LETTER

Resilience of tropical rain forests: tree community reassembly in secondary forests

Natalia Norden,[1] Robin L. Chazdon,[1]* Anne Chao,[2] Yi-Huei Jiang[2] and Braulio Vílchez-Alvarado[3]

[1]*Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269-3043, USA*

[2]*Institute of Statistics, National Tsing Hua University, Hsin-Chu 30043, Taiwan*

[3]*Escuela de Ingeniería Forestal, Instituto Tecnológico de Costa Rica, Cartago, Costa Rica*

Correspondence: E-mail: robin.chazdon@uconn.edu

Abstract

Understanding the recovery dynamics of ecosystems presents a major challenge in the human-impacted tropics. We tested whether secondary forests follow equilibrium or non-equilibrium dynamics by evaluating community reassembly over time, across different successional stages, and among multiple life stages. Based on long-term and static data from six 1-ha plots in NE Costa Rica, we show that secondary forests are undergoing reassembly of canopy tree and palm species composition through the successful recruitment of seedlings, saplings, and young trees of mature forest species. Such patterns were observed over time within sites and across successional stages. Floristic reassembly in secondary forests showed a clear convergence with mature forest community composition, supporting an equilibrium model. This resilience stems from three key factors co-occurring locally: high abundance of generalist species in the regional flora, high levels of seed dispersal, and local presence of old-growth forest remnants.

INTRODUCTION

Attempts to explain patterns of community assembly in species-rich plant communities have focused on two contrasting paradigms (Tilman 1982; Pimm 1991; Hubbell 2001). Under niche-based equilibrium theory, species dynamics are governed by deterministic processes dictated by species-specific attributes in relation to their surrounding environment (Tilman 1982). Neutral theory, in contrast, predicts that community composition is determined solely by stochastic events, historical contingencies, and random dispersal events (Hubbell 2001). Elucidating the relative importance of these processes in determining community assembly is particularly urgent in human-impacted landscapes, where recovery from disturbance has critical implications for conserving unique biodiversity and for rehabilitating ecosystem services (Chazdon 2008; Harvey *et al.* 2008). The extent to which human-impacted forests are able to recover following degradation has been a focal point for heated debate (Brook *et al.* 2006; Wright & Muller-Landau 2006; Gardner *et al.* 2007; Laurance 2007). Some researchers claim that succession is a predictable process

governed by niche-assembly rules, conferring high resilience to tropical forests after disturbance both in terms of structure and species composition (Finegan 1996; Terborgh *et al.* 1996; Letcher and Chazdon *in press*). If so, secondary forest could serve as biodiversity reservoirs for mature forest species (Aide & Grau 2004; Wright & Muller-Landau 2006). Others argue that human-impacted forests are doomed because their original functioning has been disrupted and species composition will never return to its original state (Turner *et al.* 1997; Brook *et al.* 2006).

Although it is increasingly recognized that both niche and neutral processes dictate community assembly rules (Chave 2004; Adler *et al.* 2007; Norden *et al.* 2009), placing this controversy within a conceptual framework of equilibrium vs. nonequilibrium theories sets the stage to test the relative importance of these forces in driving successional dynamics. Understanding whether forest succession proceeds towards a stable and predictable endpoint or whether it exhibits idiosyncratic successional trajectories remains a challenging task for biologists and conservationists (Ewel 1980; Chazdon 2008). Attempts to test theoretical assumptions predicting patterns of community reassembly in these

ecosystems have been hampered by several limitations. Floristic reassembly in tropical secondary forests is expected to be a very slow process, and, to our knowledge, no continuous data on vegetation change are available for any secondary forest site over longer than 20 years (Chazdon *et al.* 2007). Consequently, prior assessments of floristic reassembly in secondary forests rely solely on chronosequence-based studies, that often come from relatively small plots (≤ 0.1 ha), focus on individuals in large size classes, or lack simultaneous comparisons with data from old-growth forests (Chazdon 2003, 2008).

By examining early life stages in second-growth forests, we adopt a novel approach to investigate the relative importance of niche and neutral processes in determining community reassembly in secondary strands in the absence of long-term data. Early life stages provide a unique opportunity to address this issue because young individuals better reflect the footprint of dispersal events, stochastic demography (Hubbell 2001) and niche differences (Grubb 1977; Poorter 2007). Under a deterministic model of successional dynamics, one would expect high floristic similarity between early life stages in secondary forests and trees in mature forests, since species composition in secondary forests is expected to gradually converge with that of mature forests as these young individuals become trees (Nathan & Muller-Landau 2000). Several studies have found that the species composition of secondary forests tended to recover faster in seedling and sapling layers than in tree assemblages (Guariguata *et al.* 1997; Peña-Claros 2003; Capers *et al.* 2005; Lozada *et al.* 2007; Ochoa-Gaona *et al.* 2007), supporting this equilibrium view. In contrast, a 12-year study of recovery following severe hurricane disturbance in Nicaraguan forests demonstrated that successional trajectories exhibited manifold patterns following a catastrophic disturbance, rather supporting a non-equilibrium model of successional dynamics (Vandermeer *et al.* 2004).

