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Secondary forests of central Panama increase in similarity to old-growth forest over time in shade tolerance but not species composition

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Abstract

Question: Does species and functional composition of secondary tropical forests more closely follow a deterministic or a stochastic model of succession?

Location: The Barro Colorado Nature Monument (BCNM), central Panama. The BCNM comprises Barro Colorado Island (BCI) and five adjacent mainland peninsulas and is a mosaic of tropical old-growth (OG) and secondary forests (SF).

Methods: We studied the species and functional composition of seedling, sapling and adult tree communities in a chronosequence of SF stands ranging in age from 20 to 100 yrs since abandonment, as well as two OG stands for comparison. Functional composition was defined as the representation of species with different degrees of shade tolerance. We also examined patterns of species diversity and dominance to better understand processes driving compositional changes.

Results: Species diversity recovered rapidly, and, by 20 yrs, species richness for all size classes was equivalent if not higher in SF compared to OG. Species diversity tended to be lower and species dominance higher for seedlings than saplings or adults. Seedling, sapling and adult tree species composition did not clearly increase in similarity to OG with forest age. Instead, differences in species composition among stands reflected variation in dominance by particular species. Light-demanding species became less common and shade-tolerant species more common over stand age, with the functional composition of older secondary forests converging on that of OG. The seedling and sapling communities across the chronosequence were composed of a shade-tolerant subset of those species found in the stands as adults.

Conclusion: Our results suggest that recruitment into the seedling community of SF is determined by both predictable (e.g. selection for shade-tolerant species) and unpredictable factors (e.g. species-specific reproduction events and dispersal limitation). Recruitment into the sapling and tree communities reflects stronger, and potentially compounded, selection for shade-tolerant species. Therefore, changes in the species composition of regenerating forests in this area appear to be unpredictable, even though the functional composition follows a more deterministic and predictable trajectory with convergence on OG over time.

Introduction

Over the last century, tropical old-growth forests have been exploited for timber extraction, cleared for agriculture, pasture and roads, and degraded by wildfires and overhunting (Laurance & Peres 2006; Sodhi et al. 2007). The resulting human-modified landscapes, composed of a mosaic of old-growth forest (OG) fragments, degraded forest, regenerating forest and agricultural land, now cover large areas of the tropics. Recent estimates indicate that secondary and degraded tropical forests cover a larger area than undisturbed OG (FAO 2010). Therefore, the long-term conservation of tropical forest biodiversity is dependent on the capacity of human-modified landscapes to maintain viable populations of tropical forest species. Secondary forests (SF) are increasingly important habitats within tropical landscapes (FAO 2010), and the extent to which regenerating SF can conserve tropical forest species and ecosystem functions has been the focus of a highly publicized debate (Brook et al. 2006; Wright & Muller-Landau 2006; Gardner et al. 2007; Dent & Wright 2009). Given the rate and extent of tropical forest conversion around the world, it is imperative that we develop a better understanding of how quickly and how predictably reassembly of tree communities occurs in regenerating SF.

From chronosequence studies, it appears that regenerating forests can attain many of the structural characteristics of OG and equivalent woody plant species richness within 20–30 yrs (Guariguata & Ostertag 2001), but carbon storage may not attain old-growth levels until many decades later (Fearnside & Guimarães 1996; Denslow & Guzman 2000; Mascaro et al. 2012). Whether species composition of canopy trees in SF ever approaches OG is unknown, but the current paradigm is that SF will ultimately come to resemble intact stands within 100–500 yrs, barring further large-scale disturbances (Finegan 1996; Guariguata & Ostertag 2001; Chazdon 2003; Norden et al. 2009). However, this time frame exceeds the ages of almost all SF stands that have been studied to date.

The rate and extent to which SF species composition converges on that of OG will depend on whether compositional changes occur predominantly as the result of deterministic or stochastic processes. The accepted model of SF succession is that changes in species composition over time are determined by changes in environmental conditions, such as temperature and availability of light, nutrients and water. Therefore, community composition at different points during succession is limited to species that have the appropriate traits to reach a site, and then to establish and grow under these specific environmental conditions (Pickett 1976; Peterson & Carson 2008). As light is the limiting resource in the understorey of most wet tropical forests (Montgomery & Chazdon 2001) and light levels decline in the understorey during succession (Denslow & Guzman 2000), species composition at all levels of the forest should shift from a suite of shade-intolerant species to a suite of more shade-tolerant species over time. Under this model, environmental conditions drive changes in functional composition, supporting a deterministic model of succession. However, if species are functionally equivalent, changes in species composition may still be largely stochastic.

The future functional and species composition of SF may be predicted by examining the composition of different life stages within SF stands (Peña-Claros 2003; Lozada et al. 2007; Norden et al. 2009). If deterministic processes drive succession, similarity in species composition between seedlings in SF and adult trees in OG should be higher than similarity between adults in SF and OG. High similarity between SF seedlings and OG adults will lead to compositional convergence of SF on that of OG, as young individuals from the SF seedling bank grow up to become canopy trees. Alternatively, if community reassembly is largely a stochastic process, then similarity between SF seedlings and OG trees may be low, with each forest exhibiting idiosyncratic successional trajectories that reflect variation in local seed sources, seed production and dispersal limitation (Ewel 1980; Hubbell 2001). Previous examination of the relative importance of deterministic and stochastic processes in tropical forest succession has been limited to relatively young secondary forests (e.g. Norden et al. 2009) and has not addressed functional changes in community composition.

Here we examine whether the changes in species and functional composition of seedlings, saplings and adult trees along a tropical forest chronosequence in the Barro Colorado Nature Monument (BCNM), Panama, follow a deterministic or stochastic model of succession. The BCNM chronosequence represents the longest SF chronosequence identified to date, with forests ranging in age from 20 to 100 yrs since abandonment. As such, it provides the ability to assess whether SF converges on OG characteristics under conditions that should maximize the rate of convergence on OG characteristics, including ample seed availability, low-intensity land use prior to abandonment, and absence of invasive plants and on-going disturbance. We also study patterns of diversity and species dominance to assess how changes in these community properties contribute to patterns of species composition.

