

Successional dynamics of woody seedling communities in wet tropical secondary forests

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Summary

1 Chronosequence studies have found that shrubs and lianas are generally more abundant in early stages of tropical forest succession, whereas canopy trees and palms become more abundant and species-rich in older stages and mature forests.

2 We analysed changes in woody seedling communities over 5 years in four second-growth forests (initially 13–26 years after pasture abandonment) in Costa Rica. We recorded community-level changes in woody seedling density, species density, species richness and composition in six woody life-forms: canopy trees, subcanopy trees, canopy palms, understorey palms, shrubs and lianas. We evaluated these changes in relation to annualized recruitment and mortality rates for each life-form.

3 Seedling density declined in all four sites over the 5 years, whereas Shannon diversity and the proportion of rare species increased. Species richness and evenness increased in all but the oldest site.

4 Canopy palm, understorey palm and canopy tree seedlings increased in species richness and relative abundance, whereas shrub and liana relative abundance declined. Canopy trees accounted for 34–42% of all new recruits. Detrended correspondence analysis showed that species composition was initially highly distinct within each forest site and remained distinct over the 5-year period.

5 Shifts in life-form were correlated with declining light availability during succession. Across sites, median light availability at the end of the study period in 2003 was positively correlated with recruitment rates of understorey palms, shrubs and lianas, and was negatively correlated with mortality rates of canopy trees and palms.

6 Observed changes among seedling communities mirrored those described in chronosequence studies on plants in larger size classes, lending support to the assumptions of chronosequence studies in Neotropical forests.

7 The results demonstrate the importance of seedling recruitment and mortality in determining the course of succession. Convergence occurs in some community properties, such as relative abundance within life-forms, but not in others, such as species composition. Finally, the results illustrate the value of studying plant community dynamics at the level of woody life-forms, especially in hyperdiverse systems such as tropical forests.

Key-words: canopy trees, chronosequence, forest understorey, lianas, life-form, mortality, palms, recruitment, shrubs, succession.

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Introduction

Life-form composition, abundance and species richness of woody vegetation undergo major shifts during secondary forest succession. In Neotropical forests, lianas (Hegarty & Caballé 1991; DeWalt *et al.* 2000; Peña-Claros & de Boo 2002) and shrubs (Guariguata *et al.* 1997; Laska 1997) reach higher abundance in early successional forests than in old-growth forests, whereas palms (Guariguata *et al.* 1997; Svenning 1998; Farris Lopez 2001), canopy trees (Guariguata *et al.* 1997) and understorey treelets (Martin *et al.* 2004) show increasing abundance during later phases of succession and in mature forests. Successional shifts also occur within individual life-forms; tree species that dominate early successional forests decline in abundance in mature forests, and species abundant in mature forests may be absent or less abundant in early successional forests (Saldarriaga *et al.* 1988; Guariguata & Ostertag 2001; DeWalt *et al.* 2003). The net effect of these changes is an increase in woody species richness, evenness and species diversity (Shannon index) during the first 40–50 years of succession (Saldarriaga *et al.* 1988; Peña-Claros 2003; Ruiz *et al.* in press).

In secondary tropical forests, seedling dynamics can link communities of early successional shrubs, shade-intolerant trees and lianas with later successional communities of shade-tolerant canopy trees, palms and understorey trees, revealing how these transitions occur and, potentially, permitting inferences to be drawn about the processes involved. Community-level studies of seedlings in secondary tropical forests are lacking (but see Chazdon in press), however, and even studies that include all woody seedlings are very rare (e.g. Harms *et al.* 2000).

To date, most of our knowledge on successional dynamics of tropical forests is based on chronosequence studies, in which sites of different ages are used to represent the general condition of all sites at those ages (Pickett 1989; Chazdon in press). Although this approach is expedient, allowing work to be done in a year or two that would otherwise take decades or longer, chronosequence studies assume similar site history, environmental conditions and seed availability, assumptions that rarely are tested (Chazdon in press). Long-term studies are needed to determine whether changes that actually occur over time within individual sites conform to successional patterns described in chronosequence studies (Sheil 1999), as well as to elucidate the processes associated with these patterns.

Here we examine woody seedling dynamics over 5 years in four wet, secondary forest sites in north-east Costa Rica. Study area forests ranged in age from 13 years to 26 years in 1998 when the seedling dynamics study began. We focus on changes in density and species composition of woody seedlings in six life-forms: canopy trees, subcanopy trees, canopy palms, understorey palms, shrubs and lianas. Based on detrended correspondence analysis and an abundance-based estimator of community similarity (Chao *et al.*

2005), we also examine patterns of floristic similarity among woody seedling communities and address changes in these patterns over time.

If chronosequence assumptions are valid, we would expect to find changes in forest composition during the 5-year period of our study that mirror those observed in chronosequence studies. These would include decreases in abundance of shrub and liana seedlings and increases in abundance of palm and canopy tree seedlings. We further predict an overall decline in woody seedling density, modest or no change in species richness, increasing evenness and increasing species diversity. Previous studies in north-east Costa Rica have found higher woody seedling density and species richness in old-growth than in secondary forests (Nicotra *et al.* 1999). Similarly, in a chronosequence study of Panamanian forests, Denslow & Guzman (2000) found that seedling densities were highest in 20-year-old second-growth sites (the youngest age class studied), decreasing to a minimum in 100-year-old sites; species diversity did not differ among forests after accounting for seedling density.

Chronosequence studies in a river-bank succession in Peru (Terborgh *et al.* 1996) and secondary succession following human land use in Uganda (Sheil 1999) suggest that species composition of tree communities follows an orderly progression from successional to mature sites. However, studies of species composition within these plots over time do not support the convergence model (Sheil 1999), and long-term studies of forest successional dynamics following hurricane damage in south-east Nicaragua (Vandermeer *et al.* 2004) concluded that successional pathways were diverging over time, perhaps owing to differences in initial conditions or to later successional dynamics. Thus, whereas some community properties, such as species density, appear to converge over time in tropical forests, convergence of other properties, including species composition, may depend on the characteristics of individual sites, including proximity to mature forests and the degree of disturbance. Here we test whether the composition of woody seedling communities becomes more similar over time during secondary succession in a fragmented landscape in Costa Rica.

Our study is the first to report on the successional dynamics of woody seedling communities in tropical forests. Our focus on life-forms reveals patterns not previously evident among seedling communities but which explain changes previously observed in larger size classes. Although the lack of replication within forest age classes limits the statistical power of our analysis, the clear trends that emerge from our results provide novel insights into the role of seedling recruitment and mortality in shaping successional trajectories in Neotropical forests.

