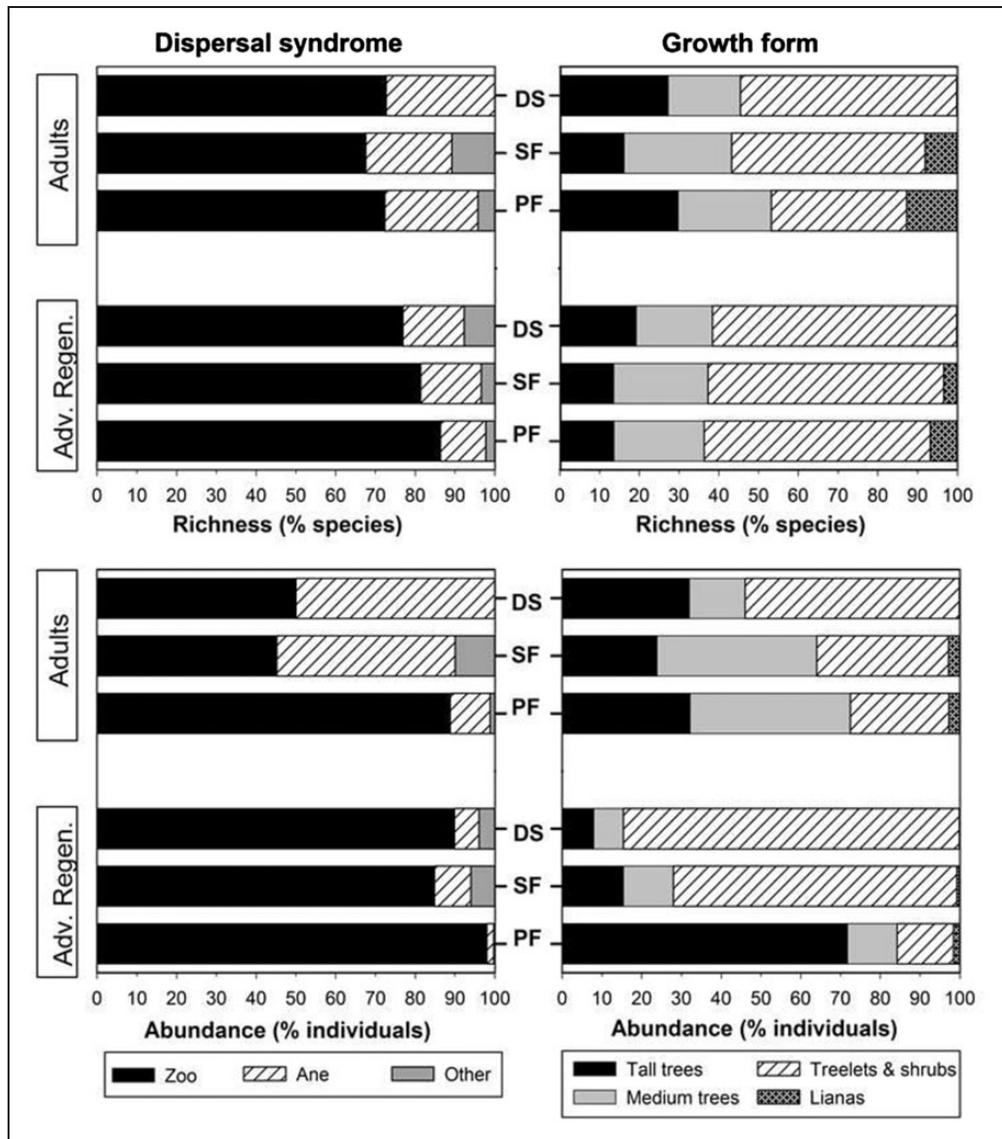


Figure 4. Proportional richness (% species) and abundance (% individuals) of the advance regeneration (Adv. Regen.) and adult vegetation (adults), grouped by dispersal syndrome (left panels) and growth form (right panels), for the dune scrub (DS), secondary forest (SF), and the protected forest (PF). Growth forms: tall trees > 15 m in height; medium trees 8 to 15 m; treelets < 8 m and shrubs; and lianas. Dispersal syndrome: endozoochorous species (Zoo); anemochorous (Ane); and other type of dispersal (see Methods section).

than it is in more humid regions (Janzen, 1988; and see reviews in Quesada et al., 2009, and Poorter et al., 2016). Janzen (1988) also mentioned that abandoned pastures in the dry tropics could be colonized and dominated over several years by a few species of fast growing, wind dispersed trees, which would impede or slow down the establishment of tree species dispersed by forest animals that usually avoid open areas. Consequently, secondary succession could be deflected toward a poorer composition that is different from that of the original forest. The fast recovery of species richness does not imply the complete recovery of composition (see Barlow et al., 2007, for a case of quick recovery in richness but not in composition in the wet tropics).

