CHAPTER 6

Lecythidaceae of a Central Amazonian Lowland Forest

Implications for Conservation

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The Lecythidaceae are often ecologically important members of Neotropical forests where they are especially abundant in lowland, nonflooded forests. In various ecological studies of lowland forests, especially in Amazonia and in the Guyana floristic province, the family often ranks among the ten most important families of trees (Black, Dobzhansky, and Pavan 1950; Cain et al. 1956; Prance, Rodrigues, and da Silva 1976; Prance and Mori 1979; Balslev et al. 1987; Mori and Boom 1987; Mori, Becker, et al. 1989). These studies, however, provide little information on sample variability—mostly because of the time and expense involved in replicating samples in the species-rich lowland forests of the tropics.

The purpose of this study was to provide information on the frequency, density, dominance, and species richness of Lecythidaceae based on a 100 ha sample from central Amazonian Brazil. The information provided herein will furnish the baseline data needed for comparing changes in the composition of Lecythidaceae as a result of forest fragmentation or climate change. Moreover, our experience with sampling diversity of Lecythidaceae provides insight into the number of hectares that should be sampled in order to reach an understanding of the species richness of this ecologically important family of tropical trees.

Study Site

The Lecythidaceae study plot is located in Reserve 1501, a 1,000 ha control reserve of the BDFFP located within more or less continuous forest. Reserve 1501 is also called Km 41 because it is situated 41 kilometers along state highway ZF-3 from federal highway BR-174 (the Manaus-Boa Vista highway) (see fig. 4.1).

The mean annual temperature for Manaus, some 80 km south of Reserve 1501, is 26.7° C with monthly means fluctuating only by about 2° C. Maximum temperatures range between 35° and 39° C and minimum temperatures between 19° and 21° C. Cool air masses, often occurring at the transition between the rainy and dry seasons, can drop temperatures to 17° C. There is a distinct dry season between July and September, and these months normally receive less than 100 mm of rain (BDFFP 1990; Lovejoy and Bierregaard 1990). Local winds may on occasion be strong enough to topple trees (Nelson 1994; Nelson, Kapos, et al. 1994), although no large blowdowns are known to

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have occurred since 1987 at Reserve 1501. The difference in day length between the longest and shortest days of the year at Manaus is about eighteen minutes (List 1950).

The plot is dissected by several small streams, especially one that flows north to south in the middle of the eastern half of the plot, and there is a plateau in the northeastern corner (Mori and Becker 1991). Although there are wetter areas along small streams and periodic small ponds form for unusually long periods during years of excessive rainfall (Mori and Becker 1991), this plot is typical of the terra firme habitat found throughout central Amazonia. As in any other tropical forest, the formation of small and mid-sized gaps is common (Denslow 1980).

The reserves of the BDFFP are located on extensive Tertiary sediments within the ancient meander plain of the Amazon. However, Reserve 1501 is not situated near any major river, and as a result there are no recent alluvial deposits in the plot. The soils in the plot are sandy or clayey latosols that have been subjected to long periods of leaching and are therefore generally poor in nutrients (Lovejoy and Bierregaard 1990). In the Lecythidaceae plot, soils dominated by clay are prevalent, but soils richer in sand occur in the northwestern and southwestern corners (P. Becker et al., unpublished data). Charcoal is ubiquitous in the soil of the plot (Bassini and Becker 1990), but there is no evidence, based on a study of plant remnants in the soil (phytoliths), that crops were ever grown there (Piperno and Becker 1996).

Reserve 1501 is situated in terra firme forest at between 80 and 110 meters altitude. The forest is dominated mostly by species of Sapotaceae, Lecythidaceae, and Burseraceae (Oliveira 1997). Palms, especially spiny ones of the genus *Astrocaryum*, are abundant in the understory. Within all of the reserves of the BDFFP, there are at least 57 families (Oliveira 1997) and over 800 species of trees (BDFFP 1990). Nee (1995) has published a preliminary vascular plant flora of the BDFFP reserves, and Oliveira (1997) has reported on total tree species richness per hectare based on a sample of all trees of at least 10 cm DBH (diameter at breast height, or 1.3 m from the ground on the uphill side of the trunk) in three hectares of the Lecythidaceae plot.

