Rapid Recovery of Biomass, Species Richness, and Species Composition in a Forest Chronosequence in Northeastern Costa Rica

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ABSTRACT

Secondary forests are a vital part of the tropical landscape, and their worldwide extent and importance continues to increase. Here, we present the largest chronosequence data set on forest succession in the wet tropics that includes both secondary and old-growth sites. We performed 0.1 ha vegetation inventories in 30 sites in northeastern Costa Rica, including seven old-growth forests and 23 secondary forests on former pastures, ranging from 10 to 42 yr. The secondary forest sites were formerly pasture for intervals of < 1–25 yr. Aboveground biomass in secondary forests recovered rapidly, with sites already exhibiting values comparable to old growth after 21–30 yr, and biomass accumulation was not impacted by the length of time that a site was in pasture. Species richness reached old-growth levels in as little as 30 yr, although sites that were in pasture for > 10 yr had significantly lower species richness. Forest cover near the sites at the time of forest establishment did not significantly impact biomass or species richness, and the species composition of older secondary forest sites (> 30 yr) converged with that of old growth. These results emphasize the resilience of tropical ecosystems in this region and the high conservation value of secondary forests.

Key words: biodiversity; ecological resilience; land use history; succession; tropical wet forest.
light forest structure (Purata 1986) and aboveground biomass (Hughes et al. 1999). In Guatemala, Ferguson et al. (2003) found lower species diversity, basal area, and density of woody stems in recently abandoned fields that were used for intensive agriculture or pasture, compared with agroforestry and swidden sites. In Puerto Rico, abandoned coffee plantations, pastures, and improved pastures show divergent tree communities, even after 50 or more years of regeneration (Aide et al. 1995, 1996; Pascarella et al. 2000; Lugo 2002; Chinea & Helmer 2003). Land-use history explained observed differences in forest composition in 20-yr-old patches of secondary forest near Manaus, Brazil. Sites that had been active pasture for > 4 yr had Vismia-dominated forests, while less intensively used sites were dominated by Cecropia spp. (Lucas et al. 2002). These early differences in tree species composition may affect the community structure of a secondary forest for many years. Cecropia spp. tend to die off after 20 yr and permit other species to regenerate, but Vismia spp. are much longer-lived and may slow the establishment of other species in the understory (Lucas et al. 2002). Thus, land-use history can drive different successional trajectories. The spatial configuration of the landscape, especially the extent and condition of surrounding forests, can also strongly impact the recovery of biomass, species richness, and species composition (reviewed in Guariguata & Ostertag 2001; Chazdon 2003, 2008; Holl 2007).

Explaining patterns of succession along a chronosequence requires an adequate level of replication at each point in the time series. In the tropics, a relatively large plot size is essential in order to capture variation in the context of such broad floristic diversity. To capture diversity in secondary forests, it is essential to measure variation in the context of such broad floristic diversity. We use these data to examine the structural and floristic components of forest regeneration. We investigate how land-use history impacts the biomass and species richness of secondary forests, and whether the biomass, species richness, and species composition of secondary forests approaches that of old-growth forests along a chronosequence.

**METHODS**

**STUDY SITE AND DATA COLLECTION.**—We studied secondary and old-growth forests in the Sarapiquí region of northeastern Costa Rica, in an area centered around La Selva Biological Station (10°26’ N, 83°59’ W; described in McDade et al. 1994). The area has an annual average temperature of 26.5°C and annual precipitation of ca 3900 mm (Sanford et al. 1994), placing it in the tropical lowland wet forest life zone (Holdridge 1967). The landscape of the Sarapíqui region consists of old-growth forest fragments surrounded by cattle pastures, extensive banana and pineapple plantations, and patches of secondary forest (Butterfield 1994, Guariguata et al. 1997).

We conducted vegetation inventories in 30 sites, seven in old-growth forest and 23 in secondary forests of 10–44 yr post-abandonment (Table S2). All the secondary forest sites were in abandoned pastures, with the exception of two sites that were formerly in rice cultivation (Sites 6 and 26), and three sites that were cut, burned, and then immediately left fallow (Sites 27, 29, and 30). Forest ages and land-use history were ascertained by a combination of aerial photographs and satellite images (where available), and interviews with landowners and neighbors. We also used aerial photos and satellite images to estimate the percent forest cover in a 1-km radius around each site at the approximate time of forest establishment (Table S2). The 30 sites occupied a fairly small geographic area, with < 25 km between the most widely separated sites, with elevations of 40–200 m asl (Table S2; Fig. 1).