Here, we reconcile these opposing views by evaluating *simultaneously* community reassembly in second-growth forest over time, across different successional stages and among multiple life stages. We examine the regeneration potential of these ecosystems—their capacity for resilience through the successful establishment of mature forest tree species in the forest understory—to achieve an integrated understanding of the stand-level recovery processes. If community reassembly is governed by niche-assembly rules, we expect successional forests to attain a single floristic equilibrium. Thus, secondary forests should show floristic convergence with mature forests (Terborgh *et al.* 1996). This convergence should increase over succession and should be reflected in all life stages, but most strongly in the earliest stages. In contrast, if community reassembly is primarily driven by dispersal limitation and demographic stochasticity,

successional patterns should show idiosyncratic trajectories, reflecting variation in the sequence and timing of species arrival (Ewel 1980; Hubbell 2001). To test these alternative predictions, we assembled a unique and robust data set on canopy tree and palm species abundance of seedlings, saplings and adult trees from six 1-ha plots in lowland forests in Costa Rica spanning three stages of succession. Specifically, we compared community structure and evaluated broad-scale compositional variation across size classes and among stands to test whether small size classes in secondary forests reflect floristic convergence with that of mature tree communities. Then, we compared species abundance between small size classes in secondary forests and trees in mature forests, to test whether compositional similarity between small stems in secondary forests and trees in mature forests increases over succession. We tested this prediction both among stands of different age since abandonment and within stands over 8 years. Finally, we compared species composition of newly recruited trees among stands, to ask whether community reassembly is occurring within larger size classes.

MATERIAL AND METHODS

Study site

The study was conducted in a lowland tropical forest at La Selva Biological Station and surrounding areas of northeastern Costa Rica. All sites were within an agricultural matrix composed of secondary and mature forests patches, pastures, and cash crops (Table 1). Among the six 1-ha plots, two are in young secondary forests (EB and JE, both 12 years in 2006), two are in 'intermediate' secondary forests (LSUR, 21 year old; and LEPS, 29 years old in 2006) and two are in old-growth forests (LEPP and SV), with no records of forest clearing over the past 200 years (McDade & Hartshorn 1994). The two intermediate sites, and one old-growth site (LEPP) are within La Selva Biological Station, approximately 1–3 km from each other. The other three sites are located in privately owned farms in Chilamate, about 6 km west of La Selva. All secondary sites were formerly pastures for several years. Tree censuses were initiated in 1997 in the two intermediate age plots, and seedlings and saplings have been monitored since 1998. Censuses in the other sites were initiated in 2005 or 2006. Each plot was 50 × 200 m, divided into 50 subplots of 10 × 10 m. Within each plot, all stems ≥ 5 cm diameter at breast height (DBH) were tagged, mapped, measured and identified to species since the beginning of the monitoring. Saplings 1–4.9 cm DBH were sampled in five strips 5 × 200 m long, running every 10 m (0.5 ha). Tree seedlings < 1 cm DBH and of height > 20 cm were sampled in five strips 2 × 200 m long, running every 10 m (0.2 ha). We

Table 1 Stand characteristics of six 1-ha monitoring plots

	Stand age in 2006 (year)	Location	Previous use	Surrounding landscape
El Bejuco (EB)	12	Chilamate	Pasture	Pasture, mature and secondary forest
Juan Enriquez (JE)	12	Chilamate	Pasture	Pasture, mature and secondary forest
Lindero Sur (LSUR)	21	La Selva	Pasture	Mature and secondary forest
Lindero El Peje secondary (LEPS)	29	La Selva	Pasture	Mature and secondary forest
Lindero El Peje primary (LEPP)	mature	Chilamate	—	Mature and secondary forest
Selva Verde (SV)	mature	Chilamate	—	Pasture, mature and secondary forest

excluded data for woody species that were not canopy trees or palms (species that exceed 15 m height in mature adult trees). For simplicity, we henceforth refer to individuals > 5 cm DBH as 'trees', including canopy palms. In most of the analyses presented here, we used data from 2006 since this was the only year for which we had data for all sites and all size classes.

Species richness and species abundance distribution

To compare species richness among sites and across size classes, we performed sample-based rarefaction adjusting for unequal number of individuals in sites by using EstimateS software (v. 8.0; Colwell 2004). EstimateS computed the mean number of species in a randomized sample based on 100 randomizations. For each 1-ha plot, tree species richness was randomly sampled in 100 10×10 m quadrats, sapling species richness in 200 5×5 m quadrats (0.5 ha), and seedling species richness in 1000 2×1 m quadrats (0.2 ha). To compare sites in terms of species richness instead of species density, EstimateS rescales the expected species accumulation curves by individuals, computing the mean number of individuals for each sampling level among resampling runs. We illustrated variation in patterns of dominance by comparing species abundance distribution among sites and across life-stages. We plotted the log-transformed values of species abundance vs. species rank abundance for each plot and each size class.

Comparing compositional similarity among sites across size classes

We evaluated similarity in canopy tree species composition among sites and across size-classes between all pairs of possible combinations, using the Chao-Jaccard abundance-based estimator (Chao et al. 2005). This estimator is an abundance based similarity index that assesses the probability that individuals belong to shared vs. unshared species, by accounting for the effect of unseen, shared species. In tropical forests, where rare species are frequent

and the sampling is incomplete, this index is less biased by sample size, and is therefore more appropriate than other similarity indices commonly used (Chao et al. 2005). Similarity estimates were computed using EstimateS, and associated standard errors were calculated based on bootstrapping 200 replications. To illustrate pairwise similarities among plots and size classes, we performed a non-metric multidimensional scaling (NMDS) using the function 'metaMDS' of the package 'VEGAN' (v. 1.13–8) (Oksanen et al. 2008) in the R statistical software (v. 2.7.2) (R Core Team Development 2008). This function finds a stable solution using several random starts, and it standardizes the scaling in the result by a principal components rotation. This maximizes the variance of the points along the first axis, so that the configurations are easier to interpret. We chose the number of dimensions equal to 4 to minimize the stress (maximize the rank correlation between the calculated similarity distances and the plotted distances). We also performed this analysis using other similarity indices, but, because the results were similar, we only report results obtained with the Chao-Jaccard estimator. To assess variation in floristic composition within vs. between forest types (secondary vs. mature), we performed non-parametric MANOVA (McArdle & Anderson 2001), an analysis of variance using distance matrices performed by the function 'adonis' of the package 'VEGAN', in the R statistical software. This function partitions sums of squares using metric or semi-metric distance matrices, such as those generated with the Chao-Jaccard estimator. The significance of the test is done using F-tests based on sequential sums of squares from permutations of the raw data.

