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Ecosystem recovery in terra firme forests after cutting and burning: a comparison on species richness, floristic composition and forest structure in the Jaú National Park, Amazonia

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Six hectares, three in a primary forest and three in a 40 year old secondary forest were inventoried for all trees with Diameter at Breast Height (DNH) of 10 cm or greater in a terra firme forest 200 km north-east of Manaus, central Amazonia in order to compare the difference between structure, species richness and floristic composition. Both species richness and tree density were significantly higher in the upland forest than in the secondary forest. The forest structure pattern analysed (DBH, basal area and estimated dry biomass) did not differ significantly between the two forest types. Similarity indices at species level were only 14%. In the 3 ha of primary forest the number of species varied from 137 to 159, the number of individuals from 639 to 713, total basal area from 32.8 to 40.2 m^2 and estimate total of above-ground dry biomass (AGBM) from 405 to 560 tons per ha. In the 3 ha of secondary forest, the number of species varied from 86 to 90, the number of individuals from 611 to 653, total basal area from 28.8 to 39.9 m^2 and estimated total AGBM from 340 to 586 tons per ha. Family Importance Value (FIV) is the sum of relative density, dominance and richness of a family. The most important families in relation to FIV were Burseraceae, Chrysobalanaceae, Lecythidaceae, Myristicaceae, Bombacaceae, Fabaceae and Mimosaceae in the 3 ha of primary forest, while Burseraceae, Lecythidaceae, Sapotaceae, Arecaceae and Cecropiaceae were the most important families in the 3 ha of secondary forest. Importance Value Index (IVI) is the sum of relative density, dominance and frequency of a species. *Alexa grandiflora* (Caesalpiniaceae), *Scleronema micranthum* (Bombacaceae) and *Pourouma guianensis* (Cecropiaceae) were the most important species in relation IVI, in the primary forest, while *Eschweilera grandiflora* (Lecythidaceae), *Protium apiculatum* (Burseraceae) and *Bertholletia excelsa* (Lecythidaceae) were the most important species in the secondary forest. We conclude that species richness was significantly different between the two forests, but that forest structure patterns analysed in this study (DBH, basal area and dry biomass) were similar. This

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demonstrates that 40 years was sufficient time for the secondary forest to recover the original structure of the primary forest, but not the original species richness. The low species similarity between the two forests indicates that the floristic composition was quite distinct and that the mixture of primary forest and disturbed forest has led to an increase in total species diversity.

ADDITIONAL KEYWORDS:—forest recovery – plant community – primary forest – secondary forest.

CONTENTS

INTRODUCTION

The Amazon region occupies an area of nearly 6 million km^2 in South America, most of which is covered by different forest types (Pires & Prance, 1985). A high percentage of Amazonia is covered by the type of non-flooded forest called 'terra firme' (Daly & Prance, 1989).

A major cause of tropical deforestation has been the conversion of forests to pastures to establish farms, also for tree plantations, roads and logging (Uhl *et al.*, 1982; Aide *et al.*, 1996). Over the last 20 years, 6 million hectares of the Amazon Basin have been deforested and converted to pasture (Toledo & Serrão 1982; Fearnside, 1995). However, large areas of pasture formed from Amazonian rain forest have been left fallow after only 4–8 years of use (Uhl, 1987; Buschbacher, Christopher & Serrão, 1992). Uhl *et al.* (1989, 1989) reported that despite the adverse effects of cutting and burning, the natural vegetation does not lose all of its ability to recover. However, the rate and extent of this recovery depends on the degree of disturbance and the age since abandonment.

The object of this study was to compare forest structure, species richness and floristic composition between a primary forest and a 40 year old secondary forest in order to determine whether secondary forest can attain the structure, richness and floristic composition of primary forest over a 40 year period.

MATERIAL AND METHODS

Study area

The study site is located in the Jaú National Park (JNP) 200 km north-east of Manaus, Brazil (1° 90′–3° 00′S, 61° 25′–63° 50′W). With 22 000 km^2, Jaú is the world's largest park of continuous tropical forest; 65% of this area is terra firme.

Terra firme in the JNP is characterized by dense vegetation with a large number of stems of small diameter, and canopy height varying from 20 to 30 m, with emergent species ranging from 35 to 40 m, and characterized by a high species richness and diversity (Ferreira & Prance, 1998). The soils are predominantly clay on the plateaux, with sand in the river valleys.

The climate is hot and humid (Koepen's Afi type). Mean monthly temperature ranges from 26.3° to 27.2°C. Mean total annual precipitation varies from 1700 to 2500 mm. The rain is irregularly distributed throughout the year, showing a marked dry season from June through September, and a rainy season from December through May (Radambrasil, 1978).