Methods and materials

STUDY PLOTS

Four 1-ha monitoring plots were established in 1997 in the Caribbean lowlands of north-east Costa Rica, Sarapiquí

Table 1 Site descriptions of 1-ha monitoring plots in north-east Costa Rica. Seedling communities in the four second-growth sites were monitored for 5 years

Site abbreviation (full name)	Location	Age in 1998 (years)	Previous land use	Landscape matrix	Mean tree height > 10 cm d.b.h., 1999 (m)*	Light (median %T at 0.5 m, 2003, range in parentheses)	Number of trees > 25 cm d.b.h. in 1997*
LSUR (Lindero Sur)	La Selva Biological Station	13	Cattle pasture	Adjacent to large tract of old-growth	16.90	1.38 (0.80, 8.49)	63
TIR (Tirimbina)	Finca de Arturo Salazar, adjacent to Tirimbina Research Center	16	Cattle pasture	Surrounded by matrix of pasture and second-growth	16.10	2.13 (1.18, 31.21)	78
LEP (Lindero El Peje)	La Selva Biological Station	21	Cattle pasture	Adjacent to large tract of old-growth	19.50	1.41 (0.71, 10.75)	165
CR (Cuatro Rios)	La Virgen de Sarapiquí	26	Cleared for cattle pasture, little or no grazing	Surrounded by matrix of pasture and second-growth	20.21	1.18 (0.73, 5.11)	208

*Chazdon (in press).

County, Heredia Province. The natural vegetation in the area is classified as Tropical Wet Forest (*sensu* Holdridge *et al.* 1975). Annual temperature and rainfall average 26 °C and 3800 mm, respectively, at La Selva Biological Station (Sanford *et al.* 1994). Soils in our study areas are derived from weathered granite (Fisher 1995) and are primarily classified as ultisols (Sollins *et al.* 1994). Much forest in the area was cleared for agriculture during the 1960s and 1970s, although some was abandoned later (Butterfield 1994; Table 1). The area is now a mosaic of primary forest, secondary forest, agricultural land and active pastures. The sites where the four monitoring plots were established had been cleared and grazed lightly for several years before being abandoned (Chazdon *et al.* in press). Land-use history was determined based on aerial photographs, satellite images and interviews with residents and land-owners. Two sites (LSUR, 13 years since agricultural pasture, and LEP, 21 years old) were within La Selva Biological Station (10°26' N, 84°00' W), approximately 3 km from each other. Two others (TIR, 16 years since abandonment, and CR, 26 years old) were on privately owned farms about 12 km south-west of La Selva and 5 km from each other and are more isolated from mature forest areas. LEP and TIR plots were 50 × 200 m in size. Because of roads (CR) and uneven topography (LSUR), two adjacent 0.5-ha plots, of 50 × 100 m, were created at LSUR and CR. All had closed canopies, although canopy height varied with age (Table 1).

Light levels were measured in 2002–03 at 5-m intervals, at one corner of each seedling plot (see below), using a red : far-red (R : FR) light meter (Skye SKR 110 sensor, Skye Instruments, Llandrindod Wells, UK) mounted on a tripod, then converting the R : FR ratio to percentage diffuse transmittance (%T) using the technique of Capers & Chazdon (2004). All light readings were made in diffuse light conditions and at a

height of 50 cm (Table 1). Differences among %T were analysed with analysis of variance and a post-hoc least significant difference (LSD) test.

At each site, 144 seedling plots were created, each of 1 × 5 m, with a total area of 0.072 ha. Initial seedling censuses were conducted in 1998 (1–28 April at LEP, 27 April–20 May at LSUR, 21 May–3 June at CR and 12 June–3 July at TIR). All woody stems > 20 cm in height and < 1 cm d.b.h. were identified to species level, assigned a number and tagged. Seedlings were identified by experienced field assistants (Marcos Molina and Orlando Vargas), and vouchers were collected to compare with specimens identified at the La Selva Herbarium and the Costa Rican Institute for Biodiversity. Each species was assigned to a life-form (canopy tree, subcanopy tree, canopy palm, understorey palm, shrub or liana). Life-form categories were determined by Orlando Vargas, an experienced naturalist, and were also used in previous studies by Chazdon *et al.* (2003). Two species in LSUR, one in LEP and one in CR were unidentified and could not be assigned to life-form; these were excluded from the life-form analysis but treated as separate species otherwise. Every 4 months, censuses were conducted to identify newly recruiting seedlings and seedlings that had died. Stem height of all seedlings was measured at 8-month intervals. When the stem at 20 cm above the ground reached a diameter of 1 cm, a seedling was advanced to the sapling size class. The final census (the 17th) was completed in August 2003.

SEEDLING ABUNDANCE AND SPECIES RICHNESS

From the complete data set, we extracted seedling abundance data for all species at the 1st, 5th, 9th, 13th and 17th census in each of the four sites. These data

were used to evaluate change in species richness and seedling abundance by life-form. Shannon diversity was calculated, and evenness was measured as J , the observed value of the Shannon index as a proportion of its maximum value, which equals the natural logarithm of the number of observed species with perfect evenness. Rareness was measured as the percentage of species represented in a community by only one stem (singletons). We used sample-based rarefaction (Gotelli & Colwell 2001) to adjust for unequal numbers of seedlings in sites and to compare species richness and tree species richness at the beginning and the end of the study period. This was done using EstimateS software (Version 7.5, Colwell 2005), computing the mean number of species in a randomized sample of 1375 seedlings (340 tree seedlings), based on 200 randomizations. We used analysis of variance to determine if mean species density in 5-m² quadrats differed among sites at the first census or the final census.

Analysis of variance also was used to determine if mean seedling density in 5-m² quadrats differed among sites and whether it changed within sites. G -tests were used (incorporating Williams' correction, Sokal & Rohlf 1995) to determine if the distribution of seedlings among life-forms changed within sites over the 5-year study period and if the life-form distribution differed among sites, for both seedling density and species density. We used paired t -tests with the four sites as replicates to assess whether mean seedling density and mean species density changed during the study period, overall or among life-forms.

We used detrended correspondence analysis (DCA) to determine whether the four seedling communities diverged or became more similar over time. All species with a minimum of eight seedlings at some point during the 5-year period were included ($n = 120$). Abundance of seedlings in five censuses for each site were entered in the DCA, which was executed in PC-ORD for Windows (McCune & Mefford 1997). We also evaluated similarity in woody species composition (including all species) between all pairs of sites at the beginning and the end of the study period using a new, abundance-based Jaccard index that corrects for rare species missing from samples but likely to be present and shared (Chao *et al.* 2005).

