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Species Dynamics During Early Secondary Forest Succession: Recruitment, Mortality and Species Turnover

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ABSTRACT

The "Initial Floristic Composition" hypothesis is applied to secondary tropical rain forest succession in abandoned agricultural fields with light previous land-use and close to seed sources. This hypothesis predicts that both pioneer and shade-tolerant species colonize a site directly after abandonment, and as the canopy closes, the recruitment of pioneers sharply declines, while recruitment of shade-tolerant species continues. It also predicts higher mortality among pioneers. Consequently, recruited and dead trees are expected to differ in species composition, with highest species richness for the recruits. During 18 mo, we monitored recruitment and mortality of trees with height $\geq$ 1.5 m in eight plots in abandoned cornfields with initial fallow age of 1–5 yr, in SE Mexico. Shade-tolerant species established in the first years of succession, albeit in low numbers. As predicted, recruited and dead trees differed in species richness and composition, and in shade-tolerant frequency. In contrast to our expectations, over 50 percent of recruits were from pioneer species, as high stand-level mortality opened new opportunities for continued pioneer colonization. Species turnover starts very early in succession but is not always a gradual and continuous process, complicating prevailing succession models. The strong spatial and temporal variability of succession emphasizes the need to monitor these dynamics in permanent plots across a range of initial stand ages, with multiple plots in a given age class.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: initial floristic composition; Mexico; secondary forest dynamics; tropical wet forest.

SECONDARY FOREST SUCCESSION ON ABANDONED AGRICULTURAL FIELDS has been described as the colonization and replacement of functional groups of species, which differ in life history attributes such as seed dispersal rates, establishment requirements, growth rates, longevity and size at maturity (*e.g.*, Huston & Smith 1987, Bazzaz 1996). The variety of temporal patterns of species colonization and replacement is immense, and depends on site and species availability and characteristics (Picket & Cadenasso 2005). Across-site variation in these patterns has been related to environmental factors such as soil characteristics (*e.g.*, Donfack *et al.* 1995, Chinea 2002, Lu *et al.* 2002), previous land-use (*e.g.*, Uhl *et al.* 1988, Pascarella *et al.* 2000), distance to seed sources (*e.g.*, Purata 1986, Mesquita *et al.* 2001), and characteristics of dominant species (Mesquita *et al.* 2001).

The Initial Floristic Composition (IFC) hypothesis of Egler (1954) is predicted to apply to tropical postagricultural secondary succession where previous land-use was of low intensity and seed sources are nearby (Gomez-Pompa & Vazquez-Yanes 1981, Finegan 1984). Such conditions are found in many regions of the tropics, especially where traditional small-scale shifting cultivation practices still prevail or where agricultural colonization is recent (*e.g.*, Lawrence *et al.* 1998, Kammesheidt 2002, Gemerden *et al.* 2003). According to the IFC hypothesis, most species that will later dominate the community will colonize the site at the onset of succession. The proposed sequential physiognomic dominance of species, first light-demanding species of increasing longevity, and finally shade-tolerant species, unfolds largely due to differences in growth rates, longevity, and shade-tolerance among tree species that happen to colonize the site at abandonment (Gómez-Pompa & Vazquez-Yanes 1981, Finegan 1984).

The IFC hypothesis does not provide an unambiguous testable hypothesis, and accordingly it has been interpreted in different ways (Wilson *et al.* 1992, McCook 1994). Therefore, to address this hypothesis clear predictions have to be formulated about successional replacement among functional groups, making interpretations and assumptions explicit. In this study, we formulated and evaluated the following predictions. Both pioneer and shade-tolerant species are present in the first phase of succession although pioneer species are more abundant (Gómez-Pompa & Vazquez-Yanes 1981, Finegan 1996). After canopy closure, recruitment of the dominant pioneer species becomes limited, while recruitment of shade-tolerant species continues (Swaine & Whitmore 1988). Mortality is relatively high among the dominating pioneer species compared to shade-tolerant species (*e.g.*, Álvarez Buylla & Martínez Ramos 1992, Davies 2001). In consequence of these three aspects, recruits and dead trees constitute distinct groups of species, while the surviving initial assemblage can be expected to represent a transitional species composition (*i.e.*, high potential of species replacement).

Shade-tolerant taxa form a much larger species pool than pioneer taxa (Budowski 1965, Saldarriaga *et al.* 1988, Finegan 1992), though pioneer species seem to be more widely distributed than

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many shade-tolerant species (Holmgren & Poorter, in press). Unlike shade-tolerant taxa, few pioneers have narrowly localized or disjunctive areas, and generally occur at much higher densities (Richards *et al.* 1996, Holmgren *et al.* 2004). Hence, we expect that species richness and evenness of recruits will be higher than that of the species assemblage of earlier established trees. For the same reasons, we expect that species richness and evenness of the group of trees that die will be lower than that of recruited trees.

We know of only one community-level study that explicitly, but partially, addressed these predictions in the context of tropical rain forest succession. This chronosequence study in the Bolivian Amazon demonstrated that the understory had higher species diversity and approached the composition of nearby old-growth forests faster than the canopy (Peña-Claros 2003). However, a complete examination of the rate and patterns of species colonization and replacement requires monitoring of permanent plots (Picket 1989, Bakker *et al.* 1996, Foster & Tilman 2000). We are aware of only two studies focusing on advanced (initial fallow age ≥ 55 yr) secondary succession (Lang & Knight 1983, Milton *et al.* 1994), of two studies on sites with initial fallow age between 12 and 25 yr (Chazdon *et al.* 2005, 2007; B. Finegan, pers. comm.), and two further studies that monitored the first years of post-clearance succession (Swaine & Hall 1983, Uhl 1987). These studies monitored mortality, recruitment, and changes in species composition over periods ranging between 5 and 17 yr, but none explicitly addressed the above-stated predictions on species colonization and replacement.