Methods

Study area

This study took place in central Panama in and around the Barro Colorado Nature Monument (BCNM). The BCNM comprises Barro Colorado Island (BCI; 9°9′ N, 79°51′ W) and five adjacent peninsulas (see Denslow & Guzman 2000; DeWalt et al. 2000). BCI was set aside as a biological reserve in 1923, and in 1979 the five surrounding mainland peninsulas were incorporated into the BCNM. Old-growth forests of the BCNM are possibly the world's most thoroughly studied tropical forests. Detailed descriptions of the soils, geology, climate and vegetation of BCI can be found in Croat (1978), Leigh et al. (1982) and Windsor (1990). The area receives ca. 2600 mm of rainfall annually, predominantly during the 7-mo wet season from May to December (Windsor 1990). Soils of the BCNM are oxisols and alfisols, both high in nitrogen and phosphorus availability (Yavitt 2000). The vegetation is classified as tropical moist forest and canopy height reaches ca. 30 m, with emergent trees approaching 50 m (Holdridge &

Budowski 1956). The canopy of the OG is characterized by emergent trees in the Fabaceae and Malvaceae. Smaller-stature trees such as *Cordia alliodora* (Boraginaceae), *Spondias mombin* (Anacardiaceae), *Annona spraguei* (Annonaceae) and *Miconia argentea* (Melastomataceae) are common in the SF (DeWalt et al. 2003).

The BCNM is a patchwork of OG and SF stands of different ages. Old-growth forest occupies about half of BCI (Leigh et al. 1982) and small areas on the surrounding peninsulas. Secondary forests within the BCNM are located on lands that were used for cattle pasture or fruit production between the 1880s and the establishment of BCNM in 1979. Detailed accounts of land-use history of the BCNM are provided in Leigh et al. (1982).

Stand selection

This study was conducted in a chronosequence consisting of two replicate stands of 20, 40, 70 and 100-yr-old SF and two stands of OG (>500 yrs). The SF stands all experienced agricultural land use prior to abandonment including pasture, swidden farming and plantation farming, but for undetermined lengths of time. Study stands were located on relatively level topography and had not been subject to subsequent human disturbance once fallowed. They are representative of stands of similar ages and histories within the BCNM. Stand ages were estimated using historical records, aerial photographs and interviews with long-time residents (for details see Denslow & Guzman 2000). There is no indication that the OG stands have ever been logged or cultivated (Piperno 1990). Further descriptions of the forest history, soil properties, understorey light levels and geographic locations of the stands can be found in Denslow & Guzman (2000).

Vegetation sampling

In 1994, in nine of the ten stands, vegetation was sampled in two parallel 160 m × 10 m transects separated by at least 10 m and composed of contiguous nested quadrats. The configuration of one 20-yr-old stand (Saino) was sufficient only for the establishment of a single transect, which was interrupted in two places by creeks. A nested sampling design was used to sample different size classes of vegetation. All trees ≥ 5 cm diameter at breast height (DBH) were measured for diameter and identified to species in 16 10 m × 10 m quadrats in each transect (3200 m^2 per stand; Denslow & Guzman 2000). We define trees ≥ 5 cm DBH as 'adults' to distinguish them from seedlings and saplings, but they are not necessarily reproductive at this size. Tree saplings ≥ 1 m in height and <5 cm DBH were sampled in contiguous 5 m × 5 m subplots for the length of each transect (1600 m^2 per stand). Tree seedlings (≥ 0.2 m and <1.0 m in height) were sampled in contiguous 1 m × 1 m subplots along the centre of each transect (320 m^2 per stand). In the single transect at Saino, adults ≥ 5 cm DBH were measured in only one 160 m × 10 m transect (1600 m^2), saplings were sampled in 32 5 m × 5 m subplots (800 m^2) and seedlings were sampled in 160 1 m × 1 m subplots (160 m^2). Because we were interested in compositional changes, all analyses for trees and saplings were performed on genets; no multiple stems were included and so each stem represents an individual. To enable us to make direct comparisons among the three size classes, analyses were restricted to those species that become canopy or mid-storey trees at maturity (Garwood 2009; R. Foster unpublished data).

Data analysis

Species richness and dominance

To compare levels of species richness among stands and size classes, we used Mao-Tau sample-based rarefaction adjusting for unequal numbers of individuals (EstimateS v. 8.0; http://purl.oclc.org/estimates). For each stand except Saino, species richness was randomly sampled in 32 10 m × 10 m quadrats for trees, 64 5 m × 5 m quadrats for saplings and 320 1 m × 1 m quadrats for seedlings. To assess differences in diversity of adult tree communities with forest age, we calculated Fisher's α and the abundance-based coverage estimator (ACE; EstimateS v. 8.0). We compared variation in species dominance among stands and size classes with rank-abundance curves, Simpson's evenness statistic and the percentage of individuals composed by the five most common species for each stand.

Similarity in species composition among stands and across size classes

We used the Morisita–Horn abundance-based similarity index to compare species composition between pairs of assemblages. The Morisita–Horn index is robust to uneven and insufficient sampling, and is ideally suited to determine if reassembly of OG communities occurs in SF in terms of relative abundance because the index is based on the probability that two individuals taken from each of two communities belong to the same shared species (Chao et al. 2005, 2006). To further remove biases associated with under-sampling, we applied the jackknife method recommended by Schechtman & Wang (2004) to the Morisita–Horn index (henceforth, S_{MH}). For further details about similarity indices, refer to Chao et al. (2005, 2006) and Jost (2006). Dissimilarity in species composition ($1 - S_{MH}$) was calculated for all pair-wise comparisons among sites to generate a dissimilarity matrix that was used for further analyses using functions in the 'vegan'

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package of R (R Development Core Team, R Foundation for Statistical Computing, Vienna, AT).

