BIOTROPICA 0(0): 1–11 2014 10.1111/btp.12136

Species Richness, Forest Structure, and Functional Diversity During Succession in the New Guinea Lowlands

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ABSTRACT

Much of the world's tropical forests have been affected by anthropogenic disturbance. These forests are important biodiversity reservoirs whose diversity, structure and function must be characterized across the successional sequence. We examined changes in structure and diversity along a successional gradient in the lowlands of New Guinea. To do this, we measured and identified all stems ≥5 cm diameter in 19 0.25 ha plots ranging in age from 3 to >50 yr since disturbance. We also measured plant functional traits related to establishment, performance, and competitive ability. In addition, we examined change in forest structure, composition, species diversity, and functional diversity through succession. By using rarefaction to estimate functional diversity, we compared changes in functional diversity while controlling for associated differences in stem and species density. Basal area and species density increased with stand age while stem density was highest in intermediate secondary forests. Species composition differed strongly between mature and secondary forests. As forests increased in basal area, community-weighted mean wood density and foliar carbon increased, whereas specific leaf area and proportion of stems with exudate decreased. Foliar nitrogen peaked in medium-aged forests. Functional diversity was highest in mature forests, even after accounting for differences in stem and species diversity. Our study represents one of the first attempts to document successional changes in New Guinea's lowland forest. We found robust evidence that as succession proceeds, communities occupy a greater range of functional trait space even after controlling for stem and species density. High functional diversity is important for ecological resiliency in the face of global change.

Abstract in Melanesian pidgin is available in the online version of this article.

Key words: forest regeneration; functional diversity; New Guinea; plant traits; secondary succession; tropical forests.

Over half of all temperate and tropical forested areas have been classified as regenerating, young secondary forests (Dupuy & Chazdon 2006, FAO 2010). These areas are important reservoirs of biodiversity in increasingly fragmented landscapes (Chazdon 2003), and significant sources of timber and non-timber products (Chazdon & Coe 1999, Ticktin 2004). Secondary forests are by definition successional, thus any point on the landscape also represents a point along a time course of forest recovery. To understand the overall impacts of secondary forests on biodiversity conservation and provisioning of ecosystem services, the patterns of diversity, structure, and function must be characterized across the successional sequence. This can be challenging as the trajectory of ecological succession in secondary forests can vary due to factors such as fire, characteristics of remnant vegetation, past land-use history and intensity, and soil properties (Moran *et al.* 2000, Guariguata & Ostertag 2001, Hooper *et al.* 2004).

Forest structural changes, and their effect on environmental conditions during succession, have been documented in a number of tropical forests, many in the Neotropics (Saldarriaga *et al.* 1988, Corlett 1995, Denslow & Guzman 2000, Bischoff *et al.* 2005, Ruiz *et al.* 2005, Chazdon 2008, Lebrija-Trejos *et al.* 2008, 2010, 2011, Norden *et al.* 2009) and some in the Paleotropics and Africa (Richards 1996, Sheil 2001, Slik *et al.* 2003, Mo *et al.* 2013). In general, as stand age increases basal area increases, whereas stem density generally peaks at intermediate age (Oliver & Larson 1990). Recovery of structure is normally quite rapid (Letcher & Chazdon 2009) but recovery of pre-disturbance species composition is less predictable and depends largely on pre-disturbance history (Chazdon 2008, Letcher & Chazdon 2009). Structural changes are accompanied by changes in environmental conditions and light levels, soil temperature, and air temperature under the canopy, all decrease as basal area increases during succession (Lebrija-Trejos *et al.* 2010).

Received 20 October 2013; revision accepted 7 May 2014.

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Classical niche theory (Hutchinson 1957, Grubb 1977) predicts that differences among species in the environmental conditions required for germination and establishment are important factors determining species coexistence and turnover during succession. Given changing resource conditions during succession, we expect that secondary tropical forests will move from dominance of species with resource acquisitive strategies to those with resource conservation strategies (Adler *et al.* 2014). These shifts in life-history strategies are associated with shifts in plant function (Wright *et al.* 2004, 2010, Lasky *et al.* 2014a, Lohbeck *et al.* 2014). The resource acquisitive to resource conservation continuum involves species with fast growth rates, high mortality rates and high, early fecundity on the acquisitive end while those on the conservative end of the spectrum have slow growth rates, low mortality rates and low fecundity. Classic functional traits associated with these life-history characteristics include rates of photosynthesis and respiration, leaf tissue allocation (specific leaf area; SLA), leaf nitrogen (N) and carbon (C), and wood density (Wright *et al.* 2004, Chave *et al.* 2009).

While studies exist that examine shifts in traits through succession, a key question emerging in research on tropical secondary forests is how overall functional diversity changes through time (Lohbeck *et al.* 2012). Functional diversity could be stable as diverse species with resource acquisitive strategies are replaced by diverse species with resource conservation strategies. Alternately, since species richness generally increases through succession one might expect that if those species represent a broader range of functions, then functional diversity should increase with stand age (but see Lasky *et al.* 2014a). As heterogeneity of environmental conditions increases with stand age in many forests (Lebrija-Trejos *et al.* 2011), we also expect a broader range of strategies represented in later successional forests and thus higher functional diversity.