In this study we examine, in detail, community-level species dynamics in the initial years of secondary tropical rain forest succession. We analyze mortality, recruitment, and subsequent changes in species abundance, diversity, and evenness and composition in eight 1- to 5-yr-old fallows in a swidden agricultural landscape with light previous land-use and in proximity of old-growth forest remnants over a period of 18 mo. Our specific objectives were: (1) to describe early secondary patterns of species richness and composition and short-term changes therein; (2) to test the predictions derived from the IFC hypothesis.

METHODS

STUDY AREA.—The study was conducted at the Marquéz de Comillas region, to the south of the Montes Azules Biosphere Reserve (approximately 16°04′ N, 90°45′ W), Chiapas, Mexico. Annual temperature and rainfall is *ca* 23°C and 3000 mm, respectively. There is a dry season from February to April (< 100 mm/mo) (Ibarra-Manríquez & Martínez-Ramos 2002). The original vegetation consists mainly of lowland tropical rain forests and semideciduous forests. A more extensive description of the natural vegetation in the region is given by Ibarra-Manríquez and Martínez-Ramos (2002).

The region is a mosaic of small-scale agriculture, pastures, mostly young (< 10 yr) secondary forests, and remnants of old-growth forests. Méndez-Bahena (1999) found that secondary vegetation succession in the study region varied with former land-use, more specifically abandoned pastures versus abandoned cornfields, and with geomorphology. It was not our objective to study such relationships; therefore, we selected secondary growth plots with similar geomorphology and land-use history. Plots were selected on abandoned cornfields ("milpas") in areas with undulating hills, between 115 and 300 m asl., with a complex acidic soil (pH 4–5), derived from sedimentary rocks (sandy and clay) that have low total nitrogen (0.4 kg/m^2) and phosphorous (< 0.01 kg/m^2) content (Siebe *et al.* 1996, Celedón 2006). The cornfields had been established after clear-cutting the original old-growth forest, used for corn cultivation once, and subsequently abandoned. Initial fallow age ranged from 1 to 5 yr. All plots were bordering remnants of old-growth forest or connected to them by another secondary forest plot. Fallow age and land-use history was determined based on information of landowners and other local residents.

INVENTORY.—We selected eight secondary forests, and established plots of 10 × 50 m in each of them. At the beginning of the study all free-standing woody perennials (trees, shrubs, and treelets) with a diameter at 1.3 m aboveground (dbh) ≥ 1 cm were recorded, tagged, and identified to lowest possible taxonomic level. In the case of individual plants with multiple stems, all stems with dbh ≥ 1 cm were included. Henceforth we will refer to individual plants as "trees," independent of their life form, for convenience. After 6 mo, a census was conducted to record mortality and recruitment. At this time all trees with dbh ≤ 1 cm but height ≥ 1.5 m were included as well, but dbh was not measured. Hereafter we will refer to the first census as "census 0" and to the latter as 'census 1'. Approximately 18 mo (± 15 d) after census 1, recruitment and mortality were monitored again (census 2). Here we report data from this 18-mo study period. Henceforth, we will deal with five tree groups: (1) trees with height ≥ 1.5 m at census 1, initial assemblage (IA); (2) trees with height ≥ 1.5 m at census 2; (3) trees of census 1 that survived until census 2 (surviving trees, ST); (4) trees alive at census 1 and recorded dead at the end of the study period (dead trees, D); and (5) trees that grew over the lower size limit of 1.5 m height after census 1 and were alive at census 2 ('recruitment.' R).

Based on data and observations from long-term studies on the distribution of seedlings and young saplings, conducted at Los Tuxtlas Tropical rain forest (*e.g.*, Ibarra-Manríquez *et al.* 2001) and in our own study region (M. Martínez-Ramos *et al.*, pers. comm.), 118 of a total 142 species were classified in two broad regeneration groups (pioneer and shade-tolerant). We defined pioneers as those light-demanding species that establish and persist only under higher-light conditions and, accordingly, their distribution as seedlings and saplings is largely confined to gaps and early secondary vegetation. We defined shade-tolerant species as those able to establish and persist below the closed canopy of old-growth forests. Note that this classification includes a wide array of alternative life histories (Martínez-Ramos *et al.* 1989). For example, within the pioneer group we included short- and long-lived species, and within the shade-tolerant group understory, mid- and upper-canopy species.

ANALYSES.—To measure species evenness we used Smith and Wilson's index (E_{var}) (Smith & Wilson 1996):

$$E_{\mathrm{var}} = 1 - 2/\pi \ \arctan\left\{\sum_{S=1}^{S}\left(\ln(x_s) - \sum_{t=1}^{S}\ln(x_t)/S\right)^2 \Big/ S\right\}$$

With $S =$ the number of species in a plot, $x_s =$ the abundance of the s^{th} species, and arctan in radians. Values range from 0 to 1, with 0 representing minimum evenness, and 1 the maximum (Smith & Wilson 1996).