Methods

The area for the 100 ha plot was selected by Becker in consultation with Marc van Roosmalen to include the major types of topography. A factor in plot selection was proximity to the camp at Reserve 1501. The plot was professionally surveyed, and care was taken to ensure that each 20 × 20 m quadrat contained 400 m^2 in horizontal projection, as was subsequently recommended by Dallmeier (1992). A stake was placed at the corners of all of the 20 × 20 m quadrats, and a plaque marked with the *x* and *y* coordinates was affixed to the stake. Each of the 100 hectares is identified by the *x,y* coordinates of its southwesternmost stake.

All individuals of Lecythidaceae at least 10 cm DBH were located by experienced woodsmen under the supervision of a Brazilian student intern and confirmed by Mori. Individuals of Lecythidaceae are relatively easy to identify because of the fibrous nature of their bark (Mori, Becker, et al. 1987), but mistakes, especially in distinguishing between species of Annonaceae and species of Lecythidaceae, are sometimes made. The position of each individual was then recorded by measuring the distance and azimuth to the individual from one of the corner stakes.

After the trees were marked and meas-

TABLE 6.1. Density, Dominance, and Diversity of Lecythidaceae per Hectare in a 100 ha Plot at Reserve 1501

Hectare Coordinates	Density (trees/ha)	Dominance (m²/ha)	Diversity (spp./ha)
0,0	142	5.26	12
0,5	89	4.24	15
0,10	107	3.57	13
0,15	113	5.06	22
0,20	109	4.05	18
0,25	92	3.50	18
0,30	122	5.65	20
0,35	125	4.38	15
0,40	87	2.54	16
0,45	93	4.60	19
5,0	90	4.04	20
5,5	86	3.16	19
5,10	73	3.34	15
5,15	99	4.01	18
5,20	149	5.71	18
5,25	117	4.12	22
5,30	82	4.00	17
5,35	86	3.02	19
5,40	75	2.65	15
5,45	79	3.33	24
10,0	50	2.26	17
10,5	65	2.64	16
10,10	73	3.85	21
10,15	103	3.69	18
10,20	77	3.63	20
10,25	116	4.34	18
10,30	69	3.33	16
10,35	89	3.58	18
10,40	75	5.11	20
10,45	84	3.42	18
15,0	45	3.19	18
15,5	62	2.40	15
15,10	68	2.67	12
15,15	64	2.89	13
15,20	80	3.67	20
15,25	82	3.01	20
15,30	91	4.08	18
15,35	74	3.74	15
15,40	60	2.64	18
15,45	72	4.50	16
20,0	100	4.25	21
20,5	78	3.51	18
20,10	72	4.49	13
20,15	74	4.34	18
20,20	68	3.12	16
20,25	76	3.85	17
20,30	81	6.56	18
20,35	69	4.31	20
20,40	64	4.55	15
20,45	74	4.77	20
25,0	72	3.84	17
25,5	51	2.13	11
25,10	71	2.92	14
25,15	70	4.15	18
25,20	58	4.59	20
25,25	65	3.48	16
25,30	55	3.24	23
25,35	87	5.00	18
25,40	82	5.35	18
25,45	70	3.51	19
30,0	65	2.76	15
30,5	51	4.84	18
30,10	49	3.11	13
30,15	90	5.01	13
30,20	77	3.78	18
30,25	90	4.83	16
30,30	84	4.09	17
30,35	90	2.92	19
30,40	100	4.64	21
30,45	85	4.12	18
35,0	61	2.62	16
35,5	52	2.85	13
35,10	75	3.34	15
35,15	85	4.13	16
35,20	54	2.23	14
35,25	79	4.59	20
35,30	83	2.80	17
35,35	95	3.49	20
35,40	85	3.72	16
35,45	102	2.83	21
40,0	45	3.04	13
40,5	73	3.50	17
40,10	64	3.33	15
40,15	55	2.69	13
40,20	78	4.25	16
40,25	70	2.98	14
40,30	58	3.91	19
40,35	65	5.00	21
40,40	74	3.11	18
40,45	65	3.11	19
45,0	89	3.65	17
45,5	73	4.85	19
45,10	79	4.64	21
45,15	52	2.77	18
45,20	53	4.03	17
45,25	57	3.84	16
45,30	56	3.01	15
45,35	59	3.93	17
45,40	63	3.74	15
45,45	60	3.43	18
Totals	7,791	376.34	