We used a modified Gentry transect (Phillips & Miller 2002) to survey vegetation in 0.1 ha at each site. The transect consisted of a series of five parallel strips of 2 × 100 m, each separated by 10 m (this design maintains the sampling effort in a fairly limited local area, yet avoids oversampling clusters of clonally reproducing plants; Phillips & Miller 2002). Within the transect, we recorded diameter at 1.3 m height (dbh) and species identification for all woody stems ≥ 2.5 cm dbh for trees/shrubs and ≥ 0.5 cm dbh for lianas. We chose a smaller diameter size threshold for lianas because they produce far greater biomass for an equivalent stem diameter (Gehring et al. 2004), and their low diameter growth rate leads to an absence of large-diameter liana stems in young secondary forest (DeWalt et al. 2000). Following the methods of Gentry (Phillips & Miller 2002), we also measured and recorded giant herbs (e.g., Heliconia spp.) if their stem diameter exceeded 2.5 cm. Where a plant had multiple stems, we recorded it as one individual, but took separate diameter readings for each stem. The data for all stems were used to calculate biomass and relative life form abundance, but species richness and species composition were calculated based on individuals.

We took a voucher specimen for each species at each site, where possible, and we verified species identifications using the collection of the Instituto Nacional de la Biodiversidad (INB) in Santo Domingo de Heredia, Costa Rica. All specimens are filed at INB, with duplicates of fertile specimens at the Museo Nacional de Costa Rica. For soil analysis, at each transect site we took three evenly spaced 2 × 30 cm soil cores, one at the base of the first 2 × 100 m strip, one at the center of the second strip, and one at the extreme of the fifth strip. The three cores from each site were combined.

**ANALYTICAL METHODS.**—We estimated aboveground biomass using allometric regression equations based on diameter (in this analysis, non-woody stems were omitted, because they generally contribute only
a small amount of biomass, and accurate regression equations are not readily available; Saldarriaga et al. 1988, Uhl et al. 1988). To select appropriate models, we used equations that were developed in similar forest types and/or with diameter ranges overlapping the range in our data set. For lianas, we used the equations in Gehring et al. (2004), based on the largest available liana biomass dataset. For trees, we used two sets of equations: Brown’s (1997) wet forest equation, calibrated near La Selva, was used for trees $Z5 cm dbh, while Nelson et al.’s (1999) equation, calibrated with smaller stems (1.2–28.6 cm dbh) in secondary forest in the Amazon, was used for stems $5 cm dbh.

To incorporate wood density variation into the estimates of biomass accumulation, we used the equation from Chave et al. (2004) with wood density estimates taken from Chave et al. (2006) and Brown (1997). Of the 180 tree species with individuals $10 cm dbh, species-level wood density estimates were available for 98. For 69 species, we used genus-level estimates, and for the 13 species with no reported wood density values we used the regional average of 0.645 g/cm³ (Chave et al. 2006). Because Chave’s (2004) equation is only valid for stems $10 cm dbh, in this case we used the equations from Nelson et al. (1999) to estimate biomass of trees 2.5–9.9 cm dbh. We also report basal area measurements (Table S2), calculated from diameter of all stems, to facilitate comparison with data from sites where no appropriate allometric regression equations are available.

Species richness was estimated by rarefaction in order to control for differences in stem density among sites (Colwell & Coddington 1994), using the program EstimateS (Colwell 2007). Unidentified species were excluded from species richness estimation, but we did include eight consistent morphospecies corresponding to undescribed species (N. Zamora, pers. comm.). For the rarefaction process, we divided the data from each transect into 50 samples of 10 m each, and randomized the order of sampling 100 times. We also calculated the Abundance-Based Coverage estimator (ACE; Chao et al. 2005), a non-parametric estimator of species richness.

To examine chronosequence trends in biomass accumulation and species richness, sites were grouped by age: 10–15 yr ($N=6$), 16–20 yr ($N=6$), 21–30 yr ($N=6$), 31–44 yr ($N=5$), and old growth ($N=7$). Biomass and species richness data were compared using GLM procedures with Bonferroni post-hoc tests, using Minitab Version 14 (Minitab Inc. 2003).