Data collected

Three sites of primary forest and three of secondary forest (the result of slash-and-burn shifting agriculture, where the principal crop was cassava, *Manihot esculenta*) were inventoried. At each site, a 1000 metre trail was cut. Four perpendicular 500 m transects were randomly placed along the trail. Along each of these four transects, six 10 × 40 m plots were also placed at random locations. In one of the four transects, seven plots were randomly placed to produce a total of twenty-five 400 m^2 (or an equivalent 1 ha total area) plots at each site.

In each plot all trees 10 cm DBH (Diameter at Breast Height) or larger were marked using numbered aluminium tags. Voucher specimens were identified and some collected and deposited in the INPA herbarium. The Cronquist System of classification was used in the taxonomic treatment for this study (Nee, 1995).

Data analysis

We used two-way analysis of variance (Sokal & Rohlf, 1995) to test for differences between location and site sampled for species richness, tree density, DBH, basal area and biomass. Where site effects were not significant, the data were lumped by location for one-way analysis of variance (Sokal & Rohlf, 1995). The dependent variables were log-transformed.

We calculated for each species an Importance Value Index (IVI), which is the sum of relative density, dominance and frequency of a species (Cottam & Curtis, 1962). For each family we derived a Family Importance Value (FIV), which is the sum of relative density, dominance and richness of a family (Mori *et al.*, 1983).

We used Jaccard's Coefficient (J) to quantify the species composition overlap among forest types (the complete species lists in each forest). J is defined as: $J = A/(A + B + C)$ where A = the number of species found in both paired locations, B =

species in location A but not in location B, and C = species in location B but not in location A (Magurran, 1988).

We used a non-metric multidimensional scaling ordination to determine distribution of species in the plots in the primary and secondary forests (McCune & Mefford, 1995).

The above-ground dry biomass (AGBM) was calculated using the following allometric equation: $(\exp\{3.232 + [2.546 \times \ln(\mathrm{DBH}/100)]\}) \times 600$. The 319 trees used to derive the equation ranged from 5 to 120 cm DBH and were destructively sampled to determine AGBM. Estimates of AGBM for each plot were derived by carefully measuring the diameters of all trees >10 cm diameter-at-breast-height (DBH) (Laurance *et al.*, 1997).

There were no significant transect effects for family richness, species richness, tree density, DBH, basal area and biomass ($P=0.101$, $P=0.082$, $P=0.788$, $P=0.858$, $P=0.492$ and $P=0.668$, respectively, Table 1), so we combined transect data by site (25 plots = 1 ha) in subsequent analyses.

RESULTS

Species richness and forest structure

The primary forest had a significantly higher number of families ($\bar{X}=38.0$), species richness ($\bar{X}=146.7$) and tree density ($\bar{X}=673.7$) than the secondary forest, ($\bar{X}=33.0$; $\bar{X}=88.7$ and $\bar{X}=631.3$, respectively, Table 2). Mean DBH and total basal area and biomass were not significantly different between the two forest types (Table 2).

The slope of the curve for each hectare on the primary and secondary forest declined as sample area increased, but the curves did not approach an asymptote (Fig. 1). Distribution of DBH classes in the hectares of primary and secondary forest shows the same inverse J-shape curve, with a high proportion of trees, 90% and 91%, of between 10 and 30 cm DBH, respectively (Fig. 2).

Thirty-one species attained diameters >60 cm in the primary forest. Examples include, in descending order of number of trees represented, *Scleronema micranthum* (Bombacaceae), *Copaifera* sp.1 (Cesalpiniaceae), *Bertholletia excelsa* (Lecythidaceae), *Caryocar villosum* (Caryocaraceae), and *Micrandra elata* (Euphorbiaceae). Thirty species attained diameters >60 cm in the secondary forest. The most important, in descending order of number of trees, were *Bertholletia excelsa* (Lecythidaceae), *Goupia glabra* (Celastraceae), *Scleronema micranthum* (Bombacaceae), *Caryocar glabrum* (Caryocaraceae) and *Copaifera multijuga* (Caesalpiniaceae).

Family composition

In terms of FIV the Burseraceae, Chrysobalanaceae, Lecythidaceae and Myristicaceae were the most important families in the primary forest (Table 3), while Burseraceae, Lecythidaceae, Caesalpiniaceae and Sapotaceae were the most important in the secondary forest (Table 4). Bignoniaceae (*Tabebuia serratifolia*) was restricted to the secondary forest, while Araliaceae (*Didymopanax morototoni*),

TABLE 1. Two way ANOVA results (F) and probabilities (P) of the number of families, species and trees, mean DBH, basal area and biomass in relation to forest type, area and interaction

Source of Variation	DF*	Number of families	Number of species	Number of trees	Mean DBH	Total basal area	Total biomass (ton)
Forest type	1	$F=32.06$	96.96	5.31	3.21	0.659	0.338
		$P=0.0001$	0.0001	0.082	0.075	0.418	0.562
Transect	3	$F=1.94$	1.39	1.15	2.56	2.1	2.28
		$F=0.13$	0.25	0.332	0.058	0.10	0.082
Forest type* transect	$3F=2,11$	$F=2.11$	2.28	0.35	0.25	0.81	0.522
		$P=0.101$	0.082	0.788	0.858	0.492	0.668

