

Composition and Dynamics of Functional Groups of Trees During Tropical Forest Succession in Northeastern Costa Rica

Robin L. Chazdon^{1,4}, Bryan Finegan², Robert S. Capers¹, Beatriz Salgado-Negret^{2,5}, Fernando Casanoves³, Vanessa Boukili¹, and Natalia Norden¹

¹ Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269-3043, U.S.A.

² Production and Conservation in Forests Program, Tropical Agricultural Centre for Research and Higher Education (CATIE), Apartado 93-7170, Turrialba, Costa Rica

³ Biostatistics Unit, Tropical Agricultural Centre for Research and Higher Education (CATIE), Apartado 93-7170, Turrialba, Costa Rica

ABSTRACT

We compared the functional type composition of trees ≥ 10 cm dbh in eight secondary forest monitoring plots with logged and unlogged mature forest plots in lowland wet forests of Northeastern Costa Rica. Five plant functional types were delimited based on diameter growth rates and canopy height of 293 tree species. Mature forests had significantly higher relative abundance of understory trees and slow-growing canopy/emergent trees, but lower relative abundance of fast-growing canopy/emergent trees than secondary forests. Fast-growing subcanopy and canopy trees reached peak densities early in succession. Density of fast-growing canopy/emergent trees increased during the first 20 yr of succession, whereas basal area continued to increase beyond 40 yr. We also assigned canopy tree species to one of three colonization groups, based on the presence of seedlings, saplings, and trees in four secondary forest plots. Among 93 species evaluated, 68 percent were classified as regenerating pioneers (both trees and regeneration present), whereas only 6 percent were classified as nonregenerating pioneers (trees only) and 26 percent as forest colonizers (regeneration only). Slow-growing trees composed 72 percent of the seedling and sapling regeneration for forest colonizers, whereas fast-growing trees composed 63 percent of the seedlings and saplings of regenerating pioneers. Tree stature and growth rates capture much of the functional variation that appears to drive successional dynamics. Results further suggest strong linkages between functional types defined based on adult height and growth rates of large trees and abundance of seedling and sapling regeneration during secondary succession.

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

Key words: forest regeneration; functional types; growth rates; mortality; recruitment; secondary succession; tree height; vegetation dynamics.

NEW FORESTS ARE REGENERATING THROUGHOUT THE TROPICS in areas where agricultural land is abandoned and nearby remnant forest patches provide seed sources (Chazdon *et al.* 2003, Cramer & Hobbs 2007, Myster 2008). Secondary forests in tropical regions are increasing not only in extent but also in importance, as sinks for carbon, areas for biodiversity conservation, and for sources of timber and nontimber products (Brown & Lugo 1990, Chazdon & Coe 1999, Feldpausch *et al.* 2004, Silver *et al.* 2004). Although much progress has been made in understanding key processes of secondary forest succession in the tropics (Finegan 1996, Chazdon 2008), few studies have applied concepts of plant functional groups to land-use transitions in tropical regions (Denslow 1996, Verburg & van Eijk-Bos 2003, Delcamp *et al.* 2008, Zhang *et al.* 2008). Functional traits are key elements determining tree regeneration in mature forests (Bazzaz & Pickett 1980, Hubbell & Foster 1986, Swaine & Whitmore 1988, Clark & Clark 1992, Condit *et al.* 1996, Wright *et al.* 2003, Poorter *et al.* 2008). Functional type classifications of trees have also been used to model forest dynamics following logging and small-scale natural disturbances (Favrichon 1994, Köhler *et al.* 2000, Shugart 2003, Slik 2005). Therefore, it is

likely that functional types of trees will be useful in describing and understanding successional changes in tropical forests.

Here, we develop a new approach that links functional attributes of tree species with studies of forest recovery and regional land-use transitions (Chazdon *et al.* 2007). Grouping species according to their functional attributes or demographic rates provides insight into both applied and theoretical questions, such as selecting species for reforestation programs, assessing ecosystem services, and understanding community assembly processes in tropical forests (Diaz *et al.* 2007, Kraft *et al.* 2008). In previous studies, tree species have been grouped based on four sets of criteria: (1) population size distribution and demographic rates; (2) functional traits; (3) shade tolerance/intolerance of juveniles and associated growth characteristics; or (4) response to fire or hurricanes (Knight 1975, Swaine & Whitmore 1988, Lieberman *et al.* 1990, Thomas & Bazzaz 1999, Turner 2001, Burslem & Swaine 2002, Baker *et al.* 2003, Wright *et al.* 2003, Gourlet-Fleury *et al.* 2005, Poorter & Bongers 2006, Easdale *et al.* 2007, Poorter *et al.* 2008). Since we have data on leaf and wood functional traits for only a subset of the species in our study sites, we based our functional type classification on information for a large number of tree species obtained through vegetation monitoring studies.

Conceptual approaches to successional forest dynamics have been largely based on the distinction between two major groups of tree species, *shade-intolerant pioneer* species and *shade-tolerant late successional* species (Swaine & Whitmore 1988). As succession

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⁴Corresponding author; e-mail: robin.chazdon@uconn.edu

⁵Current address: Centro de Estudios Avanzados en Ecología & Biodiversidad, Departamento de Ecología, Pontificia Universidad Católica de Chile, Alameda 340, Santiago, Chile.

unfolds, however, pioneer and shade-tolerant species vary widely in their longevity and in the timing of their colonization and peak abundance, suggesting that this dichotomy may be inadequate for describing the full range of ecological diversity of trees. Characterizing shade tolerance for trees in secondary forests is particularly challenging, as individuals may have established under very different conditions than they are currently experiencing. In both mature and successional forests, some species do not conform to this simple dichotomy because of ontogenetic shifts in responses to light availability (Clark & Clark 1992, Dalling *et al.* 2001, Poorter *et al.* 2005, Niinemets 2006, Poorter 2007). Moreover, shade tolerance alone does not explain why some tree species are abundant in seedling, sapling, or tree size classes of secondary forests. Initial colonization and seedling recruitment in secondary forests is often strongly limited by dispersal (Martínez-Garza & González-Montagut 1999, Holl *et al.* 2000, Cubiña & Aide 2001, Dalling & Hubbell 2002, Günter *et al.* 2007).

Our approach avoided preconceived notions of successional behavior or shade tolerance of tree species by developing an objective and independent classification of functional types based on vegetation monitoring data from permanent sample plots in mature and secondary forests of northeastern Costa Rica (Finegan *et al.* 1999, Chazdon *et al.* 2007). We apply an independent, prior classification of 293 tree species from our study region into five functional types,

based on two species attributes: canopy strata and diameter growth rates for individuals ≥ 10 cm dbh (Finegan *et al.* 1999, Salgado-Negret 2007). We compare functional type composition of trees in eight secondary forest monitoring plots with logged and unlogged mature forest plots in the same region. Based on long-term data on species composition, we track changes in functional type composition over time within these secondary forest plots. In another set of four secondary forest plots (12–30 yr post abandonment), where we collected detailed seedling and sapling data, we assigned tree species to one of three colonization groups, based on the presence of seedlings, saplings, or trees ≥ 10 cm dbh. Finally, we synthesize both approaches by assessing functional type composition among regenerating seedlings and saplings in these four secondary forest plots. Our results demonstrate strong linkages between functional types defined by adult height and growth rates of large trees and colonization groups based on the timing of seedling, sapling, and tree recruitment in secondary forests.