We compared the similarity of species composition of groups (census 1 vs. census 2; recruitment vs. dead trees; recruitment and dead trees vs. surviving trees from census 1) using the Chao–Jaccard abundance-based similarity estimator (Chao *et al.* 2005). Standard errors and confidence intervals were calculated by a bootstrapping procedure, with 200 resample trials. The estimator varies from 0 (no similarity) to 1 (complete similarity). Similarity index values differed significantly from a complete similarity when the value 1 fell outside the calculated confidence intervals. Note that the Chao–Jaccard Abundance Index provides a conservative estimate of similarity; the Jaccard Index based on presence–absence data and the Morisita Index based on abundance data (Krebs 1999) give much lower similarity values.

To evaluate whether these plot-wise analyses reflected a general pattern of successional species replacement, we performed a detrended correspondence analysis (DCA) on species abundance by plot × group combinations (24 combinations). Groups were: Recruited (R); Dead (D); and Surviving trees from census 1 (ST). We performed the DCA using the CANOCO (version 4.5) software (Ter Braak & Smilauer 1998), with abundance data square-root transformed prior to analysis. We included only species with five or more sampled individuals per plot (76 species). These species represented 99 and 97 percent of the sampled individuals and 61 and 75 percent of the total number of species of the initial assemblage and recruits, respectively.

Differences in species richness might proceed from differences in tree density (Denslow 1995, Chazdon *et al.* 1998). Therefore, when indicated in the results, we compared species richness at the lowest abundance level among groups using a bootstrapping procedure (Krebs 1999, Quinn & Keough 2002). This procedure implies random resampling, with replacement, from the original group to calculate test statistics. Calculations were done in the EcoSim 7.0 package (Gotelli & Entsminger 2001), using its rarefaction procedure. Calculated test statistics were the mean and 95 percent confidence intervals. We used the same bootstrapping procedure (using 1000 repetitions) to calculate the expected species richness and E_{var} assuming random mortality, and we tested differences between expected and observed values with one-sample *t*-tests (Quinn & Keough 2002).

RESULTS

SPECIES RICHNESS.—Across plots, tree density varied between 426 and 1786 (mean 906 ± 155 SE), and variation in species richness can simply be a consequence of these large differences (Denslow 1995, Condit *et al.* 1996). There was no significant relationship, however, between tree density and species richness in any of the two censuses (least square linear regression, census 1: $P > 0.95$, census 2: $P > 0.47$), and therefore we used actual observed species richness for across-plot comparisons.

At census 1, the number of recorded species in the plots (S_i) ranged from 24 to 54 (mean 40 ± 3.6 SE) and was positively related to fallow age (Fig. 1A). During the 18-mo study period,

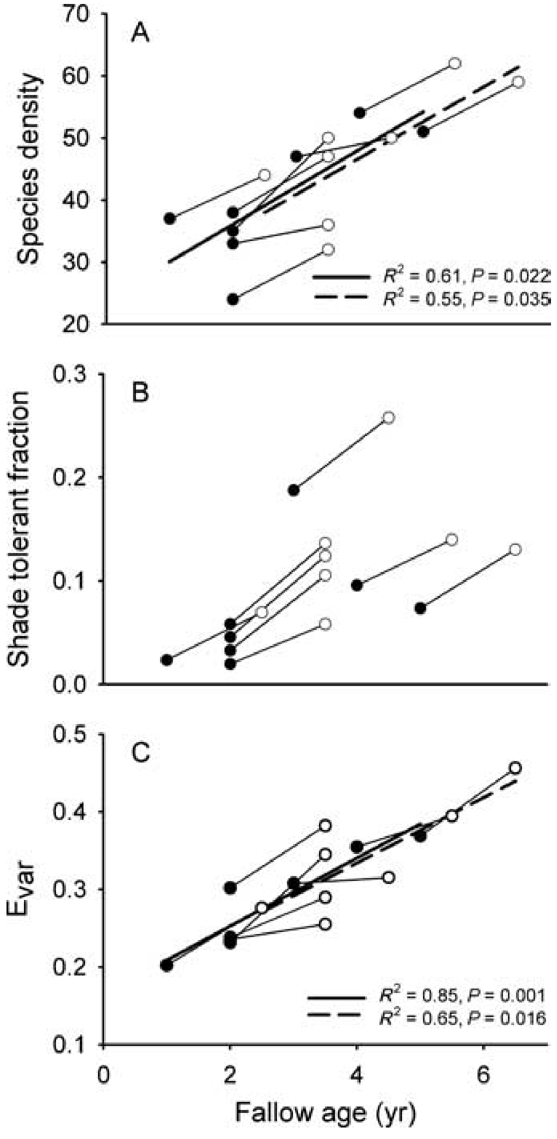

FIGURE 1. Early secondary succession trends in community attributes of trees ≥ 1.5 m height at Marquéz de Comillas, Southern Mexico. (A) Species density (number of species/500 m^2); (B) Fraction of total number of trees belonging to shade-tolerant species; and (C) Smith and Wilson's measure of evenness (E_{var}). Closed circles: census 1; open circles: census 2. The bold continuous and dashed lines give the linear regressions of the variables of census 1 and 2, respectively, on fallow age.

species density increased to 32–62 species/plot (mean 47.5 ± 3.6 SE), representing a 20 percent increase on average (6.4–42.9%). Species density continued to be significantly related to fallow age (Fig. 1A), with statistically similar regression slopes ($F = 0.00$, df $= 12$, $P = 0.95$) and interception points ($F = 0.10$, df $= 13$, $P = 0.75$) compared with those of the first census.

Shade-tolerant species constituted on average 7 percent (± 2 SE) of the total number of individuals, but 42 percent (± 5 SE) of all species. The fraction of shade-tolerant trees increased on average 2.3 (± 0.3 SE) times to an average of 13 percent (± 2 SE). In none of the two censuses was the shade-tolerant fraction related to fallow age (Fig. 1B), but the increase of this fraction was negatively related to fallow age ($R^2 = 0.59$, $P = 0.025$).