To determine if geographic location explained patterns in species composition of the different aged forests, we performed Mantel tests ('mantel' function in R) of three matrices of pair-wise distances between stands: Euclidean distance in space, Euclidean difference in forest age and dissimilarity in species composition ($1 - S_{MH}$). For these analyses only, we assigned OG stands an age of 500 yrs to be able to include these stands in the distance matrix for forest age.

We visually examined similarities in species composition among stands and size classes with non-metric multidimensional scaling (NMDS). We used similarity matrices generated from both the S_{MH} abundance-based and Sørensen incidence-based similarity indices. The Sørensen index is based solely on species presence/absence; we calculated this index as well as the abundance-based index to investigate whether OG species were present in SF even when patterns of relative species abundance were still quite different from OG. We calculated and plotted two dimensions for the S_{MH}, but used three dimensions for the Sørensen index because the NMDS stress was too high (i.e. >20) when calculated for just two dimensions. NMDS was performed using the 'metaMDS' function in the 'vegan' package of R (McArdle & Anderson 2001).

We directly examined whether species composition of SF converged on OG over time by comparing the similarity in composition (S_{MH}) of each size class in each SF stand to each of the OG stands. For each size class, we calculated similarity for all possible comparisons between SF and OG stands and used linear regressions to identify the relationship between forest age and similarity to OG. We used ANOVA to assess whether similarity indices between OG adult and SF sapling communities were significantly different from similarity indices between OG adult and OG sapling communities; we ran equivalent analyses for comparisons of adult and seedling communities. For data presentation, we calculated mean (±1 SE) similarity indices by forest age.

To determine whether the species composition across size classes within each stand became more similar with increasing stand age, we calculated the Morisita–Horn multiple community similarity index among size classes within each stand using species prediction and diversity estimation (SPADE; http://chao.stat.nthu.edu.tw.).

Functional composition in relation to forest age and size class

To examine changes in the functional composition of SF and OG, we examined the degree of shade tolerance for each size class in each forest stand using quantitative and categorical metrics. The quantitative metric was a community-weighted mean of a species-specific light requirement index developed by Rüger et al. (2009) as an estimate of how light availability affects recruitment into the sapling community of the BCI 50-ha plot in relation to light. The light requirement index could be assigned to 77% of the species in the chronosequence, and ranged from −0.39 (*Licania platypus*, Chrysobalanaceae – very shade tolerant) to 3.28 (*Spondias mombin*, Anacardiaceae – very shade intolerant). Additionally, we assigned each tree species to a light-requirement category (shade tolerant, intermediate or light-demanding) based on classifications published in Comita et al. (2007), Hubbell et al. (1999), Condit et al. (1995, 1996) and Welden et al. (1991). Species-specific light requirement categories were available for 88% of chronosequence species. These classifications are primarily based on the recruitment, mortality and distribution of species within the BCI 50-ha plot (Hubbell et al. 1999). We then calculated the proportions of adults, saplings and seedlings represented by each light requirement category for each forest stand.

Using only data from SF stands, analysis of covariance (ANCOVA) was used to determine whether light requirement index varied significantly with forest age and size class. Linear regressions were used to describe relationships between light requirement index and SF age within each size class. For each size class, ANCOVA was used to determine changes in the proportional representation of different light requirement categories with forest age. Unless otherwise stated, all statistical analyses were conducted with R (v. 2.15).

Results

Patterns of species diversity among stands and across size classes

There were no distinguishable patterns in species diversity in adult, seedling or sapling communities in relation to forest age (Table 1; Appendices S1 and S2). By 20 yrs, rarefied species richness, ACE and Fisher's α diversity were equivalent if not higher in SF compared to OG. Across the ten stands, the size of the species pool for the different size classes differed, with 163, 134 and 108 canopy and mid-storey species present in the adult, sapling and seedling communities, respectively. For a given number of individuals, adults were represented by more species than either saplings or seedlings (Table 1). Species dominance generally was higher for seedlings than for either saplings or adults, as seen by the higher percentage of individuals represented by the five most abundant species (46%, 44% and 64% in the adult, sapling and seedling communities, respectively), lower Simpson's evenness (0.35, 0.45 and 0.26 for adult, sapling and seedling communities, respectively) and steeper rank-abundance curves for seedlings than the other

Table 1. Approximate stand age, site code (used in Fig. 1) and species diversity and dominance statistics for eight secondary forest and two old-growth forest stands in central Panama. ACE and Fisher's α diversity are presented for the adult community only. The number of species in each stand was rarefied to 120 individuals for each size class, and 95% confidence intervals are presented in parentheses. Dominance was measured as the percentage of individuals represented by the five most common species in each stand.

Site	Age (yrs)	Site code	Fisher's α	ACE	Rarefied species number (CI)			Simpson's evenness			Dominance (%)		
					Adults	Saplings	Seedlings	Adults	Saplings	Seedlings	Adults	Saplings	Seedlings
Pedro Gomez	20	20-P	33.8	86.9	49 (40–59)	38 (29–45)	33 (25–41)	0.507	0.440	0.223	31.7	31.5	59.2
Saino	20	20-S	11.4	38.6	26 (18–34)	31 (21–40)	23 (15–31)	0.326	0.842	0.106	59.0	37.0	74.4
Enders	40	40-E	28.6	83.5	47 (37–57)	30 (22–38)	31 (23–40)	0.579	0.484	0.383	28.3	37.6	49.3
Fosters	40	40-F	18.7	56.2	36 (27–45)	35 (26–44)	32 (24–40)	0.443	0.453	0.250	43.9	42.6	52.4
Bohio	70	70-B	16.3	57.6	32 (23–41)	22 (15–29)	20 (12–27)	0.188	0.276	0.297	58.5	61.1	79.4
Poachers	70	70-P	25.2	88.7	44 (34–54)	27 (19–33)	29 (21–37)	0.493	0.258	0.202	33.8	50.2	66.1
Barbour	100	100-B	14.9	59.2	27 (20–34)	26 (18–33)	28 (20–37)	0.074	0.312	0.476	72.0	53.8	54.5
Pearson	100	100-P	24.8	80.0	43 (33–52)	30 (21–38)	32 (23–42)	0.408	0.537	0.377	38.0	45.2	57.3
Armour	>500	OG-A	27.2	81.5	45 (36–55)	36 (27–44)	23 (16–30)	0.256	0.520	0.176	40.4	34.4	76.3
Zetek	>500	OG-Z	22.5	81.0	38 (29–47)	29 (21–36)	25 (18–32)	0.241	0.325	0.136	53.7	45.6	74.6
Mean			22.3	71.3	39	31	28	0.352	0.445	0.263	45.9	43.9	64.4
SD			6.94	16.9	8.2	4.9	4.6	0.161	0.173	0.119	14.2	9.3	11.2

