Successional Change and Resilience of a Very Dry Tropical Deciduous Forest Following Shifting Agriculture

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ABSTRACT

We analyzed successional patterns in a very dry tropical deciduous forest by using 15 plots differing in age after abandonment and contrasted them to secondary successions elsewhere in the tropics. We used multivariate ordination and nonlinear models to examine changes in composition and structure and to estimate forest recovery rates and resilience. A shrub phase characterized early succession (0–3 yr); afterwards, the tree Mimosa acantholoba became dominant. Below its canopy, species composition may therefore recover soon as suggested by convergence toward mature forest species composition. The time trend of plant density also differed from humid forests for it lacked its characteristic density decline, presumably because of differences in regeneration mechanisms between very dry and other less water-stressed forest types. As opposed to the prevailing hypothesis, resilience was not higher than in moister forests, and thus factors other than structure relative simplicity must be accounted for when assessing resilience.

Key words: chronosequence; forest recovery; Mexico; Mimosa acantholoba; seasonally dry forests; secondary succession; successional models; tropics.

Tropical dry forests (TDF) covered large areas in México, Central and South America, Africa, India, Southeast Asia, and Australia (Gerhardt & Hytteborn 1992), but their current distribution represents only a fraction of their original cover, mostly due to conversion to agriculture or other land uses (Janzen 1988, Maas 1995, FAO 2007). For example, in Mexico less than 27 percent remains undamaged (Trejo & Dirzo 2000) and in other areas it is even less (Venezuela 10% of potential cover, Fajardo et al. 2005; Central America 2%, Janzen 1988; New Caledonia 2%, Guillespie & Jaffré 2003). After field abandonment in many TDF rural areas, secondary forests develop naturally (Swaine 1992, Lugo et al. 2002). Understanding secondary vegetation development is fundamental to achieve restoration and management goals for such successional areas (e.g., Aide et al. 2000).

While research in tropical rain forests (TRF sensu lato; Richards 1996) has produced reasonable insight into their secondary succession (e.g., Finegan 1996, Guariguata & Ostertag 2001, Chazdon 2008), research in TDF lags far behind (Sánchez-Azofeifa et al. 2005, Vieira & Scarlotti 2006), despite the increased attention recently received (e.g., Kennard 2002, Pereira et al. 2003, McLaren et al. 2005, Ruiz et al. 2005, Molina Colón & Lugo 2006). TDF are very heterogeneous in community and ecosystem properties (Murphy & Lugo 1986, Gerhardt & Hytteborn 1992, Mooney et al. 1995, Vieira & Scarlotti 2006) and we expect TDF succession to be equally heterogeneous.

Successional TDF pathways may differ substantially from those in TRF, rendering knowledge extrapolations from TRF to TDF inappropriate (Ewel 1980, Sánchez-Azofeifa et al. 2005, Viera & Scarlotti 2006), particularly to TDF at the dry end of their range, where processes operating in less water-stressed forests may encounter greater difficulties. Several characteristics affecting succession account for the differences. TDF host a greater proportion of wind-dispersed species (Bullock 1995), seedling survival is typically unsuccessful (Gerhardt & Hytteborn 1992, Swaine 1992), while coppicing contributes greatly to regeneration (Murphy & Lugo 1986, Perera 2001, Vesk & Westoby 2004). The processes and mechanisms determining late colonists invasion in TRF gap dynamics (Finegan 1996, Guariguata & Ostertag 2001) may not be as relevant in dry forests, for in mature TDF most dead trees remain standing (Durán et al. 2002), gap formation rates and sizes are low (Dickinson et al. 2001), and light conditions are not overriding for seedling establishment (Lieberman & Li 1992, Gerhardt 1996). For example, Pooter and coworkers (Pooter et al. 2006, Marksteijn et al. 2007, Pooter & Kitajima 2007) found that seedling and sapling traits usually related to light requirement gradients deviate from expectations in short stature, dry forests.