Species dominance and evenness.—Evenness (E_{var}) values were low, varying between 0.20 and 0.37 (Fig. 1C), but increased during the 18-mo study period in all plots. At the beginning and end of this period, E_{var} was positively related to fallow age (Fig. 1C) with statistically similar regression slopes ($F = 0.01$, df $= 12$, $P = 0.91$) and interception points ($F = 0.07$, df $= 13$, $P = 0.80$).

Low evenness values reflect the dominance (high relative abundance) of few species in these early successional assemblages. Across plots only 11 species (9% of total number of species) had more than 50 individuals in census 1, while 62 species (51%) had less than five individuals. Only seven species had a relative abundance (RA) ≥ 10 percent in at least one plot (Fig. 2B), of which *Trichospermum mexicanum* (DC.) Baill. (mean RA 26%, range: 1.5–59%), *Trema micrantha* (L.) Blume (mean RA 19.6%, range: 0–64%), and *Cecropia peltata* L. (mean RA 16.4%, range: 1–53%) were by far the most abundant ones. At census 1, in one plot the single most abundant species alone comprised on average 48 percent (± 4 SE) of total number of trees and the group of five most abundant species on average 82 percent (± 3; Fig. 2A).

Changes in dominance over the 18-mo study period seem to have been small, with only a slight decline of the share of dominant species in all plots (circles in Fig. 2A). However, the relative abundance of individual dominant species changed rather drastically in several plots (Fig. 2B) due to high mortality (see below). Populations of the early pioneer species *T. micrantha* dominated two plots (closed circles and open triangles in Fig. 2B) but collapsed due to extreme high mortality (89% and 93%) and were replaced by the early pioneer *T. mexicanum* as the most dominant species. The latter was partly the result of a high absolute increase (260% and 126%, respectively) due to recruitment, and partly a direct consequence of the decrease of *T. micrantha*. In one plot (open diamonds, Fig. 2), 76 percent mortality of the most abundant species *C. peltata* resulted in an increase of the relative dominance of *T. mexicanum*, even while absolute number of *T. mexicanum* trees decreased by 7 percent.

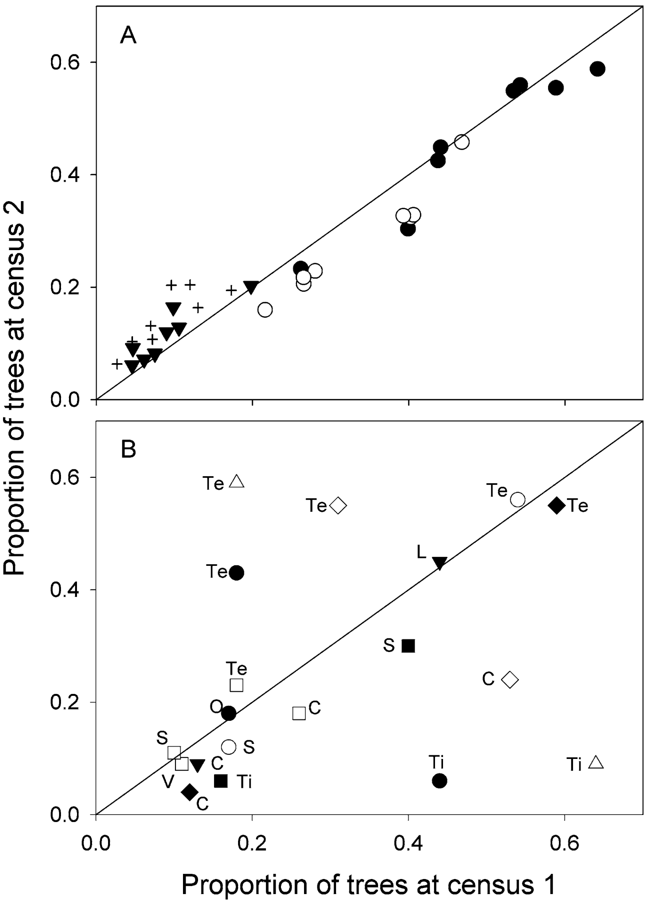

FIGURE 2. Change in proportional abundance of pioneer tree species during 18 m (from census 1 to census 2) in young secondary forest at Marquéz de Comillas, Southern Mexico. (A) Species are grouped according to dominance and every symbol represents a group-plot combination. Closed circles: single most dominant species per plot; open circles: 2nd to 5th most dominant species; triangles: 6th to 10th most dominant species; crosses: all other species. (B) Individual species that had a relative abundance of at least 10 percent in one or both censuses. Every point is a species-plot combination and different symbols represent different plots. Species are indicated as follows: Te = *Trichospermum mexicanum*; Ti = *Trema micrantha*; C = *Cecropia peltata*; L = *Luehea speciosa*; S = *Schizolobium parahyba*; O = *Ochroma pyramidale*; V = *Vernonia patens.*

Recruitment and mortality.—On average, 59 percent (± 6 SE) of the recruits were classified as pioneer, 34 percent (± 6) as shade-tolerant, and 7 percent (± 3) was unclassified, although among-plot variation was high (Fig. 3A). This variation is partly explained by among-plot differences in stand basal area mortality. Between 22 percent and 74 percent of the initial basal area in our study plots was lost due to the death of canopy trees during the study period, and the proportion of pioneers among the recruits was positively related with this percentage (least square linear regression, $R^2 = 0.69$, $P = 0.01$).