TABLE 6.2. Frequency, Density, Dominance, and Within Family Importance Values for Species of Lecythidaceae in a 100 ha Plot at Reserve 1501

Species[1]	Absolute frequency[2]	Absolute density[3]	Absolute dominance[4]	Relative frequency[5]	Relative density[6]	Relative dominance[7]	WFIV[8]
ALLI	5	5	.46	0.3	0.1	0.1	0.5
BEEX	1	1	1.04	0.1	<0.1	0.3	0.3
CADE	29	40	4.35	1.7	0.5	1.2	3.4
CAMI	27	29	9.93	1.6	0.4	2.6	4.6
COAL	75	192	15.85	4.3	2.5	4.2	11.0
CORI	63	208	13.81	3.6	2.7	3.7	10.0
CUGU	18	21	1.79	1.0	0.3	0.5	1.8
CULO	14	14	.36	0.8	0.2	0.1	1.1
CUMU	20	24	1.29	1.2	0.3	0.3	1.8
CUST	41	77	5.31	2.4	1.0	1.4	4.8
CUTA	2	3	.09	0.1	<0.1	<0.1	0.1
ESAF	51	190	11.26	2.9	2.4	3.0	8.3
ESAT	96	571	24.50	5.5	7.3	6.5	19.3
ESBR	61	105	1.51	3.5	1.3	0.4	5.2
ESCA	8	10	1.01	0.5	0.1	0.3	0.9
ESCO	28	55	2.35	1.6	0.7	0.6	2.9
ESCR	95	1,539	64.85	5.5	19.8	17.2	42.5
ESCY	75	275	31.47	4.3	3.5	8.4	16.2
ESGR	93	335	8.63	5.4	4.3	2.3	12.0
ESLA	41	57	3.89	2.4	0.7	1.0	4.1
ESMI	73	180	12.25	4.2	2.3	3.3	9.8
ESPE	61	100	1.43	3.5	1.3	0.4	5.2
ESPS	48	118	8.18	2.8	1.5	2.2	6.5
ESRC	68	309	8.91	3.9	4.0	2.4	10.3
ESRN	13	16	1.48	0.8	0.2	0.4	1.4
ESTE	84	250	6.49	4.8	3.2	1.7	9.7
ESTR	95	1,321	53.52	5.5	17.0	14.2	36.7
ESWA	99	926	22.90	5.7	11.9	6.1	23.7
GUEL	30	111	2.64	1.7	1.4	0.7	3.8
LEBA	53	105	2.22	3.1	1.3	0.6	5.0
LEGR	31	40	3.64	1.8	0.5	1.0	3.3
LEPA	22	30	4.72	1.3	0.4	1.3	3.0
LEPI	36	46	4.96	2.1	0.6	1.3	4.0
LEPR	90	362	23.23	5.2	4.6	6.2	16.0
LERE	7	11	.90	0.4	0.1	0.2	0.7
LEZA	29	51	10.59	1.7	0.7	2.8	5.2
LE01	7	8	.23	0.4	0.1	0.1	0.6
LE05	40	51	3.39	2.3	0.7	0.9	3.9
INDETS	4	4	.92	0.2	0.1	0.2	0.5
TOTAL	1,733	7,791	376.35	≈100.0	≈100.0	≈100.0	≈300.0