* DF = Degrees of freedom

TABLE 2. Summary of species richness and structure patterns on the hectares sampled in the primary and secondary forests analysed in this study

Forest type	Number of species	Number of families	Number of trees	Mean DBH (cm)	Total basal area (m^2)	Total biomass (ton)
Primary	144	36	639	21.9	32.8	405
	159	41	669	22.1	37.8	529
	137	37	713	22.1	40.2	559
mean (SD)	146.7 (9.2)	38 (2.2)	673.7 (30.4)	22.0 (0.1)	36.9 (3.1)	497.7 (66.7)
Secondary	86	32	636	21.2	28.8	340.5
	90	32	650	23.2	37	485.8
	90	35	608	24.3	39.9	585.9
mean (SD)	88.7 (1.9)	33.0 (1.4)	631.3 (17.5)	22.9 (1.3)	35.2 (4.7)	470.7 (100.7)

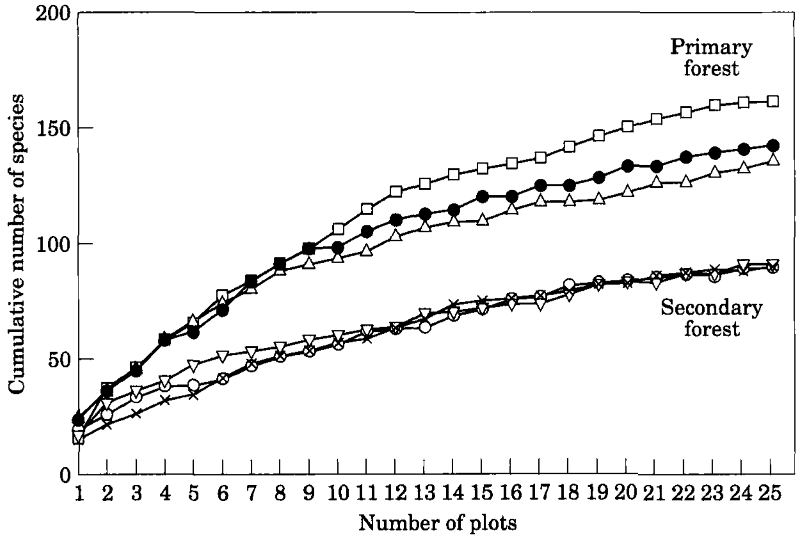

Figure 1. Number of tree species as a function of sample area in of hectares of primary and secondary forests sampled in this study.

Dichapetalaceae (*Tapura amazonica*), Lacistemaceae (*Lacistema aggegratum*), Loganiaceae (*Strychnos* sp.1), Nyctaginaceae (*Neea* cf. *altissima*), Olacaceae (*Minquartia guianensis*), Quiinaceae (*Quiina negrenesis*), Verbenaceae (*Vitex triflora*) were restricted to the primary forest.

Species composition

In terms of IVI *Alexa grandiflora* (Cesalpiniaceae), *Scleronema micranthum* (Bombacaceae) and *Pourouma guianensis* (Cecropiaceae) were the most important species in the primary forest (Table 5) while *Eschweilera grandiflora* (Lecythidaceae), *Protium apiculatum* (Burseraceae), *Bertholletia excelsa* (Lecythidaceae), *Iryanthera juruensis* (Myristicaceae) were the most important in the secondary forest (Table 6).

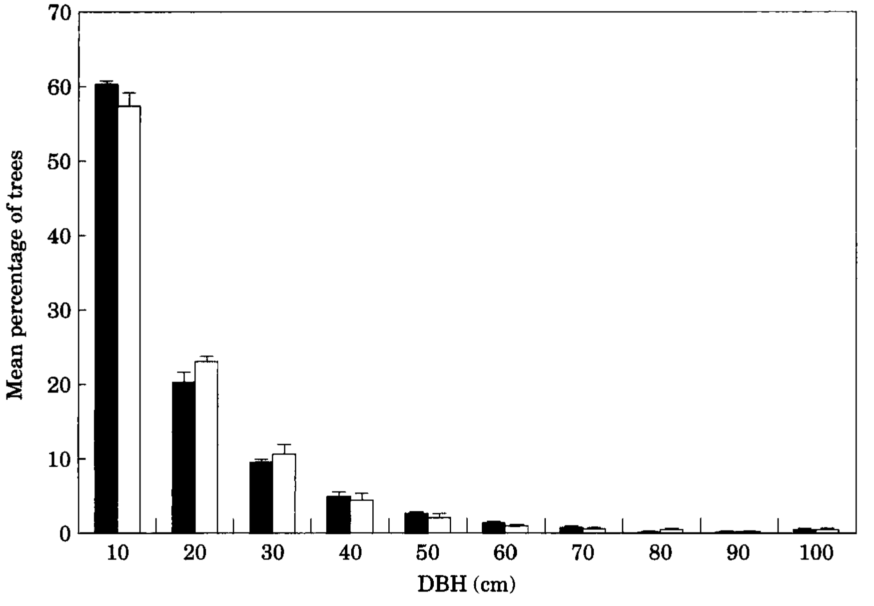

Figure 2. Mean tree DBH distribution in the hectares of primary (■) and secondary (□) forest sampled in this study.