Mature TDF have lower species richness (but see Janzen 1988, Trejo & Dirzo 2002), smaller stature, lower basal area, fewer canopy strata, lower leaf area index, and more frequent vegetative reproduction than their TRF counterpart (Murphy & Lugo 1986, Swaine...
In line with these differences, and from height growth comparisons between the two forest types, Ewel (1977, 1980) stated that TDF succession is floristically simpler, comprises fewer seral stages and, as recovery to predisturbed forest height was faster, that TDF are more resilient than TRF. Later, this difference was nuanced in a resilience model (Ewel 1983), but the idea of TDF being more resilient rooted in later secondary succession theory (Murphy & Lugo 1986, Kennard 2002, Fajardo et al. 2005, Vieira & Scario 2006, Chazdon 2008, but see Lugo et al. 2002). Evaluating resilience as the speed of return to preexisting mature forest conditions after perturbation, is a relative task that depends on how fast the same phenomenon occurs in other forests, and that involves the particular community attribute discussed (Molina Colón & Lugo 2006), the quality of the reference mature forest (lower quality, faster recovery; Kennard 2002), the land use history of the disturbed sites (higher use intensity, slower recovery; Uhl et al. 1988), the sampling criteria used, especially when analyzing species diversity and composition (recovery speed increases with decreasing size-class sampled; Peña-Claras 2003), and the degree of isolation of the successional patch and the related propagule availability (Wijdevven & Kuzee 2000). Considering the large heterogeneity of TDF systems, the scarcity of studies, and the dependence of speed of relative recovery on several factors, the assertion of higher resilience of TDF is insufficiently supported and needs further evaluation.

As part of a long-term project, we study forest development in permanent fallow plots in a TDF of southern Mexico whose climatic regime corresponds to the driest end of TDF distribution. Here we analyze development patterns and compare them to other dry and rain forest examples to further understand the variability and particularities of TDF succession. We also model and analyze the degree and velocity of recovery (resilience) in this TDF.

**METHODS**

**STUDY AREA.**—The study was conducted near Nizanda (16°39'30" N, 95°00'40" W), a village on the Pacific slope of the Isthmus of Tehuantepec (Oaxaca), southern Mexico. Mean annual temperature is ca 26°C and mean total annual precipitation is ca 900 mm (T/P [×100] = 2.89), with 90 percent falling between late May and mid-October (García 2004, Pérez-García et al. 2005; Fig. 1). These features correspond to a transition from subtropical very dry forest to subtropical dry forest sensu Holdridge (1979).

The landscape is hilly, with elevations of around 250 m asl, and is dominated by phyllite of Mesozoic age. Lithosols (shallow soils dominated by rock fragments) predominate in the region but medium textured Haplic Phaeozems (porous dark soils, rich in organic matter, with a mollic A horizon) also occur on gentle hillslopes (Pérez-García et al. 2001). The mature TDF has a low canopy stature, ca 7–8 m, with few prominent trees of Bursera and Lonchocarpus attaining 15 m. It has neither a clear vertical stratification nor a distinct dominance of any species; in fact, many are rare (Pérez-García et al. 2001, Gallardo-Cruz et al. 2005). Although the region still has large areas of well-preserved mature forest (some officially under protection), patches of secondary forest derived from abandoned agricultural fields (mostly maize) occur on many hills around the village. Agricultural fields are small, rarely exceeding 0.5 ha but mostly smaller, and they are normally sown for 1 or 2 yr only. Heavy machinery is never used in the region’s hills. Fallow periods vary but the minimum span is 5–7 yr, coinciding with recovery times of soil nutrients (L. Galicia, pers. comm.).

**SITE SELECTION AND PLOT ESTABLISHMENT.**—Chronosequence approaches have limitations due to unrealistic assumptions regarding similarities in environmental conditions, site history, and seed availability across sites. Nevertheless, when these variables are carefully addressed, results of studies following changes in time mirror those from chronosequences in important aspects such as density, richness, diversity, life-form composition, and rate of change (Capers et al. 2005). We carefully selected 15 sites after detailed interviews with local landowners: one recently abandoned field, fallows of 1, 3, 5, 7, 10, 12, 14, 18, 22, 27, 32, 37, and 40 yr, and a mature forest site. Selection was based on homogeneity of the site's land-use history (i.e., few years of cultivation without pasture use before abandonment), geological substrate, and topographic position, giving preference to mid-slope hillsides, or piedmonts.
For the comparisons, our mature forest plot was supplemented with nine 100-m² mature forest plots studied by Pérez-García and Meave (2004). These plots were mainly used to set the mature forest confidence intervals. We use ‘mature forests’ to refer to sites that have never been cleared, to the knowledge of current inhabitants, and have the structure and composition of intact or under ‘good conservation’ status Mexican TDF (Trejo & Dirzo 2002, Gordon et al. 2004, Gallardo-Cruz et al. 2005); i.e., over 100 trees/0.1 ha, 7–12 m in height and 20–40 cm dbh, characteristic species such as Amphipterygium adstringens, Apoplanesia paniculata, Bursera spp., Ceiba parvifolia, Euphorbia schlechtendalii, Lysiloma divaricatum, and Krugiodendron ferreum, among others, and a continuous layer of native treelets and shrubs.