If we look at the large adult plants of the 17-year-old SF, we can see that the closed secondary canopy is dominated by just a few wind dispersed species (*Cedrela*, *Tecoma*, *Diphysa*, and *Gliricidia*) and some that are dispersed by livestock (*Enterolobium*, *Guazuma*, and *Leucaena*). *Bursera simaruba*, the only endozoochorous tree (dispersed by birds) that could be regarded as dominant in the secondary canopy, is widely planted as a living fence in the area, so there were plenty of sources of this species' seeds nearby when the pasture was abandoned. These observations would lead us to believe that secondary succession in the dry tropics is very slow and also that a first wave of a few colonizer species that do not depend on frugivorous fauna for dispersal could be

stopping or at least slowing down the establishment of late successional species dispersed by birds and bats. However, when we look at the smaller woody plants (DBH < 5 cm) that are part of the AR stage in this SF, two things stand out: there are very few or no immature individuals of the first colonizers of the site in its understory, and yet there are plenty of seedlings, saplings, and juveniles of several bird- and bat-dispersed species (e.g., *B. alicastrum*, *N. salicifolia*, *Ehretia tinifolia*, and *Diospyros acapulcensis*, among others) growing under the light shade of the current secondary tree canopy. This explains in part why several quadrats of the SF had a high degree of similarity with those of the primary forest (Figure 2), and also why overall similarity among sites (Table 2) was highest in the AR between these two sites. Shade tolerant species that are already present in the AR but have slow growth rates and long life cycles will be recruited as adults in the future, increasing the similarity of its floristic composition to that of the nearby preserved forest. SF in the dry tropics may appear to be dominated by a small subset of fast growing, easily dispersed species of early secondary succession phases, but a careful examination of the understory reveals that mid- to late successional species have already established there and their growth is facilitated by the light shade of the first successional wave of early colonizers (see also Lebrija-Trejos, Perez-García, Meave, Bongers, & Poorter, 2010b; Norden et al., 2009b).

These trends were evident on just over 5 ha of the large 6 ha plot of SF that we studied; however, within the same plot, there was a compact patch of almost 1 ha that had a very different structure and composition. This patch was almost exclusively dominated by *L. leucocephala*, whose short, slender trees (3–4 m tall, DBH < 8 cm) formed a thin, deciduous tree canopy, under which the African grass *P. maximum* was still growing profusely, covering 100% of the ground. The only other tree species in this patch were *Diphysa americana*, *Tecoma stans*, and *B. simaruba*, whose stunted and widely scattered individuals were indicative of the stressful conditions for woody plants within this patch. If our vegetation sampling had been restricted to this patch, the most likely conclusion would have been that both the cultivated grass and the ruderal *Leucaena* tree had prevented the establishment of other woody plants, thus inhibiting succession. However, the generous size of the plot (6 ha) together with its topographic heterogeneity allowed us to discern that the main factor explaining the composition of this patch was not biotic but rather abiotic and directly linked to hydric stress. It is important to note that the importance of topography in the spatial variation of vegetation was not detected the way we measured it in the field as the slope of the 5 × 5 m quadrat (see DS topography discussion below). It was only by the

direct observation of the entire plot and its internal topographic variation that we were able to determine that the area still covered in grass had the highest elevation within this plot. Because it was 2 to 3 m above the level of the rest of the plot, the water table is deeper down than in the remaining area where conditions were more mesic, and the rich, dense SF was developed. We would like to make it clear that the entire plot was used during its cattle ranching stage as a single undivided grazing unit for 20 years, and all of it was abandoned at the same time. Dispersal failure does not explain the lack of woody species in this patch given that other areas of the same plot were similar distances from seed sources and were just as attractive or unattractive to dispersal agents as this patch was. The C4 African grass *P. maximum* and the deep-rooted, ruderal tree *L. leucocephala* are both well known for their drought tolerance (Centro Internacional de Agricultura Tropical, 1992), and this explains their dominance in the patch.