Notes: [1]Species codes: ALLI, *Allantoma lineata* (Martius ex Berg) Miers; BEEX, *Bertholletia excelsa* Humboldt & Bonpland; CADE, *Cariniana decandra* Ducke; CAMI, *C. micrantha* Ducke; COAL, *Corythorphora alta* R. Knuth; CORI, *C. rimosa* W. Rodrigues subsp. *rimosa;* CUGU, *Couratari guianensis* Aublet emend. Prance; CULO, *C. longipedicellata* W. Rodrigues; CUMU, *C. multiflora* (J. E. Smith) Eyma; CUST, *C. stellata* A. C. Smith; CUTA, *C. tauari* Berg; ESAF, *Eschweilera amazoniciformis* Mori; ESAT, *E. atropetiolata* Mori; ESBR, *E. bracteosa* (Poeppig ex Berg) Miers; ESCA, *E. carinata* Mori; ESCO, *E. collina* Eyma; ESCR, *E. coriacea* (A. P. de Candolle) Mori; ESCY, *E. cyathiformis* Mori; ESGR, *E. grandiflora* (Aublet) Sandwith; ESLA, *E. laevicarpa* Mori; ESMI, *E. micrantha* (Berg) Miers; ESPE, *E. pedicellata* (Richard) Mori; ESPS, *E. pseudodecolorans* Mori; ESRN, *E. rankiniae* Mori; ESRC, *E. romeu-cardosoi* Mori; ESTE, *E. tessmannii* R. Knuth; ESTR, *E. truncata* A. C. Smith; ESWA, *E. wachenheimii* (R. Benoist) Sandwith; GUEL, *Gustavia elliptica* Mori; LEBA, *Lecythis barnebyi* Mori; LEGR, *L. gracieana* Mori; LEPA, *L. parvifructa* Mori; LEPI, *L. pisonis* Cambessèdes; LEPR, *L. prancei* Mori; LERE, *L. retusa* Spruce ex Berg; LEZA, *L. zabuajo* Aublet; LE01, *Lecythis* sp. 01; LE05, *Lecythis*, sp. 05. [2]Number of hectares in which species is found. [3]Number of trees of a species per 100 ha. [4]Basal area of a species per 100 ha. [5]Total number of occurrences of a species of Lecythidaceae/total number of occurrences of all species of Lecythidaceae. [6]Total number of trees of a species of Lecythidaceae/total number of trees of all species of Lecythidaceae. [7]Total basal area of a species of Lecythidaceae/total basal area of all species of Lecythidaceae. [8]Relative frequency + relative density + relative dominance.

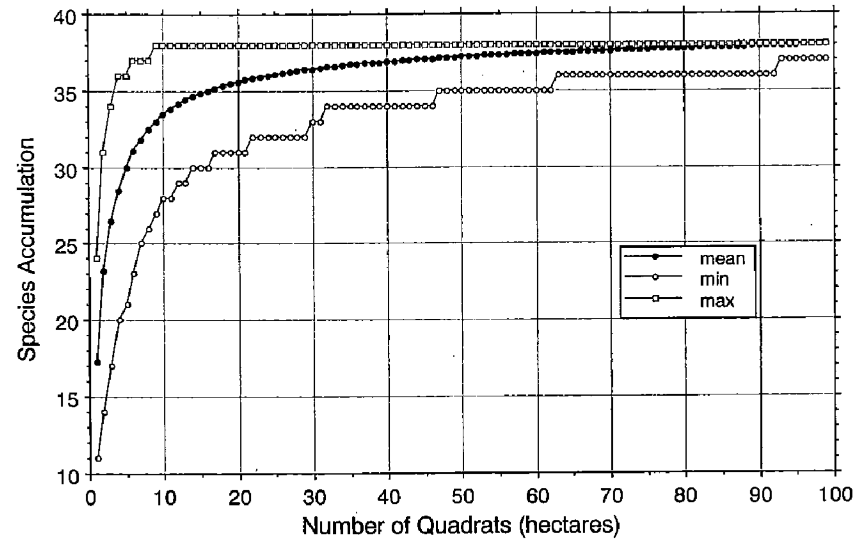

Fig. 6.1. Species-area curves generated from sampling hectare combinations without replacement. N = 10,000 except for the single and 2 ha samples which are exact solutions. The lower curve represents the minimum number of species, the middle curve the mean number of species, and the upper curve the maximum number of species for each combination of quadrats.