DATA COLLECTION.—At each site, 30 × 30 m plots were fenced. Within each enclosure, four 20 × 5 m transects, separated by 2-m corridors, were marked. Each transect was divided into four 5 × 5 m quadrats (Fig. S1). All woody and succulent plants were sampled using a size-based criterion. For each transect, sampling in one quadrat included individuals ≥ 1 cm dbh; in a second one, individuals ≥ 2.5 cm dbh; and in the remaining two, individuals ≥ 5 cm dbh. The sampling criterion of each 25-m² quadrat was assigned randomly. Smaller individuals (dbh < 1 cm, height ≥ 30 cm) were sampled in eight 2 × 2 m squares systematically placed in the plot (Fig. S1).

For individuals ≥ 1 cm dbh we recorded species name, life form, height, dbh, and two perpendicular cover diameters. For the smaller individuals only the first three variables were measured. Suckers from the same individual were considered one individual (for density calculations) but the dbh of all suckers fulfilling the sampling criterion were measured (for species and plot basal area calculations). When species identities were unknown, specimens were collected and identified using a regional reference collection of ca 900 species at the Faculty of Sciences, National Autonomous University of Mexico. Sampling was conducted in the wet season (August–October 2003).

DATA ANALYSIS.—Diversity was described by: (1) species density (S); (2) species richness, rarefied to the lowest (80; \( S_{80} \)) and to ca half of the maximum (175; \( S_{175} \)) number of individuals recorded in the plots (using Ecosim, Gotelli & Entsminger 2006); (3) Shannon diversity index (H'); and (4) Shannon evenness index (E). Shannon H' and E were chosen due to their widespread use and the comparative goal of the analysis. For a suitable comparison with the mature plots of Pérez-García and Meave (2004), we (re)calculated H' and E using data only from the four 25-m² quadrats per fallow; hence, quadrat size and sampling criteria were the same as theirs. We used EstimateS (Colwell 2005) to construct sample-based rarefaction curves, computed without replacement (to include all fallows) and scaled to individuals, to compare joint species richness (Mao Tau function) of fallows with mature forests.

Structural analyses included canopy height, density of individuals, basal area, and total crown cover (calculated for individuals ≥ 1 cm dbh, except for canopy height, as the two youngest plots lacked individuals ≥ 1 cm dbh and hence calculations included only smaller individuals). Canopy height was calculated by averaging the heights of eight individuals per plot. To avoid biases resulting from spots with particularly tall trees, we selected the tallest individual within the first and second half of each 100-m² transect, respectively (i.e., two canopy individuals from each of the four transects within a plot); thus, the sample consisted of tall individuals distributed over the entire plot but not necessarily of the eight tallest trees within the plot. Absolute crown cover was the sum of the crown areas of individuals rooted inside the plot. Density, basal area, and total crown cover were expressed on a per hectare basis for comparison with the mature forest plots.

Successional trends were described fitting a set of nonlinear models, as proposed by Huisman, Olff and Fresco (1993; HOF models henceforth), which allow exploring temporal variations within ecologically realistic bounds and without restricting the analysis to a single response type. Model I fits nonsignificant trends in time; Model II fits increasing or decreasing trends where the maximum reaches an upper bound; Model III resembles model II but the maximum remains below an upper bound; Model IV describes a symmetrical increase and decrease; and Model V depicts an increase and decrease at different rates. We used SPSS nonlinear regression module (SPSS 2003) for model fitting. The model’s upper boundary was set to the mature forest mean upper limit (mean + 1.96 SE), or to 1.2 times the highest value found in the data set, to account for possible higher values not contained in it (Bongers et al. 1999), when data from Pérez-García and Meave (2004) were not available or suitable for calculating comparable confidence intervals (i.e., species density, H', and E). Selection of the best model was based on a significant improvement of the fit by using the least squares F-statistic (Huisman et al. 1993).