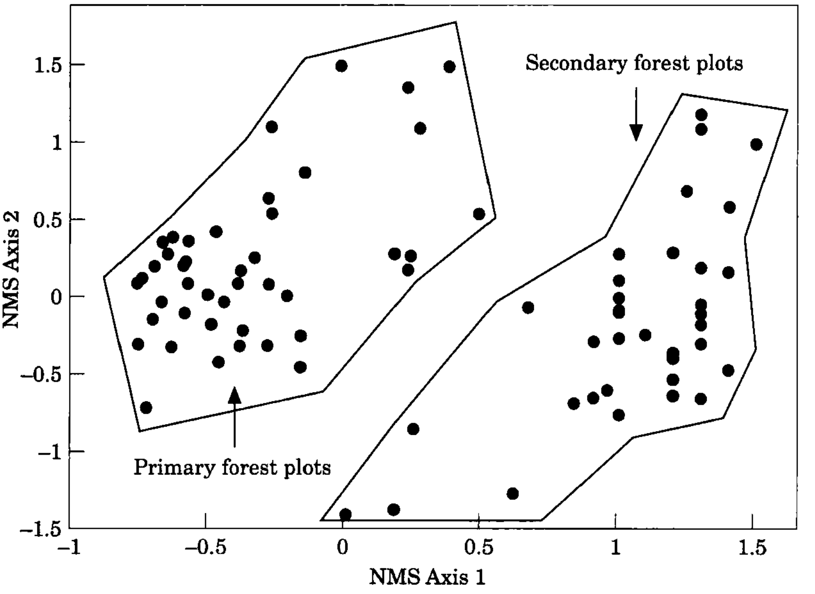

Figure 3. Ordination of plots of the primary and secondary forests derived from non-metric multidimensional scaling (NMS).

TABLE 3. Ten most important families (FIV) found in the 3 ha sampled in primary forest

Families	FIV	Relative richness	Relative density	Relative dominance (basal area)	Relative dominance (biomass)
HECTARE 1					
Chrysobalanaceae	24.9	6.9	7.5	10.5	11.0
Myristicaceae	26.1	5.6	14.1	6.4	4.8
Bombacaceae	16.8	1.4	3.8	11.6	13.9
Burseraceae	25.5	6.3	13.0	6.2	4.7
Fabaceae	19.6	2.8	7.4	9.5	9.6
Sapotaceae	19.3	8.3	5.9	5.1	4.3
Euphorbiaceae	15.0	5.6	2.7	6.8	8.5
Lauraceae	17.5	9.0	3.8	4.7	4.9
Lecythidaceae	15.9	2.8	6.7	6.4	6.4
Cecropiaceae	11.6	1.4	4.9	5.4	5.1
TOTAL	192.2	50.0	69.6	72.6	73.2
Remaining families	107.8	50.0	30.4	27.4	26.8
HECTARE 2					
Myristicaceae	25.5	6.9	11.2	7.4	5.9
Burseraceae	25.1	4.4	13.6	7.1	4.9
Mimosaceae	17.0	5.0	3.1	8.8	11.8
Bombacaceae	15.5	1.9	6.3	7.3	6.8
Lauraceae	15.6	5.0	4.9	5.6	4.9
Lecythidaceae	12.3	3.1	3.6	5.6	7.2
Euphorbiaceae	13.5	4.4	3.6	5.5	5.8
Caesalpiniaceae	12.4	4.4	3.0	5.0	5.7
Cecropiaceae	13.7	3.1	5.2	5.3	4.4
Combretaceae	6.9	0.6	0.4	5.9	9.9
TOTAL	157.6	39.0	55.0	63.6	67.3
Remaining families	142.4	61.0	45.0	36.4	32.7
HECTARE 3					
Lecythidaceae	19.4	5.1	3.2	11.1	17.6
Myristiceae	29.5	6.6	15.3	7.7	5.7
Fabacaceae	22.7	5.1	10.2	7.4	5.8
Lauraceae	21.0	7.3	7.0	6.6	5.6
Burseraceae	21.8	4.4	11.1	6.3	4.5
Caesalpiniaceae	15.4	4.4	2.9	8.0	9.4
Chrysobalanaceae	18.5	5.1	6.6	6.8	5.9
Sapotaceae	19.1	8.8	5.9	4.5	3.5
Bombacaceae	12.3	1.5	3.4	7.5	7.8
Euphorbiaceae	12.2	4.4	2.7	5.2	5.9
TOTAL	192.0	52.6	68.3	71.2	71.7
Remaining families	108.0	47.4	31.7	28.8	28.3

Species similarity indexes

The mean similarity indexes at species level was ($\bar{X}=44.6$, $SD=2.33$) between hectares in the primary forests and ($\bar{X}=41.3$, $SD=2.15$) between hectares in the secondary forests. The mean similarity indexes at species level between hectares in the primary and secondary forests was ($\bar{X}=12.1$, $SD=1.17$).