ured, Mori began the long process of identification to species. Each tree was visited, and the bark, leaves, and flowers and fruits, when available, were examined. When there was any doubt about the determination, a herbarium specimen was collected as a voucher. The vouchers are mostly deposited in the herbaria of the Instituto Nacional de Pesquisas da Amazonia (INPA), the New York Botanical Garden, and the Smithsonian Institution. A list of the vouchers is available from Mori. All identifications, locations of the trees, DBH, and other data are kept in a database (dBase III) under the supervision of Becker.

The field crew, which lived at Reserve 1501 for five years, was asked to make collections of all species that came into flower or fruit. The fertile material sometimes revealed mistakes in determination that had to be resolved on subsequent visits by the senior author to all of the trees with dubious determinations. This process was made possible by the lists of species and their locations generated from the database. Species concepts follow Mori and Lepsch-Cunha's floristic treatment of all species of Lecythidaceae known to occur in the 100 ha plot (Mori and Lepsch-Cunha 1995). In addition, Mori and Prance (1990) and Prance and Mori (1979) present taxonomic treatments, including distribution maps, of the 198 species of Neotropical Lecythidaceae known at the time of the publication of these monographs. An additional seven species have since been described (Mori 1992a, 1995; Mori and Lepsch-Cunha 1995).

Notes on the habitat preferences of the species of Lecythidaceae found at Reserve 1501 can be found in Mori and Lepsch-Cunha (1995). With the exception of *Allantoma lineata,* a species found along streams, all of the species in the Lecythidaceae plot prefer terra firme forest.

Absolute density, absolute dominance, and species richness of Lecythidaceae were tabulated for each of the hectares sampled (table 6.1), and absolute frequency, absolute

TABLE 6.3. Samples of 1, 2, 5, 10, 20, 25 and 50 Hectares

Sample size and combinations	Species richness	Frequency	Probability	Mean species richness per sample
1 ha sample				17.3
(all 100 possible	11	1	.0200	
combinations of	12	2	.0100	
1 taken out of 100)	13	8	.0800	
	14	3	.0300	
	15	12	.1200	
	16	12	.1200	
	17	10	.1000	
	18	23	.2300	
	19	8	.0800	
	20	11	.1100	
	21	6	.0600	
	22	2	.0200	
	23	1	.0100	
	24	1	.0100	
2 ha sample				23.2
(all 4,950 possible	14	1	.0002	
combinations of	15	10	.0020	
2 taken out of 100)	16	24	.0048	
	17	42	.0085	
	18	93	.0188	
	19	181	.0366	
	20	330	.0667	
	21	575	.1162	
	22	708	.1430	
	23	762	.1539	
	24	733	.1481	
	25	611	.1234	
	26	449	.0907	
	27	216	.0436	
	28	135	.0273	
	29	52	.0105	
	30	24	.0048	
	31	4	.0008	
5 ha sample				30.0
(10,000 combinations	21	1	.0001	
of 5 taken out of 100)	23	4	.0004	
	24	28	.0028	
	25	96	.0096	
	26	262	.0262	
	27	635	.0635	
	28	1,201	.1201	
	29	1,737	.1737	
	30	2,040	.2040	
	31	1,824	.1824	
	32	1,253	.1253	
	33	658	.0658	
	34	220	.0220	
	35	36	.0036	
	36	5	.0005	