To assess forest recovery, we used the HOF model selected for each community attribute to estimate the attributes’ value along the 40-yr chronosequence span. Resilience was measured as the time-referred percent recovery of the mature forest mean value (± 1.96 SE) represented by each calculated quantity. These percentages were then compared to those reported or calculated by us for our time frame for other tropical secondary successions. Compared studies were from forests growing in areas that experienced low-to-moderate land-use intensities, and had reference mature or old-growth forests that were structurally indistinguishable from undisturbed forests, i.e., > 80-yr old, according to Brown and Lugo’s (1990) criterion. This included 11 TRF (comprising both Holdridge’s 1979 moist and wet forests) and 7 TDF studies, some with sites located in more than one region; all TDF were less dry than ours (T/P ratios of 1.76–2.78). If the recovery of the focal attribute remained below 100 percent along the studied period, we used for the comparison the value at the oldest available stand or age class that was equivalent to ours; if recovery reached 100 percent within 40 yr (our studied period), then we used the stand or age class at which this maximum level of recovery was reached.

Floristic relationships between stands were examined using nonmetric multidimensional scaling ordination (NMDS; Quinn & Keough 2002). Two NMDS were performed: (1) including all individuals, to analyze overall differences between fallows (\( N = 15 \)); and (2) only considering trees and columnar cacti divided into a
lower (ind. < 1 cm dbh, 0.3–2 m height) and upper (ind. ≥ 1 cm dbh, > 2 m in height) strata, to analyze successional trends in species composition assuming that trees and cacti occurring in the lower strata will eventually dominate the upper strata (N = 28; the two youngest plots lacked upper strata individuals). A similarity matrix using the abundance-based Jaccard index adjusted for unseen species (Chao et al. 2005), calculated with EstimateS (Colwell 2005), was employed as the input matrix of analyses. We used the SPSS multidimensional scaling module (SPSS 2003) selecting the Simplex method as starting configuration; dimensions were fixed at two, as Kruskal’s measures of stress reached levels adequately representing actual dissimilarities between samples (0.132 and 0.152 for analyses 1 and 2, respectively; Quinn & Keough 2002). The first axis of the first ordination was regressed on stand age to evaluate its relationship with the main compositional variation.

RESULTS

NUMBER OF SPECIES, STAND STRUCTURE, AND ABANDONMENT TIME.—In total, 141 species (including 21 morphospecies), belonging to 46 families, were found. Among them, 54 were shrubs, 62 trees, 21 lianas, and 4 succulents. Most occurred in one (35%) or two (18%) stands only. All community attributes were related to fallow age (P ≤ 0.01 to < 0.001), which explained 60–91 percent of data variation (Figs. 2 and 3). According to the fitted models, all attributes but height would sooner or later reach their characteristic mature forest or maximum value.

Species density was one of the most variable attributes (range: 15–58 species), but showed a gradually increasing pattern along the chronosequence (Fig. 2A). S80 and S175 paralleled such increments in time although with a lower rate and variability, as expected from the relationship between density of individuals and number of species (R2 = 0.69). The sample-based rarefaction curves of mature and fallow plots (Fig. 2C) revealed that joint fallow richness is much lower than the area’s mature forest richness (61 ± 8 species vs. 112 ± 15 at 496 individuals). Shannon H’ also reflected the patterns in species richness with a gradual increase along the chronosequence (1.36–3.34). Contrastingly, E increased initially fast but varied little after 3 yr (Fig. 2B).

All structural attributes significantly increased with fallow age but differed in their relationship to time. Basal area was the only attribute that gradually increased throughout the chronosequence (0–25 m2/ha) and remained below the mean 95% CI of the region’s mature forests (32.0 ± 6.3 m2/ha; Fig. 3C). Canopy height, density of individuals, and total crown cover (range = 1.0–7.2 m, 0–7475 individuals/ha and 0–44,110 m2/ha, respectively) had steep increments within the first 15 yr of succession (Figs. 3A, B, D), but hardly changed thereafter.

CHANGES IN LIFE-FORMS AND SPECIES COMPOSITION.—Life-form spectrum drastically changed with abandonment time: the proportion of shrubs changed from > 80 percent of all individuals for the two youngest sites to a maximum of 59 percent in older fallows. From 2 yr after abandonment, life-form distribution changed little. Shrubs showed the widest range of values with 18–59 percent of individuals (mean = 34.9, SD = 12); trees between 31 and 69 percent (mean = 57, SD = 12); and lianas between 2 and 11 percent (mean = 7, SD = 3). Succulents appeared only after
18 yr and persisted with 1–8 percent of the individuals (mean = 3, SD = 3).