TABLE 4. Ten most important families (FIV) found in the 3 h sampled in secondary forest

Families	FIV	Relative richness	Relative density	Relative dominance (basal area)	Relative dominance (biomass)
HECTARE 5					
Burseraceae	29.6	1.1	16.2	12.3	9.7
Lecythidaceae	22.1	4.5	6.6	11.0	14.7
Arecaceae	31.9	9.1	15.5	7.3	4.9
Sapotaceae	19.0	6.8	5.0	7.2	7.1
Myristicaceae	20.4	6.8	9.1	4.5	3.4
Bombacaceae	14.1	2.3	3.5	8.4	9.6
Caesalpiniaceae	15.4	8.0	3.3	4.1	3.9
Lauraceae	13.9	4.5	4.7	4.6	5.0
Celastraceae	9.8	1.1	1.9	6.8	8.6
Cecropiaceae	12.6	3.4	3.9	5.2	4.9
TOTAL	188.8	47.7	69.7	71.4	71.8
Remaining families	111.2	52.3	30.3	28.6	28.2
HECTARE 5					
Burseraceae	28.1	1.1	16.2	10.8	8.8
Caesalpiniaceae	25.3	9.8	5.8	9.8	10.5
Myristicaceae	23.3	5.4	12.9	4.9	3.2
Lecythidaceae	15.0	4.3	3.0	7.7	10.6
Sapotaceae	19.0	9.8	4.5	4.8	4.5
Humiriaceae	13.4	3.3	2.7	7.5	8.9
Fabaceae	14.6	2.2	6.7	5.7	4.6
Bombacaceae	12.6	3.3	3.3	6.0	6.5
Lauraceae	14.7	5.4	4.7	4.5	3.9
Cecropiaceae	13.2	3.3	6.1	3.9	3.1
TOTAL	179.2	47.8	65.7	65.6	64.7
Remaining families	120.8	52.2	34.3	34.4	35.3
HECTARE 5					
Lecythidaceae	28.4	6.7	1.5	20.3	38.5
Sapotaceae	31.2	8.9	9.7	12.7	13.6
Myristicaceae	27.3	6.7	12.4	8.2	6.4
Caesalpiniaceae	19.7	5.6	4.6	9.5	9.4
Cecropiaceae	18.4	2.2	10.0	6.2	3.5
Burseraceae	17.1	1.1	10.8	5.2	2.8
Annonaceae	16.0	5.6	6.4	4.1	2.3
Lauraceae	12.7	5.6	4.1	3.1	1.8
Arecaceae	13.4	7.8	4.4	1.2	0.5
Mimosaceae	9.4	4.4	2.1	2.9	2.2
TOTAL	193.7	54.4	66.0	73.3	81.1
Remaining families	106.3	45.6	34.0	26.7	18.9

DISCUSSION

Forest structure

The size distribution of trees obtained in both primary and secondary forests in this study with a reverse J-shaped size-distribution is typical for other tropical forests (Ferreira & Rankin de-Mérona, 1997; Oliveira, 1997; Ferreira & Prance, in press). This indicates that 40 years since abandonment is enough time for secondary forest

TABLE 5. Ten most important species (IVI) found in the 3 ha sampled in primary forest