MORTALITY AND RECRUITMENT

To establish the importance of mortality in explaining change over time in the relative abundance of each life-form, we determined the proportion of the original cohort of seedlings that survived the 5-year period at each site. Seedlings that graduated to the sapling size class were considered to have survived for the entire 5-year period. Mortality rates for each life-form were annualized by using the equation $m = 1 - (N_t/N_0)^{1/t}$ where N_t is the number of seedlings alive at the end of the period, N_0 is the number in the original cohort and t is the time period, 5 years in this case (Sheil *et al.*

1995). Mortality rates among seedlings that recruited to the sites during the study period were calculated in the same way; a rate was calculated separately for each cohort – those newly recorded at each census – and a mean mortality rate was then calculated, weighted by the number of seedlings in each cohort. The recruitment rates, r , for each life-form were calculated in a similar way (Sheil *et al.* 2000) as $r = 1 - (1 - n_t/N_t)^{1/t}$ where n_t is the number of recruits during the period, and N_t and t are as above.

To explore the effect of mortality and recruitment on species richness, we determined the number of species present in the original census but not in the final census, calculating a 5-year species persistence rate (the proportion of species surviving the entire 5-year period) for each life-form. We also determined the number of new species recruiting to the sites during the 5-year period and the number of species in each life-form with increasing abundance and decreasing abundance. We analysed Pearson correlation coefficients to determine whether the degree of change in absolute abundance of seedlings (the difference between abundance in the first and final censuses in each of the four sites) in each life-form was affected most by annualized recruitment or mortality rates and to explore the effects of site age and light availability on these rates. Results of correlation analysis using relative abundance instead of absolute abundance were qualitatively the same and are not reported.

Results

Light availability was significantly higher in TIR than in the other sites ($F_{3,480} = 19.035$, $P < 0.0001$; Table 1). Median %T was similar to the values (0.98–2.0%) recorded in three secondary (15–20 years old) and three old-growth forest sites in the region by Nicotra *et al.* (1999), who found that mean %T did not differ between old-growth and second-growth sites. In our sites, light was most variable in TIR, with high light levels in several areas that remain quite open. LEP and CR had no canopy openings and had more uniformly low light availability.

CHANGES IN SEEDLING DENSITY, DIVERSITY AND COMPOSITION

Seedling density in 5-m² quadrats differed among sites at the beginning and the end of the study period ($F_{3,572} = 24.024$ and 32.240 , respectively, $P < 0.0001$ in both cases) and declined significantly over time ($F = 40.039$, d.f. = 1, $P < 0.0001$) from (mean $\pm$ SE) 15.9 ± 1.35 to 11.7 ± 1.00 seedlings in LSUR, 23.3 ± 1.46 to 20.5 ± 1.10 seedlings in TIR, 11.0 ± 0.65 to 9.3 ± 0.43 seedlings in LEP, and 13.2 ± 0.59 to 12.8 ± 0.70 seedlings in CR. The greatest decline (26%) was seen in the youngest site and the least (3%) in the oldest. Of the species present in the first census, 10–12% were lost during the 5-year period, but younger sites gained twice as many new species as they lost, whereas the two older sites had

Table 2 Community characteristics are shown for five times during a 5-year period in four second-growth tropical forest sites in Costa Rica. The 1-ha study sites ranged in age from 13 years to 26 years when the research began. Seedlings in each forest were censused in 144 quadrats, each 5 m² in area. Seedling density and species density in each site are totals recorded in this 0.072-ha area. % rare is the proportion of species that had no more than one seedling in a plot. The number of species lost is the number of those present at the first census that were absent from the last, and the number of species gained is the number that were absent from the first but present in the last

	Month				
	0	16	32	48	60
LSUR (13 years)					
Species number	132	130	137	142	150
Seedling number	2287	2035	1918	1751	1710
Shannon diversity	2.98	3.01	3.20	3.31	3.51
<i>J</i> , evenness	0.61	0.62	0.65	0.67	0.67
% rare	31.8	30.0	28.5	35.2	33.3
5-year species persistence (%)					89.4
No. (%) species lost					14 (11)
No. (%) species gained					32 (21)
Tree seedling species number	50	49	51	53	56
Tree seedling number	427	379	382	345	353
% rare trees	28.0	28.6	27.5	35.8	33.9
TIR (16 years)					
Species number	152	152	160	164	168
Seedling number	3350	2976	2930	2989	2978
Shannon diversity	3.06	3.16	3.33	3.41	3.49
<i>J</i> , evenness	0.61	0.63	0.66	0.67	0.68
% rare	21.6	23.0	27.5	26.8	25.6
5-year species persistence (%)					90.1
No. (%) species lost					15 (10)
No. (%) species gained					31 (19)
Tree seedling species number	58	61	62	64	67
Tree seedling number	857	822	857	926	988
% rare trees	22.4	23.0	27.4	23.4	20.9
LEP (21 years)					
Species number	165	165	159	165	164
Seedling number	1588	1524	1445	1377	1375
Shannon diversity	4.02	4.07	4.06	4.09	4.11
<i>J</i> , evenness	0.79	0.80	0.80	0.80	0.81
% rare	31.5	29.7	31.4	33.3	31.3
5-year species persistence (%)					87.9
No. (%) species lost					20 (12)
No. (%) species gained					19 (12)
Tree seedling species number	53	56	56	58	59
Tree seedling number	458	429	395	370	362
% rare trees	37.7	37.5	37.5	37.9	37.3
CR (26 years)					
Species number	154	149	154	154	158
Seedling number	1905	1717	1764	1861	1861
Shannon diversity	3.29	3.25	3.33	3.34	3.31
<i>J</i> , evenness	0.65	0.65	0.66	0.66	0.65
% rare	28.6	28.9	33.1	33.1	36.1
5-year species persistence (%)					88.3
No. (%) species lost					18 (12)
No. (%) species gained					21 (13)
Tree seedling species number	69	70	65	66	67
Tree seedling number	484	449	515	645	671
% rare trees	34.8	38.6	40.0	39.4	44.8

similar numbers of gains and losses (Table 2). As a result, species density rose more than 10% in the two younger sites and changed little in the older two.

Mean species density in 5-m² quadrats differed among sites in the first census and the final census ($F_{3,572} = 11.165$ and 26.412 , respectively, $P < 0.0001$ in both cases), because species density at TIR was significantly

higher than at the other three sites (LSD, $P < 0.0001$ for both first and final censuses; means $\pm$ SE for LSUR, TIR, LEP and CR of 6.82 ± 0.251 , 8.40 ± 0.334 , 6.76 ± 0.234 and 6.41 ± 0.231 , respectively, for the first census and 6.41 ± 0.247 , 9.17 ± 0.385 , 6.41 ± 0.215 and 6.22 ± 0.222 , respectively, for the final census). A repeated-measures ANOVA indicated that mean species

density did not change within sites during the 5-year period ($F = 0.0011$, d.f. = 1, $P = 0.97$).