We investigated the relative abundance of different life forms in different successional stages by assigning each species to one of the following life form groups: giant herbs, shrubs, lianas, small trees (usually <15 m, not reaching the canopy in old growth), canopy trees, understory palms, and canopy palms. The group designation is mainly taken from Chazdon et al. (2003). Species not included in Chazdon et al.’s (2003) data set were evaluated based on field observations and herbarium labels at INB and in the W3TROPICOS database of the Missouri Botanical Garden (available online at http://mobot.mobot.org/W3T/Search/vast.html).

To examine species composition, we calculated pairwise similarities between each pair of sites using EstimateS (Colwell 2007). We chose the Chao–Jaccard abundance-based similarity estimator, a probabilistic estimator that is demonstrably more robust to variations in sample size than traditional similarity metrics (Chao et al. 2005). We used NMDS to visualize the relationships among the plots in ordination space, and the permutation test ANOSIM (Clarke & Warwick 1994) to compare the strength of within-group vs. between-group relationships for all the plots.
using age category as the grouping variable. NMDS and ANOSIM were implemented in Primer-E Version 6 (Clarke & Warwick 1994), with 50,000 starts for the NMDS and a maximum of 999 permutations in ANOSIM.

We used the bulked soil samples from each transect site to examine the effects of soil characteristics on species composition. The soil samples were frozen after collection for a period of up to 2 yr, and then air-dried for 3–4 d, sieved to remove fine roots, and ground. Analysis was conducted at the soil lab of the University of Massachusetts, Amherst. We measured pH, carbon, and total nitrogen by catalytic combustion, and the concentrations of the following elements from a Mehlich III extraction (Mehlich 1984) and flame spectroscopy: K, Ca, Na, Mg, Zn, Mn, Cu, Fe, Pb, Al, Ni, B, S, and P. Because the soils were frozen before analysis, it was not possible to measure biologically available N and P. We performed a canonical correspondence analysis (CCA) in PC-ORD 4 (McCune & Mefford 1999) with log-transformed soil variables to investigate the relationship between soil characteristics and species abundances along the chronosequence.

To investigate the effects of landscape context, land-use history and forest age on secondary forest formation, we compared all 23 secondary forest sites. In this analysis, it was necessary to lump sites into rather broad categories to ensure sufficient replication and representation in each category. We divided sites into older (> 20 yr) vs. younger (≤ 20 yr) and light use (0–10 yr in pasture before abandonment) vs. heavy use (> 10 yr pasture). We performed ANCOVAs, using forest cover in the 1-km buffer around each site as the covariate, to investigate the relative effects of forest age and land-use history on biomass accumulation and species richness. The ANCOVAs were conducted in Minitab Version 14 (Minitab Inc. 2003).

RESULTS

In the 30 transects combined, we found a total of 8898 individuals (10,920 stems). In a few cases we were unable to collect a voucher specimen, or unable to fully determine a species from a sterile voucher. Nine individuals were completely unidentified, and five were only identified to genus level. The flora of northeastern Costa Rica is very well-characterized (Holdridge & Poveda 1975; Zamora et al. 2000, 2004; Proyecto Flora Digital 2007), permitting high taxonomic accuracy. Nonetheless, we found eight morphospecies that were internally consistent among the specimens we collected, yet could not be matched to any currently described species (N. Zamora, pers. comm.). One morphospecies was found in each of the following genera: Coccoloba, Cupania, Dussia, Licania, Odontocarya, Paulinia, Swartzia, and Unonopsis. Including these consistent morphospecies, we found a total of 477 species in 93 families (according to the APG classification; Stevens 2006). Overall, 8791 individuals (98.8%) were positively identified and matched to described species. When we include the eight morphospecies, this figure rises to 8889 individuals (99.9%).

Nearly all the species we collected were angiosperms. The only exceptions were two tree ferns, Cyathea microdonta (Desv.) Domin. and C. multiflora Sw., and the gnetophyte liana Gnetum leiboldii.

Tul. The vast majority were species native to the region; only seven exotic species (1.5%) were found, and they contributed only 15 individuals (0.15%).