Species	IVI	Relative frequency	Relative density	Relative dominance (basal area)
HECTARE 1				
Alexa grandiflora	18.7	4.2	6.4	8.0
Scleronema micranthum	18.3	3.4	3.4	11.5
Pourouma sp.1	13.2	3.6	4.4	5.2
Iryanthera sp.1	11.9	4.0	6.4	1.5
Eschweilera coriacea	11.8	3.8	5.2	2.8
Protium sp.1	10.6	3.2	5.2	2.2
Iryanthera tricordis	8.2	2.5	3.3	2.3
Orbygnia speciosa	7.9	2.7	2.5	2.7
Protium sp.2	7.6	2.7	3.8	1.1
Couepia longipendula	7.4	1.9	2.2	3.3
TOTAL	115.6	32.1	42.7	40.7
Remaining species	184.4	67.9	57.3	59.3
HECTARE 2				
Scleronema micranthum	15.1	3.0	5.1	7.0
Pourouma sp.1	9.7	2.0	3.6	4.1
Alexa grandiflora	8.4	2.2	3.3	2.8
Protium sp.1	7.6	2.2	3.9	1.4
Iryanthera sp.1	7.4	2.6	3.7	1.0
Alchomeopsis sp.1	7.3	1.8	1.5	3.9
Protium sp.2	7.0	2.6	3.3	1.1
Buchenavia sp.2	6.7	0.4	0.4	5.9
Tetragastris sp.1	6.3	2.2	2.5	1.5
Orbygnia speciosa	6.0	2.2	2.2	1.5
TOTAL	81.5	21.5	29.6	30.4
Remaining species	218.5	78.5	70.4	69.6
HECTARE 3				
Alexa grandiflora	18.0	4.1	8.8	5.1
Scleronema micranthum	12.6	2.4	2.8	7.4
Iryanthera sp.1	11.9	3.9	6.5	1.6
Protium pedicellatum	11.4	3.5	5.0	2.8
Iryanthera tricordis	10.9	3.5	4.5	2.9
Bertholletia excelsa	8.3	0.4	0.3	7.6
Micropholis sp.3	7.4	2.8	2.7	2.0
Couepia sp.1	7.1	2.4	2.0	2.7
Micrandra	7.1	1.3	1.3	4.5
Sclerolobium sp.2	6.5	1.5	1.1	3.9
TOTAL	101.3	25.7	34.9	40.7
Remaining species	198.7	74.3	65.1	59.3

to attain a forest structure (DBH distribution) similar to that of primary forest. The same pattern is also true for basal area and biomass (Table 2).

The basal area obtained in hectares sampled in the primary forest ($\bar{X} = 36.9\ m^2$, SD = 3.08) and secondary forest ($\bar{X} = 35.2\ m^2$, SD = 4.70) of this study was high in comparison with the values from other floristic inventories in Amazonian primary forests. Boom (1986), Campbell *et al.*, (1986) and Ferreira & Rankin de-Mérona (1997) recorded $21.4\ m^2$, $29.3\ m^2$ and $24.7\ m^2$, respectively. This difference was the result of the high proportion of trees of diameters >60 cm in the hectares of primary ($\bar{X} = 2.7\%$) and secondary forests ($\bar{X} = 2.1\%$), in comparison to the values found in

TABLE 6. Ten most important species (IVI) found in the 3 ha sampled in secondary forest

Species	IVI	Relative frequency	Relative density	Relative dominance (basal area)
HECTARE 5				
Protium	35.4	6.6	16.3	12.4
Eschweilera sp.1	15.7	5.0	5.8	4.9
Scleronema micranthum	14.5	3.3	3.0	8.2
Jessenia bataua	14.3	3.6	6.6	4.1
Euterpe precatoria	12.5	3.6	6.9	2.0
Licania sp.1	12.5	4.7	4.4	3.4
Pourouma sp.1	11.7	3.6	3.6	4.5
Goupia glabra	10.9	2.2	1.9	6.8
Iryanthera tricordis	7.5	3.0	3.3	1.2
Iryanthera sp.5	7.1	3.0	3.1	0.9
TOTAL	142.1	38.7	54.9	48.5
Remaining species	257.9	61.3	45.1	51.5
HECTARE 6				
Protium	34.3	6.3	16.7	11.3
Iryanthera tricordis	17.4	5.6	9.0	2.9
Alexa grandiflora	17.1	5.3	6.1	5.6
Scleronema micranthum	12.3	3.3	2.8	6.2
Saccoglotis	10.3	2.8	2.3	5.3
Conceveiba guianensis	8.9	2.8	2.9	3.2
Licania sp.1	8.7	3.0	2.9	2.8
Sclerolobium sp.1	8.0	2.5	1.8	3.7
Bertholletia excelsa	7.5	0.8	0.5	6.3
Pourouma sp.2	7.3	2.3	2.3	2.7
TOTAL	131.9	34.6	47.3	50.0
Remaining species	268.1	65.4	52.7	50.0
HECTARE 7				
Protium	21.8	5.8	10.8	5.2
Bertholletia excelsa	19.8	0.8	0.5	18.5
Pourouma sp.2	16.3	5.0	7.2	4.1
Iryanthera tricornis	14.5	4.5	7.7	2.4
Micropholis sp.1	12.9	2.9	2.9	7.1
Copaifera multijuga	8.5	2.4	2.0	4.2
Pourouma sp.1	7.8	2.9	2.8	2.1
Theobroma subincanum	7.0	2.9	3.1	1.0
Micropholis guianensis	6.2	2.1	2.3	1.8
Licania sp.1	6.2	2.6	2.0	1.6
TOTAL	114.8	29.1	39.3	46.4
Remaining species	285.2	70.9	60.7	53.6

the studies above: 0.5%, 0.6% and 0.6%, respectively. These results can be partially explained by the high density of *Bertholletia excelsa* (Lecythidaceae) in the hectares sampled in the primary forest ($\bar{X}=2.33$, SD$=2.05$) and in the secondary forest ($\bar{X}=2.33$, SD$=0.94$). The mean DBH of this species in the hectares sampled in the former was $\bar{X}=69.9$, SD$=56.9$, and in the latter $\bar{X}=126.6$, SD$=84.8$. William F. Laurance (pers. comm.) in an inventory of 66 ha plots in terra firme forests in Central Amazonia, found no trees of this species. We conclude that these huge trees did not start their growth after cutting and burning of the area, but must have been left standing by the original agriculturalists. The same pattern could also have occurred with larger trees of other species over 30 cm.