Evenness increased in the three youngest sites and was unchanged in the oldest (Table 2). The proportion of rare species (singletons) also increased in three of the four sites. After adjusting for differences in seedling abundance, species richness increased most in the youngest site (26%), rose less in sites of intermediate age (11% and 4%) and rose slightly in the oldest site (< 1%). After correcting for differences in density, species richness in the youngest site equalled that of the oldest by the end of the study period (Table 3), and canopy tree species richness in the youngest exceeded that in the oldest. Shannon diversity increased in all four sites (Table 2), rising most in the two younger sites because of substantial increases in both richness (Table 3) and evenness (Table 2).

DCA showed that each site initially had a distinct seedling community and that community composition remained distinct during the 5-year period (Fig. 1). The four sites were separated along the first axis, with younger sites on the left end and older sites on the right; only the oldest plot showed a change over time associated with the second axis.

Initially, the Jaccard-estimated abundance-based similarity index was highest between LSUR and LEP (0.88), the two sites located at La Selva Biological

Table 3 Species richness in each of four second-growth tropical forest sites after rarefaction to adjust for different seedling densities. Rarefaction of all woody seedlings estimated the number of species with seedling density of 1375 for the first and final censuses, and rarefaction of canopy tree seedlings estimated the number of species with seedling density of 340; both rarefactions were based on 200 randomizations

Site	All woody seedlings		Canopy tree seedlings	
	Census 1	Census 17	Census1	Census 17
LSUR	110	139	45	55
TIR	115	128	42	45
LEP	157	164	46	56
CR	138	139	58	46

Station, and lowest between CR and TIR (0.42), the two more isolated sites located west of La Selva (Table 4). After 5 years, the three youngest sites were less similar to each other, whereas similarity between these three sites and the oldest site (CR) changed little or not at all. However, none of the changes was statistically significant.

CHANGE AMONG LIFE-FORMS

In all four sites, absolute and relative abundance of seedlings of canopy palms and understorey palms

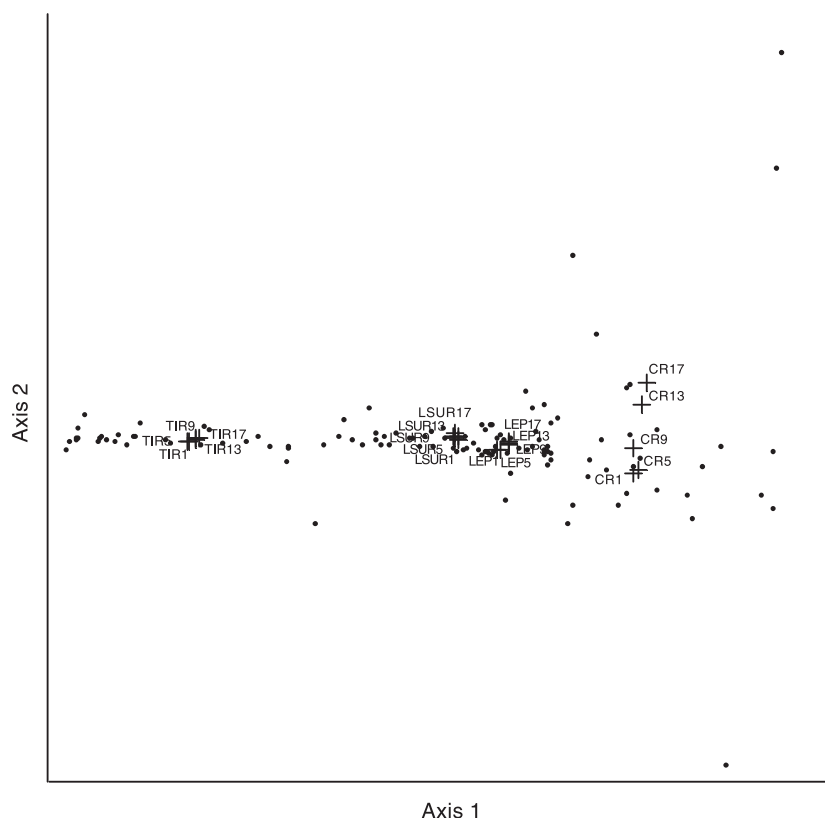


Fig. 1 Detrended correspondence analysis of 120 woody species that had a minimum of eight seedlings in at least one of the censuses at four secondary forest sites in Costa Rica. Seedling abundance at five censuses conducted during a 5-year period at each site were entered in the analysis. Each species is plotted with a small circle, based on its scores on the first two axes, and the position of each site in ordination space is shown with a cross. The communities of woody seedlings did not become more similar during the study period. The eigenvalue for Axis 1 was 0.634 and for Axis 2 was 0.093.

Table 4 Similarity between sites is shown for the first and the final census, 5 years later. Scores ($\pm$ SD) above the diagonal are for the first census, and those below are for the final census. The abundance-based Chao–Jaccard estimator, which corrects for undersampling, was used with all species present ($n = 297$)

	LSUR	TIR	LEP	CR
LSUR		0.76 $\pm$ 0.109	0.88 $\pm$ 0.084	0.47 $\pm$ 0.192
TIR	0.68 $\pm$ 0.103		0.75 $\pm$ 0.086	0.42 $\pm$ 0.163
LEP	0.78 $\pm$ 0.106	0.58 $\pm$ 0.158		0.75 $\pm$ 0.085
CR	0.49 $\pm$ 0.158	0.42 $\pm$ 0.141	0.78 $\pm$ 0.129	