Different components of tropical forest succession have been documented in many parts of the world (Saldarriaga *et al.* 1988, Guariguata & Ostertag 2001, Sheil 2001, Chazdon 2003, Chazdon *et al.* 2007, Mo *et al.* 2013) yet few studies have characterized forest structure, species richness, and functional diversity during succession in a single forest community (Lohbeck *et al.* 2012, Barrufol *et al.* 2013). The objective of this study was to simultaneously document changes in these attributes during forest recovery following small-scale (up to one hectare) shifting cultivation in the New Guinea lowlands. The understudied island of New Guinea is recognized as one of the world's largest remaining tropical wilderness areas based on the extent of relatively undisturbed forest (Mittermeier *et al.* 1998) and high levels of plant endemism (Paijmans 1976). Studies of montane habitats or small volcanic islands have described aspects of succession on New Guinea (Corlett 1987, Vanvalkenburg & Ketner 1994, Harrison *et al.* 2001) and several previous studies have described general forest characteristics across the island (Wright *et al.* 1997, Oatham & Beehler 1998, Weiblen 1998, Balun *et al.* 2000, Laidlaw in press). However, lowland rain forest succession in New Guinea is rarely documented (but see Whitfeld *et al.* 2012a) with most accounts appearing only in inaccessible journals or 'gray' literature (*e.g.*, Saulei 1988, Saulei & Kiapranis 1996, Saulei *et al.* 1999). We examined changes in forest structure (basal area, stem density); plant species richness and composition; and functional traits related to establishment, performance, and competitive ability during succession. The traits we chose relate to photosynthetic and growth rates (leaf N, leaf C, SLA, wood density) and protection from herbivores (production of exudates) and as such are closely related to species success through succession. We hypothesize that community-weighted mean foliar N and SLA will decline and wood density and leaf C will increase through succession. We also calculated several multi-trait functional diversity indices (functional richness, evenness, divergence) that included all measured traits across the successional gradient and hypothesize that functional diversity will increase through succession. This prediction is based on the expectation of increased species richness leading to a broader representation of functions. We also expect the increased heterogeneity of environmental condition in later successional stages will lead to higher functional diversity. In addition, we estimated rarified multi-trait functional diversity to deconstruct the individual and interactive effects of forest structure, species richness, and functional trait variation. We hypothesize that for a given stem or species density later successional forests will have higher functional diversity. This hypothesis is based on the same expectations as those for changes in overall functional diversity through succession.

METHODS

At present, the island of New Guinea is experiencing high rates of deforestation, particularly in the more accessible lowland areas where net forest loss between 1972 and 2002 was at least 30 percent (Shearman & Bryan 2011). However, little is known about successional trajectories following conversion in these forests.

STUDY SITE.—The study site was in Madang Province, Papua New Guinea, near the village of Wanang in the Ramu River basin (145°5′32″ E, 5°14′26″ S) (Fig. S1). This region is part of an extensive mixed evergreen forest (Hammermaster & Saunders 1995), 100–200 m above sea level, on latosols (Paijmans 1976, Wood 1982). Topography is highly varied with a mixture of low rugged hills, steep slopes, and narrow river valleys. The region has a humid climate, a mean annual rainfall of 3500 mm with a mild dry season from July to September, and a mean monthly temperature of 26°C (McAlpine *et al.* 1983). We sampled a total of 19 0.25 ha plots (50 × 50 m) representing 4.75 ha of forest. Five plots were in young secondary forest (3–9 yr since disturbance), seven plots were in intermediate secondary forest (10–30 yr since disturbance), and 7 plots were in mature forest (age unknown but >50 yr since disturbance). All plots were surrounded by contiguous lowland rain forest. Mature forest is used here rather than old growth because the exact date of last disturbance is unknown. In prior work, we called this age-class 'primary' (Whitfeld *et al.* 2012a,b). Approximate ages were obtained through interviews with landowners. A minimum age for mature forest in the area was estimated from Royal Australian Survey

Corps aerial photographs. These indicate the presence of multilayered canopy in 1973 suggesting no anthropogenic disturbance since at least the late 1950s. The common land-use history of our plots combined with the close proximity of different aged stands and relatively similar soils (Table S1) represents a best-case scenario for use of a chronosequence to study succession, an approach often criticized for including sites with varied land-use history (Chazdon 2008). In addition, the entire survey area is exposed to similar propagule input since it is part of contiguous forest without large cleared areas, pastures, or other significant barriers to dispersal. Study plots in areas with no recent disturbance provided a late-successional baseline and enabled us to investigate whether secondary forest structure and composition tended to converge on mature forests. Four of the intermediate secondary plots and four of the mature forest plots were contiguous (*i.e.*, 1-ha plots) and were part of another study that destructively sampled all trees (see Whitfeld *et al.* 2012b for a more detailed description of methods). To avoid pseudoreplication, we averaged the values from each set of contiguous plots and used each as a single data point (rather than four) in our analyses. The dominant prior land use for all plots was subsistence gardens that typically range in size from 0.25 to 1.0 ha and are planted after felling and burning of mature forest. Crops include papaya (*Carica papaya*), yams (*Dioscorea* sp.), cassava (*Manihot esculenta*), bananas (*Musa* sp.), and taro (*Colocasia esculenta*). Succession proceeds when garden plots are abandoned after 2–3 yr of low intensity cultivation. Such gardens are not grazed or mechanically cultivated. For this study, young and intermediate secondary survey plots were located in areas recently disturbed by this subsistence agriculture.

DATA COLLECTION.—In each plot, all trees with diameter at breast height (dbh) $\geq$5 cm were measured, tagged, and identified to estimate species density, stem density, and basal area. Following field identification, vouchers were collected and their identity confirmed at the Papua New Guinea Forest Research Institute herbarium (LAE). Complete sets of vouchers were deposited at LAE and the J. F. Bell Museum of Natural History (MIN) at the University of Minnesota, U.S.A., plus other herbaria (Appendix S1).