Aboveground biomass recovered rapidly along the chronosequence, such that sites 21–30 yr of age already showed values not significantly different from the biomass of old-growth forests (Fig. 2). The value for old-growth forests obtained in this study using Brown’s (1997) equations (mean ± SE of 163 ± 12 Mg/ha) compares favorably to the estimate of Clark and Clark (2000), of 161–186 Mg/ha for old-growth forests in the same region. Biomass in older secondary forests, 30–42 yr, was significantly higher than the value for old-growth forests (Fig. 2). Chave et al.’s (2006) equations incorporating wood density calculated substantially higher values overall (Fig. 2), but the pattern of rapid accumulation and overshoot did not differ.

Species richness also recovered rapidly along the chronosequence, although not as rapidly as biomass: it did not reach old-growth levels until 30–44 yr postabandonment (Fig. 3). Estimated species richness was higher than observed for all age categories (Fig. 3), indicating that species accumulation curves did not level off at 0.1 ha in these sites. However, the behavior of the estimator was identical to the behavior of the rarefied species richness: ACE values increased in each successive age category for secondary forests, reaching a level indistinguishable from old-growth values in the 30–44 yr age category.

The relative abundance of different life forms changed along the chronosequence (Fig. 4). Giant herbs were most prevalent in the youngest sites, and their abundance rapidly declined with forest
age, reaching zero in forests > 30 yr old. Shrubs and lianas also declined with forest age, although less dramatically, and they were still present even in old-growth forests. Canopy palms were almost absent from young sites; the few stems found in sites < 20 yr old probably represent remnant vegetation, because canopy palms in this region have an extended establishment phase (DeMason 1983, Schatz et al. 1985), during which they have no aboveground stem extension, and thus would not have been measured in this census. Likewise, understory palms were very rare except in old-growth forest, where they formed approximately 6 percent of stems. Tree ferns formed a negligible amount of the stems in any age category, and are not shown here.

Species composition varied consistently along the chronosequence, with older sites grouping at one extreme and younger sites at the other (Fig. 5). The NMDS plot had a 2-D stress of 0.17, indicating a meaningful level of structure in the data set (Clarke & Warwick 1994). The global P value from ANOSIM was < 0.001. Pairwise comparisons (Table 1) showed few significant differences between adjacent age groups; most significant differences occurred between groups separated by at least 10 yr in age. This analysis indicated no significant difference between the species composition of older secondary forests (30–42 yr) and old-growth forest.

Soils had little apparent effect on the species composition of regenerating forests. Soil characteristics explained a cumulative total of only 23.5 percent of the variance in species composition in the first three canonical axes. Soils were generally nutrient-poor oxisols with low pH and high aluminum. Site 6 was an apparent outlier, with the highest pH (6.5), the highest P concentration (6.5 mg/kg soil), and cation concentrations an order of magnitude higher than in other sites (pH at other sites was 4.0–5.3, and P concentrations 1.2–4.2 mg/kg). Site 6 was on a river floodplain, and it was in rice

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TABLE 1. Significance (determined by ANOSIM) for differences in species composition among sites from the five age categories. The table shows P values for pairwise comparisons between age categories, with values < 0.05 in bold.

<table>
<thead>
<tr>
<th>Age Category</th>
<th>&lt; 15 yr</th>
<th>16–20 yr</th>
<th>21–30 yr</th>
<th>&gt; 30 yr</th>
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<tr>
<td>16–20 yr</td>
<td>0.143</td>
<td></td>
<td></td>
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<tr>
<td>21–30 yr</td>
<td><strong>0.045</strong></td>
<td>0.16</td>
<td></td>
<td></td>
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<tr>
<td>&gt; 30 yr</td>
<td><strong>0.004</strong></td>
<td>0.006</td>
<td><strong>0.004</strong></td>
<td></td>
</tr>
<tr>
<td>Old growth</td>
<td><strong>0.001</strong></td>
<td>0.003</td>
<td><strong>0.002</strong></td>
<td>0.077</td>
</tr>
</tbody>
</table>
cultivation before abandonment, which may account for the unique soil properties. Nonetheless, when Site 6 was removed, the CCA showed even less relationship between environmental variables and species composition: the first three canonical axes explained only 21.3 percent of the variance in species composition in the remaining 29 sites.