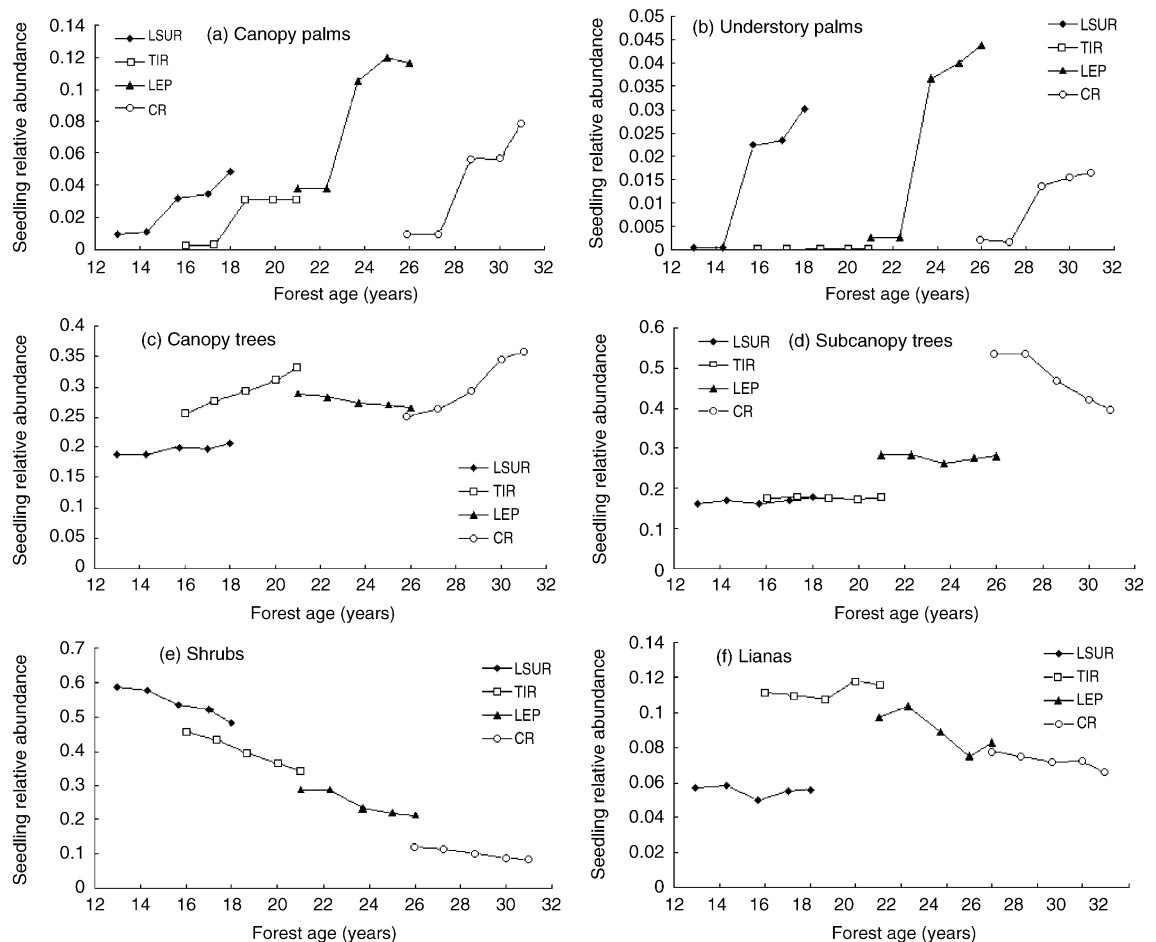


Fig. 2 The relative abundance of seedlings in six life-forms is shown for each of five censuses in four second-growth tropical forest sites in Costa Rica. The relative abundance of seedlings of canopy palms, understorey palms and canopy trees generally increased, and relative abundance of shrubs and lianas declined over time. The ages of the four sites at the beginning of the study period were: LSUR, 13 years since abandonment; TIR, 16 years; LEP, 21 years; CR, 26 years.

increased, whereas absolute and relative abundance of shrub seedlings declined (Fig. 2). Absolute abundance of liana and subcanopy tree seedlings also declined in the four sites, whereas relative abundance of liana seedlings declined in three, increasing slightly in the fourth, and relative abundance of subcanopy tree seedlings declined in three sites and was unchanged in the fourth. Canopy tree seedlings increased in absolute abundance in two sites and declined in two, and relative abundance increased in three (Fig. 2). Paired *t*-tests showed that mean seedling density for lianas was significantly lower at the end of the 5-year period ($t = 9.770$, d.f. = 3,

$P = 0.0023$), while mean canopy palm seedling density increased ($t = -7.638$, d.f. = 3, $P = 0.0047$). Mean seedling density was marginally different for understorey palms ($t = -2.675$, d.f. = 3, $P = 0.0754$) and shrubs ($t = 2.771$, d.f. = 3, $P = 0.0695$).

Species density of canopy palm and understorey palm seedlings increased in all four sites in both absolute and relative terms (Fig. 3). Absolute and relative species density of shrub seedlings declined in three sites, increasing only in TIR. Relative species density of liana seedlings declined in all four sites, although density declined in only three sites in absolute terms. The

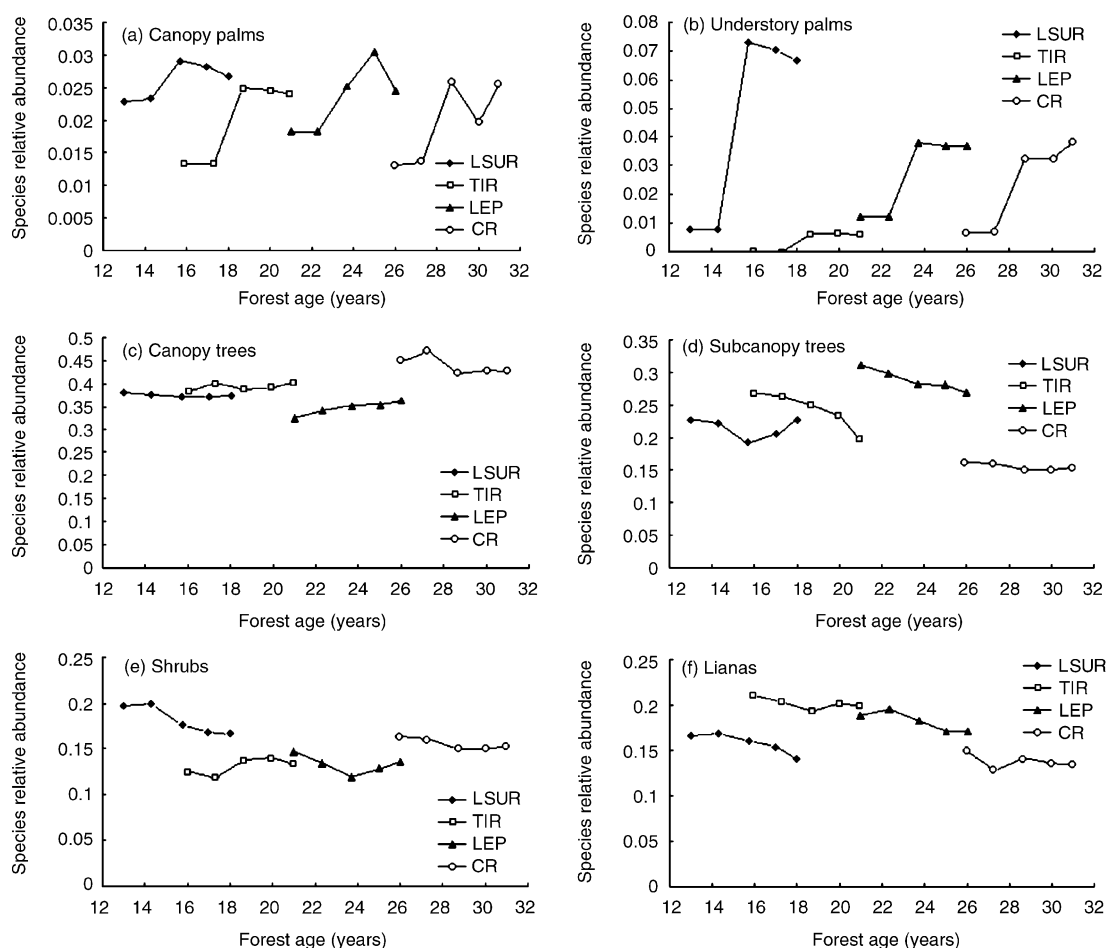


Fig. 3 Change in the proportion of species in six life-forms is shown for each of five censuses in seedling communities in four second-growth tropical forest sites in Costa Rica. Species relative abundance increased among canopy palms and understorey palms in all four sites and decreased in at least three of the sites among subcanopy trees, shrubs and lianas.

mean density of canopy palm seedling species was higher at the end of the study period ($t = -5.196$, d.f. = 3, $P = 0.0138$), and density of understorey palm seedling species was marginally higher ($t = -2.875$, d.f. = 3, $P = 0.0638$).