TABLE 6.3. (continued) Samples of 1, 2, 5, 10, 20, 25 and 50 Hectares

Sample size and combinations	Species richness	Frequency	Probability	Mean species richness per sample
10 ha sample				33.4
(10,000 combinations	28	2	.0002	
of 10 taken out of 100)	29	23	.0023	
	30	179	.0179	
	31	659	.0659	
	32	1,567	.1567	
	33	2,607	.2607	
	34	2,671	.2671	
	35	1,697	.1697	
	36	517	.0517	
	37	69	.0069	
	38	9	.0009	
20 ha sample				35.6
(10,000 combinations	31	2	.0002	
of 20 taken out of 100)	32	13	.0013	
	33	230	.0230	
	34	1,140	.1140	
	35	3,169	.3169	
	36	3,601	.3601	
	37	1,631	.1631	
	38	214	.0214	
25 ha sample				36.1
(10,000 combinations	32	1	.0001	
of 25 taken out of 100)	33	52	.0052	
	34	432	.0432	
	35	2,107	.2107	
	36	4,043	.4043	
	37	2,810	.2810	
	38	555	.0555	
50 ha sample				37.2
(10,000 combinations	34	1	.0001	
of 50 taken out of 100)	35	61	.0061	
	36	1,383	.1383	
	37	5,011	.5011	
	38	3,544	.3544	

Note: The samples were run without replacement of the hectares, and each sample run, except those of 1 and 2 ha, was performed 10,000 times.

density, and absolute dominance (Curtis and Cottam 1962) were calculated for each of the species of Lecythidaceae present in the 100 ha plot (table 6.2). Finally, relative frequency, relative density, and relative dominance of each species of Lecythidaceae in relation to all other species of the family were calculated and summed to give the Within Family Importance Value (WFIV) in the manner of Boom and Campos (1991) for the Rubiaceae (table 6.2).

Known species richness of Lecythidaceae in the Neotropics was obtained from the *Flora Neotropica* monographs of Prance and

Mori (1979) and Mori and Prance (1990), as well as from papers with new species published subsequent to these monographs (Mori 1992a; Mori and Lepsch-Cunha 1995).

Species-area curves were prepared based on exact and approximate randomization analyses (performed by Kincaid) of the number of species added to the total with each additional hectare sampled. For each sample run, the hectares were sampled randomly without replacement. Analyses were based on 10,000 sample runs for sample combinations greater than two (fig. 6.1 and table 6.3).

Results

The 100 ha plot at Km 41 harbors thirty-eight species of Lecythidaceae (table 6.2). Only one other species, *Lecythis poiteaui* Berg, is known to occur elsewhere at Km 41. The species in the Lecythidaceae plot are represented by 7,791 individuals at least 10 cm DBH, which are found throughout the entire plot.

Frequency

Individuals of Lecythidaceae are found in all of the 100 hectares (table 6.1). Five species (*Eschweilera atropetiolata, E. coriacea, E. grandiflora, E. truncata,* and *E. wachenheimii*) occur in more than 90 percent and sixteen species occur in at least half of the hectares (table 6.2). In contrast, the least frequent species is *Bertholletia excelsa* (Brazil nut), which is represented by only one individual in the entire plot. Ten species were found in fewer than 25 percent of the hectares sampled.

Density

A total of 7,791 individuals of Lecythidaceae at least 10 cm DBH were recorded in the 100 ha plot (see tables 5.1, 5.2). As few as 45 individuals were found in hectare 15,0, and as many as 149 in hectare 5,20 (table 6.1). The mean density of Lecythidaceae per hectare is 77.9 ± 19.9 (mean ± SD). Some species, such as *Eschweilera coriacea* and *E. truncata,* are abundant, with 1,539 and 1,321 individuals, respectively, in the 100 ha plot (table 6.2).

Dominance

Total basal area for all Lecythidaceae in the 100 ha plot is 376.34 m^2 (table 6.1), and average basal area per hectare is 3.76 ± 0.86 m^2 (mean ± SD). Hectare 20,30, with 6.56 m^2, possesses the greatest basal area, and hectare 25,5, with 2.13 m^2, the least basal area of Lecythidaceae. *Eschweilera coriacea* (64.85 m^2/100 ha) and *E. truncata* (53.52 m^2/100 ha), because of their high densities and relatively large sizes, are the most dominant species of Lecythidaceae in the 100 ha plot (table 6.2).