size classes (Table 1; Appendix S2). One of the 100-yr-old stands (Barbour) was an exception; species dominance by the five most abundant species was higher for adults (72%) than seedlings (55%) in this stand because the adult community was dominated by *Gustavia superba* (Lecythidaceae), which composed 53% of trees ≥ 5 cm DBH (Appendix S3), but was not common as seedlings (6%).

The composition of the five most abundant species differed among size classes, with adults dominated by, in order of decreasing abundance, *Gustavia superba*, *Protium panamense* (Burseraceae), *Alseis blackiana* (Rubiaceae), *Trichilia tuberculata* (Meliaceae) and the palm *Oenocarpus mapora* (see Appendix S3). In contrast, the most abundant species in the sapling and seedling communities was *Tetragastris panamensis* (Burseraceae), although common species in the sapling community also included *P. panamense*, *A. blackiana*, and *T. tuberculata* along with *Trichilia pallida* (Meliaceae). After *Tetragastris panamensis*, the seedling layer was dominated by *G. superba* and *O. mapora* (both abundant in the adult community), as well as *Beilschmiedia pendula* (Lauraceae) and the palm *Attalea butyracea*, which were both uncommon as adults.

The seedling community of young SF was composed of a mixture of species from both SF and OG tree communities that included some very shade-tolerant species, which were more common as adults in OG than SF (e.g. *Protium tenuifolium* and *Tetragastris panamensis*), and lacked many species that were common as adults in SF. Seven species had less than six reproductive-sized individuals across the two 20-yr-old forest stands but no seedlings recorded in the seedling layer of these same stands [*Annona spraguei* (Annonaceae), *Apeiba tibourbou* (Malvaceae), *Casearia arborea* (Salicaceae), *Cecropia peltata* (Urticaceae), *Guazuma ulmifolia* (Malvaceae), *Luehea seemannii* (Malvaceae) and *Spondias radlkoferi* (Anacardiaceae)].

Species composition across size classes and forest ages

Differences in species composition were unrelated to location of plots in the BCNM. Mantel tests used to compare differences in species composition between pairs of stands indicated that geographic distance between stands did not explain patterns in species composition for adults ($r = 0.309$, $P = 0.07$), saplings ($r = 0.053$, $P = 0.39$) or seedlings ($r = -0.153$, $P = 0.80$). Despite differences among ages, the NMDS using S_{MH} (stress = 12.1) showed no clear trajectory of species composition in SF becoming more similar to OG with increasing stand age for any of the three size classes (Fig. 1c). The sapling communities grouped together along the second axis, indicating high similarity regardless of successional age. In contrast, the seedling and adult communities were scattered across the ordination space, suggesting idiosyncratic species composition in these two size classes among stands.

Similarity in composition among the three size classes was highest in the OG stands but did not increase significantly with stand age. This result is demonstrated by adult, sapling and seedling communities of the OG stands grouping more tightly in ordination space than the other stands (Fig. 1). It is also apparent in the multi-community SPADE analysis (Fig. 2). Low similarity among the seedling, sapling and tree communities in the 100-yr-old Barbour forest stand was caused by dominance of *G. superba* in the adult community but not in the sapling and seedling communities.

In contrast to patterns of abundance, successional differences in species composition among the three size