The sharp contrast in the spatial variability of succession within this large plot serves as a warning regarding drawing conclusions based on the data from the small plots or sampling areas that are the norm in tropical secondary succession studies. It would also be prudent to exercise caution when interpreting the results of studies based on chronosequences since they assume that the structural (density, biomass, richness) and compositional characteristics of SF are mainly explained by or correlated with the time since abandonment (or elapsed successional time). By averaging the values between different plots of similar age, these studies ignore the spatial heterogeneity and local factors that can exert a strong influence on secondary succession (see also Chazdon, 2014; Power et al., 2009). Other studies have also found a high degree of spatial heterogeneity in the attributes of the AR of SF (Almazán-Núñez, Arizmendi, Eguiarte, & Corcuera, 2012; Capers et al., 2005), but our study is the first to report such striking spatial heterogeneity in a tropical seasonally dry region and within a single large area (6 ha) that was abandoned all at once and that has similar distances to seed sources.

For the DS, previous research reported frequent visits by several frugivorous birds to the woody patches of this habitat, mainly from the adjacent-preserved forest, dispersing the seeds of zoochorous woody plants between the two habitats (Ortiz-Pulido, Laborde, & Guevara, 2000; Vázquez-Balbuena, 2014). However, our results strongly suggest that few of the dispersed seeds establish successfully or are recruited as adults or juveniles in the DS. In spite of the proximity of the adjacent preserved forest and the fact that both habitats had been protected since 1977, AR in the DS was very poor and sparse in woody species, even when compared with the 17-year-old SF. Our data indicate that there is strong niche limitation in the DS and

that the limited seedling establishment of forest woody plants is not a result of dispersal failure (seed limitation *sensu* Levine & Murrel, 2003). The heterogeneous topography of the DS has important consequences in the spatial distribution of woody plants; however, this was not as important in our results (online Appendix B) as expected. This is due, in large part, to the way we measured it in the field by noting the slope of the sampled quadrat, thus we need a better estimator of variation in topography that reflects local conditions, and based on our observations and vegetation results, we suggest that elevation and the depth of the water table should be taken into account more quantitatively. The structural attributes of established adult vegetation in the dunes had more explanatory power than the slope of the sampled quadrat not only in the DS but also in the PF. This suggests that a better descriptor of canopy variation, such as for instance the degree of deciduousness of the trees on top of the site, should be used in future studies.

The largest trees in the DS were *Bursera* and *Cedrela*, but they were restricted to the deepest and therefore wettest dune slacks and they were considerably smaller than the largest conspecifics growing in the adjacent forest, highlighting the stressful hydric conditions of this habitat. Soils in this site are poorer and comprised almost of pure sand (Suárez et al., 2015), but the site is also more than 10 m higher in elevation than surrounding areas and therefore highly prone to desiccation. The DS plot is dominated by clumps of highly drought tolerant woody plants that, additionally, are able to grow in very poor sandy soils. These species include *Diphysa*, *Randia*, *Tecoma*, and *Casearia*, which are in turn surrounded by areas covered by native grasses (*Andropogon* spp., *Trachypogon plumosus*, and *Schizachyrium scoparium*, among others) growing on the dune crests and flanks, where even cacti (*Opuntia stricta*) are found (Moreno-Casasola & Travieso-Bello, 2006). Our results show that even though some woody plants are able to establish in the dune slacks, only a few of them are recruited as adults and most of them are shrubs or small trees (Figure 4). The absence or extremely low abundance in the DS of medium to tall tree species that are common in the old-growth forest of the region explains in great part the DS's much lower values of diversity and similarity when compared to the other two sites. Therefore, the successional pathway to an old-growth semideciduous tropical forest, as suggested in the literature (Moreno Casasola & Travieso-Bello, 2006), is still quite far in the future for this system. It is possible that several centuries of soil formation in the site with the accumulation of leaf litter from drought resistant woody plants are needed before the current scrub patches can expand through a nucleation process and ultimately coalesce with other patches to form a continuous arboreal cover in the site.