PLANT FUNCTIONAL TRAITS.—In addition to documenting diversity, we also measured several plant functional traits. SLA (cm^2/g) was calculated from approximately ten, 2.3 cm diameter disks cut from fully expanded, mature leaves on the outer part of the crown that were without obvious signs of pathogen or herbivore damage. The number of individuals per species sampled ranged from one to 246 with a mean of nine individuals per species. Our SLA data represent a community wide sample that includes trees from understory and canopy positions and thus foliage that varied in exposure to light. Given that SLA likely varied within species with canopy position, we calculated both average SLA and SLA at the maximum tree height sampled for a species. For those species that had individuals in the canopy, SLA at maximum tree height values should represent full sun SLA; however, some species had no individuals tall enough to be in the canopy either because they were rare canopy trees or they never reach the canopy as adults. The orthogonal regression (*i.e.*, includes variation in both x and y variables) of average SLA and SLA at maximum tree height was 0.81 (species with only one individual sampled were excluded from this analysis). Given the strong relationship, we used average SLA across all individuals to assign species means because it was usually based on a larger sample size per species (except in the case of singletons). We calculated wood density (g/cm^3) for each species occurring in the two hectares of destructively sampled vegetation (see *Study site*). Samples (2 cm sections, from the core to the cambium) were collected for up to ten individuals $\geq$5 cm dbh (mean number of individuals = 3, range = 1–10) in order to obtain species averages. Fresh volume was measured by submerging the section in a flask of water and the sections were then oven-dried at 70°C to a constant weight. For the measurement of foliar nitrogen and carbon, three randomly chosen leaves were sampled from up to four individuals per tree species. The leaves were bulked and ground by hand in liquid nitrogen or in a Tissuelyzer (Qiagen). Analysis was carried out at the University of Nebraska-Lincoln, U.S.A., using dry combustion gas chromatography on a COSTECH analytical elemental combustion system ESC 4010. The presence or absence of exudate in leaves and wood was also noted during surveys. The values for all functional traits were scaled up from the species to community level by using the community-weighted mean values, weighted by stem density (Lavorel *et al.* 2008).

DIVERSITY ESTIMATES.—For each survey plot, we calculated species density, Shannon diversity (to account for differences in species relative abundance), and the Chao1 unbiased asymptotic richness estimator (to account for differences in stem density). We used EstimateS (Colwell 2009) to calculate these diversity indices. We also calculated importance values for each species as the sum of relative dominance (species basal area divided by total basal area) (McIntosh 1957) and relative density (number of stems of one species divided by total number of stems).

To assess changes in functional structure based on all measured plant traits through succession, we calculated three multitrait metrics, using the program FDiversity (Casanoves *et al.* 2011) which incorporate different aspects of trait diversity and are considered complementary (Villeger *et al.* 2008). Functional richness is an estimation of the functional hyperspace filled by the community. It identifies extreme species and estimates the total space occupied by all intermediate species. Low functional richness indicates that parts of the total trait space are unused. By contrast, functional evenness measures the regularity of spacing and evenness in abundance distributions in the functional space. It measures how the biomass within a community is distributed in trait space. Low values suggest that some parts of the space are occupied but underused. Functional divergence estimates how species' abundance is distributed within the trait volume and how it diverges from the center of the functional space. We calculated these indices on a subset of species for which we had values for all traits (199 out of 260 species, representing 86 percent of the total basal area in all plots). Per plot, the percent of species included in the analysis ranged from 82 to 97 percent (mean 89%) and the percent of basal area ranged from 66 to 99 percent (mean 80%). We weighted abundance by the number of stems and used Euclidean distances. All values were standardized prior to analysis to have a mean of zero and standard deviation of one (*z*-score), to ensure equal contribution of each trait. In order to assess functional diversity variation among forest types while controlling for variation in stem and species richness, we constructed multi-trait rarefied assemblages (Gotelli & Colwell 2011) based on the same set of functional traits used to calculate functional structure. We generated rarefied assemblages with 5, 25, 50, 75, 100, 125, 150, 175, and 200 individuals sampled from each plot (maximum of 150 for young secondary plots and 175 for intermediate secondary plots), in addition to assemblages with 5, 10, 15, 20, 30, 40, 50, 60, 65 species sampled from each plot (maximum of 25 for young secondary plots and 35 for intermediate secondary plots). For each level of sampling, we generated 50 random assemblages using rarefaction in the 'vegan' package in R (Oksanen *et al.* 2012). For each assemblage we then calculated functional diversity as the total shared branch length in a multivariate functional dendrogram (Petchey & Gaston 2002). Functional diversity values were then taken as the average of the 50 assemblages for each plot.

STATISTICAL ANALYSIS.—We used one-way analysis of variance to compare forest structure and species diversity among estimated stand age classes. Succession involves recovery of stand biomass after disturbance (Letcher & Chazdon 2009, Lebrija-Trejos *et al.* 2011). Since basal area is correlated with biomass (Slik *et al.* 2010) and basal area recovery is closely tied to changing environmental conditions through succession (Lebrija-Trejos *et al.* 2011, Lohbeck *et al.* 2012), we examined how traits and trait diversity change as basal area recovers during succession. We conducted regression analyses that examined the relationship between plot-level community-weighted means of each functional trait, plot-level measures of functional diversity, and total basal area per plot. An underlying assumption is that as succession proceeds basal area increases. We think this a reasonable assumption even though many pioneer trees grow relatively quickly. ANOVA and regression analyses were conducted using JMP v. 8.0.1 (SAS Institute, Inc., Cary, North Carolina, U.S.A.). In addition, we used multivariate analysis to evaluate the association of species with successional stage. An exploratory correspondence analysis indicated a wide range of species abundances (gradient of 4.9) and a strong arch effect in our data (*i.e.*, the position of samples on the second ordination axis are strongly, non-linearly, dependent on their positions on the first axis) so we proceeded with unimodal detrended correspondence analysis (DCA), including all species but down weighting rare species to reduce their influence. This analysis was performed in CANOCO v. 4.5 (Ter Braak & Šmilauer 2002) and allowed us to assess whether survey plots segregated with respect to successional stage based on plant species abundance.