In the two youngest fallows, the shrubs Waltheria indica, Chamaecrista nictitans var. jaliscensis, and Melochia tomentosa accounted for 68–82 percent of all woody individuals. The two pioneer trees Mimosa tenuiflora and M. acantholoba var. eucarpia took over dominance from the 3-yr-old stand onwards, either in terms of density of individuals, crown cover, or basal area. Waltheria indica and C. nictitans var. jaliscensis were seldom found thereafter. In 3- and 5-yr-old stands, M. tenuiflora accounted for up to 95 percent of total basal area, and in 7-yr-old stands and older M. acantholoba was dominant. In the two oldest stands, several stems of the dominant Mimosa species were uprooted, snapped, or senescent. Species such as Acacia farnesiana and A. cochliacantha, recognized by locals as early successional, had low relative abundances, and others like Crescentia alata, Guazuma ulmifolia, Heliconius palleus, and Piptadenia flava, referred elsewhere to as early successional (Sabogal 1992, Rincón & Huante 1993, Bullock 1995, Miller & Kauffman 1998), occurred only sporadically.

Below the canopy of the Mimosa species, mature forest species increased gradually in abundance to become conspicuous only at later stages, i.e., from the 32-yr-old stand onwards (e.g., A. adstringens, A. paniculata, E. schlechtendalii, L. divaricatum, Senna atomaria). The two Mimosa species had no young recruits.

Successional changes in species composition are well depicted by the NMDS analyses. Fallow scores on the first axis of the ordination for all individuals had a strong logistic relationship with fallow age (Fig. 4A; $R^2 = 0.72$). When the longer-lived and physiognomically dominant forest components (i.e., trees and cacti) were stratified and analyzed (Fig. 4B), trends of change toward a mature forest composition became clearer. The dissimilarity between the upper and lower strata of any successional plot was larger than that between the upper and lower strata of the mature forest. Moreover, all but one sample within the immediate neighborhood of the mature forest samples were lower stratum samples. For most plots, lower strata samples were closer to the mature forest samples than their corresponding upper strata.

Forest recovery and resilience.—Estimated speed of recovery varied attributes. Density of individuals, crown cover, and height had the fastest recoveries (Fig 5A, B, D); the first two recovered fully (5511 ± 625 individuals/ha, and 31,283 ± 2227 m²/ha, respectively) within 8–13 yr. Canopy height recovered 75 percent of the mean mature forest height in 13 yr, but remained below full recovery (8.03 ± 0.75 m) within the modeled period. Basal area had the slowest recovery (Fig. 5C); after 40 yr, the secondary forest recovered 60–89 percent of mature forest basal area (31.9 ± 7.2 m²/ha).
Diversity attributes had intermediate recovery rates; $S_{175}$ was the only one to attain at least the lower bound of full recovery (49 ± 7 species) within the 40-yr period (Fig. 5E). In 40 yr, species density, $H'$ and $E$ reached 80–96, 86–90, and 78–85 percent of mature forest values (24.6 ± 2.2 species/100 m², 0.91 ± 0.021 and 2.9 ± 0.12), respectively (Fig. 5F; G, H).

**DISCUSSION**

Development of species composition, richness, and diversity matches patterns of steady recruitment in small-sized, low-intensity disturbed areas like ours, where propagule availability of mature forest species is not limited (Finegan 1996, Wijdeven & Kuzee 2000, Capers et al. 2005). The higher values of species richness, $H'$, and $E$ in our oldest plots relative to our mature forest match in turn the expectations of a diversity peak according to the intermediate disturbance hypothesis (Connell 1978, Huston 1979), although a sound confirmation requires the analysis of older stands. Shifts in dominance from herbs and shrubs, through pioneer trees, to mature forest tree species can be explained from differences in growth rates, life histories, and longevities of new-incoming species as compared to early-successional ones; these traits cause species turnover in tropical secondary succession (Gómez-Pompa & Vázquez-Yanes 1981, Finegan 1996, Capers et al. 2005). Fast increments in height and crown cover compared to basal area agree with processes of early allocation to resource acquisition followed by a later shift toward structural materials (Brown & Lugo 1990, Guariguata & Ostertag 2001). Likewise, factors affecting secondary succession such as temporal and spatial variations in propagule, water, and soil nutrient availability (Lieberman & Li 1992, Bullock 1995, Guariguata & Ostertag 2001, Marod et al. 2002), and predisturbance differences in composition and structure between stands, may explain the variation not accounted by time only.