Comparing floristic composition of small size stems in young and intermediate secondary stands with trees in mature stands

To evaluate similarity between seedlings/saplings in young and intermediate secondary forests with trees in mature forests, we performed a species-by-species analysis based on the Horn similarity index (Horn 1966). This index is based

on Shannon's entropy and has some optimal properties for performing pairwise *species by species* comparisons between communities (Jost 2006). One optimal property of Shannon's diversity measure is that the index for any pooled (weighted) samples is always greater than or equal to the weighted average of the indices of the samples. More detailed theoretical background, as well as the formula used here for the calculation of the Horn similarity index is found in Jost (2006). We compared seedling and sapling species abundance in each secondary stand with tree abundance in each mature stand. Because we were interested in comparing species abundance between pairs of assemblages, the Horn index was more appropriate than the Chao-Jaccard estimator, which pools all shared species together, regardless of their abundance. We applied the Jackknife method to the Horn index, so that under-sampling bias can be largely removed (Schechtman & Wand 2004). These calculations were performed in C++.

Assessing floristic reassembly of small size stems over time

Using sites of different age to reconstruct changes in compositional similarity during succession requires the assumption that similar changes occur within sites over time (Chazdon *et al.* 2007; Johnson & Miyanishi 2008). To test this assumption, we used the modified Horn index to compare changes in similarity over time between secondary forest seedling and sapling assemblages and mature forest tree assemblages. We used seedling and sapling census data from 1998 and 2006 for the two secondary forest monitoring plots that are now classified as 'intermediate' (LSUR and LEPS), and 2006 tree data for the mature forest plots. To have better insights about the actual rates of change in floristic composition occurring in the tree community, we extended our analysis to large size classes. We compared changes in species composition of newly recruited trees (> 5 cm DBH) between 2005 and 2007 with species composition in mature tree assemblages in 2006 using the modified Horn index.

RESULTS

Community structure and compositional patterns

Mature forests exhibited notably higher tree species richness and lower tree species dominance than secondary forests (Fig. 1a,b). In contrast, the structure of seedling and sapling assemblages in secondary forests was indistinguishable from that of seedling and sapling assemblages in mature forests, respectively (Fig. 1c–f). These changes in community properties across size classes were also reflected in differences in species composition. The first ordination axis

in the NMDS reflected compositional differences in tree assemblages across successional stages, with the youngest secondary sites to the left of the ordination space, the intermediate plots in the centre, and the mature sites to the right (Fig. 2). Patterns of dissimilarity among tree assemblages were independent of spatial distance among plots (Mantel partial test: $R = 0.76$, $P < 0.01$). In striking contrast to trees, small size class assemblages from secondary forests clustered together in the centre of the ordination space (Fig. 2). Differences in floristic composition between secondary and mature forests were significant for trees (non-parametric MANOVA: $F = 7.98$; df = 1; $P < 0.001$), but not for saplings (non-parametric MANOVA: $F = 2.63$; df = 1; $P = 0.35$) or for seedlings (non-parametric MANOVA: $F = 0.01$; df = 1; $P = 0.76$). In addition, the amount of variance in species abundance explained by forest type (secondary vs. mature) decreased with size class ($R^2 = 0.66$, $R^2 = 0.40$ and $R^2 = 0.01$ for trees, saplings and seedlings, respectively).