In the subset of just secondary forest sites, we examined the effects of forest age vs. land-use history (time in pasture) on biomass and species richness, using forest cover in the 1-km buffer around each site at time of forest establishment as a covariate. For biomass accumulation, forest age (but not land use) had a significant effect, explaining 49.6 percent of the variance, and the covariate was not significant ($F_{1,18} = 16.2, P < 0.01$ for age; $F_{1,18} = 0.11, P = 0.75$ for use; $F_{1,18} = 2.10, P = 0.17$ for interaction; $F_{1,18} = 0.85, P = 0.37$ for forest cover). Young forests (< 20 yr) had significantly lower biomass than their older counterparts. For species richness, both age and land-use history had significant impacts. A combined model with age and land use explained 61.7 percent of the variance in species richness; the interaction term and the covariate were not significant. ($F_{1,18} = 17.6, P < 0.01$ for age; $F_{1,18} = 12.9, P < 0.01$ for use; $F_{1,18} = 0.13, P = 0.73$ for interaction; $F_{1,18} = 1.52, P = 0.23$ for forest cover). Older forests and those with lighter use (< 10 yr pasture) had higher species richness.

**DISCUSSION**

Recently, much debate has centered on the conservation value of tropical secondary forests and their potential as reservoirs of biodiversity (Wright & Muller-Landau 2006a, b; Brook et al. 2006; Barlow et al. 2007). Rates of recovery for biomass and species richness vary widely across the Neotropics, and species composition of secondary forests often fails to converge with that of old-growth forests nearby (Chazdon 2008; Table S1). Our work indicates an encouraging prognosis for forest regeneration in northeastern Costa Rica. For woody vegetation, biomass and species richness recover rapidly, and even the species composition returns to pre-disturbance levels in a relatively short period of time.

Recent research has questioned the validity of the chronosequence approach for studying tropical forest succession (Chazdon et al. 2007, Feldpausch et al. 2007, Johnson & Miyashita 2008). Chronosequences provide a cost-effective and rapid method of investigating forest changes over time, but the critical, and often untested, assumption is that sites of different ages represent points along a predictable continuum. In comparing chronosequence predictions to the results of long-term dynamics studies, Chazdon et al. (2007) found that certain stand properties are predictable from chronosequence trends, while others fail to conform. In particular, basal area accumulation (a conservative proxy for biomass accumulation where no locally calibrated allometric biomass equation is available) is a highly predictable emergent property of forest stands during succession. Species composition at a site was found to be much less dynamic than would be predicted from a chronosequence, and hence species richness and species composition during succession are much less predictable. Feldpausch et al. (2007) monitored secondary forests in the Amazon for 4 yr, and they found that biomass accumulation was not predictable from chronosequence extrapolations. In their study site, however, forest age was confounded with land-use intensity: the oldest forests established after short-term pasture use, and the youngest forests established on lands that had been in pasture for many years. In this study, we attempted to control for the pitfalls of the chronosequence approach by rigorously verifying site ages, and by selecting multiple sites ($N \geq 5$) in each age category. We also ensured that, as much as possible, forest age was not confounded with land-use history, and we addressed the confounding of age and land-use history in our analysis.

The rapid early accumulation of aboveground biomass observed in these data compares favorably to the results of prior studies (Saldaña et al. 1988, Guariguata et al. 1997, Pascarella et al. 2000, Silver et al. 2000, Guariguata & Ostertag 2001, Peña-Claros 2003, Feldpausch et al. 2005). According to many studies, biomass accumulation is a saturating curve, rapid at first and then leveling off, with the highest standing biomass in old-growth sites (Saldaña et al. 1988, Peña-Claros 2003, Gehring et al. 2005, Howorth & Pendry 2006). This study, Denslow and Guzman (2000), and Marin-Spiotta et al. (2007) found higher biomass in intermediate-aged forests than in old growth. One might suspect that this trend was driven by an overabundance of light-wooded pioneer species in the canopy of intermediate-aged successional forests, but an analysis incorporating species-specific wood density values (Fig. 2) showed precisely the same pattern. An alternate explanation for the over-shoot in biomass is that young to intermediate secondary forests have very few large-scale gap disturbances (Montgomery & Chazdon 2001). Many species recruit from beneath the canopy rather than exploiting gaps. Late in the process of forest maturation, stand-level thinning may regulate tree distributions, a high density of stems may recruit and establish (Guariguata & Ostertag 2001, Chazdon 2008).