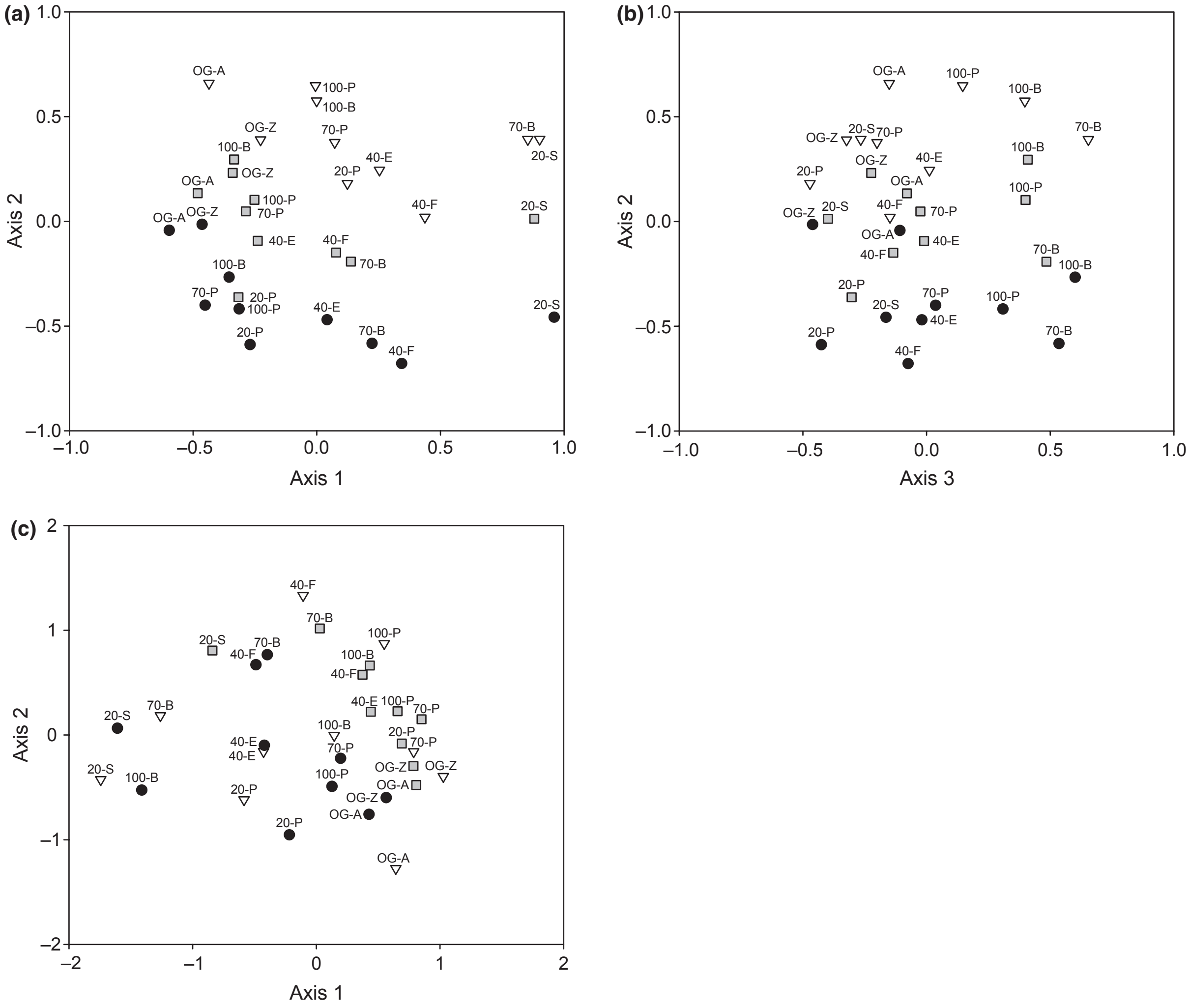

Fig. 1. Non-metric multidimensional scaling (NMDS) plots of adult trees (black circles), saplings (grey squares) and seedlings (open triangles) in two forest stands in each of five age categories: 20, 40, 70 and 100-yr-old secondary forest and old-growth forest (see Table 1 for site codes). NMDS was generated using the Sørensen index (**a** and **b**) and jackknife Morisita–Horn similarity matrix (**c**).

classes could be seen more clearly in the NMDS using the Sørensen index (stress = 14.3), which is based solely on species incidence and not abundance (Fig. 1a,b). The seedling, sapling and adult communities separated along the second axis, and the age of the forest communities tended to increase along the first axis.

Comparisons between adult, sapling and seedling species abundance in each SF stand and adult abundance in OG stands did not indicate increasing similarity to OG with stand age (Fig. 3a,d,e; trees: $R^2 = 0.01$, $P = 0.24$; saplings: $R^2 < 0.001$, $P = 0.69$; seedlings: $R^2 = 0.13$, $P = 0.16$). Similarity between adult communities in the two OG stands was 0.81, which is substantially higher than similarity between the 100-yr-old SF and OG stands (0.40 ± 0.16; Fig. 3a). High similarity between the OG stands may be due to their close proximity; however, the similarity between the OG sites was within 1 SD of the mean similarity derived from comparing randomly selected 0.32-ha areas within the BCI 50-ha plot (mean ± SD: 0.75 ± 0.11). This suggests that the similarity between the two OG plots is typical of OG across the BCNM. Similarity between OG adults and OG saplings (0.62 ± 0.07) was lower than between the OG adult communities (0.81) but was significantly higher than similarity between OG adults and SF saplings (0.35 ± 0.04; Fig. 2; $F_{1,21} = 9.03$, $P < 0.01$). However, OG adult and OG seedling communities (0.47 ± 0.06) were not more similar than OG adult and SF seedling communities (0.33 ± 0.12; Fig. 2c; $F_{1,21} = 1.29$, $P = 0.27$).

Similarity between SF and OG sapling communities and between SF and OG seedling communities did not increase significantly with stand age (Fig. 3b,c; saplings:

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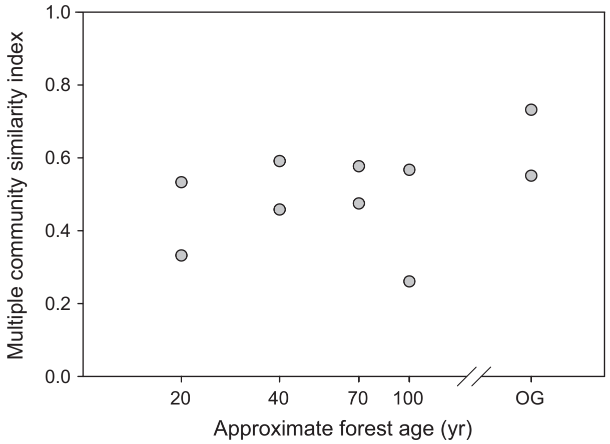

Fig. 2. Morisita–Horn multiple community similarity indices calculated across the three size classes (seedlings, saplings and adults) for each of the two forest stands in five age categories: 20, 40, 70 and 100 yr-old secondary forest and old-growth forest.

$R^2 < 0.001$, $P = 0.92$; seedlings: $R^2 = 0.08$, $P = 0.28$). Mean similarity between the two OG stands was high for sapling composition (0.76). In contrast, similarity between the two OG stands was low for the seedlings (0.34). However, this low similarity was typical of the seedling communities in general, and similarity between OG and SF seedling communities was between 0.16 and 0.32.