RESULTS

FOREST STRUCTURE.—Intermediate secondary forest contained significantly more stems per hectare than young secondary with mature forest intermediate (Table 1). Total basal area and basal area of larger trees (>10 cm dbh) was highest in mature forest. The frequency distribution of dbh size classes indicated all successional stages contained similar numbers of trees up to 30 cm dbh but larger trees became relatively more frequent in the mature forest compared to the two secondary forest stages (Fig. 1).

SPECIES DIVERSITY AND COMPOSITION.—All size classes of trees in mature forest had significantly higher species density than in either age class of secondary forests (Table 1). Species density, Shannon diversity, and asymptotic species richness (Chao1) were positively correlated with basal area (Figs. 2A–C).

In addition to changes in species richness and diversity with succession, we found changes in composition. The frequency distribution of species was relatively consistent across all three successional stages (Fig. S2) and most species were represented by ten or fewer individual stems (84%, 79%, and 84% of species in young secondary, intermediate secondary, and primary forest respectively). Five families accounted for a ~75 percent of basal area in young and intermediate secondary forest (74% and 79% respectively). However, in mature forest there was a marked

TABLE 1. *Mean (±standard deviation) stem density, tree density, and basal area per hectare by successional stage in the lowlands of New Guinea. Significant differences between successional stages for each size class are indicated by different letters (ANOVA, $\alpha = 0.05$). Young secondary (3–9 yr since disturbance), intermediate secondary (10–30 yr since disturbance), mature (>50 yr since disturbance). NB: species density is calculated per 0.25 ha, whereas stem density and basal area are per 1 ha.*

Dbh (cm):	5–10	>10	All stems*
Successional stage:			
Stem density (per ha)			
Young secondary	741 ± 61.4 a	338 ± 58.4 a	1079 ± 74.4 b
Intermediate secondary	879 ± 68.7 a	547 ± 65.4 a	1426 ± 83.1 a
Mature	724 ± 68.7 a	529 ± 65.4 a	1253 ± 83.1 ab
Basal area (m^2/ha)			
Young secondary	2.8 ± 0.2 a	9.5 ± 2.3 b	12.3 ± 2.2 b
Intermediate secondary	3.5 ± 0.3 a	14.4 ± 2.6 b	17.8 ± 2.5 b
Mature	2.9 ± 0.3 a	27.9 ± 2.6 a	30.8 ± 2.5 a
Species density (per 0.25 ha)			
Young secondary	45 ± 6.5 b	21 ± 3.6 b	50 ± 8.9 b
Intermediate secondary	54 ± 7.3 b	38 ± 4.1 b	60 ± 9.9 b
Mature	86 ± 7.3 a	65 ± 4.1 a	116 ± 9.9 a

*All stems with dbh ≥5 cm.

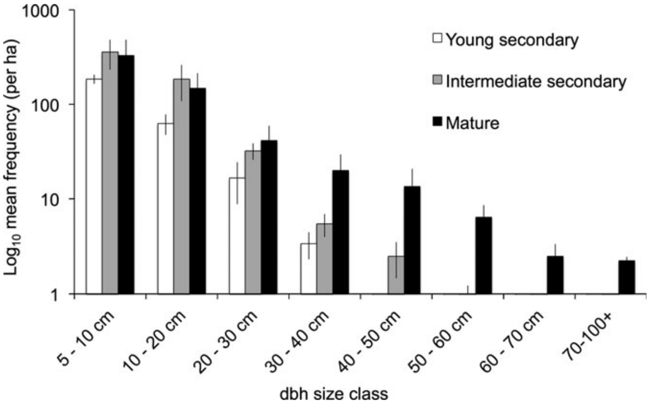

FIGURE 1. Frequency distribution of tree dbh size classes in three forest successional stages in the New Guinea lowlands. Bars represent standard error. Young secondary (3–9 yr since disturbance), intermediate secondary (10–30 yr since disturbance), mature (>50 yr since disturbance).

turnover in the dominant families (Table S2). DCA suggested that plots located in mature forest were more similar to each other in terms of species composition than to plots in young and intermediate secondary plots (Fig. 3). Strong separation between mature and secondary forests in composition suggests that the mature forests were considerably older than indicated by our aerial photos, which were censored at 50 yr.

FUNCTIONAL TRAITS AND DIVERSITY.—As with forest structure, species diversity, and species composition, we found changes in functional traits and functional diversity as basal area recovered during succession. As plot basal area increased, community-weighted mean of wood density and foliar carbon increased significantly, whereas SLA decreased (Figs. 4A–C). By contrast, community-weighted mean foliar nitrogen was significantly higher at intermediate basal areas corresponding to young forests (Fig. 4D). In all successional stages, species and stems containing exudate were more abundant than those without (Table 2). However, there were proportionally more individuals (93% compared to 74%) with exudates in young secondary forests and the probability of a tree containing exudate decreased as basal area increased (Fig. 4E). Functional richness increased significantly with basal area, whereas functional evenness did not (Figs. 2D and E) and functional divergence was only weakly correlated (Fig. 2F). Functional richness also increased with species density ($R^2 = 0.82$, $P < 0.0001$), whereas functional evenness and divergence did not. When differences in stem and species density were taken into account (*i.e.*, in rarefied analyses), functional diversity was still highest in mature forests across a broad range of stem and species densities (Fig. 5).