The distribution of seedling abundance by life-form changed from the beginning of the 5-year period to the end in all four sites (G -test, $P < 0.001$ in all cases). The distribution of species among life-forms changed in the younger two sites (G -test, $P < 0.001$ in both cases) but not the older two ($P > 0.05$). The proportion of tree species that were rare (singletons) increased in two of the four plots, peaking at 45% in the oldest site (Table 2). The proportion of shrub species that were rare increased in all four sites. Rarity of other life-forms did not change consistently within sites.

SURVIVORSHIP AND RECRUITMENT

Canopy and understorey palms survived better than other life-forms in all four sites (Fig. 4). For the three sites with understorey palms at the start of the study, 89% of the original cohort of palm seedlings survived for 5 years. Survival of the original cohort of canopy and subcanopy tree seedlings was next highest in three

of the four sites. Among the canopy tree seedlings present at the first census at LSUR, 4.5% became saplings during the 5-year period, compared with 3.8% at TIR, 1.6% at LEP and 2.1% at CR, the oldest site, suggesting that seedlings grew faster in the younger sites, where light availability was highest. Shrubs and lianas showed low rates of seedling survival ($< 50\%$ in three of the four sites for each life-form).

Annualized mortality rates for the original cohort of trees and canopy palms were lowest in the younger sites and highest in the oldest site, and this was true as well among newly appearing tree seedlings. By contrast, annualized mortality rates for the original cohort of subcanopy trees, lianas and shrubs were lowest in the oldest site and highest in one of the younger sites (Table 5). However, mortality rates for shrub and liana seedlings that recruited to the sites during the study period showed the opposite trend, increasing with site age. Recruitment rates for canopy and understorey palms were far higher than those for other life-forms except at CR, where large numbers of tree recruits were also recorded (Table 5).

Because of low mortality rates, every palm species present at a site at the beginning of the study period was present at the end; at the same time, the sites were

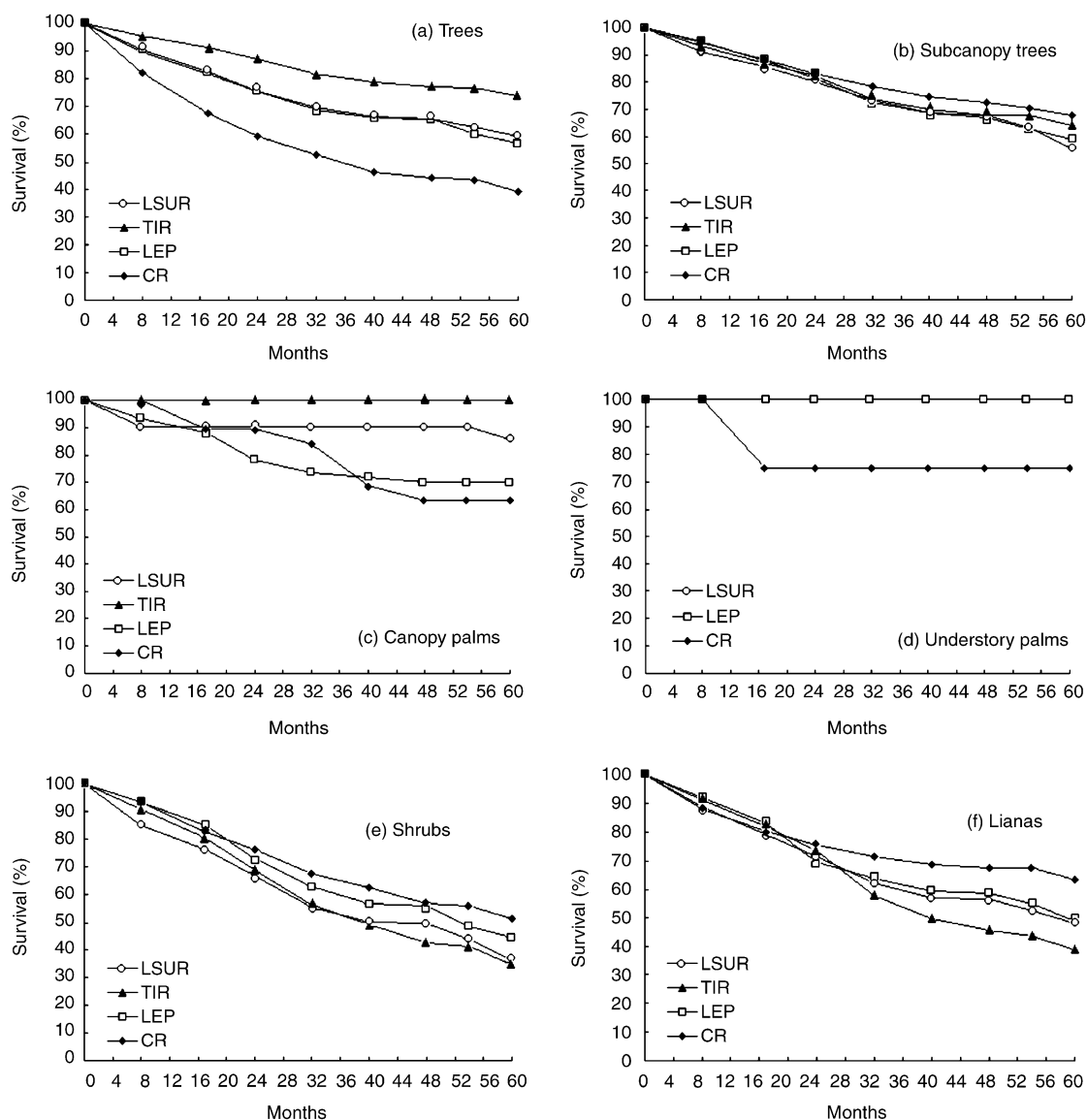


Fig. 4 Survival among the original cohort of seedlings of canopy trees (a), subcanopy trees (b), canopy palms (c) and understorey palms (d) generally was higher than among shrubs (e) and lianas (f) in four second-growth tropical forest sites, although survival within life-forms varied somewhat among sites, especially for trees and palms. No survival is shown for understorey palms in TIR because none occurred there at the beginning of the 5-year study period.

colonized by 3–10 new palm species. More than 25% of all recruiting species were palms in three of the four sites (Table 6a). Each of the four sites lost at least 15% of its original shrub species and at least 20% of its original liana species (Table 6b). In all four sites, trees represented more than one-third of recruiting species (Table 6a) and more than 25% of the species that were lost from three sites (Table 6b), indicating that much of the change in community composition involved tree species turnover.