METHODS

STUDY AREA.—Our study was conducted in Sarapiquí County, Heredia Province, in the Caribbean lowlands of Costa Rica (Table 1; Fig. S1). The natural vegetation in the area is classified as Tropical Wet Forest (*sensu* Holdridge *et al.* 1975) and all study

TABLE 1. Site information for secondary and mature forest study plots used in the comparisons of functional composition and dynamics. * denote secondary forest pasture plots sampled for the definition of colonization groups: two of these were not used for the evaluation of functional dynamics because only one enumeration had been made when the present analysis was carried out. Selectively logged mature forest plots used in some comparisons are described by Finegan and Camacho (1999). Map locations are shown in Fig. S1.

Plot	Latitude, longitude	Prior land use	Year abandoned	Location	Surrounding landscape	Plot size (ha)	Measurement period
Lindero Sur (LSUR)*	10.41° N, 84.03° W	Pasture	1985	La Selva	Mature and secondary forest	1	1997–2006
Tirimbina (TIR)	10.40° N, 84.11° W	Pasture	1982	Tirimbina	Plantations, pasture, and secondary forest	1	1997–2006
Lindero El Peje secondary (LEP sec)*	10.43° N, 84.03° W	Pasture	1977	La Selva	Mature and secondary forest	1	1997–2006
Cuatro Rios (CR)	10.39° N, 84.13° W	Pasture	1972	Tirimbina	Pasture and secondary forest	1	1997–2006
El Bejuco (EB)*	10.46° N, 84.06° W	Pasture	1995	Chilamate	Pasture, secondary and mature forest	1	2006
Juan Enriquez (JE)*	10.46° N, 84.07° W	Pasture	1995	Chilamate	Pasture, secondary and mature forest	1	2006
Arrozal	10.40° N, 84.10° W	1 yr rice cultivation	1986	Tirimbina	Pasture and secondary forest	0.3	1987–2003
Aceituno	10.41° N, 84.11° W	Cleared but not used	1972	Tirimbina	Pasture and secondary forest	1	1987–2003
Manú	10.41° N, 84.12° W	Cleared but not used	1962	Tirimbina	Pasture and secondary forest	1	1987–2003
Botarrama	10.41° N, 84.12° W	Cleared but not used	1962	Tirimbina	Pasture and secondary forest	1	1987–2003
Lindero El Peje, primary (LEP pri)	10.42° N, 84.04° W	Mature forest		La Selva	Mature forest	1	2006
Selva Verde	10.44° N, 84.07° W	Mature forest		Chilamate	Mature forest	1	2006

plots share the same source pool of species. Annual temperature and rainfall average 26°C and 3800 mm, respectively, at La Selva Biological Station (Sanford *et al.* 1994). Soils in the study areas are derived from weathered basalt and are primarily classified as ultisols (Sollins *et al.* 1994). Study areas were 50–220 m asl.

DYNAMICS OF FUNCTIONAL TYPE COMPOSITION DURING SUCCESSION.—To evaluate variation in functional type composition among forest types and over time during forest succession, we used a classification of 293 tree and palm species from our landscape into five functional types, developed by Finegan *et al.* (1999) and Salgado-Negret (2007). This classification used an independent data set for trees ≥ 10 cm dbh in fifteen 1 ha permanent sample plots in mature and selectively logged forest at two sites, Tirimbina Biological Reserve (Fig. S1) and Los Laureles del Corinto farm (Finegan & Camacho 1999, Salgado-Negret 2007). Los Laureles del Corinto farm is located approximately 30 km SE of Tirimbina in the same Holdridge life zone, and belongs to the same *Pentaclethra* forest type as delimited by Sesnie *et al.* (2009).

Tree species were assigned to one of four height categories occupied by adult trees (Finegan *et al.* 1999), based on information on specimen labels in the Missouri Botanical Garden data base (<http://www.tropicos.org>) and in consultation with Costa Rican botanical expert Nelson Zamora (Table S1). This species attribute will henceforth be referred to as ‘canopy stratum.’ The second species attribute for the functional classification was stem diameter growth rate, for which species were assigned by cluster analysis to one of five growth rate classes, based on medians and quartiles of diameter increments derived from measurements over 13–16 yr (Table S1; Finegan *et al.* 1999). Subcanopy and canopy palms, abundant in the forests of this region, were assigned to the slow growth category, due to their lack of secondary woody growth. We selected the slow growth category because the stem anatomy of palms represents a fundamental constraint on growth rates (Tomlinson 1979) and because Neotropical forest canopy or subcanopy palms may show mean height growth rates < 20 cm/yr and take many decades to reach reproductive maturity (Lugo & Rivera Batlle 1987, Pinard 1993). Although this may not be the optimal classification, it did allow us to include these abundant species in our analysis. Three reproductive traits were also recorded for each tree species: dispersal syndrome, pollination syndrome, and sexual system. None of these traits contributed to a satisfactory species grouping, however, and ultimately, the cluster analysis was based solely on adult canopy stratum and diameter growth rate class (Salgado-Negret 2007). Ward’s clustering method and Gower’s similarity with the 1-abs transformation to distance were used for clustering, using the Infostat statistical package (InfoStat 2004). Ward’s method is a widely used and effective clustering procedure (McCune & Grace 2002), while Gower similarity is appropriate for clustering on the basis of attributes represented by different types of variable (InfoStat 2004), as in the present case. Five groups of species were delimited by the analysis and represent five functional types, henceforward abbreviated as plant functional type (PFT) 1 through PFT 5 (Salgado-Negret 2007; Table S2). Thirteen tree species from the secondary forest plots were absent from the pool of

species used for the original functional type classification. These were assigned *post-hoc* to the existing PFTs using discriminant analysis (InfoStat 2004), on the basis of adult canopy stratum and diameter growth rates observed in the secondary forests.

We compared functional type composition using both static and dynamic analyses. To track changes in the abundance and basal area of the five functional types over time, we used inventory data for trees ≥ 10 cm dbh in eight secondary forest monitoring plots (Table 1). Four plots were formerly used for pasture, having been cleared and grazed lightly for several years before abandonment (Table 1), although they varied in the abundance of remnant trees (Redondo Brenes *et al.* 2001). Four plots were cleared but not subsequently used, or were used briefly for annual crops (Table 1; Chazdon *et al.* 2007). All forest plots had closed canopies from the initiation of vegetation monitoring, although canopy height varied with age. Three of the nonpasture plots and all of the pasture plots were 1 ha in size; one nonpasture plot was 0.3 ha. Trees ≥ 10 cm dbh were monitored for growth, recruitment, and mortality. Assessment of change over time was based on annual monitoring in the four pasture plots during 1997–2006, and measurements at multiyear intervals during the 1987–2003 period in the four nonpasture plots. Census data for all trees ≥ 10 cm dbh were used to compute mortality rates (%/yr), and number of newly recruited trees for species from each of the five functional types during two time intervals for the pasture (1997–2002, 2002–2006) and nonpasture plots (1989–1995, 1995–2003). PFT 1 lacked sufficient abundance to compute mortality rates for both time intervals. The youngest nonpasture plot also had insufficient data to compute mortality rates during the first time interval. We compared rates across functional types using ANOVA on arc-sin square-root transformed data (mortality) and untransformed data (number of recruits). We also used annual (1997–2006 for pasture plots) and multiannual (1989–1992, 1995, 1998, 2003 for nonpasture plots) census data to chart changes in abundance and basal area for the five functional types.

For static comparisons, we also inventoried trees ≥ 10 cm dbh in two 1 ha plots in unlogged, old growth forests and in five selectively logged forest plots from the set used for the functional type classification (Table 1; Fig. S1; Finegan *et al.* 1999). We used data from the most recent census in each case (2003 for the selectively logged plots, 2006 for all the others) to compare functional type abundance and basal area among four forest types: mature (logged and unlogged) and second growth (pasture and nonpasture), using one-way ANOVA and *post-hoc* tests.