Functional composition in relation to forest age and size class

Across all size classes, the shade tolerance of SF communities increased with stand age (effect of age in ANCOVA: $F_{1,23} = 5.12$, $P = 0.036$) and differed significantly among size classes (Fig. 4; effect of size class: $F_{2,20} = 4.31$, $P = 0.029$). There was no significant interaction between forest age and size class. light requirement indices indicated that the sapling community was the most shade tolerant (0.58 ± 0.06); adults were the least shade tolerant (0.93 ± 0.09); and seedlings were intermediate (0.75 ± 0.07). In line with these findings, the proportion of the community represented by light-demanding, intermediate and shade-tolerant species differed among size classes (Appendices S4 and S5; ANCOVA, $F_{2,4} = 8.19$, $P < 0.001$); the adult community had the highest proportion of light-demanding species (0.38), and the sapling community had the highest proportion of shade-tolerant species (0.72).

Discussion

This study exemplifies uninterrupted forest succession following clearance, agriculture and then land abandonment in a tropical moist forest site in central Panama. The study area is representative of regeneration throughout much of Central America, where forests regenerate on abandoned agricultural land embedded in a mosaic of farmland, OG and SF patches (Asner et al. 2009), but likely represents a 'best case' scenario. Thus, the patterns we observed demonstrate that community reassembly following large-scale human disturbance may be highly idiosyncratic even in a relatively undisturbed landscape where seed banks, seed sources and disperser communities are relatively intact, and succession is uninterrupted by repeated clearing of regenerating forests (Chazdon 2003; Helmer et al. 2008). We caution, however, that our inferences are limited because only two stands, each less than 0.5 ha, per forest age were examined and we have not yet examined the dynamics of these stands to test the validity of the chronosequence approach. Given that landscape and site history affect the accumulation of OG species in SF (Chazdon et al. 2009; Dent & Wright 2009), we must be cautious in our interpretation of chronosequence data (Johnson & Miyanishi 2008; Norden et al. 2009). Currently, we are following the BCNM stands to be able to combine chronosequence and forest dynamics approaches to determine whether functional and compositional changes within individual stands reflect patterns seen across the chronosequence.

Recovery of species diversity

According to the patterns observed over the BCNM chronosequence in central Panama, species diversity for all size classes recovered rapidly after land abandonment, and by 20 yrs tree species richness was equivalent if not higher in SF compared to OG. These results are in accordance with studies of lianas along this chronosequence (DeWalt et al. 2000) and trees in secondary tropical forests elsewhere (Aide et al. 2000; Peña-Claros 2003; Letcher & Chazdon 2009; Chai & Tanner 2011). Rapid recovery of species richness depends on unlimited seed availability and dispersal (Guariguata & Ostertag 2001), and the configuration of the BCNM allows for high connectivity and seed dispersal among forest patches.

Species richness tended to be lower in the seedling community compared to saplings and adults along the BCNM chronosequence. A study in old-growth forest on BCI also found that species richness of seedlings was lower than that of reproductive-sized trees and suggested that the seedling layer is composed of a subset of those species present as trees (Comita et al. 2007). Our results contrast, however, with findings from other neotropical secondary forests, where the diversity of woody species was higher in smaller size classes (Gómez-Pompa & Vázquez-Yanes 1981; Peña-Claros 2003). This pattern of higher diversity in smaller size

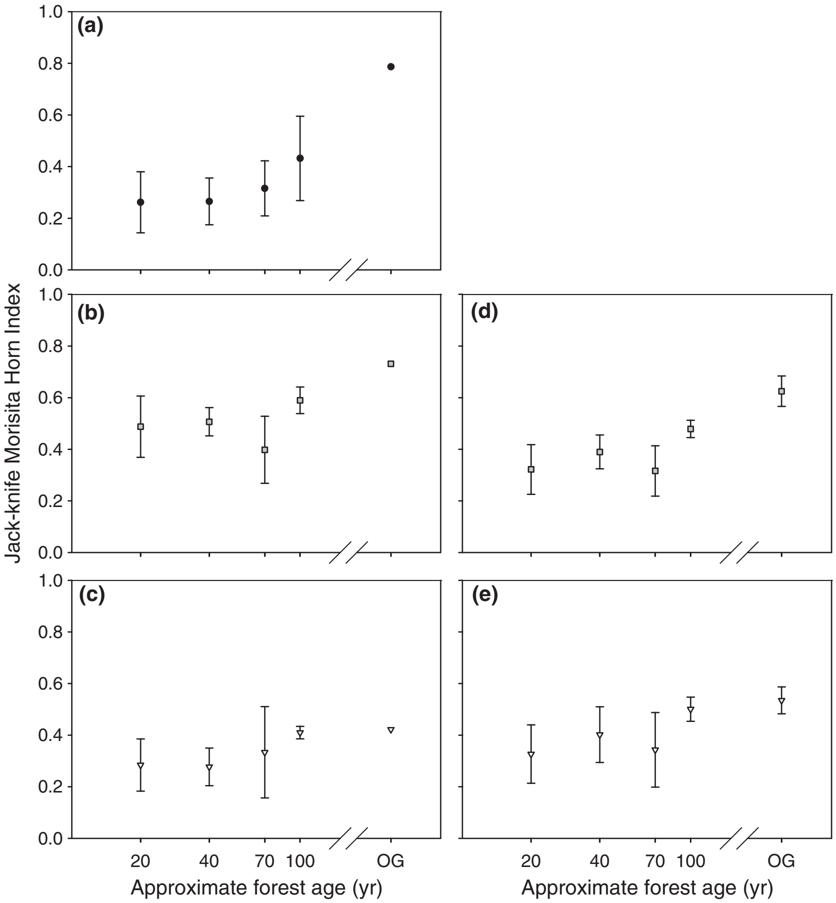

Fig. 3. Jackknife Morisita–Horn similarity indices between old-growth forest (OG) adults and secondary forest (SF) adults (**a**), OG saplings and SF saplings (**b**), OG seedlings and SF seedlings (**c**), OG adults and SF saplings (**d**) and OG adults and SF seedlings (**e**). Each point represents the mean (±1 SE) similarity index of all possible comparisons between the two SF plots in each age category (20, 40, 70 and 100 yrs old) and the two OG plots ($N = 8$). The OG points represent comparisons between the two OG plots.

classes tends to occur in early to mid-successional forests when the understorey is composed of a diverse mix of long-lived pioneers and shade-tolerant species but the canopy is still dominated by a less speciose group of fast-growing pioneer species (Finegan 1996; Toriola et al. 1998). Long-lived pioneers and shade-tolerant species are already present in the canopies of all forests in the BCNM chronosequence, suggesting that forests in this study are too old to exhibit this pattern. However, the difference between our results and those of other studies may also be due to the exclusion of shrubs and understorey trees our analysis, which would disproportionately reduce diversity in the forest understorey compared to the canopy.