Most recruits (across plot average 77% ± 7) belonged to species with less than 1 percent of total plot basal area at census 0 (including new species). Ten percent (± 7) of recruits belonged to species that constituted between 1 and 10 percent of the plot basal area, and 13 percent (± 5) to the group of species that constituted at least 10 percent of the plot basal area (Fig. 4A). For convenience we will refer to the latter group as 'canopy dominants.' Only six species belonged to this group in at least one of the study plots, all of

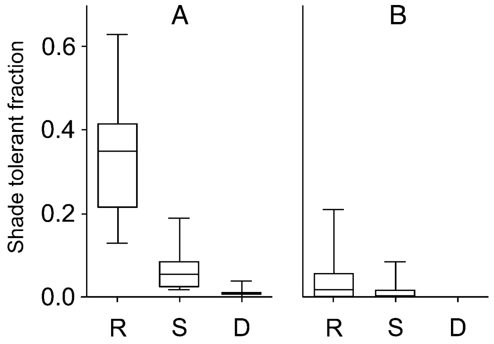

FIGURE 3. Dynamics of the fraction of shade-tolerant trees in early successional communities. Shade tolerant fraction of the trees of the initial assemblage that survived the study period (S) and of the groups of trees that recruited (R) and that died (D) between censuses 1 and 2. Different lower size limits were used to define the initial group of trees as well as recruitment: (A) height ≥ 1.5 m; (B) dbh ≥ 2.5 cm. Boxes show median, the 25th and 75th percentiles and the whiskers give the extent from lowest to highest values.

them pioneer species. Four of these species hardly recruited in the plots where they formed the canopy dominants, with across-plot averages (± SE; number of plots) of: *T. micrantha* 0.7 percent (± 0.5; 4); *Schizolobium parahyba* (Vell.) S. F. Blake 1.1 percent (± 1.1; 3); *Ochroma pyramidale* (Cav. ex Lam.) Urb. 0.4 percent (± 0.4; 4); *C. peltata* 2.6 percent (± 1.2; 4). These averages were much higher for two other pioneer species: *T. mexicanum* 17 percent (± 8.5; 4); and *Luehea speciosa* Willd. 18 percent (— 1). In five plots, the canopy dominants were represented by > 10 percent of the recruits (Fig. 4A), and these percentages were largely due to high recruitment of these two species.

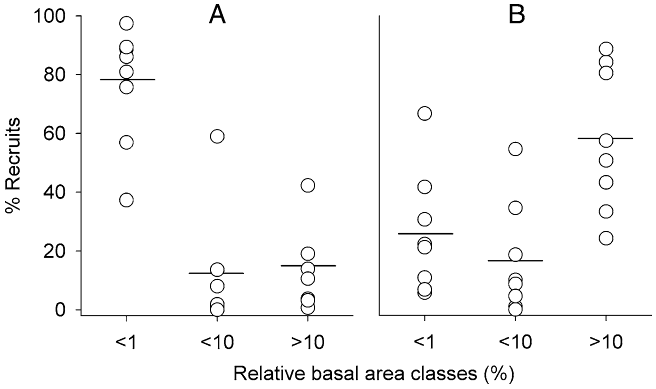

FIGURE 4. Frequency distribution of recruitment among relative basal area classes. Relative basal area is calculated as the percentage of the plot basal area at census 0. Species were grouped in classes according to their relative basal area, with class limits as indicated on the x-axis, and the percentage of total number of recruits in a plot was calculated for each class. The among-plots means are indicated by horizontal lines. Different lower size limits were used to define the initial group of trees as well as recruitment: (A) height ≥ 1.5 m; (B) dbh ≥ 2.5 cm.

Redefining the size class to take into account only larger stems with dbh > 2.5 cm resulted in rather different recruitment patterns. A lower fraction of the recruitment in this class was shade tolerant (Fig. 3B) and, on average, most recruits in this class belonged to the group of species with more than 10 percent of total plot basal area (at census 0), with considerably higher between-plot variation (Fig. 4B). Comparing Figures 3A and 3B, on one hand, and 4A and 4B, on the other hand, shows that most of the species dynamics discussed in the previous paragraph occurred in the lower size classes (notably stems < 2.5 cm dbh).

Mortality was high, ranging between 17 percent and 63 percent (mean 39% ± 6 SE) of the initial individuals. The Smith and Wilson index (E_{var}) of the group of dead trees was lower than expected by random mortality in all plots (bootstrap procedure, with plot-wise repeated random sampling of a number of individuals equal to the number of dead trees in the plot, *t*-test, df = 999, $P < 0.001$). This suggests relatively high mortality among the most abundant species in each plot. In all plots mortality among the pioneer species (mean = 43.3% ± 5.8) was more than three times higher than the across-plot mean of the shade-tolerant group (13.0% ± 2.6). Across plots this difference was highly significant (paired samples *t*-test, $t = 5.6$, $P = 0.001$).

Species richness of the dead trees (S_d) ranged from 12 to 20 (mean 16) species, and between one and six species per plot disappeared during the 18-mo interval (mean 2.8 ± 0.6 SE). Species richness of recruited trees (S_r) varied between 19 and 40 (mean 28). Between 5 and 19 new species entered the plots (mean 10.4 ± 1.4), which constituted on average 38 percent (23–61%) of the species richness of the recruited trees. In all plots, the number of new species surpassed the number of species lost, and consequently absolute species richness increased (Fig. 1A). The recruited community was not only richer in species than the group of dead trees, but also had higher evenness values (0.63 ± 0.06, and 0.27 ± 0.02, respectively).