Some studies have demonstrated a great difference in basal area and biomass accumulation between sites subjected to disturbance and primary forests. Aide *et al.* (1996) reported that age since abandonment was the best predictor of forest recovery in abandoned pastures in subtropical moist and wet forests in Puerto Rico, and suggested that 60 years is sufficient time for an abandoned pasture to regain a basal area comparable to that of undisturbed forest. Saldarriaga (1987), in a study of biomass-accumulation following slash-and-burn agriculture in northern Amazonia reported that 200 years would be required for the area to attain the biomass of primary forest. Buschbacher, Christopher & Serrão (1992), in a study of reforestation of degraded pasture in eastern Amazonia, which was subjected to light use, reported that 100 years would be required. The high number of larger (>60 cm DBH) trees found in both the primary and secondary forest sites in this study suggests that many trees did not die at the time of slash-and-burn, but either regenerated from stump sprouts or were left standing. The importance of stump and root sprouting in the recovery of cut tropical forests has frequently been mentioned (e.g. Ducke & Black, 1950; Prance, 1975). Uhl *et al.* (1982) reported that after cutting, Amazonian caatinga forest regenerated via sprouting.

An additional factor is probably the light use of our secondary forest study area, which resulted in little loss of soil nutrient concentration (Buschbacher, Christopher & Serrão 1992). In their study, Uhl *et al.* noted that there was no significant soil difference between the cut and burned treatment plots after 3 years. Saldarriaga (1987) reported that potassium stocks in the soils were similar in stands of different ages in Amazonian terra firme forest in San Carlos, Venezuela. These factors may be the reason for the rapid recuperation of total basal area and biomass of secondary forests of this study.

Species richness and floristic composition

Many factors can control succession following slash-and-burn in shifting agriculture in Amazonia, but the most important one is the degree of disturbance of the area. Uhl *et al.* (1982) reported that ecosystem recovery in Amazon caatinga forest was directly dependent on the intensity of disturbance, with early successional vegetation varying from primary forest trees (cut treatment) to successional woody species (cut and burned treatment) to forbs and grasses (bulldozed treatment). Prance (1975) and Uhl *et al.* (1981, 1982), reported that burning after cutting dramatically changes the nature of plant succession. The temperature during fires is high enough to kill shoots and to reduce significantly the size of the seed bank. Additionally, the practice of weeding largely eliminates the possibility of on-site regeneration and the only way for woody species to re-establish is by seed dispersal. The distance from primary forest is another important factor and in the case of our study area the distance was no more than 500 m.

In marked contrast to tree size and biomass, great differences in species richness were evident between the two forest types. Species richness was 1.65 times higher in primary than in secondary forest, demonstrating that 40 years after abandonment may not be sufficient time for recuperation of the original species richness of the primary forest. Ducke & Black (1950) and Jacobs (1988) reported that after some centuries a secondary forest can resemble the surrounding primary forest so closely that only an expert, through a detailed examination of its species composition, could detect any difference. Saldarriaga (1987), reported that abandoned sites of shifting cultivation in Amazonian terra firme forests in the upper Rio Negro region will probably eventually return to primary forest.

The similarity in forest structure (DBH, basal area and biomass) in the hectares sampled of primary and secondary forest in this study shows that a gap of 40 years was sufficient for the secondary forest to recuperate to a similar structure as that of the primary forest. However, differences in the number of trees, species and family richness (and especially floristic composition) show that this length of time was not nearly enough for recuperation of the original species richness. The low species similarity between the hectares of primary and secondary forest sampled also indicates that the composition is quite different, and that therefore it will take considerably longer to resemble the original forest. On the other hand, this difference in floristic composition also means a greater total diversity. Total diversity may be increased by a moderate level of disturbance, but larger areas of disturbed forest are likely to contain a significantly different species make-up from areas of primary forest.

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REFERENCES

Aide TM, Zimmerman JK, Rosario M, Marcano H. 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in Northeastern Puerto Rico. *Biotropica* **28**(4a): 537–548.

Boom B. 1986. A forest inventory in Amazonian Bolivia. *Biotropica* **18:** 287–294.