To understand which species contribute most to the compositional similarity patterns found across size classes and among stands, we correlated mean species abundance of both seedlings and saplings in secondary forests with mean species abundance of trees in (i) secondary forests and in (ii) mature forests. The composition of canopy tree and palm species in seedling and sapling assemblages of the secondary sites consisted of a mixture of species from both secondary and mature forests, displaying a wide variety of life-history characteristics (Fig. 3). Although the variance in mean seedling and sapling abundance in secondary stands was better explained by mean tree abundance in secondary stands ($R^2 = 0.35$ and $R^2 = 0.52$ for seedlings and saplings, respectively; Fig. 3a), these variables also showed a strong positive correlation with mean tree abundance in mature stands ($R^2 = 0.26$ and $R^2 = 0.31$ for seedlings and saplings, respectively, Fig. 3b). The seedling assemblage in the secondary stands comprised many shade-tolerant tree species that showed high abundance in old-growth stands, but which appeared to be rare as trees in the second-growth stands (Fig. 2; e.g. *Brosimum lactescens*, *Hirtella media*, *Minquartia guianensis*, *Welfia regia*). Among the 86 species occurring as seedlings in the secondary forest plots, 15 (17%) had no trees in any of these plots, indicating that a significant fraction of the seedling community consisted of non-locally dispersed species. Out of these 15 species, 14 occur in mature plots as trees. Yet, an average of 86% of the individuals composing the seedling layer in secondary forest plots belonged to species occurring in these plots as trees. Regenerating secondary stands were dominated by several generalist species occurring in both secondary and mature plots in all size classes (Fig. 2; e.g., *Euterpe precatoria*, *Iriartea deltoidea*, *Pentaclethra macroloba*, *Socratea exorrhiza*).
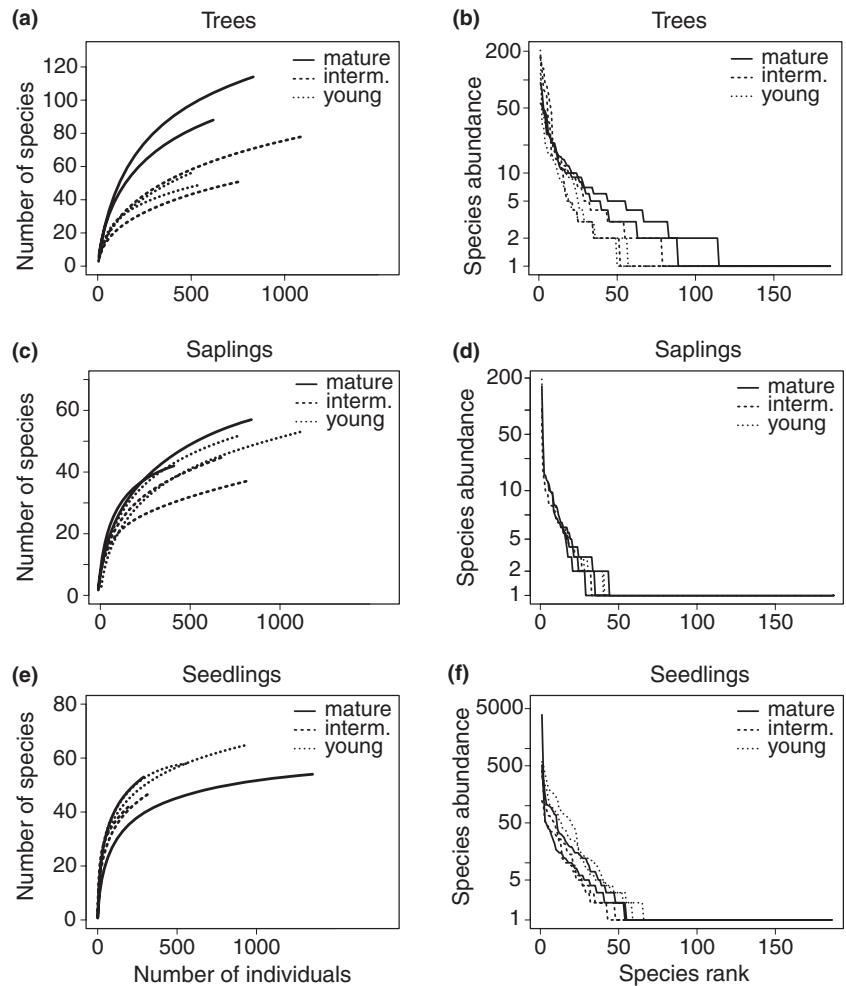
Figure 1 Species accumulation and species abundance distribution curves for trees (a,b), saplings (c,d) and seedlings (e,f) in each of the six study plots in young (EB, JE), intermediate (LEPS, LSUR) and mature (LEPP, SV) plots.
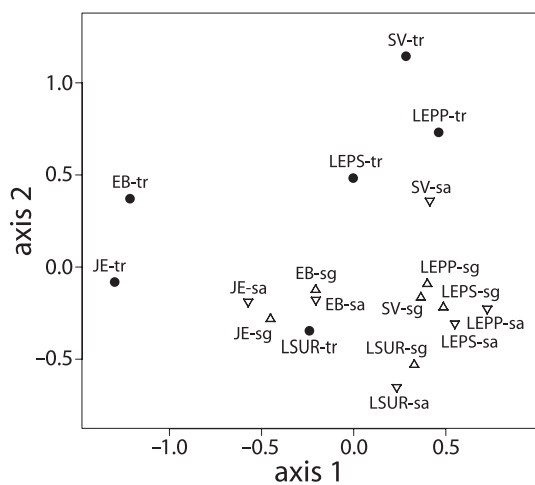

Figure 2 Non-metric dimensional scaling plot of adults (tr, filled circles), saplings (sa, open down triangles) and seedlings (sg, open up triangles) in young (EB, JE), intermediate (LSUR, LEPS), and mature (LEPP, SV) plots.

Community reassembly over succession

Pairwise comparisons between seedling/sapling species abundance in each secondary stand and tree abundance in each mature stand showed that both seedlings and saplings from intermediate secondary stands were more similar to trees from mature stands than seedlings and saplings from young secondary stands (Fig. 4a,b). Indeed, seedling assemblages in mature stands did not show increased similarity with their own tree assemblage compared to seedling assemblages in intermediate secondary stands (see Supporting Information Table S1). Similarity between seedling assemblages in secondary stands and tree assemblages in mature stands also increased over 8 years (Fig. 4c). Saplings showed the same pattern only in one of the two intermediate sites (LSUR). In the other site (LEPS), the sapling assemblage showed a decline over time in similarity with both mature tree assemblages. Finally, trees recruited between 2005 and 2007 in intermediate secondary forests were more similar to tree communities in
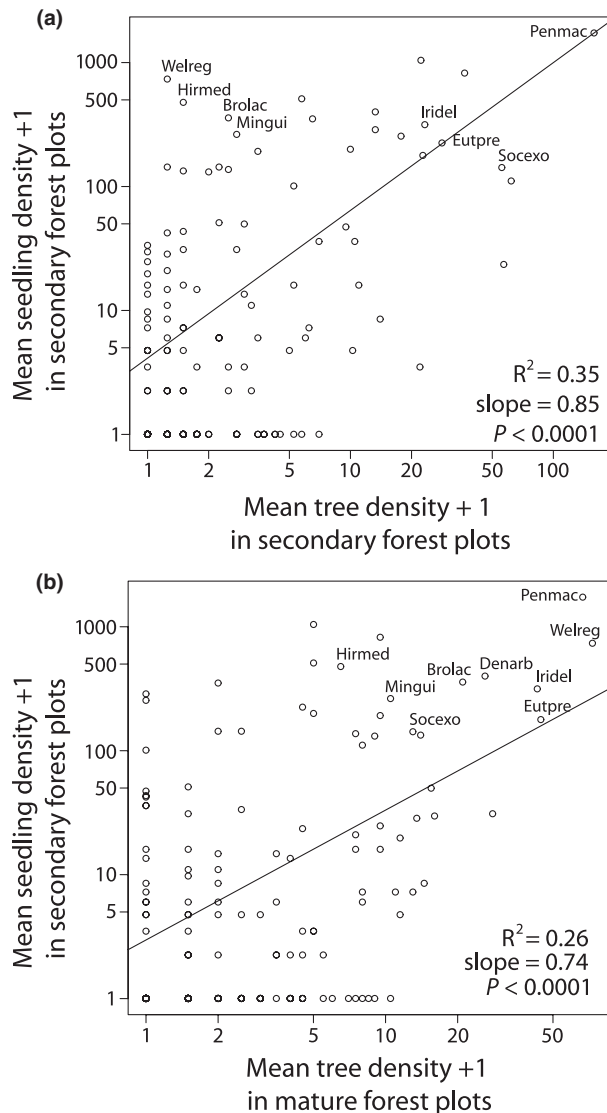
Figure 3 Relationship between mean seedling abundance in secondary forests plots and mean tree abundance in (a) secondary and (b) mature plots. Note that the values are log-transformed, so that a value of 1 is equivalent to a null abundance. Species abbreviations correspond to the first three letters of the genus and species given in the supplementary Table S3.