DISCUSSION

The island of New Guinea is recognized as one of the world's largest remaining tropical wilderness areas based on the extent of relatively undisturbed forest (Mittermeier *et al.* 1998) and high levels of plant endemism (Paijmans 1976). Lowland tropical forests are currently threatened by intensification of timber harvesting making studies of succession timely. Overall, patterns of recovery of forest structure, species diversity and composition in New Guinea, paralleled those in other more intensively studied tropical forests (Saldarriaga *et al.* 1988, Sheil 2001, Chazdon *et al.* 2007, Letcher & Chazdon 2009, Mo *et al.* 2013). Shifts in structure, composition and species richness were accompanied by shifting plant functional traits. Combining structure, composition and trait data into an analysis of functional diversity supported the hypothesis that as forests become more diverse in species through succession, those species occupy a larger proportion of the functional trait space perhaps through increasing heterogeneity of environmental conditions and species interactions.

NEW GUINEA SUCCESSION.—The long-isolated island of New Guinea includes elements of Gondwanan and Southeast Asian flora (Paijmans 1976), but lacks seed dispersing primates and large ground-dwelling herbivores (Primack & Corlett 2005). Previous studies suggest species' spatial arrangement are strongly correlated with seed dispersal traits with large-fruited animal dispersed species being the most diffuse (Seidler & Plotkin 2006). The lack of wide ranging, large mammals in New Guinea may mean large-fruited tree species are more aggregated leading to lower alpha diversity. Compared to other parts of the tropics for which comparable data exist, rarefied diversity of large trees (dbh ≥10 cm) was indeed lower in mature forests of New Guinea compared to Malaysia, Borneo, Sarawak and Ecuador but was higher than Panama (Kochummen & LaFrankie 1990, Leigh *et al.* 2004, Valencia *et al.* 2004). Shannon diversity of early successional forests in Papua New Guinea was similar to subtropical forests in Australia (Williams *et al.* 1969). In general, species richness in the New Guinea lowlands appears to fall within the range documented across the tropical zone. However, we sampled a relative small area in this study. Currently, survey and analysis is underway of a 50-ha plot near our study area that will provide a much stronger basis for comparisons with other tropical areas.

As expected, based on observations from Neotropical forests (Saldarriaga *et al.* 1988, Ruiz *et al.* 2005, Letcher & Chazdon 2009), overall stem density in our survey plots was highest in intermediate secondary forest before the onset of stem exclusion. Density of stems in the small size class (5–10 cm dbh) or large size class (>10 cm dbh) did not change through succession perhaps because of the broadly defined age classes that may obscure differences within each age class. This would be exacerbated if the stem exclusion period is short. In addition, disturbance regimes in New Guinea are characterized by frequent landslides (Johns 1986) that may lead to higher than expected stem densities, even in mature forests. Whether or not these factors account for the observed differences in stem density between our study site and other tropical forests deserves more detailed study. Total basal area and basal area of large trees increased during succession in line with predictions based on prior work (Guariguata *et al.* 1997, Chazdon *et al.* 2007).

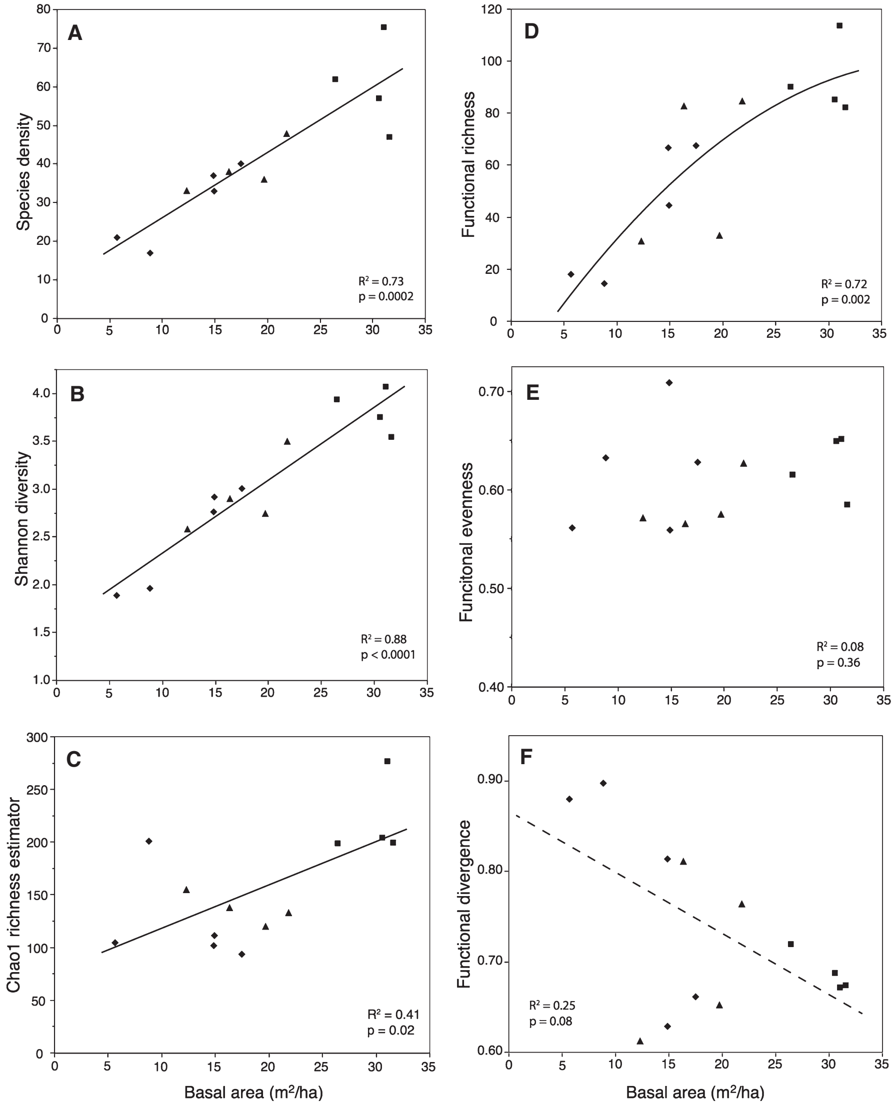

FIGURE 2. (A) Species density (#/ha), (B) Shannon diversity, (C) Chao1 asymptotic richness estimator, (D) functional richness, (E) functional evenness, and (F) functional divergence vs. basal area (m^2/ha). Each point represents one 0.25 ha survey plot in the New Guinea lowland forest. Young secondary (3–9 yr since disturbance = diamond), intermediate secondary (10–30 yr since disturbance = triangle), mature (>50 yr since disturbance = square). Contiguous plots in intermediate secondary and mature forests were averaged and are represented by single points on the figure. Dotted line represents marginal significance.