When the species richness of the initial assemblage (S_i) was compared pairwise with S_r and S_d, considering the lowest abundance level of recruitment and dead trees ($S_{i\,(\mathrm{rarefied})}$; Gotelli & Entsminger 2001), S_r was significantly higher than $S_{i\,(\mathrm{rarefied})}$ in seven of eight plots, and S_d was in all cases lower than $S_{i\,(\mathrm{rarefied})}$. Likewise, we compared S_r with S_d at the lower abundance level of the recruitment, and S_r was significantly higher than $S_{d\,(\mathrm{rarefied})}$ in all cases (data not shown).

SPECIES COMPOSITION AND TURNOVER.—None of the eight plots showed a significant change in species composition over 18 mo. Similarity values (Chao–Jaccard Abundance Estimator; Chao *et al.* 2005) ranged from 0.95 to 1.00 with none being significantly different from 1 (Table 1). In all but two plots, species composition of the assemblage of recruits did not differ significantly from the assemblage of surviving trees. Similarity between dead and recruited trees was on average lower, but the difference was only significant in 4 of the 8 plots (Table 1).

TABLE 1. *Similarity between species assemblage of censuses 1 (C1) and 2 (C2), and between recruitment (R), dead trees (M), and surviving trees (S) assemblages. Chao–Jaccard abundance-based similarity estimators are given ± standard error. Bold values indicate that the value is significantly different from 1. The number in the plot names indicates plot age at census 1.*

Plot	C1 × C2	S × M	S × R	M × R
R1	0.98 ± 0.04	0.90 ± 0.14	0.83 ± 0.16	**0.35 ± 0.16**
F2	0.95 ± 0.05	0.87 ± 0.10	0.86 ± 0.15	0.74 ± 0.23
H2	1.00 ± 0.03	0.83 ± 0.17	0.96 ± 0.10	0.78 ± 0.27
P2	0.98 ± 0.04	0.83 ± 0.14	0.94 ± 0.14	0.73 ± 0.30
R2	0.97 ± 0.03	0.99 ± 0.07	**0.54 ± 0.14**	**0.57 ± 0.20**
G3	1.00 ± 0.00	0.98 ± 0.13	1.00 ± 0.06	0.85 ± 0.28
F4	1.00 ± 0.01	0.93 ± 0.17	0.78 ± 0.19	**0.38 ± 0.21**
R5	1.00 ± 0.01	0.97 ± 0.08	**0.39 ± 0.13**	**0.39 ± 0.20**

The three groups did differ with respect to the share of shade-tolerant trees. In all plots, the fraction of shade-tolerant trees in the recruitment group was higher than in the group of survivors from the initial assemblage (after log transformation, paired sample *t*-test, $t = -5.93$, $P = 0.006$). The shade-tolerant fraction of the surviving trees was higher than that of the dead trees (after log transformation, paired sample *t*-test, $t = 4.81$, df $= 7$, $P = 0.002$ (Fig. 3).

The variation explained by the first two axes of the DCA was only 27.6 percent (axis 1 = 19.8%; Fig. 5). The first axis was most strongly correlated with the variables 'recruits' and 'dead,' but with opposite sign ($r = -0.55$ and 0.63, respectively), indicating a separation between the composition of species that entered (recruitment) and left (mortality) our secondary succession plots. Correlation of the first axis with fallow age was $r = -0.47$. The shade-tolerant species had a significant lower mean score on the first axis than the pioneer species ($t = -4.8$, df $= 66$, $P < 0.001$). These results suggest a pattern of species turnover, starting the replacement of pioneer species by shade-tolerant species as succession progresses.

DISCUSSION

In this study, we addressed species colonization and replacement dynamics during the first years of secondary succession. More specifically, we evaluated the prediction that the IFC hypothesis (Egler 1954) applies to succession on abandoned agricultural fields with light use and proximity to old-growth forests patches (Gómez-Pompa & Vázquez-Yanes 1981; Finegan 1984, 1996). To meet these conditions, all sites were selected on abandoned milpas that had been in use for one single harvest, and adjacent or close to other forest fragments. There is no clear consensus regarding how to understand and interpret the IFC hypothesis (Wilson *et al.* 1992, McCook 1994). Therefore, we formulated specific predictions concerning species dynamics on community level that will be examined in the following paragraphs.

Patterns of species richness and composition.—Species density was as high as 54 species/500 m^2 in these very early stages of secondary succession (Fig. 1B). When differences in density were taken into account, species richness reached about one-third of the values of old-growth forest within the same region: after rarefaction, the mean old-growth forest species richness was 56 species/188 trees (M. Martínez-Ramos, pers. obs.), while the average secondary forest value was 17 species/188 trees (range: 9–22, census 1). About 60 percent of the species encountered in our sites was also found in five 0.5-ha old-growth forest plots in the same region on similar soils (M. Martínez-Ramos, pers. obs.). Dominance of the species differed, however, between secondary and old-growth forests. While the five most dominant species in the secondary forest plots represented 66 percent of all trees, they represented less than 1.3 percent of all trees with dbh ≥ 10 cm in the old-growth forest. On the other hand, five of the six most abundant species in the old-growth forest (together representing 33% of total stems with dbh ≥ 10 cm in 2.5 ha), were present in one to six of our eight secondary forest plots. They occurred in low numbers however (1–5 individuals per plot).

The relationships between species density and fallow age were the same for census 1 and census 2, suggesting that the chronosequences gave a good estimate of general trends of increasing species density, at least over a time interval of a few years. Despite such consistent results, however, rate of increase of species richness varied considerably among plots (Fig. 1B). This supports the suggestion that time studies are very much needed to recognize such a variation and to analyze the underlying patterns of mortality and recruitment, as advocated earlier by Swaine and Hall (1987), Finegan (1996), and Chazdon *et al.* (2005).