Within Family Importance Value

The ecologically most important species of Lecythidaceae in the 100 ha plot are: *Eschweilera coriacea* (WFIV = 42.5), *E. truncata* (36.7), *E. atropetiolata* (19.3), *E. cyathiformis* (16.2), *Lecythis prancei* (16.0), *Eschweilera grandiflora* (12.0), *Corythophora alta* (11.0), *Eschweilera romeu-cardosoi* (10.3), and *Corythophora rimosa* (10.0). These nine species account for 58 percent of the possible 300-point WFIV index.

Species Richness

The total number of species in the 100 ha plot is thirty-eight (table 6.2). A single other species, *Lecythis poiteaui,* is also known from the reserve, but it does not occur in the plot (Mori and Lepsch-Cunha 1995). Hectare 25,5, with only eleven species, and hectare

5,45, with twenty-four species of Lecythidaceae, represent the least and most species-rich hectares, respectively. The mean number of species per hectare in the plot is 17.3 ± 2.6 (mean ± SD).

We generated three simulated species-area curves for the 100 ha Lecythidaceae plot (fig. 6.1). The lower curve represents the fewest and the upper curve the greatest number of species sampled per specified number of hectares. The middle curve gives the mean number of species sampled. Species richness was calculated for 1, 2, 5, 10, 20, 25, and 50 ha samples—each, except for the 1 and 2 ha samples, based on a draw of 10,000 combinations of the number of hectares sampled from the 100 ha plot. For example, a sample of 10 hectares yields as few as 28 (P = 0.0002), as many as 38 (P = 0.0009), and a mean of 33.4 species (table 6.3). A 20 ha sample yields as few as 31 (P = 0.0002), as many as 38 (P = 0.0214), and a mean of 35.6 species.

Discussion

The high frequency, density, and species richness of Lecythidaceae in the 100 ha plot at Reserve 1501 suggest that central Amazonia may harbor the world's greatest number of individuals and species richness of Lecythidaceae.

At least 45 and as many as 149 individuals of Lecythidaceae were found in 100 percent of the 100 ha sampled (table 6.1), demonstrating that this family is found everywhere in the terra firme habitat of this area. A mean density of 77.9 ± 19.9 (mean ± SD) individuals of Lecythidaceae per hectare is considerably higher than that found in any other study. The next highest reported density of Lecythidaceae is the 50.3 individuals/ha found in central French Guiana by Mori and Boom (1987).

The mean basal area of Lecythidaceae in the 100 ha plot of 3.76 ± 0.86 m^2 (mean ± SD) per hectare is considerably lower than the 5.47 m^2 reported for the family in central French Guiana (Mori and Boom 1987). The average basal area per tree of Lecythidaceae in the 100 ha plot is 483.0 cm^2 (calculated from data provided in tables 5.1 and 5.2) in contrast to 1,086.7 cm^2 per tree in central French Guiana (Mori and Boom 1987) indicating that, at least for Lecythidaceae, the French Guianan forest possesses considerably larger trees. Although this has not yet been tested, the forests of central Amazonia appear to be relatively small in stature in contrast to some other areas, such as central French Guiana (Mori, pers. obs.). Small tree size in this part of central Amazonia may be attributed to some combination of the relatively poor soils, low quantity, and seasonality of rainfall found in the area.

Oliveira (1997), in his study of overall tree diversity among individuals of trees at least 10 cm DBH in hectares 10,10; 25,30; and 5,35 of the Lecythidaceae plot, found 285 species among 618 individuals, 280 species among 654 individuals, and 280 species among 644 individuals in these hectares, respectively. His data demonstrate that central Amazonia possesses overall tree species richness in the at least 10 cm size class comparable to that found by Gentry (1988) of about 300 species/hectare in Amazonian Peru and by Valencia, Balslev, and Paz y Miño (1994) of 307 species/hectare in Amazonian Ecuador.