LINKING SURVIVAL AND RECRUITMENT TO LIFE-FORM CHANGE

Across sites, change in seedling abundance of canopy trees and subcanopy trees was more strongly correlated with recruitment rates than mortality (Table 7), whereas

change in abundance of canopy palms and lianas was more strongly correlated with mortality rates than recruitment. Change in shrub seedling abundance was correlated with both recruitment and mortality rates. Change in understorey palms was not strongly correlated with recruitment or mortality of newly recruiting seedlings. None of the correlations was statistically significant because of the low number of sites ($n = 4$).

Across the four sites, median light availability was more highly correlated with recruitment rates (positively) than with mortality rates for understorey palms, shrubs and lianas, but it was more highly correlated (negatively) with mortality rates for canopy trees and canopy palms (Table 7). Forest age was most strongly and positively correlated with change in abundance of canopy palms, subcanopy trees and shrubs, and it was negatively correlated with change in abundance of subcanopy trees.

Table 5 Annualized mortality and recruitment rates, expressed as percentages, are shown for seedlings in six life-forms in four secondary tropical forests in Costa Rica. Mortality rates are shown separately for the original cohort of seedlings in the sites and for seedlings recruiting in the second and subsequent censuses. The age of the sites at the beginning of the 5-year study period is shown in parentheses

Site	Canopy trees	Canopy palms	Understorey palms	Subcanopy trees	Shrubs	Lianas
Mortality rates – original cohort						
LSUR (13)	9.9	3.0	0	11.0	18.2	13.6
TIR (16)	5.9	0	–*	8.6	19.2	13.6
LEP (21)	10.6	6.9	0	10.1	15.0	13.3
CR (26)	17.2	10.4	5.6	7.6	12.4	8.7
Mortality rates – newly appearing seedlings						
LSUR (13)	25.0	13.9	9.9	10.5	17.1	19.4
TIR (16)	5.6	9.0	0	8.3	13.8	22.0
LEP (21)	30.3	11.6	1.6	11.9	21.4	18.9
CR (26)	47.7	15.3	6.6	8.9	26.6	33.8
Recruitment rates						
LSUR (13)	7.0	25.0	49.0	9.0	9.6	8.0
TIR (16)	8.6	42.1	100.0	7.7	12.4	13.4
LEP (21)	9.3	23.2	45.6	6.9	7.1	5.4
CR (26)	21.1	46.1	42.6	2.6	6.0	4.2

*No understorey palms occurred at TIR in the original census.

Table 6 (a) The percentage of species recruiting to second-growth tropical forest seedling communities that were in each life-form and (b) the percentage of the original species that were lost, by life-form

Site	Canopy trees	Subcanopy trees	Canopy palms	Understorey palms	Shrubs	Lianas
(a) Species recruiting to communities						
LSUR	34	19	3	28	6	9
TIR	42	10	6	3	19	13
LEP	41	11	5	21	5	16
CR	38	10	10	24	10	10
(b) Species lost from communities						
LSUR	36	14	0	0	21	29
TIR	27	33	0	0	20	20
LEP	10	45	0	0	15	30
CR	56	6	0	0	17	22

Discussion

Predicted trends in life-form composition and seedling density from chronosequence studies were supported by our observations over time in the four secondary forests. Woody seedling density declined during the 5-year study period in all four sites and declined with site age, whereas species density, evenness and the proportion of rare species generally increased within sites. The greatest changes in the seedling communities were relative increases in the abundance and species richness of trees and palms and corresponding declines among shrubs and lianas. Evenness and the proportion of rare species appear to increase for at least 30 years after pasture abandonment, although at declining rates.

In species-rich tropical forests, many species are rare (Gentry 1988; Dallmeier *et al.* 1996). The increasing proportion of rare species in our four sites resulted in part from the increasing representation of canopy tree species that recruited from outside the study plots. In three of the four sites, more than 85% of the canopy tree

species that occur as singletons among the seedlings had no potential parent (trees > 25 cm d.b.h.) within the same monitoring plot (R.L.C., unpublished data). The proportion of rare species is likely to continue to rise as trees that have large, animal-dispersed seeds recruit to the sites. This view is supported by the increase of animal-dispersed palms. The abundance of tree species (including palms) with animal-dispersed seeds is higher and the abundance of those with ballistically dispersed seeds is lower in old-growth than secondary-growth forests in the Sarapiquí region of Costa Rica (Chazdon *et al.* 2003).

Mean seedling density declined with age in our sites, as previously found in Panama (Denslow & Guzman 2000). It is likely that decreasing seedling density results at least in part from declining light levels in secondary forests and that density rises again late in succession as structural complexity and light heterogeneity increase with the occurrence of large gaps (Nicotra *et al.* 1999; Chazdon in press). Density values in Panama (1.0–2.25 seedlings m⁻²) were lower than those in our Costa

Table 7 Pearson correlation coefficients are shown between change in absolute abundance of seedlings in each of six life-forms and annual recruitment rates, mortality rates for the original cohort of seedlings (MortOrig) and for seedlings that appeared later (MortNew), site age and light availability. Correlation between Median %T and Site age was negative ($r = -0.5032$). The analysis for understory palms does not include MortOrig because one site (TIR) had no seedlings in this life-form at the beginning of the study period. None of the correlation coefficients was statistically significant because values were available for only four sites

	Change	Recruitment	MortOrig	MortNew
Canopy trees				
Recruitment	0.7058			
MortOrig	0.3116	0.8815		
MortNew	0.1179	0.7800	0.9793	
Site age	0.4764	0.8876	0.8033	0.7654
Median %T	0.2046	-0.5151	-0.8587	-0.9330
Canopy palms				
Recruitment	0.4974			
MortOrig	0.7869	0.1402		
MortNew	0.2555	0.0334	0.7558	
Site age	0.9825	0.4632	0.8819	0.4308
Median %T	-0.3451	0.2244	-0.8506	-0.9254
Understorey palms				
Recruitment	-0.8250			
MortNew	0.4693	-0.6286		
Site age	-0.0185	-0.4377		-0.1281
Median %T	-0.7157	0.9833		-0.5032
Subcanopy trees				
Recruitment	0.9526			
MortOrig	0.7395	0.8206		
MortNew	0.3693	0.3105	0.7309	
Site age	-0.8276	-0.9489	-0.7072	-0.0578
Median %T	0.5816	0.4807	-0.0927	-0.4669
Shrubs				
Recruitment	-0.9062			
MortOrig	-0.9701	0.9462		
MortNew	0.9366	-0.9624	-0.9925	
Site age	0.9596	-0.7905	-0.9399	0.8958
Median %T	-0.6491	0.9069	0.7680	-0.8334
Lianas				
Recruitment	0.1254			
MortOrig	-0.6973	0.6140		
MortNew	0.8419	-0.4145	-0.9728	
Site age	0.3710	-0.6850	-0.8466	0.7712
Median %T	0.0916	0.9561	0.5749	-0.3846