Seedling Carpets of *B. alicastrum* and the Absence of a Keystone Animal

A noteworthy result of this study is the detection of dense seedling carpets of *B. alicastrum* beneath the crowns of conspecific adults in the preserved forest, since these carpets are usually found in more humid tropical forest (Álvarez-Loayza & Terborgh, 2011). Almost three decades ago, Delfosse (1990) working in the same forest patch noted that seedling carpets of this canopy tree species were only evident during mast seeding years and that they were ephemeral, since most if not all of them would die off during the dry season. Another peculiarity of this forest at the time was the very low density of tree seedlings and saplings in the understory relative to that of other tropical forests (Blain & Kellman, 1991). The organism mainly responsible for these phenomena was the red land crab, *Gecarcinus lateralis* Frem., which was very abundant in our study site prior to 2000 (with 50–100 thousand crabs/ha in the 1980s; Delfosse, 1990). The crabs were observed to feed heavily on the medium-sized to large seeds of woody plants (Capistrán-Barradas, Moreno-Casasola, & Defeo, 2006; Delfosse, 1990).

These crabs are now absent from the site and the seedling density we recorded beneath the crowns of large *B. alicastrum* adults was very high and similar to that recorded in 1987 by Delfosse (1990) inside crab enclosures constructed beneath the crowns of large *B. alicastrum* adults. The absence of this crab has changed the understory dramatically, as the forest floor is now covered year round with a continuous layer of decaying leaf litter and has higher densities of seedlings and saplings (see also Sherman, 2002). To the best of our knowledge, this is the first report of the absence of this crab from this study site and is also the first record of the defaunation (*sensu* Dirzo et al., 2014) of an invertebrate in a seasonally dry tropical forest (SDTF) having remarkable effects on its understory. That being said, the numerical dominance of *B. alicastrum* in the AR stage of the preserved forest does not mean that the future canopy of this site will be dominated by this tree; seedlings that form part of dense carpets are rarely or never recruited as juveniles (Álvarez-Loayza & Terborgh, 2011). Future studies, and specifically the resampling of our 25 m² permanent quadrats (with all individuals recorded in the AR), will tell us which woody species are thriving and which are not in this recently defaunated (no land crabs) forest.

Implications for Conservation

Although seasonally dry tropical forests are thought to be less resilient than tropical rain forest and their recovery slower and much more difficult, this idea could be the result of having notably fewer studies of seasonally dry

areas. Our results show that in spite of the poor sandy soils of our study area and the long-term use of one of the sites to raise cattle, this type of forest can recover if agricultural practices are stopped and if there are seed sources nearby. In less than two decades, our SF derived from an abandoned pasture had already attained a remarkable richness and density of mid- to late successional tree species that have high probabilities of being recruited as adults in the site. Our results also show that even in a landscape with a long history of human use, forest recovery is not only possible; but when allowed to proceed, it also provides extra space for the recruitment of more individuals of canopy and subcanopy tree species in the landscape. SF could be mistaken for a degraded and species poor forest when only the fast growing, taller adult trees are sampled; however, late successional and slow growing forest trees may have established as saplings or juveniles in the understory, which thus harbors a significant proportion of native forest biodiversity. To assess the true potential of SF as biodiversity reservoirs and future mature forest, the AR stage must be included

purposely in the sampling protocol as we did in this study.

Overall, our results suggest that seed limitation may not be a problem for most of the woody species in our study area, but rather that niche limitation might be stronger. As in studies on secondary succession done elsewhere (Chazdon, 2014; Lebrija-Trejos et al., 2010a; Martínez-Ramos & García-Orth, 2007; Norden et al., 2009b), at CICOLMA, we found that the species recorded in the AR stage were different from the adult trees and shrubs growing directly above them, indicating that the seedlings and saplings growing in the quadrat had to have come (been dispersed) from adults outside of the site, whether near or far. Another key finding is that in spite of being surrounded by extensive pastures and sugar cane fields, the relatively small fragment (≈ 40 ha) of SDTF preserved in the CICOLMA reserve is not being invaded by exotic or invasive plant species that could interfere with or hamper the regeneration of native forest plants. Not even in the SF do we find any evidence of invasive plants stopping or slowing down forest recovery.