COLONIZATION GROUPS.—We classified tree species into three colonization groups based on a 2006 sampling of tree seedlings and saplings in four of the 1 ha secondary forest monitoring plots in pasture (11–29 yr post abandonment; Table 1).

Trees ≥ 10 cm dbh were sampled in the entire ha; saplings 5–9.9 cm in dbh were sampled in five strips of 5×200 m (0.5 ha); and tree seedlings were sampled in five strips of 2×200 m (0.2 ha). We excluded data for woody species that were not subcanopy or canopy trees or palms (species > 15 m height in mature adult trees). For each species, we tallied the total number of individuals

≥ 10 cm dbh in each plot ('trees') and the total number of seedlings and saplings/ha ('regeneration'). Analyses at the plot level were based on presence/absence, regardless of species abundance. This approach allowed us to include all species and to avoid arbitrary thresholds. Each species in each plot was classified into one of three colonization groups, regardless of abundance: (1) nonregenerating pioneers (species with trees ≥ 10 cm dbh but no seedlings or saplings); (2) regenerating pioneers (species with trees and seedlings/saplings); or (3) forest colonizers (species occurring only as seedlings or saplings). We also assessed colonization groups based on pooled abundance data across all four secondary forest plots. For this combined analysis, we excluded species with fewer than five individuals in the pooled data to avoid biasing results by insufficient sampling of rare or infrequent species.

FUNCTIONAL TYPE COMPOSITION OF REGENERATING VEGETATION.—Based on the pooled abundance data, we assessed the functional type composition of the seedlings and saplings inventoried in the four secondary forest pasture plots. Forest colonizers were assessed separately from regenerating pioneers, as these represent two distinct colonization groups. Nonregenerating pioneers were excluded from this analysis because they lacked individuals in regeneration stages, by definition. The relative abundance of species and of individuals in each of these colonization groups was determined for each PFT represented with the exception of PFT 1, as the 2006 regeneration data excluded understory trees.

RESULTS

DESCRIPTION OF PFTs.—Three PFTs were restricted to a single canopy stratum (Salgado-Negret 2007). PFT 1 was composed of understory tree species with a range of diameter growth rates, whereas PFT 2 comprised subcanopy tree species exhibiting very slow and slow growth rates (Table S2). Trees in PFT 5 were emergent species with moderate to very fast growth rates. The other two functional types spanned two canopy strata. PFT 3 comprised subcanopy and canopy tree species with moderate to very fast growth rates, whereas PFT 4 was made up of canopy or emergent tree species with very slow to moderate growth rates. Thus, PFT 2 and 4 were comprised of slow-growing species, whereas PFT 3 and 5 were fast-growing species. To simplify, we refer to these two major categories as slow- vs. fast-growing trees.

COMMUNITY COMPOSITION OF PFTs.—In mature, unlogged and logged forests, slow-growing subcanopy trees (PFT 2) had the highest mean relative abundance among all PFTs (Fig. 1A). In the eight secondary forests, in contrast, fast-growing emergents (PFT 5) were the most abundant (41–47%) and PFT 2 was the second most abundant group (24–28%). Relative abundance differed significantly across the four forest types for understory trees (PFT 1; $P = 0.01$, $F = 5.67$), slow-growing canopy/emergent trees (PFT 4; $P = 0.012$, $F = 5.59$) and fast-growing emergents (PFT 5; $P = 0.03$, $F = 4.16$). Relative abundance of the five PFTs did not differ significantly between mature and logged forests or between pasture and nonpasture secondary forest plots. (*post-hoc* tests; $P > 0.05$;

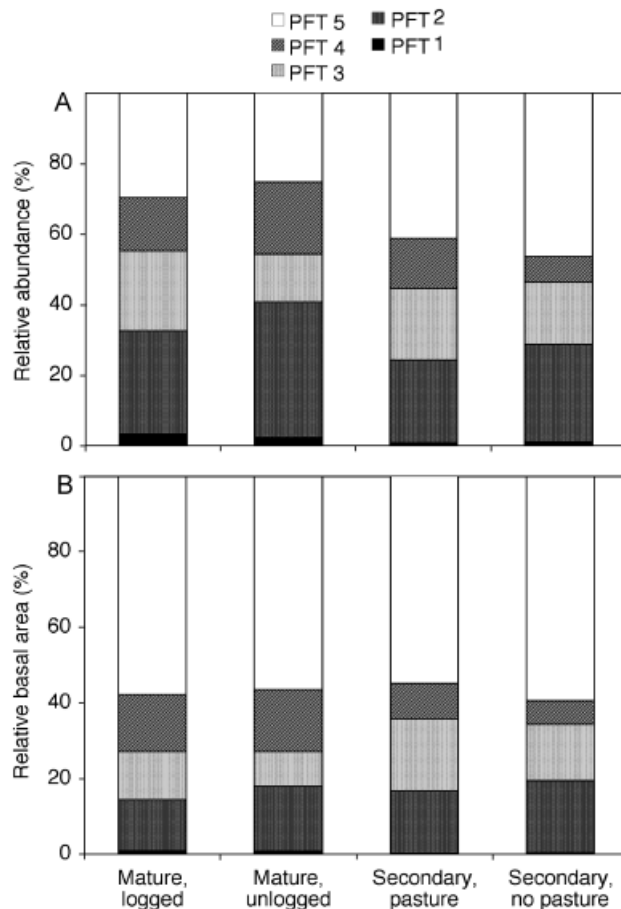


FIGURE 1. Relative abundance (A) and relative basal area (B) of five plant functional types in four forest types. Data for mature, logged forests are for five plots studied by Finegan *et al.* (1999) and for two mature, unlogged plots listed in Table 1. Data for secondary forests are from 2006 (four pasture plots) and 2003 (four nonpasture plots).

Fig. 1A, B). Understory trees (PFT 1) represented a low proportion of trees ≥ 10 cm dbh, but their relative abundance was significantly higher in mature than secondary forests (*post-hoc* test; $P < 0.05$). Slow-growing canopy/emergent trees (PFT 4) had higher relative abundance in mature than secondary forests, whereas fast-growing emergents (PFT 5) had lower abundance in mature forests (*post-hoc* tests; $P < 0.05$; Fig. 1A).

Fast-growing emergents (PFT 5) dominated all of the forest plots in terms of basal area, with no significant difference among forest types ($P > 0.05$; Fig. 1B). On the other hand, relative basal area of understory trees (PFT 1) and slow-growing canopy/emergent trees (PFT 4) differed significantly across forest types ($P = 0.017$ and 0.001 , respectively); both groups showed significantly higher values in mature than secondary forests (*post-hoc* test; $P < 0.05$; Fig. 1B).

The distribution of species richness across the five PFTs was similar in all forest types (Table S2). PFT 3 had the largest percentage of species, followed by PFT 2, and PFT 1 had the lowest percentage of species (Table S2).

TABLE 2. Mortality and recruitment of five functional types in secondary forest plots. Mortality rates are percent mortality of the original cohort in each time interval. Recruitment is measured as the number of new recruits during the time interval. Values are means \pm 1 SD. Mortality rates could not be calculated for the youngest nonpasture plot (Arrozal) during 1989–1995 or for trees in PFT 1 for any plot. Single-factor ANOVAs were used to compare rates across PFTs.