Recruitment.—The predictions that both pioneer and shade-tolerant species co-occur since the initial phase of succession is supported by our data. Because of differences in criteria used and a degree of subjectivity in species grouping, comparisons between studies have to be made with care. However, the 2 percent shade-tolerant trees in our 1-yr-old site is in the same order of magnitude as those in 1-yr-old plots in Ghana (5.4%; Swaine & Hall 1983), and in the Venezuelan Amazon (2%; Uhl 1987).

Resprouting from surviving stumps from trees of the original forest can be an important regeneration mode (Kammesheidt 1998, Bond & Midgley 2001) that might make it inherently more likely that a succession will fulfill IFC predictions, as opposed to a situation in which 'shade-tolerant' species have to recolonize mainly or totally through seed dispersal. Data on resprouting in secondary forest succession are scarce though. In the Venezuelan plot of Uhl (1987), 5 yr after abandonment 21 percent of the shade-tolerant individuals were sprouts on stumps of trees from the original forest. In the study site in Ghana (Swaine & Hall 1983), 1 yr after abandonment all shade-tolerant plants (13% of all plants) were coppice shoots of trees

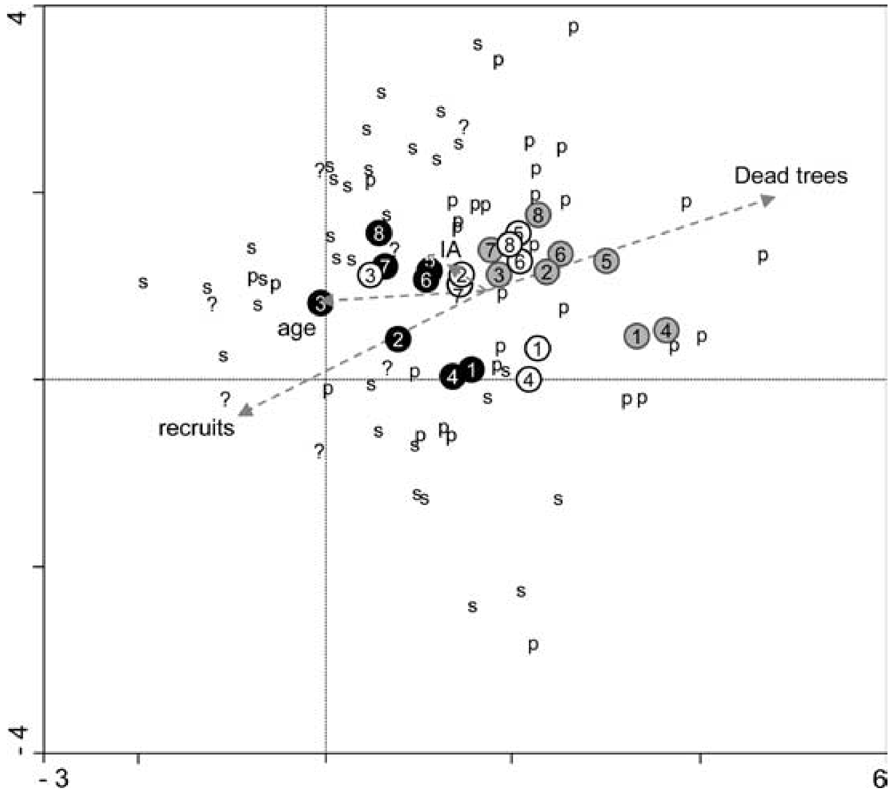

FIGURE 5. Ordination of groups in secondary forest plots with species (letters) and samples (circles). P: pioneer species; S: shade tolerant species; ?: not classified. Samples were plot × group combinations, with groups being: open circles: trees from the initial assemblage (census 1) that survived the study period (IA), black circles = recruits, and gray circles = trees of the census 1 that died during the study period. Numbers indicate plots. Groups were included as dummy variables (arrows). A detrended correspondence analysis (DCA) was used, and species numbers were square root transformed prior to analysis.

of the original forest, but in the 5 yr following the initial census no more resprouting was observed. In our 3-yr-old site, resprouts on surviving trunks constituted at least 32 percent of the stems and represented 65 percent of the shade-tolerant species in the plot. In the other sites, resprouting from original vegetation seemed to be rare or absent, but this was difficult to assess reliably, since resprouting also occurred from surviving belowground root systems (M. van Breugel, pers. comm.).

Our results contrast with the IFS prediction that dominant pioneer species recruit poorly after initial canopy closure (Finegan 1984, 1996). All our plots had a closed canopy at the time of the first census yet, on average, more than half of the recruitment belonged to pioneer species. Uhl (1987) also reported recruitment of pioneer species in year 2–5 of postagriculture succession, despite the presence of a relatively high leaf area index in these years. High stand-level mortality in young secondary forests, however, results in a highly dynamic stand structure (Breugel *et al.* 2006), and we found a positive relationship between stand-level mortality and the proportion of pioneers among the recruits. Uhl (1987) reports enhanced recruitment of pioneer trees following increased mortality of the dominant *Vismia* spp. 4 yr after succession started. These findings suggest that high mortality rates during early succession might provide new recruitment opportunities for pioneer species after initial canopy closure.