The biomass of secondary forests was not significantly impacted by the amount of time that the land was in pasture before regeneration. This contradicts the results of numerous other studies (e.g., Aide et al. 1995, Hughes et al. 1999, Steininger 2000, Kammesheidt 2002), in which biomass accumulation was impacted by prior land use, although Zarin et al. (2001) found no significant difference in biomass accumulation between former pastures and former slash-and-burn fallsows. Biomass accumulation in the Sarapiquí region may be more resilient due to the higher soil fertility in Costa Rica (Guariguata et al. 1997) than in other regions where similar work has been conducted (Pascarella et al. 2000, Feldpausch et al. 2005, Toledo & Salick 2006). Alternately, the division of land-use categories may have been too crude to capture true differences in the effects of land-use history on biomass accumulation. Steininger (2000) detected a significant difference in the biomass accumulation after 1 yr vs. 4 yr fallsows. There may be a threshold level above which further use no longer affects biomass accumulation, and having too few sites in the light-use category, we may have failed to capture that effect. However, it would be difficult to make...
a finer-scale test of the effects of land-use history on biomass accumulation in this region of Costa Rica, because use intensity is confounded with forest age here (Guariguata et al. 1997). Due to the economic history of the region, very few recently abandoned forest sites had light use: most of the clearing took place in the 1960s–1980s, and regeneration has begun sporadically since then (Butterfield 1994, Guariguata et al. 1997, Read 1999).

Similarly, we found that biomass accumulation was not affected by the amount of forest cover in the 1-km buffer around each site at the time of forest establishment. This result again contradicts many studies showing that forest regeneration is slower in landscapes with less existing forest cover (e.g., Aide et al. 1995, Hughes et al. 1999, Steininger 2000, Kammesheidt 2002, Holl 2007, Martínez-Ramos & García-Orth 2007). Compared with other tropical regions, though, deforestation in the Sarapiquí area has been relatively modest (Read 1999). Forest clearing was mainly conducted by smallholders (Butterfield 1994). Deforestation spread out from the road network, but remote areas remained under forest cover, leaving large forest remnants in the landscape (Butterfield 1994, Read 1999; Fig. 1). In the San Juan Biological Corridor, a roughly 30 × 60 km strip of land overlapping most of the study region, an estimated 26 percent of the area was forested in 2001 (this figure includes old-growth and secondary forest; Wang 2008). None of our study sites were established in completely denuded areas; the lowest forest cover in the 1-km buffer around a site at the time of establishment was 20 percent (Sites 17 and 18; Table S2). Landscape context also had no apparent effect on the aboveground biomass or species richness of old-growth forests. Sites 22, 28, and 25 were located in forest fragments, with site 25 being closest to a forest edge (Fig. 1). Sites 8, 9, 10, and 11 are located in a large contiguous area of protected old-growth forest. Yet the distribution of species richness (site 25 > 8 > 28 > 11 > 9 > 22 > 10) and biomass (site 8 > 25 > 28 > 9 > 11 > 22 > 10) does not reflect any negative effects of the landscape context on these parameters in old-growth forest. Schedlbauer et al. (2007) also failed to detect any edge effects on biomass in 20–30 yr old edges between old-growth forest and pasture in the Sarapiquí region. Perhaps in a more fragmented landscape the effects of fragmentation would be easier to detect.

Guariguata et al. (1997) estimated that up to 15 percent of the secondary forest biomass in this region of Costa Rica may be contributed by remnant trees. This may have contributed to the rapid biomass accumulation we observed, and our failure to detect any effect of surrounding forest cover on forest recovery. Lacking highly detailed records of the location of remnant trees before regeneration, however, it is difficult to develop objective criteria for separating remnant trees from true secondary forest. Growth rates are extremely rapid in the humid tropics—Piotto et al. (2003) report annual diameter increments of 1.5 to almost 3 cm/yr for plantation trees in this region of Costa Rica, and growth rates may be even higher in isolated trees during early regeneration. It is possible for trees to reach diameters > 60 cm in the first 20 yr of growth. In some cases, remnant trees can be identified based on their species identity: large individuals of slow-growing, non-pioneer species can be safely considered remnant trees. However, in our data set, the large-diameter trees (> 60 cm) in secondary forests were all species that are commonly found in secondary forests in the region: Pentaclethra macroloba (Willd.) Kuntze, Styrophodon microstachyum Poeppl. & Endl., Tapirira guianensis Aubl., Vochysia ferruginea Mart., and V. guatemalensis Donn. Sm. Omitting the seven individuals > 60 cm dbh in secondary forests from the analysis (two in forests 16–20 yr, one in forests 21–30 yr, and four in forests 31–44 yr) reduced the estimates of biomass accumulation, but did not change the pattern of rapid increase and overshoot (data not shown). Remnant trees in some sites may have facilitated the rapid successional process documented in this study: Schlawn and Zahawi (2008) found higher species richness and stem density in secondary forests in the vicinity of remnant trees in northeastern Costa Rica.