Plots/interval	Plant functional type					F	P
	PFT 1	PFT 2	PFT 3	PFT 4	PFT 5		
Mortality rate (% mortality)							
Pasture plots							
1997–2002	NA	6.7 \pm 2.9	18.2 \pm 6.2	8.7 \pm 6.2	5.9 \pm 2.8	5.07	0.02
2002–2006	NA	10.1 \pm 5.6	18.6 \pm 11.7	11.9 \pm 4.0	9.2 \pm 2.6	1.21	0.35
Nonpasture plots							
1989–1995	NA	19.3 \pm 9.3	17.2 \pm 5.2	13.6 \pm 3.9	7.3 \pm 2.3	3.13	0.09
1995–2003	NA	33.5 \pm 4.8	45.3 \pm 31.0	15.2 \pm 10.6	19.1 \pm 1.8	2.74	0.09
Average number of recruits							
Pasture plots							
1997–2002	1.5 \pm 1.9	23.5 \pm 9.1	18 \pm 10.9	20.8 \pm 17.3	22.0 \pm 21.4	1.68	0.21
2002–2006	0.8 \pm 1.0	12.8 \pm 4.3	7.8 \pm 5.2	21.0 \pm 26.1	12.0 \pm 7.9	1.39	0.28
Nonpasture plots							
1989–1995	1.7 \pm 2.1	27.0 \pm 31.1	20.7 \pm 23.7	7.3 \pm 11.8	11.7 \pm 10.7	1.15	0.37
1995–2003	0.7 \pm 1.2	42.7 \pm 30.4	30.0 \pm 30.0	8.7 \pm 5.1	25.7 \pm 5.0	2.80	0.06

MORTALITY AND RECRUITMENT OF PFTs IN SECONDARY FOREST.—In the four secondary forest pasture plots, fast-growing subcanopy trees (PFT 3) showed significantly higher rates of mortality than other functional types between 1997 and 2002, although this trend was not statistically significant from 2002 to 2006 (Table 2). In nonpasture plots, fast-growing subcanopy trees (PFT 3) also had the highest mean mortality rate (45%) during the second time interval, but this was not significantly different from other functional types (Table 2). The number of recruited trees did not vary significantly among functional types for either group of secondary plots (Table 2). Slow-growing tree species (PFT 2 and PFT 4) showed high rates of recruitment in former pasture plots and subcanopy species (PFT 2) showed high recruitment rates in the three older nonpasture plots (Table 2).

CHANGES IN DENSITY OF FUNCTIONAL TYPES.—Changes in density of the five functional types were most pronounced in the youngest nonpasture plot, which was 3 yr old in 1989 (Fig. 2A). Fast-growing subcanopy trees (PFT 3) rapidly reached high density in the plot, over 700 individuals/ha, but then declined over the next 13 yr (Fig. 2A). These are relatively short-lived trees that colonized early following abandonment. Slow-growing subcanopy trees (PFT 2) and fast-growing emergents (PFT 5) showed steady increases in density over the first 20 yr following abandonment in this plot (Fig. 2A). Understory trees (PFT 1) and slow-growing canopy/emergent trees (PFT 4) were the least abundant and showed small increases in density over the first 20 yr (Fig. 2A). Temporal trends in basal area for these functional types closely resembled trends in density (data not shown). Similar trends were observed in the LSUR plot, which was 12 yr old in 1997; by this age, fast-growing

subcanopy trees (PFT 3) were already declining in density, whereas fast-growing emergents (PFT 5) were increasing in density (Fig. 2B). Slow-growing trees (PFT 2 and 4) increased steadily but slowly in density, whereas understory trees (PFT 1) showed negligible changes in density (Fig. 2B).

Secondary plots varied in the density of different functional types and in their temporal changes, often due to dynamics of

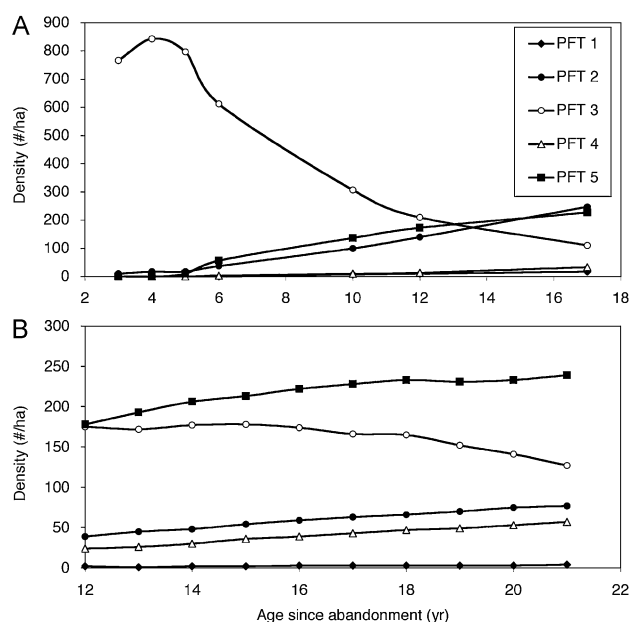


FIGURE 2. Changes in density of trees in five plant functional types in the (A) Arrozal plot over 14 yr and (B) LSUR plot over 9 yr.

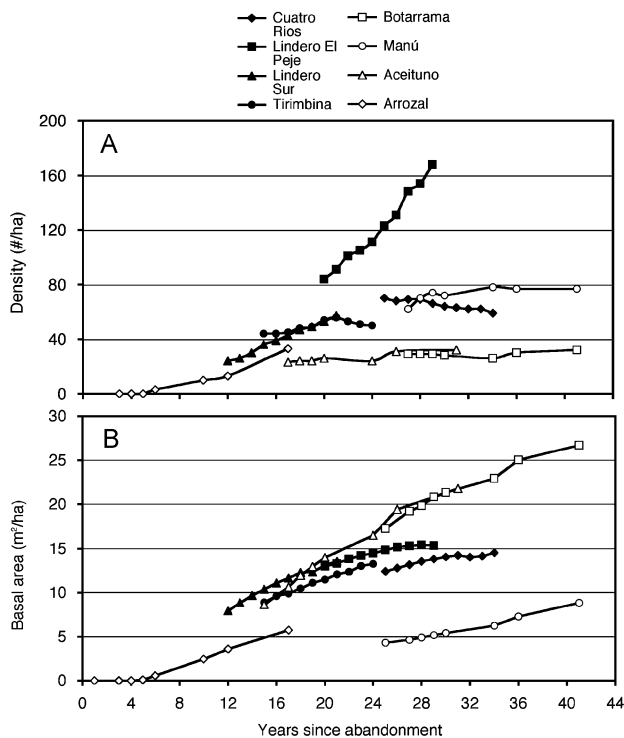


FIGURE 3. Changes in (A) density of trees in PFT 4 and (B) basal area of PFT 5 in eight secondary forest plots. Closed symbols are former pasture plots; open symbols are nonpasture plots.

particular species or species groups. For example, slow-growing canopy/emergent trees (PFT 4) doubled in density over 9 yr in the LEP plot (Fig. 3A). This change was largely due to high recruitment of two species of canopy stilt palms, *Iriartea deltoidea* and *Socratea exorrhiza*. In contrast, the three older nonpasture plots showed little or no change in density of this functional type (Fig. 3A). Increasing basal area of fast-growing emergent trees (PFT 5) was a consistent trend among all secondary forest plots, despite declines in density of this functional type in plots older than 20 yr (Fig. 3B). Slow-growing canopy/subcanopy trees (PFT 4) also increased gradually in basal area in all but one of the secondary forest plots (data not shown).