PLANT TRAITS.—Plant species growing at different points on a successional gradient in closed canopy forests differ in their environmental requirements as light levels, temperature, and relative humidity change (Lebrija-Trejos *et al.* 2010, 2011, Lohbeck *et al.* 2013). Biotic and abiotic variables can act on plant functional traits to constrain species to a particular set of environmental conditions—their regeneration niche (Grubb 1977). If these predictions are supported, we expect that species with certain combinations of traits should be associated with different successional stages (Dent *et al.* 2013). The overall trait patterns we observed in lowland New Guinea support such expectations as does previous work in other wet tropical forests (Lohbeck *et al.* 2013). Species in mature forests tended to have leaves with lower SLA and higher carbon, and stems with higher wood density compared to species in secondary forests suggesting a shift in life-history strategy from resource acquisition to resource conservation as environmental conditions change during succession. Foliar nitrogen, an important component of proteins involved in photosynthesis, did not follow expectations, peaking in plots with medium levels of basal area, whereas we expected it to be highest in lowest basal area (*e.g.*, the youngest plots). The fact that foliar nitrogen peaked in medium basal area plots may be explained in part by their species composition. In four out of five of these plots, at least a quarter (up to 88% in one case) of the basal area was comprised of species (all non-legumes) with levels of foliar nitrogen in the upper half of the observed range from this site. The success of

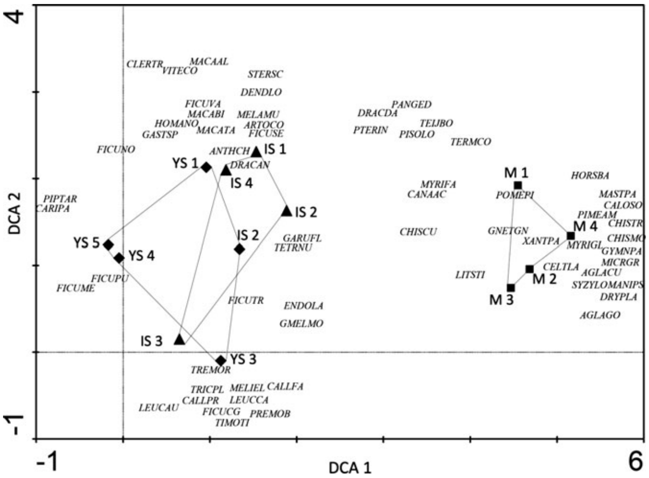

FIGURE 3. Detrended correspondence analysis (DCA) of species association with successional stage in lowland New Guinea rain forest. Young secondary (3–9 yr since disturbance) plots are represented by diamonds (YS), intermediate secondary (10–30 yr) plots by triangles (IS), and mature (>50 yr) plots by squares (M). For clarity, only the 64 species best characterized by the ordination were included on the figure. First canonical axis eigenvalue = 0.786 and percent variance of species data explained = 23.9 (33% for the axes 1 and 2). (Table S3 contains a list of taxa names included in this figure.)

TABLE 2. *Percent of stems and species containing exudate in three forest successional stages in the New Guinea lowlands. Young secondary (3–9 yr since disturbance), intermediate secondary (10–30 yr since disturbance), mature (> 50 yr since disturbance).*

	Exudate present (%)		
	Young secondary	Intermediate secondary	Mature
Stems	93	84	74
Species	78	90	86

species with high foliar nitrogen suggests the importance of fast growth rates in the highly competitive, secondary tropical forest community.

We found a higher occurrence of leaf exudates in early successional forests that suggests trees in young forests rely on an alternative herbivore deterrent strategy (compared to the structural defenses of mature forest species) while still maximizing their ability to acquire resources in the highly competitive young forests. Previous work at this site (Whitfeld *et al.* 2012b) indicated that caterpillar abundance was 71 percent higher and leaf-miner abundance was 70 percent higher on trees where exudate was absent in secondary and mature forests. The higher proportion of young secondary trees with exudate (Table 2) and the lower abundance of leaf herbivores on these trees suggest this trait is an important defense against herbivores in leaves that are otherwise poorly defended (Farrell *et al.* 1991, Agrawal 2004, Agrawal & Fishbein 2006). We focused on the presence or absence of exudate but a recent study examining the relationship between exudate volume and SLA found these traits to be negatively correlated suggesting a more nuanced relationship between these defense strategies (Lasky *et al.* 2014b). Antiherbivore defenses also represent an important mechanism driving and maintaining diversity in tropical forests. Closely related co-occurring species tend to differ in their chemical defenses suggesting that possessing unique defense traits may increase fitness (Kursar *et al.* 2009). In addition, defense compounds tend to be more diverse where insect herbivores are more specialized, suggesting a close link between phytophage pressure and host plant diversity (Becerra 2007). The presence of leaf exudates also tends to be evolutionarily convergent (Whitfeld *et al.* 2012b, Lasky *et al.* 2014b) perhaps indicating that exudate production is driven by adaptation to resource availability.