Three major aspects in our forest differ from other studies and the main reason is probably site water availability. First, density of individuals rose at early stages but did not decrease as typically observed in TRF (see reviews of Brown & Lugo 1990, Guariguata & Ostertag 2001, and recent studies by DeWalt et al. 2003, Breugel et al. 2006). Studies conducted in TDF that agree with the TRF pattern (e.g., Aweto 1981, Kennard 2002, Ruiz et al. 2005) come from areas with higher water availability (lower T/P ratios and shorter drier seasons; 1.75–2.1, and 4–5 mo, respectively), while others with behaviors similar to ours are from drier sites (González-Iturbe et al. 2002 and Pereira et al. 2003; T/P of 2.8–4.0, and 5–6 mo dry season). Read and Lawrence (2003) provide a good regional scale example in this respect: reductions in density were smaller in increasingly dry sites (T/P ratios of 1.76, 2.18 and 2.80, respectively).

The second difference is the pattern of species dominance and replacement, and the recognized successional phases. We found no group of species equivalent to the long-lived pioneers typical of TRF. Our forest succession starts with a short phase dominated by herbs and shrubs, followed by a pioneer tree phase. In TRF, this second phase of pioneer trees is replaced, within 10–30 yr, by a group of long-lived pioneers that dominate the forest during 75–150 yr before mature forest species do so (Finegan 1996, Guariguata & Ostertag 2001). In our forest, the two Mimosa tree species that represent the second phase of succession dominated up to the 40-yr-old stand, and they will be replaced by the typical mature forest species that are growing below their dying canopy.

Thirdly, our group of pioneer trees consists of a few native legume species only (Mimosa and Acacia spp.). This is surprising as our study region (Mexico’s Pacific tropical watershed) hosts one of the highest floristic diversities of its kind (over 5600 species for TDF; J. L. Villaseñor, pers. comm.), and only in Nizanda over 900 plant species have been recorded (Pérez-García et al. 2005). This also contrasts with the pioneer species richness generally found in secondary TRF within a region (e.g., Peña-Claros 2003, Breugel et al. 2006). Dominance by a few species, without implying arrested succession, has been observed in other deciduous forests at the dry

**FIGURE 4.** NMDS ordination for fallows ranging from recently abandoned field to 40-yr old and a mature forest stand using the abundance-based Jaccard index adjusted for unseen species of Chao et al. (2005) as input matrix. (A) Including all species sampled; fallows are symbolized by their age in years preceded by the letter P. (B) Only considering trees and columnar cacti divided into a lower (L; ind. < 1 cm dbh & between 0.3 and 2 m height) and upper (U; ind ≥ 1 cm dbh & > 2 m tall) stratum; the number following the letter is the age of the fallow to which each strata belong.
end of their range (e.g., Rico-Gray & García-Franco 1992, Nansen et al. 2001, Pereira et al. 2003), and it may be an ecological feature proper of these forests. The dominant pioneer species in our fallows are virtually absent from the natural regeneration dynamics of the mature forest. This seems to be in contrast with most secondary successions in TRF, where species that colonize fallows are generally the same ones involved in their gap dynamics.

Observed differences in patterns can be related to general differences between TDF and TRF. Low pioneer species diversity may derive from a pool containing only a few species adapted to the water-stressed early-successional conditions (Ewel 1977) and lacking mature forest species specialized to large gaps. Alternatively, it may result from a synergism between recurring disturbance (i.e., repetitive felling) and resprouting (e.g., Rico-Gray & García-Franco 1992), a trait commonly found among TDF species (Brown & Lugo 1986, Miller & Kauffman 1998, Vesk & Westoby 2004). In turn, competition leading to the patterns of density decline (Niklas et al. 2003) may be prevented in TDF by processes derived from its characteristic regeneration mechanisms: on the one hand, drought-related poor seedling establishment prevents a dense packing of individuals (Ewel 1980, Liebermann & Li 1992, Gerhardt 1996); on the other, a high sprouting incidence produces low individual density and slowed individual and species turnover (Kruger & Midgley 2001, Lebrija-Trejos 2004). Moreover, competition not only decreases with low recruitment (Schwinning & Weiner 1998, Niklas et al. 2003) but also with increasing environmental stress (e.g., drought; Menge & Sutherland 1987, Bunker and Carson 2005). It is also likely that the characteristic high rainfall variability of TDF (Murphy & Lugo 1986) together with the consequent variability in recruitment and survival rates (e.g., Swaine et al. 1990, Ceccon et al. 2004), simply result in an indefinite, highly variable pattern of plant abundance.