COLONIZATION GROUPS.—On average, 19 percent of the canopy tree species in secondary forests were nonregenerating pioneers with no seedlings or saplings recorded (Fig. 4). In the oldest site, LEP secondary, this fraction reached 31 percent (Fig. 4). The remaining canopy tree species were divided evenly among forest colonizers (40.3%) and regenerating pioneers (40.4%; Fig. 4). Pooling data from the four sites and removing species with fewer than five individuals led to an increase in the proportion of species of regenerating pioneers (67.0%) and a decrease in the proportion of forest colonizers (26.6%) and nonregenerating pioneers (5.3%).

Within individual plots, regenerating pioneers were by far the most abundant class of seedlings and saplings. An average of 82 percent of all seedlings and saplings were species with trees present in the plot, whereas only 18 percent were forest colonizers.

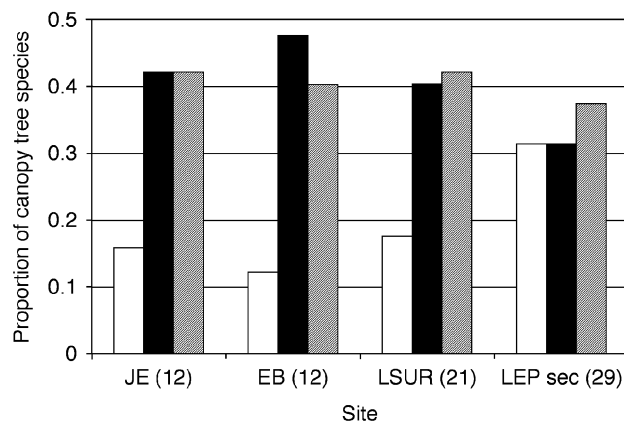


FIGURE 4. Composition of three colonization groups in four secondary forest plots in 2006. Plot ages are shown in parentheses. Open bars are nonregenerating pioneers; black bars are forest colonizers; shaded bars are regenerating pioneers. Full plot names and plot descriptions are given in Table 1.

COMPOSITION OF FUNCTIONAL TYPES IN REGENERATING VEGETATION.—Ninety-three species of regenerating subcanopy and canopy tree and palm species in four secondary forest plots based on 2006 data were included in the functional types classified (Table S3). Among the 25 species of forest colonizers (no adult trees present), 50 percent of individuals were slow-growing subcanopy trees (PFT 2) and 22 percent were slow-growing canopy/emergent trees (PFT 4; Fig. 5A). Thus, 72 percent of the seedlings and saplings with no trees present were slow-growing species. Only 11 percent of seedlings and saplings were fast-growing emergent trees (PFT 5). In contrast, seedlings and saplings of regenerating pioneers were dominated by fast-growing trees in PFT 3 and 5, with 18 and 45 percent of individuals, respectively. These trends were even more pronounced for species composition (Fig. 5B). Forest colonizers are strongly dominated by slow-growing species, whereas regenerating pioneers are strongly dominated by fast-growing species.

DISCUSSION

We conducted the first objective and quantitative characterization of changes in functional type composition of trees during succession and in forests with different histories and intensities of land use. These results allow us to move beyond earlier conceptual frameworks of tropical forest secondary succession developed by Finegan (1996) and Chazdon (2008) based on subjective groupings, such as pioneers and shade-tolerant species (Swaine & Whitmore 1988). PFTs based on only two species attributes—adult height and diameter growth rates—captured much of the functional variation that drives successional dynamics. Most trees that colonize early during succession are fast-growing species in PFT 3 and 5. Many of the species in PFT 3 occupy subcanopy positions as adults, reach reproductive maturity early, and die within 10–30 yr. These are the classically termed ‘pioneer’ species (Swaine & Whitmore 1988) though we emphasize that the PFT as defined here groups a large number of fast-growing and presumably

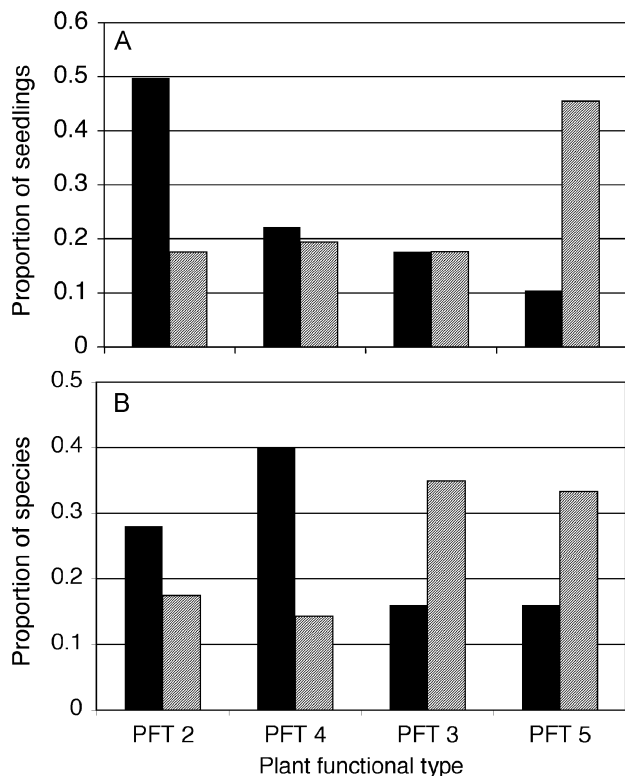


FIGURE 5. Relative abundance (A) and species composition (B) of four plant functional types (PFTs) in the seedling and sapling pool of four secondary forest plots in 2006. Seedlings and saplings are grouped according to colonization groups: black bars are forest colonizers; shaded bars are regenerating pioneers. PFTs are defined in the text.

short-lived species (*e.g.*, *Inga* spp.) with well-known pioneers such as *Cecropia* spp. (see Table S3). Emergent, fast-growing species of PFT 5 increase rapidly in basal area, dominate forest structure throughout succession, and achieve the highest fraction of basal area in mature forests. Many of these species are shared between secondary and mature forests. Meanwhile, populations of slow-growing trees (PFT 2 and 4) slowly accumulate beneath the young forest canopy and gradually become more dominant in the forest (Finegan 1996, Chazdon 2008). Understory trees (PFT 1) are the slowest functional type to repopulate regrowing forests, despite the range in growth rates that they encompass.

Reproductive traits, such as dispersal mode, pollination mode, and sexual system, were ultimately not useful in delimiting tree functional types for the tree species examined here (Salgado-Negret 2007). Thus, although reproductive traits do vary quantitatively in abundance between secondary and mature forests in our landscape (Chazdon *et al.* 2003), they do not seem to be important drivers of successional dynamics of trees ≥ 10 cm dbh. For seedlings, however, dispersal mode and seed size are likely to play an important role in community dynamics during succession (Dalling & Hubbell 2002).

Our functional type classification is similar to others developed in studies of forest dynamics in that one axis is defined by

growth rate and the other is defined by tree stature (Gourlet-Fleury *et al.* 2005). These axes may be considered to be statistically independent (Gourlet-Fleury *et al.* 2005), although several studies suggest that they are correlated. Adult tree height was correlated with both growth and mortality rates in a Malaysian mixed Dipterocarp forest (King *et al.* 2006). Asymptotic tree height was correlated with photosynthetic capacity, growth rates, and allometric characteristics of 28 Malaysian tree species (Thomas 1996, Thomas & Bazzaz 1999). Poorter and Bongers (2006) also found that light demand for juvenile trees (based on an index of crown exposure) was significantly positively correlated with adult stature among 54 Bolivian tree species. Crown exposure and adult stature were useful in delimiting four tree functional types and captured the major variation in functional traits found among these 54 species (Poorter *et al.* 2006). Zhang *et al.* (2008) classified tropical forest vegetation of Hainan Island, China, into seven functional types based on growth form, successional status, and plant size. Successional status was determined based on wood density and seed size. Functional types varied significantly in abundance and species richness across eight landscape types, including early forests of different successional stages and selectively logged forests in lowland and montane zones (Zhang *et al.* 2008).