Woody species richness recovers rapidly, reaching the level of old-growth forest after as little as 30 yr, although the recovery is less rapid in sites with more intense land use. These results corroborate many published studies (e.g., Purata 1986, Aide et al. 2000, Pascarella et al. 2000, Guariguata & Ostertag 2001, Peña-Claros 2003, Feldpausch et al. 2005, Toledo & Salick 2006, Marín-Spiotta et al. 2007). However, it is important to note that the analysis of species richness presented here made no consideration of stem size. Much of the diversity in older secondary forests comes from stems in small size classes (Guariguata et al. 1997, Peña-Claros 2003; this study), and it may take hundreds of years for the size class distributions of individual species to match those displayed in old-growth forests. In addition, secondary forests lack some of the structural characteristics of old-growth forests—standing dead trees, large woody debris, etc.—that form important wildlife habitat (Saldarriaga et al. 1988, Dewalt et al. 2003, Dunn 2004). Faunal succession may be more delayed than vegetational succession, due in part to the structural differences between old-growth and secondary forests (DeWalt et al. 2003, Dunn 2004, Barlow et al. 2007).

Species composition in secondary forests of northeastern Costa Rica converges with the composition of old-growth forests, rather than taking divergent successional pathways (Fig. 5). This is an encouraging indication of forest recovery. In Puerto Rico, numerous studies have documented the incursion of exotic invasive species into secondary forests (e.g., Aide et al. 2000, Pascarella et al. 2000, Marín-Spiotta et al. 2007). The species richness of the forest may recover, but the constituent species are different. In this study, we documented a very small number of non-native species, which contributed only a vanishing percentage of the species richness in secondary forests. One of the most pernicious invaders in Puerto Rico, Spathodea campanulata P. Beauv. (Aide et al. 2000, Pascarella et al. 2000), is widely planted as an ornamental tree near some of the sites included in this study (S. Letcher, pers. obs.), but it was not present in any of the transects and not observed in the forest. The absence of invasives in these sites does not guarantee that the forest will remain free of them: elsewhere in the Sarapiquí region, invasions of numerous exotic species have been observed: Euterpe oleracea Mart., Hevea brasiliensis (Willd. ex A. Juss.) Müll. Arg., Coffea canephora Pierre ex Froehner, and Musa velutina H. Wendl. & Drude (Chazdon et al., in press). Also, the small diameter threshold used in this study may have contributed to the high similarity between late
secondary and old-growth sites. In secondary forests in our study area, Guariguata et al. (1997) found stronger similarity to old-growth species composition in the sapling layer (stems ≥ 1 m tall and 5 cm dbh) than in the canopy (stems ≥ 10 cm dbh), suggesting that the inclusion of small stems makes it easier to detect convergence between the species composition of secondary and old-growth forest.

This study underscores the importance of secondary forests as reservoirs of biodiversity in tropical landscapes. At least in northeastern Costa Rica, tropical forests are highly resilient systems (sensu Holling 1973): after anthropogenic disturbance, they are capable of rapid recovery. After as little as 30 yr, secondary forests harbor as many woody species as old-growth forests, and in this region, the species composition converges with that of old-growth forests as well. Secondary forests contain large numbers of useful timber species (Redondo et al. 2001, Chazdon 2003) and non-timber forest products (Chazdon & Coe 1999), and the use of secondary forests as extractive reserves could take some pressure off old-growth forests (Kammermeid 2002). Although many conservation plans still focus almost exclusively on old-growth forests, it is imperative to take a more holistic view of tropical landscapes (Chazdon 2003, Bawa et al. 2004, Chazdon et al., 2009). The rapid recovery of biodiversity and forest structure in secondary forests provides hope that they may, after all, help to stem the tide of extinctions in the tropics (Wright & Muller-Landau 2006a,b).

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SUPPORTING INFORMATION

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

**TABLE S1.** Published chronosequence data sets for neotropical rain forests.

**TABLE S2.** Description of sites.

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