In addition to changing functional traits through succession, we also observed that suites of species were closely associated with young or mature forests, whereas other species were common in both successional stages. Overall, survey plots located in mature forest were more similar to each other in terms of species composition but they consistently contained more species and higher functional richness. By contrast composition of secondary forest plots was variable, perhaps as a result of high stochasticity in seed rain that determines initial plot composition, but always contained fewer species and lower functional richness than mature forests. Furthermore, mature forest was dominated by species from several major clades across the plant phylogeny (Rosids, Magnoliids, Asterids), whereas the most abundant secondary forest species were all from a single clade (Rosids) (Table S2).

FUNCTIONAL DIVERSITY.—We observed increases in multi-trait functional richness as forests regained basal area following disturbance. This pattern was expected based on previous work at this site which indicated increased phylogenetic diversity across the same successional gradient (Whitfeld *et al.* 2012a). Assuming some degree of niche conservatism (Wiens *et al.* 2010), higher phylogenetic diversity is likely to lead to increased functional diversity. Further supporting this interpretation, we found higher species richness was also associated with higher functional richness, a pattern also reported in several other studies (Lohbeck *et al.* 2012, Lasky *et al.* 2014a). Differences in stem and species density through succession can influence observed changes in biodiversity (Gotelli & Colwell 2011). Thus, the relationship between functional diversity and species richness begs the question of whether functional diversity is higher in mature forests when stem and species density are standardized. Our multi-trait rarified functional diversity results demonstrate that increased functional diversity through succession is indeed due to greater functional diversity across a range of stem and species densities. Overall, our study provides robust evidence that during secondary succession communities become more diverse in terms of life history and occupy a greater range of functional trait space in late vs. early succession. Previous studies (Lohbeck *et al.* 2014) have shown that functional traits are constrained, and functional diversity lower, during early succession reflecting the limitations of the

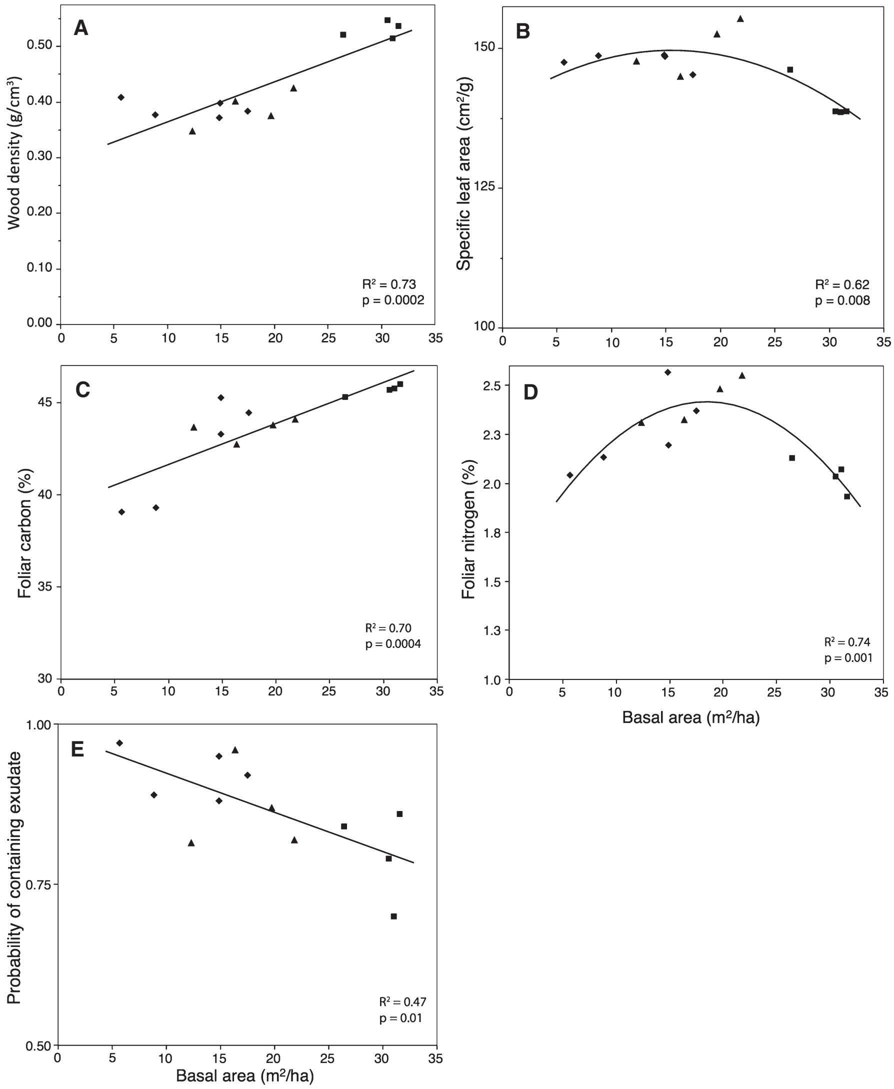

FIGURE 4. Regressions of community-weighted mean trait values per plot vs. total basal area per hectare for traits in three successional stages in the New Guinea lowlands. Young secondary (3–9 yr since disturbance = diamond), intermediate secondary (10–30 yr since disturbance = triangle), mature (>50 yr since disturbance = square). (A) wood density (g/cm^3), (B) specific leaf area (cm^2/g), (C) percent foliar carbon (g/g), and (D) percent foliar nitrogen (g/g) (E) Proportion of stems with exudate. Each point represents one 0.25 ha survey plot. Contiguous plots in intermediate secondary and mature forests were averaged and are represented by single points on the figure.

harsher conditions (hotter, drier) during the first stages of forest regeneration. Later, as light decreases, competitive interactions increase and resource partitioning becomes an important way of limiting similarity. The result is higher functional diversity in later successional stages (Lohbeck *et al.* 2014). These results are significant as communities with high functional diversity are more likely to contain functional redundancy and complementarity (Reich *et al.* 2012) and may therefore confer resilience in the face of climate change or other large-scale environmental perturbations. However, it should be noted that resilience may also be affected by factors other than functional diversity including tree size (McGroddy *et al.* 2013). High functional diversity is also associated with higher productivity in subtropical forests and is a driver of re-growth following disturbance (Barrufol *et al.* 2013).