Swaine and Hall (1983) found that none of the species that dominated the canopy at the end of the first year recruited thereafter, while the dominating *Vismia* spp. in Uhl's (1987) study plot continued to recruit in relatively large numbers up to the fourth year. The contrasting results of these early single-plot studies could lead to different conclusions, but in fact they fit well within the variation at local scale that we found in this study (Fig. 4), stressing the necessity of using multiple plots within the same age class.

MORTALITY.—As predicted, mortality among pioneers exceeded mortality of shade-tolerant species in all plots. Moreover, mortality was biased toward the dominant species. These and similar observations in 12- to 25-yr-old plots (Chazdon *et al.* 2005) and in a 60-yr-old plot (Lang & Knight 1983) indicate a gradual shift in canopy dominance from pioneers to shade-tolerant species.

In the first years of succession, shade-tolerant species are still mainly confined to the understory (Peña-Claros 2003) and competition for a canopy position is mainly between species with the same early successional status. In this study, all plots were dominated by pioneer species with a maximum life span that exceeds the 6.5 yr covered by our chronosequence study system. Nonetheless, interspecific variation in mortality rates was very high, and caused a strong shift in canopy dominance in five of eight study plots, despite the short study period (Fig. 2). Illustrative is the 1-yr-old plot, where relative abundance of *C. peltata* and *T. mexicanum* was 53 and 31 percent, respectively. Both species are early successional species with about the same life span of 25–35 yr, are very abundant, and often co-occur in our study region. The two species accounted for 86 percent and < 5 percent of total stem mortality, respectively and, in consequence, *T. mexicanum* replaced *C. peltata* as canopy dominant. Similar patterns were also reported for early succession in Ghana, where the initially dominating *Musanga cecropioides* gave way to *Harungana madagascariensis* due to differences in mortality rates (Swaine & Hall 1983). A different example is given by the catastrophic mortality among the dominant *T. micrantha* (> 90% of trees) in two other plots. Mortality affected these trees irrespective of their size or canopy position (M. van Breugel, pers. obs.), suggesting an outbreak of pathogens as the more likely cause of death, as has been shown earlier for cohorts of pioneer species in old-growth tropical forest (Augspurger 1984, Augspurger & Kelly 1984). This enabled another pioneer (*T. mexicanum*) to recruit massively and dominate the canopy within 18 mo. In old-successional (*e.g.*, Lussier *et al.* 2002) and young-successional temperate forests (Fujihara 1996, Toyohara & Fujihara 1998) pathogen outbreaks have been shown to alter succession in a similar fashion. These examples indicate that interspecific differences in mortality rates play an important role in the dynamics of early years of secondary forest succession.

SPECIES TURNOVER.—The recruitment group showed consistently higher species richness and evenness than the dead tree group, as predicted. On average, four times more new species entered than disappeared from the plots, hence species diversity increased strongly in all plots. Nonetheless, similarity estimates suggested that species composition hardly changed after 1.5 yr. An explanation of this lies in the strong dominance by few species, as a result of which the numerical influence of the recruitment of new species was low. In one plot with an initial richness of 35 species, for example, 19 new species recruited were represented by only 42 individuals, about 10 percent of the initial tree density in that plot.

A more sensitive indication for an ongoing shift in species composition was therefore given by the dissimilarity between the species composition of the trees that entered (recruitment group) and left (dead group) the tree community. The differences between these two groups indicated successional species replacement that was not evident when only net changes from census 1 to 2 were considered. The separation of the composition of recruits and dead trees along the first axis of the correspondence analysis suggested similar successional patterns. The shade-tolerant fraction was relatively high in the recruitment group, while mortality was almost entirely confined to pioneer trees. These results indicate that successional species turnover, in which pioneer species are being replaced by shade-tolerant species as a consequence of differential recruitment and mortality rates, already starts at the very early years of succession.

Species composition of the recruited and dead tree groups did not, however, differ in all plots. In some plots still a considerable fraction of recruits belonged to pioneer and canopy-dominant species. Consequently the degree of species turnover and functional group replacement varied considerably among plots. Further studies should disentangle effects of species differences (*e.g.*, seed dispersal modes, establishment requirements, susceptibility to natural enemies affecting growth and mortality rates) and landscape factors (dispersal limitations, local species pool available for colonization). Applying a larger size limit (2.5 cm dbh instead of 1.5 m height) clearly showed that most of species and functional group recruitment in these initial years are confined to the smaller size classes, in line with earlier suggestions from Okimori and Matius (2000) and Peña-Claros (2003). This stresses the need to include small size limits in the study of successional species dynamics, at least in these early communities.

CONCLUSION.—We conclude that the highly dynamic and spatially variable nature of secondary succession makes it difficult to explain successional species replacement patterns based on static data, and support calls (Finegan 1996; Chazdon *et al.* 2005, 2007) for community-level studies that monitor recruitment, mortality, and growth. This study demonstrates the benefits of setting up permanent plots across a range of initial stand ages. This approach effectively complements direct observation with space-time substitution when long-term monitoring of secondary sites is problematic, and addresses questions on community dynamics in different phases of secondary forest succession.

Successional species turnover, resulting in replacement of pioneer species by shade-tolerant species, already started in the beginning of succession. However, the fraction of canopy dominants and pioneer species among recruits, and consequently the species turnover rate, varied considerably among sites. We suggest that secondary succession is not always a gradual and continuous process of functional group replacement, but that high mortality during the first years of secondary forest succession may open new recruitment windows for pioneer species. Overall, our study supports the IFC hypothesis, but we urgently need the development of new approaches (stochastic and/or deterministic) to explain the high levels of intersite variation observed in the early stages of the secondary succession process in tropical abandoned agricultural fields.

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