Buschbacher R, Christopher U, Serrão EAS. 1992. Reforestation of degraded Amazon pasture lands. Ecosystem Rehabilitation. In: Wali MK, ed. *Ecosystem analysis and synthesis*. Netherlands: Academic Publishing Press, 257–274.

Campbell DG, Daly DC, Prance GT, Maciel UN. 1986. Quantitative ecological inventory of terra firme and várzea tropical forest on the Rio Xingú Brazilian Amazon. *Brittonia* **38:** 369–393.

Cottam G, Curtis JT. 1962. *Plant ecology workbook*. Minneapolis: Burgess Publishing Co.

Daly DC, Prance GT. 1989. Brazilian Amazon. In: Campbell DG, Hammond HD, eds. *Floristic inventory of tropical countries*. New York: The New York Botanical Garden, 401–426.

Ducke A, Black GA. 1950. Phytogeographical notes in the Brazilian Amazon. *Academia Brasileira de Ciências* **25:** 1–46.

Fearnside PM. 1995. Potential impacts of climatic change on natural forests and forestry in Brazilian Amazonia. *Forest Ecology and Management* **78:** 51–70.

Ferreira LV, Rankin de-Mérona J. 1997. Floristic composition and structure of a one-hectare plot in terra firme forest in Central Amazonia. In: Dallmeier F, Comiskey JA eds. *Forest Biodiversity in*

North, Central and South America and the Caribbean: Research and monitoring. Man and Biosphere series, Vol. 22. Carnforth, UK: Parthenon Publishing, 655–668.

Ferreira LV, Prance GT. 1998. Species richness and floristic composition in four hectares in the Jaú National Park in upland forest in Central Amazonia. *Biodiversity and Conservation* **7:** 1349–1364.

Jacobs M. 1988. *The tropical rain forest: A first encounter.* New York: Springer-Verlag.

Laurance WF, Ferreira LV, Rankin de-Mérona J, Hutchings R. (in press). Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. *Ecology.*

Laurance WF, Laurance SG, Ferreira LV, Rankin de-Mérona J, Gascon C, Lovejoy, TE. 1997. Biomass Collapse in Amazonian forest fragments. *Science* **278:** 1117–1118.

Magurran AE. 1988. *Ecological Diversity and its Measurement.* Princeton, NJ: Princeton University Press.

McCune BJ, Mefford MJ. 1995. *PC-ORD. Multivariate version 2.0.* Gleneden Beach, Oregon, USA: MjM Software Design.

Mori SA, Boom B, Carvalho AM, Santos TS. 1983. Ecological importance of Myrtaceae in a Eastern Brazilian wet forest. *Biotropica* **15:** 68–70.

Nee M. 1995. *Flora preliminar do Projeto Dinâmica Biológica de Fragmentos Florestais (PDBFF).* New York Botanical Garden and INPA/SI.

Oliveira AA. 1997. Diversidade, estrutura e dinâmica do componente arbóreo de uma floresta de terra firme de Manaus, Amazonas. Unpublished Ph.D. Thesis. Universidade de São Paulo.

Pires JM, Prance GT 1985. The vegetation types of the Brazilian Amazon. In: Prance GT, Lovejoy TE, eds. *Amazonia: key environment.* London: Pergamon Press, 109–145.

Prance GT. 1975. The history of the INPA capoeira based on ecological studies of Lecythidaceae. *Acta Amazonica* **5(3):** 261–263.

Radambrasil. 1978. *Projeto Radambrasil. Levantamento e recursos naturais.* Manaus: Ministério das Minas e Energia, Brazil.

Saldarriaga JC. 1987. Recovery following shifting cultivation. In: Jordan CF, ed. *Amazonian Rain Forests, Ecosystem Disturbance and Recovery. Ecological Studies 60.* New York: Springer-Verlag, 23–33.

Sokal RR, Rohlf FJ. 1995. *Biometry,* 3rd ed. New York: WH Freeman.

Toledo JM, Serrão EAS. 1982. Pasture and animal production in Amazonia. In: Hecht SE, ed. *Amazonia: agriculture and land-use research.* Cali, Colombia: CIAT 281–310.

Uhl C. 1987. Factors controlling succession following slash-and -burn agriculture in Amazonia. *Journal of Ecology* **75:** 377–407.

Uhl C, Clark K, Clark H, Murphy P. 1981. Early plant succession after cutting and burning in the upper Rio Negro region of the Amazon Basin. *Journal of Ecology* **69:** 631–649.

Uhl C, Jordan C, Clark K, Clark H, Herrera R. 1982. Ecosystem recovery in Amazonia caatinga forest after cutting, cutting and burning, and bulldozer clearing treatments. *Oikos* **38:** 313–320.

Uhl C, Nepstad D, Buschbacher R, Clark K, Kauffman B, Subler S. 1989. Disturbance and regeneration in Amazonia: lessons for sustainable land-use. *The Ecologist* **19**(6): 235–240.