Appendix

Appendix A. Advanced regeneration species list and species abundance per sampled site. Nomenclature follows: The Plant List (2013).

Species Name	Family	Abundance		
		Protected Forest	Secondary Forest	Dune Scrub
<i>Achatocarpusnigricans</i>	Achatocarpaceae	1	5	–
<i>Pistacia</i> spp.	Anacardiaceae	–	1	–
<i>Desmopsistrunciflora</i>	Annonaceae	–	4	–
<i>Sapranthusmicrocarpus</i>	Annonaceae	2	5	–
<i>Stemmadeniaobovata</i>	Apocynaceae	2	18	4
Unidentified genus_1	Apocynaceae	–	2	–
<i>Dendropanaxarboreus</i>	Araliaceae	1	1	–
<i>Verbesinapersicifolia</i>	Asteraceae	–	5	8
<i>Tabebuiarosea</i>	Bignoniaceae	1	1	1
<i>Tecomastans</i>	Bignoniaceae	–	11	4
<i>Cordia alba</i>	Boraginaceae	–	1	–
<i>Cordia diversifolia</i>	Boraginaceae	–	2	2
<i>Ehretia tinifolia</i>	Boraginaceae	–	1	–
<i>Rochefortialundellii</i>	Boraginaceae	–	16	–
<i>Bursera simaruba</i>	Burseraceae	7	57	9
<i>Capparisbaducca</i>	Capparidaceae	9	12	–
<i>Cynophalla verrucosa</i>	Capparidaceae	9	7	–
Unidentified genus_2	Capparidaceae	1	–	–
<i>Carica papaya</i>	Caricaceae	1	–	–
<i>Cassinexylocarpa</i>	Celastraceae	8	–	–
<i>Crossopetalumuragoga</i>	Celastraceae	76	108	40
<i>Mygindagaumeri</i>	Celastraceae	–	1	–

(continued)

Appendix A. Continued

Species Name	Family	Abundance		
		Protected Forest	Secondary Forest	Dune Scrub
<i>Schaefferia frutescens</i>	Celastraceae	11	3	3
Unidentified genus_3	Celastraceae	1	–	–
<i>Rourea glabra</i>	Connaraceae	2	–	–
<i>Diospyros acapulcensis</i>	Ebenaceae	7	30	2
<i>Erythroxylum areolatum</i>	Erythroxylaceae	–	–	11
<i>Erythroxylum havanense</i>	Erythroxylaceae	–	2	–
Unidentified genus_4	Euphorbiaceae	–	1	–
<i>Acacia cornigera</i>	Fabaceae	1	7	2
<i>Bauhinia divaricata</i>	Fabaceae	–	53	–
<i>Dalbergia brownei</i>	Fabaceae	1	–	–
<i>Diphysa americana</i>	Fabaceae	–	6	–
<i>Gliricidia sepium</i>	Fabaceae	–	1	–
<i>Leucaena leucocephala</i>	Fabaceae	–	48	–
<i>Mimosa tricephala</i>	Fabaceae	–	–	1
<i>Piscidia piscipula</i>	Fabaceae	–	1	–
<i>Pithecellobium dulce</i>	Fabaceae	–	1	–
<i>Pithecellobium insigne</i>	Fabaceae	–	5	–
<i>Casearia aculeata</i>	Flacourtiaceae	3	1	–
<i>Casearia corymbosa</i>	Flacourtiaceae	3	116	19
<i>Casearia guevarana</i>	Flacourtiaceae	–	4	–
Unidentified genus_5	Flacourtiaceae	1	–	–
<i>Xylosmapanensis</i>	Flacourtiaceae	4	1	–
<i>Nectandra salicifolia</i>	Lauraceae	232	10	7
<i>Malpighia glabra</i>	Malpighiaceae	9	34	–
Unidentified genus_6	Malpighiaceae	4	6	–
<i>Malvaviscus arboreus</i>	Malvaceae	–	1	–
<i>Cedrela odorata</i>	Meliaceae	–	9	1
<i>Trichilia hirta</i>	Meliaceae	1	8	1
<i>Brosimum alicastrum</i>	Moraceae	1435	61	2
<i>Macluratinctoria</i>	Moraceae	–	6	–
<i>Eugenia capuli</i>	Myrtaceae	26	10	9
<i>Psidium guajava</i>	Myrtaceae	–	–	1
Unidentified genus_7	Myrtaceae	1	–	–
<i>Pisonia aculeata</i>	Nyctaginaceae	–	3	–
<i>Ximelia americana</i>	Olacaceae	–	1	–
<i>Piper amalago</i>	Piperaceae	35	56	–
<i>Piper auritum</i>	Piperaceae	1	–	–
<i>Coccolobababbaridensis</i>	Polygonaceae	1	3	–
<i>Coccolobahumboldtii</i>	Polygonaceae	15	1	1
<i>Coccolobaliebmanni</i>	Polygonaceae	6	–	–
<i>Rhamnushumboldtiana</i>	Rhamnaceae	–	5	3
<i>Chiococca alba</i>	Rubiaceae	1	–	–
<i>Exostemamexicanum</i>	Rubiaceae	6	–	–
<i>Psychotria erythrocarpa</i>	Rubiaceae	48	44	26
<i>Randia aculeata</i>	Rubiaceae	3	6	–