Rican sites (mean values of 9–23 seedlings per 5-m² quadrat), possibly because Denslow & Guzman (2000) defined seedlings as 20–100 cm tall, whereas many of ours exceeded that height without reaching the 1-cm d.b.h. limit for our seedling size class. On the other hand, a number of differences have been identified between the forests of north-east Costa Rica and other Neotropical sites. Sites at the La Selva Biological Station have lower liana density (Mascaro *et al.* 2004), higher palm density (DeWalt & Chave 2004) and a more dense understorey herb layer (Harms *et al.* 2004) than several other Neotropical forests. Sites in north-east Costa Rica also have higher soil fertility (Harms *et al.* 2004) than many Neotropical sites and may have been less intensively used than former agricultural land in some areas (Guariguata *et al.* 1997).

The rate of change in the seedling communities declined with site age. Abundance declined and species density rose dramatically in sites 13–16 years old at the beginning of our study but changed less in 21- and 26-

year-old sites. A similar decline in the rate of change with site age was observed for trees of > 10 cm d.b.h. in the four sites (Chazdon *et al.* in press). Together, these results suggest that change in at least some community properties – species richness and evenness among them – occurs primarily within the first 30 years after agricultural abandonment and that values of these properties in successional forests quickly converge on those in old-growth forests. In support of this suggestion, species richness in our secondary forest seedling communities appears to be similar to that of mature forests in the region (Chazdon *et al.* 1998). Li *et al.* (1996) recorded 194 species in a total of 6281 identified seedlings in old-growth sites during a 6-year study. Our site with the highest seedling abundance (TIR) included a total of 5076 seedlings over the course of 5 years, and these seedlings were of 185 species. Denslow & Guzman (2000) reported that seedling species richness was relatively constant in 20- to 100-year-old secondary forests and in old-growth forest, after adjusting for differences

in density, and similar findings were reported by DeWalt *et al.* (2003) for trees of > 5 cm d.b.h. in a chronosequence of Panamanian sites that included old-growth forests.

Although species richness in secondary forests approaches or equals that in mature forests within 40–70 years, community composition remains different for much longer, possibly for centuries (Finegan 1996; DeWalt *et al.* 2003; Chazdon in press). Similarity analysis and the DCA provided no evidence that composition of our seedling communities became more similar over time. Compositional differences among the communities, particularly those outside of La Selva Biological Station, indicate that seedling communities are drawn from different source communities and/or that colonization is highly stochastic. Thus, secondary forests that are young and rapidly accumulating new species are more likely to diverge in composition over time if they exist in a fragmented landscape, as do our study sites. Convergence may occur later in succession in our sites, with the arrival of late-successional species and their recruitment as mature individuals. Convergence is also possible in early successional sites if they are surrounded by continuous areas of intact forest, although the effects of soil fertility and disturbance remain to be tested. Evidence of community convergence in chronosequence studies has been equivocal. DeWalt *et al.* (2003) found that secondary forest tree communities became more similar to old-growth forest during succession. Guariguata *et al.* (1997) found that similarity among canopy trees of > 10 cm d.b.h. was neither higher nor lower but was more variable in secondary than old-growth forests, and Chazdon (in press) showed that community similarity in our four sites was unrelated to site age for both canopy trees of > 10 cm d.b.h. and saplings.

Although the total number of species changed little in our communities during the 5-year period, life-form representation changed dramatically. Palm seedling abundance and species richness increased sharply in all four sites at approximately the same time, between January and May 2000, possibly in response to unusually wet conditions. January and February are relatively dry months at La Selva, although still averaging a combined 430 mm (unpublished data available from La Selva at <http://www.ots.ac.cr/en/laselva/metereological.shtml>), but rainfall during January–February in 2000 (1027 mm) was the highest recorded since 1958. These unusually wet conditions may have favoured palm germination and rapid growth.

Declining light availability in older sites appeared to be particularly important in reducing shrub and liana recruitment and increasing mortality among canopy trees and palms, although these losses were overcome among palms by even higher recruitment rates. Unlike the other sites, substantial numbers of new liana and shrub species continued to recruit at TIR, the site with the highest light levels (Table 1). The low numbers of palm species and palm seedlings at TIR could be due to

low abundance of mature palms there (R.L.C., unpublished data) and its isolation from old-growth forest fragments that could serve as seed sources. This isolation probably contributes as well to the low tree species richness of the site, after rarefaction (Table 3).

Mortality rates among canopy tree seedlings were similar to those in other studies of Neotropical seedlings, varying from 6% to 17% on an annual basis among the original cohort of seedlings and from 6% to 48% among newly recruiting seedlings. De Steven (1994) found first-year mortality of 31–50% in three tree species, declining to 10% or lower in the second year for seedlings that were > 50 cm in height. Mortality rates in our sites were strongly influenced by performance of individual species. High canopy tree seedling mortality in CR, for instance, was greatly influenced by the very high abundance at that site of *Pentaclethra macroloba*, which had very high 5-year mortality there (95.3%).

Although we focused on within-site changes, the general trends observed within sites were strongly supported by comparison across the sites: species richness and evenness were higher in the oldest site than the youngest. Tree species increased as a proportion of all species with successional age (Table 2), and the proportion of rare tree species was higher in the oldest site than the youngest. Canopy palm abundance increased with successional age, and shrub seedling abundance declined until 31 years after agricultural abandonment (Fig. 2), while lianas represented a declining proportion of all seedling species with successional age (Fig. 3). Overall, the changes we observed among seedling communities mirror those seen in chronosequence studies on plants in larger size classes, lending support to the assumptions of chronosequence studies in Neotropical forests.

Secondary succession in Neotropical plant communities is influenced by many factors, including the availability of seed sources and the declining availability of light. Although much further research is needed on the interaction of factors that drive change in seedling communities, it is clear that the distinctive life-form composition of secondary tropical forests is produced in the seedling communities and can be fruitfully studied among seedlings. It also appears that, although community composition does not converge quickly, life-form composition does show consistent trends within and across sites. Studies focusing on abundance and composition of different woody life-forms may be particularly useful in understanding and predicting successional dynamics in tropical forests and other hyperdiverse systems.

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