mature forests than trees recruited in young secondary forests (Fig. 4e).

DISCUSSION

Resilience in floristic reassembly

Our study provides strong evidence supporting an equilibrium model of successional dynamics. Community composition in secondary forests showed a clear directional trend towards convergence with mature forests, observed across

size classes, successional stages, and over time within sites. Such pattern stems from the fact that canopy tree and palm species from mature forests were able to recruit successfully as seedlings, saplings and young trees in the studied secondary stands. Young life stages therefore represent a transition in species composition between second- and old-growth canopy tree communities.

Floristic reassembly in tree and palm species composition is occurring gradually over succession. Seedling and sapling assemblages, as well as the species composition of newly recruited trees, were more similar to mature forest tree assemblages in intermediate than in young secondary stands. Secondary and mature stands in this region are thus expected to progressively converge in their tree species composition, as small size class individuals grow up. Although it will require decades for seedling and sapling recruits to become trees (Connell & Green 2000)—even with high rates of survival—the fact that recruited trees showed the same pattern of reassembly provides an optimistic assessment for canopy tree community reassembly in the regrowing forests of this region. For instance, intermediate secondary sites recruited many individuals of canopy palms (e.g. *Euterpe precatoria*, *Iriartea deltoidea*, *Socratea exhorriza*) and trees (e.g. *Brosimum lactescens*, *Pterocarpus rohrii*) typical of mature forests in the region; whereas the young secondary sites recruited several individuals of pioneer species (e.g. *Cecropia obtusifolia*, *Rollinia pittieri*, *Simarouba amara*), which were no longer recruited in the intermediate secondary sites.

Floristic reassembly in secondary stands was also due to the presence of several generalist species occurring in both secondary and mature plots in all size classes. For example, *Pentaclethra macroloba* ranked among the five most abundant tree and seedling species in all plots. Canopy palms such as *Euterpe precatoria*, *Iriartea deltoidea* and *Socratea exhorriza* were also abundant in all size classes in both secondary and mature forests. The high abundance of these species as seedlings in all plots probably arises from the fact that they show continuous fruit production year-round, providing a constant source of propagules (Vilchez *et al.* 2007). Indeed, these species form a group of oligarchic species (*sensu* Pitman *et al.* 2001) dominating across hundreds of km^2 in Central and South America. Their wide geographic range distribution suggests that these species combine long-distance dispersal abilities with an ample tolerance to environmental heterogeneity (Pitman *et al.* 2001). These characteristics give a panmictic character to community reassembly, that goes against neutral expectations of dispersal limitation.

Overall, the successful establishment of mature forest species in secondary forests understory and the presence of abundant generalist species in the area provide high levels of resilience to the system, as predicted by deterministic models of succession. This situation is conditional to the proximity of mature forests and the presence of a relatively
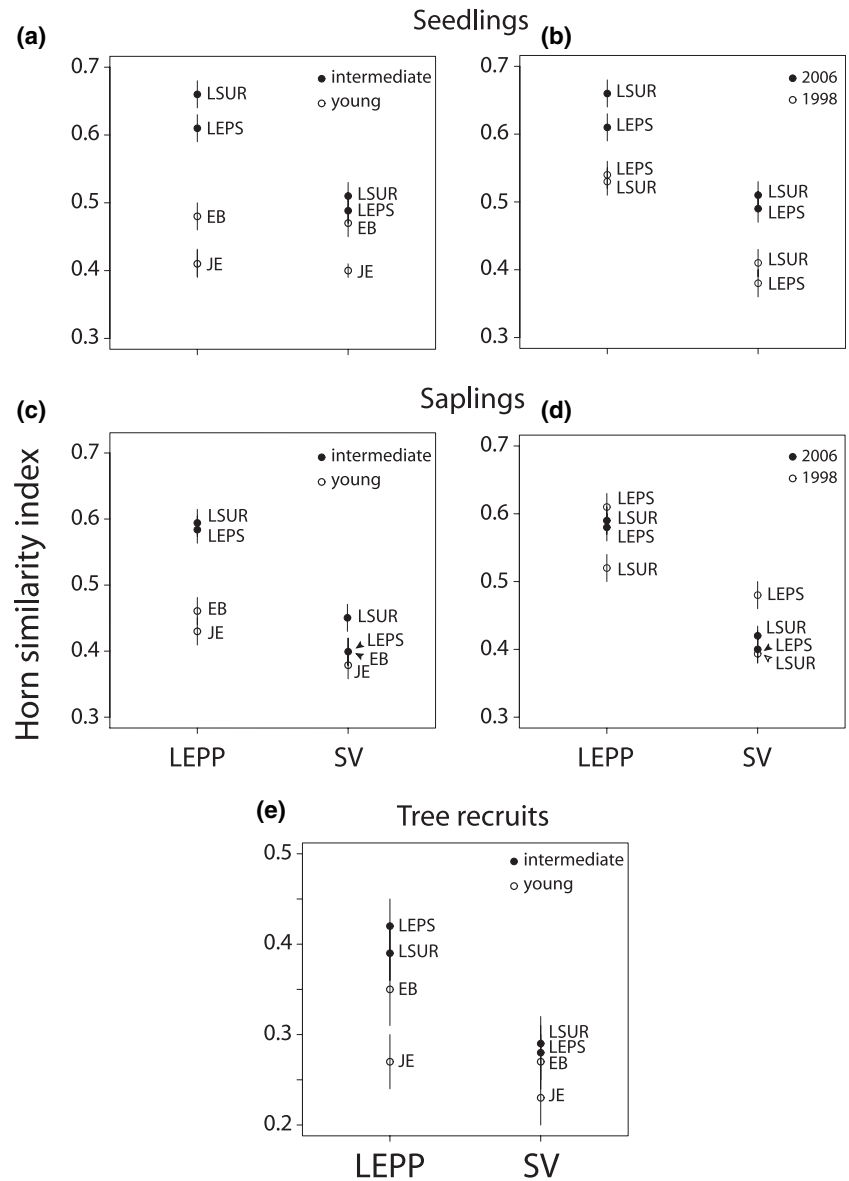
Figure 4 Jackknifed Horn species-by-species similarity index comparing (a,b) seedlings, (c,d) saplings and (e) recruited trees from young (EB, JE) and intermediate (LSUR, LEPS) plots with trees from matures plots (LEPP, SV). Open and filled circles correspond to young and intermediate secondary forest, respectively.