(continued)

Appendix A. Continued

Species Name	Family	Abundance		
		Protected Forest	Secondary Forest	Dune Scrub
<i>Randiaetevirens</i>	Rubiaceae	–	11	52
<i>Randiamonantha</i>	Rubiaceae	5	4	–
Unidentified genus_8	Rubiaceae	5	–	–
Unidentified genus_9	Rutaceae	1	–	–
<i>Cupaniadentata</i>	Sapindaceae	1	–	–
<i>Pristimeracelastroides</i>	Sapotaceae	15	4	–
<i>Sideroxyloncelastrinum</i>	Sapotaceae	–	9	–
<i>Cestrum dumetorum</i>	Solanaceae	–	7	–
<i>Solanum diphyllum</i>	Solanaceae	–	5	–
<i>Bonelliamacrocarpa</i>	Theophrastaceae	10	73	–
<i>Heliocarpus pallidus</i>	Tiliaceae	2	–	–
<i>Turneradiffusa</i>	Turneraceae	–	–	8
<i>Celtiscaudata</i>	Ulmaceae	9	8	5
<i>Celtisiguanaea</i>	Ulmaceae	1	7	–
Unidentified genus_10	Ulmaceae	3	–	–
<i>Callicarphaacuminata</i>	Verbenaceae	–	8	–
<i>Lantana camara</i>	Verbenaceae	2	–	5
<i>Petreavolubilis</i>	Verbenaceae	15	–	–
Unidentified genus_11	Verbenaceae	1	–	–
Unidentified genera (9 spp.)	Unidentified family	7	19	2

Appendix B. Summary of the R^2 values of the variance partitioning analysis of AR abundance per quadrat (25 m^2) and local variables among the three sites (All sites: 90 quadrats) and within each site (PF = protected forest; SF = secondary forest; DS = dune scrub; with 30 quadrats per site). Local variables per quadrat include: topography (T: slope in degrees); adult plants (A: vegetation attributes; including richness, abundance and basal area of adults); canopy (CA: % of tree canopy cover and LAI); cover (CO: ground cover in % including grass, herbs, litter and bare ground). The values that make the greatest contribution to variance are in bold (see text).

	All Sites	PF	SF	DS
Topography (T)	0.080	0.029	0.000	0.024
Adults (A)	0.093	0.231	0.093	0.603
Canopy (CA)	0.031	0.061	0.067	0.470
Covers (CO)	0.040	0.043	0.104	0.480
T + A	0.171	0.239	0.000	0.617
T + CA	0.093	0.089	0.000	0.484
T + CO	0.108	0.115	0.000	0.491
A + CA	0.124	0.314	0.152	0.713
A + CO	0.138	0.254	0.210	0.761
CA + CO	0.063	0.119	0.155	0.677
T + A + CA	0.187	0.322	0.000	0.733
T + A + CO	0.208	0.269	0.000	0.776
T + CA + CO	0.121	0.189	0.000	0.681
A + CA + CO	0.155	0.333	0.000	0.813
T + A + CA + CO	0.218	0.343	0.258	0.821

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