Our classification of colonization groups defies the traditional dichotomy between 'late successional' shade-tolerant and 'early successional' pioneer species. Many tree species, classified here as regenerating pioneers on the basis of their population structure in secondary forests, are common in both young secondary forest and mature forests in this region (Guariguata *et al.* 1997), and many are important timber species (Vilchez *et al.* 2008). These generalists are by far the most abundant species of seedlings and saplings, conferring a high degree of resilience in the wet tropical forests of NE Costa Rica (Norden *et al.* 2009, Letcher & Chazdon 2009). The high abundance of regenerating pioneers in seedling and sapling size classes clearly shows that species with shade-tolerant seedlings can also recruit as trees early in succession. For these species, early tree colonization enhances seedling and sapling recruitment during the first 20–30 yr of succession, due to local seed rain. Species abundance and size distribution depend strongly on chance colonization events early in succession (Chazdon 2008). Other studies have shown that mature forest species are able to colonize early in succession (Finegan 1996, van Breugel *et al.* 2007, Franklin & Rey 2007, Ochoa-Gaona *et al.* 2007), emphasizing the importance of initial floristic composition in the determination of successional pathways and rates of forest regrowth. On the other hand, significant numbers of species in our sites (40% overall and the majority of rare species) colonized only after canopy closure, and these species may not occur as mature individuals until decades after agricultural abandonment.

Further, our analysis illustrates linkages between functional types defined on the basis of adult size and growth rates of large trees, and patterns in the abundance of seedlings and saplings during secondary succession. Tree species that colonize following canopy closure (*i.e.*, forest colonizers) have very slow to moderate growth rates (PFT 2 and 4; Fig. 5). These species are more abundant in tree communities of mature forests than in secondary forests

(Fig. 2A). In contrast, species of nonregenerating pioneers are dominated by moderate to very fast-growing trees (PFT 3 and 5). These linkages illustrate a trade-off between functional traits that confer high rates of seedling establishment and survival in shade and traits that influence high growth rates in adult trees (Bazzaz & Pickett 1980, Denslow 1987, Rees *et al.* 2001). Our study is the first to illustrate these trade-offs during tropical forest succession.

Clearly, seedling and sapling recruitment are also affected by factors not taken into account by our functional type classification. One such factor is dispersal limitation. Species lacking trees in secondary forests (forest colonizers) have lower abundance as seedlings and saplings, suggesting that seed dispersal could be limiting recruitment. In contrast, fast-growing trees (PFT 3 and 5) predominate among the abundant regenerating pioneer species (Fig. 5). Fast-growing trees may reach reproductive maturity at smaller sizes in young secondary forests, thus increasing local seed availability. Moreover, wind dispersal is found principally among fast-growing emergent tree species (PFT 5), which may account for the increased representation of this group in abundant seedlings and saplings (Fig. 5; Chazdon *et al.* 2003, Salgado-Negret 2007).

Our study has several important limitations. First, with regard to colonization groups, the small number of nonregenerating pioneer species we observed may partly reflect the exclusion of understory trees from our analysis. In young secondary forests, many of the small trees are shade-intolerant species with little or no regeneration after canopy closure, such as *Vismia* and *Miconia* species. Therefore, our sampling excluded some early successional pioneers that are present in these communities, often at high abundance. Second, a classification system for functional types should define response groups that behave homogeneously under a large range of disturbance regimes (Gitay & Noble 1997). In contrast to the PFTs, classification of colonization groups is affected by chance dispersal events, making them inherently inconsistent across plots. As we did not monitor vegetation dynamics in secondary forest plots immediately after abandonment, we assumed that species present only as seedlings or saplings recently colonized the plot and that tree species present in the stand ≥ 10 cm dbh colonized early during succession. The presence of remnant trees in an abandoned pasture can favor early establishment of trees that otherwise may not colonize the site until decades later (Schlawin & Zahawi 2008). Among our secondary forest sites, El Bejuco has the greatest abundance and species richness of remnant trees; this site also had the highest proportion of forest colonizers, suggesting that remnant trees enhanced recruitment of animal-dispersed species not yet present as trees during secondary forest regeneration (Fig. 4).

Mortality and recruitment rates did not always differ significantly across functional types (Table 2), suggesting that canopy strata and growth rates measured in mature forests may not be directly linked with dynamics of trees ≥ 10 cm dbh in secondary forests. Our study did not examine vegetation dynamics in relation to functional types in mature forests of the region, but this is certainly a worthwhile avenue for further study. Gourlet-Fleury *et al.* (2005) argue that the best strategy for grouping tree species in tropical forests is to consider separate groupings for recruitment, growth, and mortality. Such an approach would be impossible for

secondary forests, as rates of growth, mortality, and recruitment can vary dramatically within species across successional stages (Chazdon *et al.* 2005, Palomaki *et al.* 2006). Classifying functional types based on functional traits with low plasticity, such as wood density and seed size, could potentially serve as robust proxies for demographic variables (Poorter *et al.* 2008, Zhang *et al.* 2008).

In the absence of functional trait data for a large number of tree species in our study areas, our investigation represents a starting point in assessing how functional types of trees can be used to understand secondary succession and other land-use transitions in tropical regions. Functional types classification can provide an indispensable tool for tracking changes in both forest degradation and recovery and for predicting future changes in vegetation characteristics, ecosystem properties, and ecosystem services in response to land-use change (Diaz *et al.* 2007). Future work should focus on expanding collection of functional trait data to explore these patterns in more detail and to assess linkages between species dynamics, functional types, and functional traits during land-use transitions in the tropics.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Functional traits used to define functional types for 293 tree species.*

TABLE S2. *Functional types of tree species grouped using cluster analysis based on adult height and growth rate trait states.*

TABLE S3. *Colonization groups and Plant Functional Types (PFT) for 93 subcanopy and canopy tree and palm species occurring in secondary forest plots in 2006.*

FIGURE S1. Map of permanent sample plots in NE Costa Rica. Plot details are given in Table 1.

