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

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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.
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.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Latitude, longitude</th>
<th>Prior land use</th>
<th>Year abandoned</th>
<th>Location</th>
<th>Surrounding landscape</th>
<th>Plot size (ha)</th>
<th>Measurement period</th>
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<td>Lindero Sur (LSUR)*</td>
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<td>1985</td>
<td>La Selva</td>
<td>Mature and secondary forest</td>
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<td>Plantations, pasture, and secondary forest</td>
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<td>Pasture</td>
<td>1995</td>
<td>Chilamate</td>
<td>Pasture, secondary and mature forest</td>
<td>1</td>
<td>2006</td>
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<td>10.46° N, 84.07° W</td>
<td>Pasture</td>
<td>1995</td>
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<td>1 yr rice cultivation</td>
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<td>Tirimbina</td>
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<td>1972</td>
<td>Tirimbina</td>
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<tr>
<td>Manú</td>
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<td>Tirimbina</td>
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<tr>
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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, Cubíña & Aide 2001, Dalling & Hubbell 2002, Günter et al. 2007).

Our approach avoided misconceptions 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 \( \geq 10 \text{ cm dbh} \) (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 \( \geq 10 \text{ cm dbh} \). 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
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, henceforth 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 x 200 m (0.5 ha); and tree seedlings were sampled in five strips of 2 x 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
Z \geq 10 \text{ 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 $\geq 10$ 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; $P > 0.05$; Fig. 1A, B). Understory trees (PFT 1) represented a low proportion of trees $\geq 10$ 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).
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

### 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± 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.

<table>
<thead>
<tr>
<th>Plots/interval</th>
<th>PFT 1</th>
<th>PFT 2</th>
<th>PFT 3</th>
<th>PFT 4</th>
<th>PFT 5</th>
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<th>P</th>
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<tr>
<td>Mortality rate (% mortality)</td>
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<td>1997–2002</td>
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<td>5.9 ± 2.8</td>
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<td>2002–2006</td>
<td>NA</td>
<td>10.1 ± 5.6</td>
<td>18.6 ± 11.7</td>
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<td>1989–1995</td>
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<td>19.3 ± 9.3</td>
<td>17.2 ± 5.2</td>
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<td>1995–2003</td>
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<td>45.3 ± 31.0</td>
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<td>Average number of recruits</td>
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<td>1997–2002</td>
<td>1.5 ± 1.9</td>
<td>23.5 ± 9.1</td>
<td>18 ± 10.9</td>
<td>20.8 ± 17.3</td>
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<td>2002–2006</td>
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<td>1989–1995</td>
<td>1.7 ± 2.1</td>
<td>27.0 ± 31.1</td>
<td>20.7 ± 23.7</td>
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<td>1995–2003</td>
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<td>30.0 ± 30.0</td>
<td>8.7 ± 5.1</td>
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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.
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, \textit{Iriartea deltoidea} and \textit{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.

**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
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 2009). 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 \(\geq 10 \text{ cm dbh}\). 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. 2007). 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.

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.
that tree species present in the stand present only as seedlings or saplings recently colonized the plot and as we did not monitor vegetation dynamics in secondary forest PFTs, classification of colonization groups is affected by chance response groups that behave homogeneously under a large range of 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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