The lack of change in functional evenness through succession in New Guinea suggests little change in the way species are distributed in niche space. The marginally significant decrease in functional divergence indicates a trend toward a decreased proportion of species with extreme trait values. Taken together, these results suggest that despite an overall increase in functional space through succession, there appears to be no corresponding change in the way that this space is filled as forests recover basal area. Previous studies (Kraft & Ackerly 2010) suggest evenly distributed trait values within a community are indicative of niche

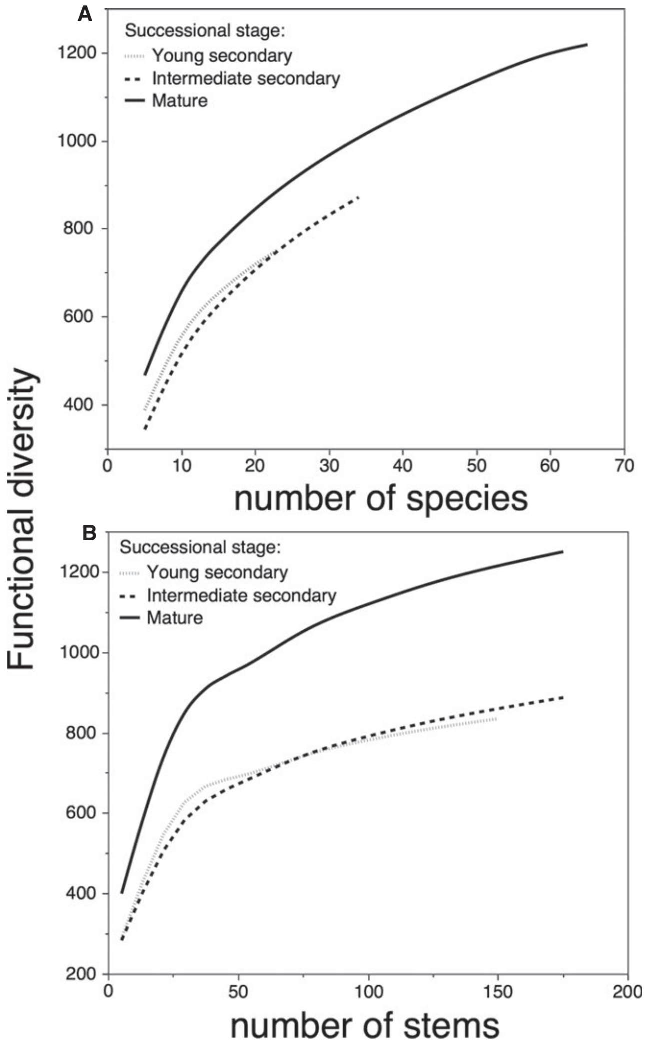

FIGURE 5. Rarefied functional diversity as a function of (A) stem density and (B) species density in the lowland rain forest of New Guinea. Young secondary (3–9 yr since disturbance = diamond), intermediate secondary (10–30 yr since disturbance = triangle), mature (>50 yr since disturbance = square). Functional diversity is calculated as the total shared branch length along a multivariate functional dendrogram among co-occurring species, scaled to the maximum possible branch length.

partitioning or enemy-mediated density dependence. That we observed no change in functional evenness through succession suggests that in the New Guinea lowlands the relative importance of this mechanism of community assembly does not change as forests recover basal area.

In summary, by all measures we found that diversity was lower in secondary forests in the New Guinea lowlands than their mature counterparts. These forests appear to be more functionally homogeneous than mature forest so may be less resilient to large-scale environmental change. Since an increasingly large area of New Guinea and the global tropical region is being converted to and maintained as secondary forest, this loss of diversity may bode ill for the long-term resiliency of these communities.

ACKNOWLEDGMENTS

We thank George Weiblen, Vojtech Novotny, and staff at the New Guinea Binatang Research Center for vital field and logistical support, Wanang landowners for access to field sites and assistance, Billy Bau and staff at PNG Forest Research Institute for assistance with fieldwork and plant species identification, and Sascha Lodge for assistance with analysis. This manuscript was improved by comments from Robin Chazdon, Lourens Poorter and one anonymous reviewer. This work was supported by a US National Science Foundation grant (DEB-0515678), the Czech Science Foundation under grants P505/10/0673 and 206/09/0115, the Arnold Arboretum (Deland Award for student research), the Society of Systematic Biologists (award for Graduate Student Research), the Systematics Association (Systematics Research Fund), and University of Minnesota (Department of Plant Biology; Department of Ecology, Evolution, and Behavior, Dayton and Rothman fellowships; Office of International Programs; Carolyn Crosby Fellowship, and Graduate School Doctoral Dissertation Fellowship).

SUPPORTING INFORMATION

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

APPENDIX S1. Voucher distribution.

FIGURE S1. Location of study site near Wanang, Madang Province, Papua New Guinea.

FIGURE S2. Species frequency distribution for 19 survey plots in the lowlands of New Guinea.

TABLE S1. *Soil chemical and physical properties from the New Guinea lowlands.*

TABLE S2. *Stem density, basal area, relative dominance, relative density, and importance values in the lowland rain forest of New Guinea.*

TABLE S3. *Species abbreviations from Fig.* 3 *with full names.*

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