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LITERATURE CITED

- BAKER, T. R., M. D. SWAINE, AND D. BURSLEM. 2003. Variation in tropical forest growth rates: Combined effects of functional group composition and resource availability. *Perspect. Plant Ecol. Evol. Syst.* 6: 21–36.
- BAZZAZ, F. A., AND S. T. A. PICKETT. 1980. Physiological ecology of tropical succession: A comparative review. *Annu. Rev. Ecol. Syst.* 11: 287–310.
- VAN BREUGEL, M., F. BONGERS, AND M. MARTINEZ-RAMOS. 2007. Species dynamics during early secondary forest succession: Recruitment, mortality and species turnover. *Biotropica* 35: 610–619.
- BROWN, S., AND A. E. LUGO. 1990. Tropical secondary forests. *J. Trop. Ecol.* 6: 1–32.
- BURSLEM, D., AND M. D. SWAINE. 2002. Forest dynamics and regeneration. In R. L. Chazdon and T. C. Whitmore (Eds.), *Foundations of tropical forest biology: Classic papers with commentaries*, pp. 577–583. University of Chicago Press, Chicago, Illinois.
- CHAZDON, R. L. 2008. Chance and determinism in tropical forest succession. In W. Carson and S. A. Schnitzer (Eds.), *Tropical forest community ecology*, pp. 384–408. Wiley-Blackwell Publishing, Oxford, UK.
- CHAZDON, R. L., AND F. G. COE. 1999. Ethnobotany of woody species in second-growth, old-growth, and selectively logged forests of northeastern Costa Rica. *Conserv. Biol.* 13: 1312–1322.
- CHAZDON, R. L., A. R. BRENES, AND B. V. ALVARADO. 2005. Effects of climate and stand age on annual tree dynamics in tropical second-growth rain forests. *Ecology* 86: 1808–1815.
- CHAZDON, R. L., S. CAREAGA, C. WEBB, AND O. VARGAS. 2003. Community and phylogenetic structure of reproductive traits of woody species in wet tropical forests. *Ecol. Monogr.* 73: 331–348.
- CHAZDON, R. L., S. G. LETCHER, M. VAN BREUGEL, M. MARTINEZ-RAMOS, F. BONGERS, AND B. FINEGAN. 2007. Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philos. Trans. R. Soc. Lond., Ser. B: Biol. Sci.* 362: 273–289.
- CLARK, D. A., AND D. B. CLARK. 1992. Life history diversity of canopy and emergent trees in a Neotropical rain forest. *Ecol. Monogr.* 62: 315–344.
- CONDIT, R., S. P. HUBBELL, AND R. B. FOSTER. 1996. Assessing the response of plant functional types in tropical forests to climatic change. *J. Veg. Sci.* 7: 405–416.
- CRAMER, V. A., AND R. J. HOBBS (Eds.). 2007. *Old fields: Dynamics and restoration of abandoned farmland*. Island Press, Washington, DC.
- CUBIÑA, A., AND T. M. AIDE. 2001. The effect of distance from forest edge on seed rain and soil seed bank in a tropical pasture. *Biotropica* 33: 260–267.
- DALLING, J. S., AND S. P. HUBBELL. 2002. Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. *J. Ecol.* 90: 557–568.
- DALLING, J. S., K. WINTER, S. P. HUBBELL, J. L. HAMRICK, J. D. NASON, AND D. A. MURAWSKI. 2001. The unusual life history of *Alseis blackiana*: A shade-persistent pioneer tree? *Ecology* 82: 933–945.
- DEL CAMP, M., S. GOURLET-FLEURY, O. FLORES, AND E. GARNIER. 2008. Can functional classification of tropical trees predict population dynamics after disturbance? *J. Veg. Sci.* 19: 209–220.
- DENSLOW, J. S. 1987. Tropical rainforest gaps and tree species diversity. *Annu. Rev. Ecol. Syst.* 18: 431–452.
- DENSLOW, J. S. 1996. Functional groups diversity and recovery from disturbance. In R. Dirzo, G. H. Orians, and J. H. Cushman (Eds.), *Biodiversity and ecosystem processes in tropical forests*, pp. 127–152. Springer-Verlag, Berlin, Germany.
- DIAZ, S., S. LAVOREL, F. DE BELLO, F. QUETIER, K. GRIGULIS, AND T. M. ROBSON. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proc. Natl. Acad. Sci. USA* 104: 20684–20689.
- EASDALE, T. A., J. R. HEALEY, H. R. GRAU, AND A. MALIZIA. 2007. Tree life histories in a montane subtropical forest: Species differ independently by shade-tolerance, turnover rate and substrate preference. *J. Ecol.* 95: 1234–1249.
- FAVRICHON, V. 1994. Classification des espèces abréces en groupes fonctionnels en vue de la réalisation d'un modèle de dynamique de peuplement en forêt guyanaise. *Rev. Ecol. (Terre Vie)* 49: 379–403.
- FELDPAUSCH, T. R., M. A. RONDON, E. C. M. FERNANDES, S. J. RIHA, AND E. WANDELLI. 2004. Carbon and nutrient accumulation in secondary forests regenerating on pastures in central Amazonia. *Ecol. Appl.* 14: S164–S176.
- FINEGAN, B. 1996. Pattern and process in neotropical secondary forests: The first 100 years of succession. *Trends Ecol. Evol.* 11: 119–124.
- FINEGAN, B., AND M. CAMACHO. 1999. Stand dynamics in a logged and silviculturally treated Costa Rican rain forest, 1988–1996. *For. Ecol. Manage.* 121: 177–189.
- FINEGAN, B., M. CAMACHO, AND N. ZAMORA. 1999. Diameter increment patterns among 106 tree species in a logged and silviculturally treated Costa Rican rain forest. *For. Ecol. Manage.* 121: 159–176.
- FRANKLIN, J., AND S. J. REY. 2007. Spatial patterns of tropical forest trees in Western Polynesia suggest recruitment limitations during secondary. *J. Trop. Ecol.* 23: 1–12.
- GITAY, H., AND I. R. NOBLE. 1997. What are functional types and how should we seek them? In T. M. Smith, H. H. Shugart, and F. I. Woodward (Eds.), *Plant functional types*, pp. 3–19. Cambridge University Press, New York, New York.
- GOURLET-FLEURY, S., L. BLANC, N. PICARD, P. SIST, J. DICK, R. NASI, M. D. SWAINE, AND E. FORNI. 2005. Grouping species for predicting mixed tropical forest dynamics: Looking for a strategy. *Ann. For. Sci.* 62: 785–796.
- GUARIGUATA, M., R. CHAZDON, J. DENSLow, J. DUPUY, AND L. ANDERSON. 1997. Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica. *Plant Ecol.* 132: 107–120.
- GÜNTER, S., M. WEBER, R. ERREIS, AND N. AGUIRRE. 2007. Influence of distance to forest edges on natural regeneration of abandoned pastures: A case study in the tropical mountain rain forest of Southern Ecuador. *Eur. J. For. Res.* 126: 67–75.
- HOLDRIDGE, L. R., W. G. GRENKE, W. H. HAHEWAY, T. LIANG, AND J. A. TOSI. 1975. *Forest environments in tropical life zones*. Pergamon Press, New York, New York.
- HOLL, K. D., M. E. LOIK, E. H. V. LIN, AND I. A. SAMUELS. 2000. Tropical montane forest restoration in Costa Rica: Overcoming barriers to dispersal and establishment. *Restoration Ecology* 8: 339–349.
- HUBBELL, S. P., AND R. B. FOSTER. 1986. Canopy gaps and the dynamics of a neotropical forest. In M. J. Crawley (Ed.), *Plant ecology*, pp. 77–96. Blackwell Scientific Publications, London, UK.
- INFOSTAT. 2004. *InfoStat, versión 2004: Manual del Usuario*. Grupo InfoStat, FCA, Universidad Nacional de Córdoba. Editorial Brujas, Córdoba, Argentina.
- KING, D. A., S. J. DAVIES, AND N. S. M. NOOR. 2006. Growth and mortality are related to adult tree size in a Malaysian mixed dipterocarp forest. *For. Ecol. Manage.* 223: 152–158.