intact disperser assemblage in the area, however (Murray *et al.* 2008). Continuous dispersal and successful seedling establishment are required to ensure the representation of these species as trees in future decades. Thus, the rapid reassembly of tropical communities in human-impacted lands is promoted by the conjunction of three key local factors: presence of old-growth forest remnants, high levels of seed dispersal, and high abundance of generalist species in the regional tree flora.

Historical contingencies and variation in successional trajectories

Support for an equilibrium view of successional dynamics does not imply that succession will always follow a unique

trajectory. Land use, environmental factors and surrounding forests fragments have been shown to strongly affect community reassembly in secondary forests (Chazdon 2008). In our study, some of the variability in successional patterns found between sites of similar age is the result of these complex interactions. For example, although the two youngest sites, El Bejuco (EB) and Juan Enriquez (JE), are very close to each other, EB exhibited considerably higher species-by-species similarity with trees in mature sites than JE. EB was indeed the only study plot where many isolated mature forest trees remained in the pasture, suggesting that remnant trees may have long-lasting positive effects on forest recovery (Schlawin & Zahawi 2008). Other studies in the same region found that initial colonization of woody species was significantly richer in areas that were allowed to

regenerate shortly after logging or that were used for pasture for less than ten years, than in areas intensively used for pasture (Chazdon *et al.* 2007; Letcher and Chazdon *in press*).

Given these considerations, several authors have questioned the central assumption of the chronosequence approach—that the sites represent points along a continuum, as if all sites have followed the same history (Chazdon *et al.* 2007; Johnson & Miyanishi 2008). We controlled for this limitation by using available long-term data on seedling and sapling dynamics in the two intermediate secondary stands studied. Seedling assemblages in intermediate secondary stands did show floristic reassembly over an 8-year study period, confirming that the observed differences between young and intermediate secondary sites reflect dynamic processes occurring within sites. Saplings, however, showed the same pattern only in one of the two sites (LSUR). The sapling assemblage in LEPS showed a decline in similarity over time with both tree assemblages in mature stands. This decline was largely due to a pulse of recruited saplings of two canopy palm species, *Socratea exhorriza* and *Iriartea deltoidea*, between 1998 and 2006 (see Supporting Information Fig. S1 and Table S2). The likely cause for such pattern is the occurrence of a pulse in seedling recruitment resulting from either mast fruiting events or temporal environmental variability (Chesson & Warner 1981). The large populations of *Socratea* and *Iriartea* might be regulated by density-dependent patterns, allowing other species to fill out the free space, and presumably reverting to a more balanced species composition. Otherwise, they might remain large, leading the community towards a distinct successional trajectory (Vandermeer *et al.* 2004). Because density-dependence mechanisms are more likely to operate during the earliest life stages (Harms *et al.* 2000), we forecast that LEPS will show a distinct tree assemblage in future decades, marked by the overpopulation of these two species.

Geographic or edaphic variation in species composition is another factor that may lead to differences among successional trajectories. The two mature sites, SV and LEPP showed distinct floristic composition; in particular SV had a species composition distinguishable from the other sites. Such variability was probably responsible for the observed differences in pairwise comparisons between small size class assemblages in secondary stands and tree assemblages in mature stands (Fig. 4). Due to the intensive nature of our sampling protocol, we could not extensively replicate our study plots. Yet, they exhibited relatively similar patterns within each age category, suggesting that the large area sampled in each plot compensated for the small number of plots. Further, our results are strengthened by consistent findings in extensive chronosequence studies across a large number of smaller plots within the same region (Guariguata *et al.* 1997; Chazdon *et al.* 1998,

2007; Letcher and Chazdon *in press*). These studies confirm rapid recovery of woody seedling and sapling composition in secondary forests 15–45 year post-abandonment. The establishment of a coordinated long-term network of monitoring sites in secondary forests, combined with theoretical approaches, will bring critical insights for a more complete understanding of spatial and temporal turnover in tree species composition in regenerating secondary forests.