**FOREST RESILIENCE.**—Considering that the study site is at the dry end of the TDF range, recovery of some mature forest attributes seems fast (in no more than 13 yr for density of individuals and crown cover), but not of others: $H'$, $E$, and basal area failed to reach mature forest values within the studied period. How resilient is then our forest compared to others?

Crown cover (sometimes compared with leaf biomass) was the only attribute for which no forest was more resilient than ours, whether TRF (Saldarriaga et al. 1988, Brown & Lugo 1990) or TDF (Kennard 2002, Molina Colón & Lugo 2006). Regarding height, the attribute used by Ewel (1977) to assert that TDF were more resilient than TRF, 11 of 17 compared forests were indeed less resilient than ours. Three TDF and two TRF were equally resilient (Moran et al. 2000, Read & Laurence 2003, Ruiz et al. 2005, Molina Colón & Lugo 2006), and only one TRF growing on a nutrient rich soil had higher resilience (Moran et al. 2000). The situation is different regarding the slowest recovering attributes. In all studies that evaluated $H'$ and $E$, resilience was higher than in ours (Saldarriaga et al. 1988, Peña-Claros 2003, Ruiz et al. 2005, Toledo & Salick 2006). This was also true for species density in almost all sites (6 TRF and 4 TDF; with remarkable recoveries of up to 55–92% of old-growth forest values only 8 yr after use as pasture; Uhl et al. 1988). Only in one TDF (Molina Colón & Lugo 2006), stands growing in the previously most disturbed sites recovered at a slower (house sites) or similar (farm sites) speed than ours. As for species richness, recovery in our forest was, at best, similar to both TRF and TDF (Gualiguata et al. 1997, Ruiz et al. 2005). Regarding
basal area, resilience was also higher in most forests (10 TRF and 4 TDF) than in ours. Read and Lawrence (2003) exemplified again the relevance of water availability, even within TDF, as while all of their study sites recovered faster than ours, the difference in speed decreased with increasing T/P ratios (1.8–2.8). Finally, density of individuals showed the highest similarity in resilience with respect to other forests; five TRF and two TDF showed comparable recovery speeds; two of each forest types were more resilient and only the most disturbed sites of Molina Colón and Lugo (2006) were less resilient. As found by Lugo et al. (2002) when comparing between Puerto Rican forests, high relative resilience of our TDF as an absolute statement cannot be sustained; the assumption that a lower structural complexity would lead to a shorter time to reach maturity does not hold for most attributes.

Our results on species convergence indicate that species composition could have a faster recovery to maturity in our TDF, as expected by Ewel (1980) and Murphy and Lugo (1986) from a lower floristic complexity (of the pioneer’s group) and the resulting reduction in several stages. A small set of effective pioneer species without long life spans leaves less room for compositional variation and thus may lead to earlier convergence between secondary and mature forests. Such convergence would not take place before 40 yr of regrowth but is possible for it to occur earlier than the 75–150 yr estimated for TRF (Finegan 1996, Guariguata & Ostertag 2001).

CONCLUDING REMARKS.—Despite chronosequence’s limitations, we are confident of its usefulness (given the high $R^2$ values in regressions on time) to overcome the lag in knowledge of TDF secondary succession, and as a way of generating new hypotheses that are site specific (as long as assumptions are carefully addressed). Indeed, valuable information on major secondary succession patterns and trends can be extracted in short time periods. We stress that a series of studies encompassing the entire range of conditions in which TDF occur, especially in very dry ones in which the early-successional floras differ completely from those of TRF, are needed to fully establish and understand patterns and particularities of TDF secondary succession; differences with respect to TRF should not be neglected. Focus on factors related to water availability is essential.

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SUPPLEMENTARY MATERIAL

The following supplementary material for this article is available online at: www.blackwell-synergy.com/loi/btp