- KNIGHT, D. H. 1975. A phytosociological analysis of species-rich tropical forest on Barro Colorado Island, Panama. *Ecol. Monogr.* 45: 259–284.
- KÖHLER, P., T. DITZER, AND A. HUTH. 2000. Concepts for the aggregation of tropical tree species into functional types and the application to Sabah's lowland rain forests. *J. Trop. Ecol.* 16: 591–602.
- KRAFT, N. J. B., R. VALENCIA, AND D. ACKERLY. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322: 580–582.
- LETCHER, S. G., AND R. L. CHAZDON. 2009. Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. *Biotropica* 41: 608–617.
- LIEBERMAN, D., G. HARTSHORN, M. LIEBERMAN, R. PERALTA, AND A. GENTRY. 1990. Forest dynamics at La Selva Biological Station, 1969–1985. *In* A. H. Gentry (Ed.). *Four neotropical rainforests*, pp. 509–521. Yale University Press, New Haven, Connecticut.
- LUGO, A. E., AND C. T. RIVERA BATLLE. 1987. Leaf production, growth rate and age of the palm *Prestoea montana* in the Luquillo experimental forest, Puerto Rico. *J. Trop. Ecol.* 3: 151–161.
- MARTÍNEZ-GARZA, C., AND R. GONZÁLEZ-MONTAGUT. 1999. Seed rain from forest fragments into tropical pastures in Los Tuxtlas, Mexico. *Plant Ecol.* 145: 255–265.
- MCCUNE, B., AND J. B. GRACE. 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, Oregon.
- MYSTER, R. W. (Ed.). 2008. *Post-Agricultural Succession in the Neotropics*. Springer, New York, New York.
- NIINEMETS, U. 2006. The controversy over traits conferring shade-tolerance in trees: Ontogenetic changes revisited. *J. Ecol.* 94: 464–470.
- NORDEN, N., R. L. CHAZDON, A. CHAO, Y.-H. JIANG, AND B. VILCHEZ-ALVARADO. 2009. Resilience of tropical rain forests: Tree community reassembly in secondary forests. *Ecol. Lett.* 12: 395–394.
- OCHOA-GAONA, S., F. HERNANDEZ-VAZQUEZ, B. H. J. DEJONG, AND F. D. GURRIGARCIA. 2007. Perdida de diversidad florística ante un gradiente de intensificación del sistema agrícola de roza-tumba-quema: un estudio de caso en la Selva Lancandona, Chiapas, Mexico. *Bol. Soc. Bot. Mex.* 81: 65–80.
- PALOMAKI, M. B., R. L. CHAZDON, J. P. ARROYO, AND S. G. LETCHER. 2006. Juvenile tree growth in relation to light availability in second-growth tropical rain forests. *J. Trop. Ecol.* 22: 223–226.
- PINARD, M. 1993. Impacts of stem harvesting on populations of *Iriartea deltoidea* (Palmae) in an extractive reserve in Acre, Brazil. *Biotropica* 25: 2–14.
- POORTER, L. 2007. Are species adapted to their regeneration niche, adult niche, or both? *Am. Nat.* 169: 433–442.
- POORTER, L., AND F. BONGERS. 2006. Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* 87: 1733–1743.
- POORTER, L., L. BONGERS, AND F. BONGERS. 2006. Architecture of 54 moist forest tree species: Traits, trade-offs and functional groups. *Ecology* 87: 1289–1301.
- POORTER, L., F. BONGERS, F. J. STERCK, AND H. WOLL. 2005. Beyond the regeneration phase: Differentiation of height-light trajectories among tropical tree species. *J. Ecol.* 93: 256–267.
- POORTER, L., S. J. WRIGHT, H. PAZ, D. D. ACKERLY, R. CONDIT, G. IBARRA-MANRÍQUEZ, K. E. HARMS, J. C. LICONA, M. MARTÍNEZ-RAMOS, S. J. MAZER, H. C. MULLER-LANDAU, M. PEÑA-CLAROS, C. O. WEBB, AND I. J. WRIGHT. 2008. Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. *Ecology* 89: 1908–1920.
- REDONDO BRENES, A., B. VILCHEZ ALVARADO, AND R. L. CHAZDON. 2001. Estudio de la dinámica y composición de cuatro bosques secundarios en la región Huetar Norte, Sarapiquí, Costa Rica. *Rev. For. Centroam.* 20–26.
- REES, M., R. CONDIT, M. CRAWLEY, S. PACALA, AND D. TILMAN. 2001. Long-term studies of vegetation dynamics. *Science* 293: 650–655.
- SALGADO-NEGRET, B. E. 2007. Tipos funcionales de especies arbóreas en un bosque muy húmedo tropical: definición, correlación filogenética y relación a la rareza local. MSc Dissertation, CATIE, Turrialba, Costa Rica.
- SANFORD, R. L. JR., P. PAABY, J. C. LUVALL, AND E. PHILLIPS. 1994. Climate, geomorphology, and aquatic systems. *In* L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (Eds.). *La Selva: Ecology and natural history of a neotropical rain forest*, pp. 19–33. University of Chicago Press, Chicago, Illinois.
- SCHLAWIN, J., AND R. ZAHAWI. 2008. Nucleating succession in recovering neotropical wet forests: The legacy of remnant trees. *J. Veg. Sci.* 19: 485–492.
- SESNIE, S. E., B. FINEGAN, P. GESSLER, AND Z. S. RAMOS. 2009. Landscape-scale environmental and floristic variation in Costa Rican old-growth rain forest remnants. *Biotropica* 41: 16–26.
- SHUGART, H. 2003. *A theory of forest dynamics: The ecological implications of forest succession models*. Blackburn Press, New York, New York.
- SILVER, W. L., L. M. KUEPPERS, A. E. LUGO, R. OSTERTAG, AND V. MATZEK. 2004. Carbon sequestration and plant community dynamics following reforestation of tropical pasture. *Ecol. Appl.* 14: 1115–1127.
- SLIK, J. W. F. 2005. Assessing tropical lowland forest disturbance using plant morphological and ecological attributes. *For. Ecol. Manage.* 205: 241–250.
- SOLLINS, P., F. SANCHO M., R. MATA CH., AND R. L. JR. SANFORD. 1994. Soils and soil process research. *In* L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (Eds.). *La Selva: Ecology and natural history of a neotropical rain forest*, pp. 34–53. University of Chicago Press, Chicago, Illinois.
- SWAINE, M. D., AND T. C. WHITMORE. 1988. On the definition of ecological species groups in tropical rain forests. *Plant Ecol.* 75: 81–86.
- THOMAS, S. C. 1996. Asymptotic height as a predictor of growth and allometric characteristics Malaysian rain forest trees. *Am. J. Bot.* 83: 556–566.
- THOMAS, S. C., AND F. A. BAZZAZ. 1999. Asymptotic height as a predictor of photosynthetic characteristics in Malaysian rain forest trees. *Ecology* 80: 1607–1622.
- TOMLINSON, P. B. 1979. Systematics and ecology of the Palmae. *Ann. Rev. Ecol. Syst.* 10: 85–107.
- TURNER, I. 2001. *The ecology of trees in the tropical rain forest*. Cambridge University Press, Cambridge, UK.
- VERBURG, R., AND C. VAN EIJK-BOS. 2003. Effects of selective logging on tree diversity, composition and plant functional type patterns in a Bornean rain forest. *J. Veg. Sci.* 14: 99–110.
- VILCHEZ, B., R. L. CHAZDON, AND V. MILLA QUESADA. 2008. Dinámica de la regeneración en cuatro bosques secundarios tropicales de la región Huetar Norte, Costa Rica: Su valor para la conservación o uso comercial. *Recur. Nat. Ambient* 55: 118–128.
- WRIGHT, S. J., H. C. MULLER-LANDAU, R. CONDIT, AND S. P. HUBBELL. 2003. Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology* 84: 3174–3185.
- ZHANG, Z. D., R. G. ZANG, AND Y. D. QI. 2008. Spatiotemporal patterns and dynamics of species richness and abundance of woody plant functional groups in a tropical forest landscape of Hainan Island, South China. *J. Integr. Plant Biol.* 50: 547–558.