Conservation considerations

The regeneration potential of regrowing forests is poorly known for most tropical regions. Our comprehensive study shows that mature forest species are successfully regenerating in secondary stands from NE Costa Rica. Furthermore, we encountered eight species with either vulnerable or endangered status occurring as trees and/or regenerating individuals in the secondary forest sites (see Supporting Information Table S3). These findings strongly indicate that secondary forests can serve as habitat refugia and biodiversity reservoirs for many mature tropical forest tree species. Although our results might illustrate a best-case scenario of floristic reassembly under ideal conditions, other studies point to similar findings in other regions, such as the Bolivian Amazon (Peña-Claros 2003) and Eastern Brazil (Alves & Metzger 2006; D. Piotto, personal communication). Unfortunately, such hopeful prospects are not the case for many tropical regions, where mature forest patches are lacking or are highly degraded, and seed dispersing fauna have become locally extinct (Turner *et al.* 1997). The regeneration potential of canopy tree species declines as intensity of previous land-use and distance from mature forests increase (Aide & Cavelier 1994; Hooper *et al.* 2005). As old-growth forests continue to be logged, we urgently need an integrated understanding of the stand-level recovery processes occurring through regeneration. Our study underscores the role of regenerating canopy trees for inferring successional pathways in different stages of regeneration. Because most of our knowledge on succession has relied upon chronosequence-based studies focusing on large individuals, our novel approach brings new insights for predicting future species composition in regenerating forests, and shows strong support for targeting secondary forests for conservation. In the context of high rates of forest clearance in many tropical regions, we expect our findings to be a template for future conservation actions to ensure sustained regeneration potential of tropical forest trees. Protection of local forest remnants and native seed dispersing fauna, are critical tools to promote resilience and tree community reassembly of secondary forests in human-managed tropical landscapes (Harvey *et al.* 2008).

REFERENCES

Adler, P.B., HilleRisLambers, J. & Levine, J.M. (2007). A niche for neutrality. *Ecol. Lett.*, 10, 95–104.

Aide, M.T. & Cavelier, J. (1994). Barriers to tropical lowland forest regeneration in the Sierra Nevada de Santa Marta, Colombia. *Restor. Ecol.*, 2, 219–229.

Aide, T.M. & Grau, R. (2004). Globalization, migration and Latin American ecosystems. *Science*, 305, 1915–1916.

Alves, L.F. & Metzger, J.P. (2006). A regeneração florestal em áreas de floresta secundária na Reserva Florestal do Morro Grande, Cotia, SP. *Biota Neotropica*, 6 (Available at: http://www.biota-neotropica.org.br/v6n2/pt/abstract?article+bn00406022006).

Brook, B.W., Bradshaw, C.J.A., Pin Koh, L. & Sodhi, N.S. (2006). Momentum drives the crash: mass extinction in the tropics. *Biotropica*, 38, 302–305.

Capers, R.S., Chazdon, R.L., Redondo-Brenes, A. & Vílchez-Alvarado, B. (2005). Successional dynamics of woody seedling communities in wet tropical secondary forests. *J. Ecol.*, 93, 1071–1084.

Chao, A., Chazdon, R.L., Colwell, R.K. & Shen, T.J. (2005). A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecol. Lett.*, 8, 148–159.

Chave, J. (2004). Neutral theory and community ecology. *Ecol. Lett.*, 7, 241–253.

Chazdon, R.L. (2003). Tropical forest recovery: legacies of human impact and natural disturbances. *Perspect. Plant Ecol. Evol. Syst.*, 6, 51–71.

Chazdon, R.L. (2008). Chance and determinism in tropical forest succession. In: *Tropical Forest Community Ecology* (eds Carson, W.P. & Schnitzer, S.A.). Blackwell, Malden, pp. 384–408.

Chazdon, R.L., Colwell, R.K., Denslow, J.S. & Guariguata, M.R. (1998). Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of northeastern Costa Rica. In: *Forest Biodiversity Research, Monitoring and Modeling: Conceptual Background and Old World Case Studies* (eds Dallmeier, F. & Comiskey, J.). Parthenon Publishing, Paris, pp. 285–309.

Chazdon, R.L., Letcher, S.G., van Breugel, M., Martínez-Ramos, M., Bongers, F. & Finegan, B. (2007). Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philos. Trans. R. Soc. Lond.*, 362, 273–289.

Chesson, P.L. & Warner, R.R. (1981). Environmental variability promotes coexistence in lottery competitive-systems. *Am. Nat.*, 117, 923–943.

Colwell, R.K. (2004) EstimateS: statistical estimation of species richness and shared species from samples. v. 8.0 (Available at: http://purl.oclc.org/estimates).

Connell, J.H. & Green, P.T. (2000). Seedling dynamics over thirty-two years in a tropical rain forest tree. *Ecology*, 81, 568–584.

Ewel, J. (1980). Tropical succession: manifold routes to maturity. *Biotropica*, 12(Suppl.), 2–7.

Finegan, B. (1996). Pattern and process in neotropical secondary rain forest: the first 100 years of succession. *Trends Ecol. Evol.*, 11, 119–124.

Gardner, T.A., Barlow, J., Parry, L.W. & Peres, C.A. (2007). Predicting the uncertain future of tropical forest species in a data vacuum. *Biotropica*, 39, 25–30.

Grubb, P.J. (1977). Maintenance of species-richness in plant communities: importance of regeneration niche. *Biol. Rev. Camb. Philos. Soc.*, 52, 107–145.

Guariguata, M.R., Chazdon, R.L., Denslow, J.S., Dupuy, J.M. & Anderson, L. (1997). Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica. *Plant Ecol.*, 132, 107–120.

Harms, K.E., Wright, S.J., Calderón, O., Hernández, A. & Herre, E.A. (2000). Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*, 404, 493–495.

Harvey, C.A., Komar, O., Chazdon, R.L., Ferguson, B.G., Finegan, B., Griffith, D.M. *et al.* (2008). Integrating agricultural landscapes with biodiversity conservation in the Mesoamerican hotspot. *Cons. Biol.*, 22, 8–15.