Stochastic versus deterministic successional trajectories

Across the BCNM chronosequence, species composition of the forest canopy did not clearly increase in similarity to OG with forest age, and even 100-yr-old forests only shared 38% of species with OG. Species composition was also unrelated to the distribution of plots across the landscape. Thus, similarity in species composition of tree communities within the BCNM appears unrelated to either forest age or geographic location.

Changes in species composition with forest age were not directional, and there was considerable variation among stands due to idiosyncratic species composition at a few sites, particularly in the seedling and adult size classes. For example, in one 20-yr-old stand (Pedro-Gomez), species composition of all three size classes was very similar to that of older SF and OG, and dissimilar to that of the other 20-yr-old stand (Saino). Differences in the length of farming between the two 20-yr-old stands may contribute to this difference; aerial photographs indicate that Pedro-Gomez was farmed for ca. 10 yrs, whereas Saino was farmed for > 40 yrs (D.H. Dent unpublished data). In addition, the low similarity in adult species composition between one of the 100-yr-old stands (Barbour) and OG was due to the

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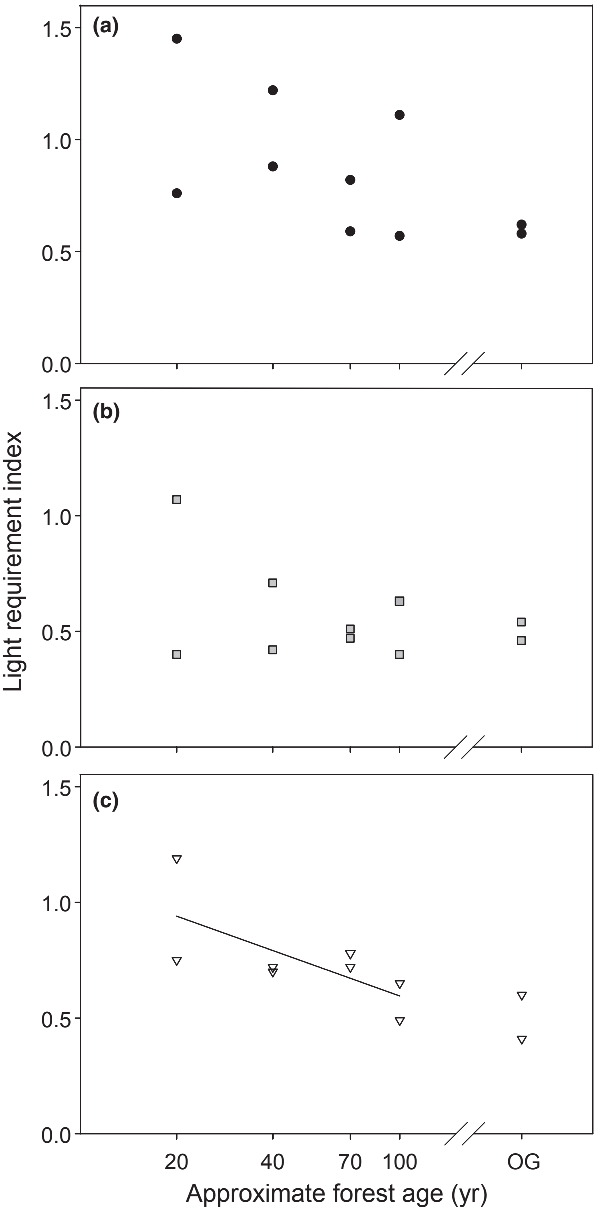

Fig. 4. The community weighted mean light requirement index of adults (**a**; $R^2 = 0.19$, $n = 8$, $P = 0.28$), saplings (**b**; $R^2 = 0.13$, $n = 8$, $P = 0.38$) and seedlings (**c**; $R^2 = 0.48$, $n = 8$, $P = 0.052$) plotted against forest age for eight SF stands and two OG stands in central Panama. Only regression lines where $P < 0.1$ are shown.

dominance of *Gustavia superba* (53% of individuals) at this site. This species composed no more than 7% of individuals in the other old SF and OG stands. The dominance of this species in the adult size class but low abundance in the seedling size class at Barbour was also reflected in the low multiple community measure for this stand (Fig. 2). *Gustavia superba* dominates SF elsewhere in the Panama Canal watershed, and its abundance in some regenerating SF sites may be because its large seeds are dispersed into disturbed sites by rodents and seedling survival in open pasture is high (Hooper et al. 2004).

The seedling community of SF in the BCNM did not reflect the species composition of adult trees in OG, or even the adult trees within the same stand. This lack of correspondence between size classes may be due to patchy and unpredictable species abundances, especially in the seedling community. Tropical tree species vary in their ability to disperse seeds (Nathan & Muller-Landau 2000; Seidler & Plotkin 2006), and limited dispersal can cause spatial aggregation of pioneer species in the seedling layer (Dalling et al. 1998). In the seedling community, species were clustered in their distributions and the most common species differed from stand to stand, leading to low similarity in species composition among stands – even in stands of the same forest age. For example, in one 40-yr-old stand, the seedling community was dominated by *Gustavia superba* (17% of seedling individuals), while *Attalea butyracea* dominated the other 40-yr-old stand (26%). Similarly, *Beilschmiedia pendula* was the most common seedling in one OG stand (35% of individuals), but this species was not present in the seedling community of the other OG stand, where *Tetragastris panamensis* was the most common (39%). These results are in accordance with patterns in the BCI 50-ha plot, where the most common species in the census (*B. pendula*) composed 9.5% of all seedlings and yet occurred in fewer than 6% of the 1 m × 1 m plots (Comita et al. 2007). Seed production of trees in tropical forests is known to differ substantially from year to year, reflecting both species- and community-level variation (De Steven & Wright 2002; Norden et al. 2007). Therefore, the patchy distribution of species in the seedling layer may be the result of both temporal and spatial variability in seed production at the species level, as well as dispersal limitation.