Hooper, E., Legendre, P. & Condit, R. (2005). Barriers to forest regeneration of deforested and abandoned land in Panama. *J. Appl. Ecol.*, 42, 1165–1174.

Horn, H. (1966). Measurement of "overlap" in comparative ecological studies. *Am. Nat.*, 100, 419–424.

Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton.

Johnson, E.A. & Miyanishi, K. (2008). Testing the assumptions of chronosequences in succession. *Ecol. Lett.*, 11, 419–431.

Jost, L. (2006). Entropy and diversity. *Oikos*, 113, 363–375.

Laurance, W.F. (2007). Have we overstated the tropical biodiversity crisis? *Trends Ecol. Evol.*, 22, 65–70.

Letcher, S. & Chazdon, R.L. Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. *Biotropica*, in press.

Lozada, T., de Koning, G.H.J., Marché, R., Klein, A.M. & Tscharntke, T. (2007). Tree recovery and seed dispersal by birds: Comparing forest, agroforestry, and abandoned agroforestry in coastal Ecuador. *Perspect. Plant. Ecol. Evol.*, 8, 131–140.

McArdle, B.H. & Anderson, M.J. (2001). Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology*, 8, 290–297.

McDade, L. & Hartshorn, G.S. (1994). La Selva Biological Station. In: *La Selva: Ecology and Natural History of a Neotropical Rain Forest* (eds McDade, L., Bawa, K.S., Hespenheide, H. & Hartshorn, G.S.). University of Chicago Press, Chicago, pp. 6–14.

Murray, K.G., Willet-Murray, K., Roberts, J., Horjus, K., Haber, W.A., Zuckowski, W. *et al.* (2008). The roles of disperser behavior and physical habitat structure in regeneration of

post-agricultural fields. In: *Post-agricultural Succession in the Neotropics* (ed. Myster, R.W.). Springer, New York, NY, pp. 192–215.

Nathan, R. & Muller-Landau, H.C. (2000). Spatial patterns of seed dispersal, their determinants and consequence for recruitment. *Trends Ecol. Evol.*, 25, 278–285.

Norden, N., Chave, J., Belbenoit, P., Caubère, A., Châtelet, P., Forget, P.M. *et al.* (2009). Interspecific variation in seedling responses to seed limitation and habitat conditions for 14 Neotropical woody species. *J. Ecol.*, 97, 186–197.

Ochoa-Gaona, S., Hernández-Vásquez, F., de Jong, B.H.J. & Gurri-García, F.D. (2007). Pérdida de diversidad florística ante un gradiente de intensificación del sistema agrícola de roza-tumba-quema: Un estudio de caso en la selva Lacandona, Chiapas, México. *Bol. Soc. Bot. Mex.*, 81, 65–80.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Stevens, M.H.H. *et al.* (2008) VEGAN: community ecology package, v. 1.13-8 (Available at: http://vegan.r-forge.r-project.org/).

Peña-Claros, M. (2003). Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon. *Biotropica*, 35, 450–461.

Pimm, S.L. (1991). *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities*. University of Chicago Press, Chicago, Illinois, USA.

Pitman, N.C.A., Terborgh, J.W., Silman, M.R., Núñez, V.P., Neill, D.A., Cerón, C.E. *et al.* (2001). Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology*, 82, 2101–2117.

Poorter, L. (2007). Are species adapted to their regeneration niche, adult niche, or both? *Am. Nat.*, 169, 433–442.

R Core Team Development (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. v. 2.7.2 (Available at: http://www.R-project.org).

Schechtman, E. & Wand, S. (2004). Jackknifing two-sample statistics. *J. Stat. Plan. Infer.*, 119, 329–340.

Schlawin, J.R. & Zahawi, R.A. (2008). Nucleating' succession in recovering neotropical wet forests: the legacy of remnant trees. *J. Veg. Sci.*, 19, 485–492.

Terborgh, J., Foster, R.B. & Núñez , V.P. (1996). Tropical tree communities: a test of the nonequilibrium hypothesis. *Ecology*, 77, 561–567.

Tilman, D. (1982). *Ressource Competition and Community Structure*. Princeton University Press, Princeton.

Turner, I.M., Wong, Y.K., Chew, P.T. & bin Ibrahim, A. (1997). Tree species richness in primary and old secondary tropical forest in Singapore. *Biodivers. Conserv.*, 6, 537–543.

Vandermeer, J., Granzow de la Cerda, I., Perfecto, I., Boucher, D., Ruiz, J. & Kaufmann, A. (2004). Multiple basins of attraction in a tropical forest: evidence for a nonequilibrium community structure. *Ecology*, 85, 575–579.

Vilchez, B., Chazdon, R.L. & Alvarado, W. (2007). Fenología reproductive de las especies del dosel superior en seis sitios de la Región Huetar Norte de Costa Rica. *Kuru: Revista Forestal Costa Rica*, 4, 1–16.

Wright, S.J. & Muller-Landau, H.C. (2006). The future of tropical forests species. *Biotropica*, 38, 287–301.

SUPPORTING INFORMATION

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

Figure S1 Correlation between tree abundance in mature plots (LEPP and SV) in 2006 and sapling abundance in LEPS in 1998 and 2006.

Figure S2 A map of the study area, showing the locations of the six 1-ha plots in relation to roads, rivers, and forest cover in the year 2000.

Table S1 Jackknifed Horn's species-by-species similarity index (± SE) between seedling/sapling assemblages from all sites and tree assemblages in the two mature sites in 2006.

Table S2 Jackknifed Horn's species-by-species similarity index (± SE) between sapling assemblages in the intermediate secondary plots in 1998 and 2006 and trees from mature plots, when excluding *Socratea exhorriza* and *Iriartea deltoidea*.

Table S3 List of the 186 canopy tree and palm species occurring as trees, saplings or seedlings in secondary and mature forest plots in 2006.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.