In contrast to patterns found with species composition, functional composition of SF converged on that of OG. Community-level shade tolerance increased with stand age, suggesting that over succession the SF tree community was increasingly dominated by individuals with slow growth and high survival (Wright et al. 2010). This gradual replacement of early-successional species with more shade-tolerant species that persist in the shaded understorey is predicted by classic successional theory and gap dynamics: when a canopy tree dies, the gap that forms is usually filled by pre-existing seedlings and saplings that established in the shade, prior to gap formation (Horn 1974; Brokaw & Scheiner 1989; Connell 1989). We see the results of this process in the dominance of light-demanding species in the canopy of young SF but prevalence of shade-tolerant species in the seedling and sapling communities. This process of gradual replacement of light-demanding species with shade-tolerant species in the forest canopy appears to be occurring in SF within the BCNM, indicating that there is convergence on the functional composition of OG even though species composition is highly variable.

Low similarity between the adult and understorey communities in SF may also reflect the functional bias towards shade-tolerant species in the understorey compared to the forest canopy. Ecological filtering at the seedling stage selects for shade-tolerant species that can germinate and persist in the seedling bank of the dark forest understorey. In contrast, light-demanding species may be entirely absent from the seedling bank, even when adults are present in the forest canopy. These species are rarely captured as seedlings or saplings because they either die quickly in the shade or grow rapidly from seeds to adult trees in high light (Wright et al. 2003). All seven species that had less than six reproductive adult trees in the 20-yr-old forest stands but no seedlings present in these same stands were light-demanding species. Although absent from the seedling community, four of these light-demanding species (*Casearia arborea*, *Cecropia peltata*, *Guazuma ulmifolia* and *Luehea seemannii*) were present in the seed bank of these 20-yr-old forests (Dalling & Denslow 1998), which illustrates their growth strategy; these species either germinate from the soil seed bank or arrive to gaps via dispersers and then grow rapidly in high-light conditions. The seedling census in the 50-ha forest plot on BCI also reported low similarity in species composition between the seedling and adult communities (Comita et al. 2007; Comita & Hubbell 2009). The adult tree community contained a mixture of shade-tolerant guilds, whereas the seedling community was dominated by a subset of shade-tolerant canopy species.

Like seedlings, saplings were composed of a subset of shade-tolerant species, but, unlike them, the composition of sapling communities was strikingly similar across forest ages. These compositional similarities suggest that strong abiotic or biotic filters are present and acting on individuals as they transition between the seedling and sapling communities (De Steven 1991; Bustamante-Sánchez et al. 2011). Therefore, recruitment into the seedling community may be a rather unpredictable process, dependent on species-specific reproduction events and dispersal limitation, whereas recruitment into the sapling and, ultimately, adult communities is more deterministic, with selection for shade-tolerant, slow-growing species (Finegan 1996; Norden et al. 2009).

Effects of previous land use and landscape composition

Our results support the idea that the composition of SF seedling communities is driven by both stochastic and deterministic processes, whereas sapling and tree communities are shaped more by deterministic processes that select for species with high shade tolerance. However, the rate at which SF tree communities accumulate these late-successional species is strongly affected by initial site conditions and the surrounding landscape (Chazdon et al. 2009; Letcher & Chazdon 2009). For example, the high proportion of shade-tolerant species in the 20-yr-old stand, Pedro-Gomez, may be explained by site history and context; this site was only farmed for ca. 10 yrs and is embedded within undisturbed OG forest, and so has a suite of characteristics that promote rapid forest succession, such as low soil disturbance and high colonization potential for seeds and wildlife. Thus, even though the processes that dictate forest succession may be consistent across sites, landscape characteristics interact with local site factors to determine the rate at which succession proceeds (Chazdon 2003).

Site conditions and the regional species pool may explain similarities and differences in successional pathways between this study in central Panama and other study sites. Although our study suggests that the functional composition of SF converges on that of OG, convergence in species composition appears to be delayed in comparison with many other studies. Convergence in species composition has been reported from considerably younger SF than we investigated, from sites in Brazil (Piotto et al. 2009), Bolivia (Peña-Claros 2003) and Costa Rica (Guariguata et al. 1997; Letcher & Chazdon 2009; Norden et al. 2009). In this study, high proportions of shade-tolerant species in the understorey and relatively low similarity across size classes within 70 and 100-yr-old forest suggest that convergence of old SF on OG is still ongoing.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Species accumulation curves for adults, saplings and seedlings in two forest stands in each of five age categories: 20, 40, 70 and 100-yr-old secondary forest and old-growth forest.

Appendix S2. Species relative abundance distributions for adults, saplings and seedlings in each of five age

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categories: 20, 40, 70 and 100 yr-old secondary forest and old-growth forest.

Appendix S3. The most abundant species and their proportional abundance for seedlings, saplings and adults, and for eight secondary forest and two old-growth forest stands in central Panama.

Appendix S4. Summary of the analysis of deviance for the proportional representation of different light requirement categories among different size classes (adults, saplings and seedlings) across all ten forest study plots.

Appendix S5. Proportion of adults (**a**), saplings (**b**) and seedlings (**c**) that are composed of light-demanding (open symbols), intermediate (grey symbols) or shade-tolerant species (black symbols) plotted against forest age.