In the hectares studied by Oliveira, the Lecythidaceae comprise 21 species among 73 individuals, 23 species among 55 individuals, and 19 species among 86 individuals, respectively (table 6.1). In these hectares, Lecythidaceae comprise 6.8 to 8.2 percent of the total species and 8.4 to 13.4 percent of the total individual trees at least 10 cm DBH.

The presence of thirty-eight species of

Lecythidaceae in such a limited area is far higher than that heretofore reported for the family. Thirty-one species of Lecythidaceae have been found in central French Guiana (Mori and collaborators 1987; Mori, unpublished data), but that figure is from an unspecified and much larger area. Mori (1990) has pointed out that slightly more than 50 percent of Neotropical Lecythidaceae are found in Amazonia, a finding that agrees with Gentry's claim (1982) that Amazonia is a center for overall species richness of trees and lianas. Therefore, reserves in Amazonia, more than anywhere else in the Neotropics, will protect disproportionately high numbers of trees and lianas. Moreover, because trees are the structural species that provide the habitat for interstitial species (e.g., herbs, shrubs, epiphytes) (Huston 1994), conservation programs designed to protect tree species richness also conserve numerous other associated species of plants and animals.

The per-hectare species richness of Lecythidaceae in the 100 ha plot is the highest heretofore reported for this family. The mean species richness for the 100 ha of 17.3 ± 2.6 (mean ± SD) species/ha is similar to the eighteen species that Prance, Rodrigues, and da Silva (1976) found in a single hectare of comparable forest in central Amazonia. Such high species diversity of trees in a family per hectare, however, is not unusual in Amazonian forests. For example, Valencia, Balslev, and Paz y Miño (1994) found 20 species of *Pouteria*, 19 species of *Inga*, and 14 species of *Protium* in a hectare surveyed in Amazonian Ecuador.

The high species richness of central Amazonian Lecythidaceae is partially the result of a mixture of species from western Amazonia (e.g., *Eschweilera bracteosa* and *E. tessmannii*), species from the Guyana floristic province (e.g., *Eschweilera collina* and *Lecythis poiteaui*), and widespread species (e.g., *Couratari guianensis* and *Eschweilera coriacea*) that may have migrated into central Amazonia after the recession of a lake (Lago Amazonas) that covered large expanses of central Amazonia in the late Pleistocene into the early Holocene (Frailey et al. 1988; Mori 1991). Others (Tuomisto, Ruokolainen, and Salo 1992), however, argue that the presence of lacustrine sediments in Amazonia can be explained by mechanisms other than the presence of a Pleistocene Lago Amazonas.

The occurrence of possible endemic taxa of Lecythidaceae in central Amazonia (e.g., *Corythophora rimosa* subsp. *rimosa*, *Couratari longipedicellata*, *Eschweilera amazoniciformis*, *E. cyathiformis*, *E. seudodecolorans*, *E. rankiniae*, *E. romeu-cardosoi*, *Gustavia elliptica*, *Lecythis barnebyi*, *L. gracieana*, *L. parvifructa*, and *L. retusa*) may be an artifact of incomplete botanical exploration as noted by Nelson, Ferreira, et al. (1990) for other taxa. These species, however, may also represent peripheral populations of forest species cut off from more widespread ancestral species by savanna habitats caused by climatic fluctuations or by the appearance and disappearance of water barriers, occurring in the Pleistocene and Holocene. It is unlikely that these endemics are the result of adaptations to habitat heterogeneity (Tuomisto et al. 1995) because they are found today in habitats similar to those of their relatives. For example, the morphologically most similar species to *L. barnebyi* and *E. amazoniciformis* are the Guianan species *L. poiteaui* and the eastern to central Amazonian species *E. amazonica* R. Knuth (Mori 1990). In both cases, the ranges of the two species pairs overlap in central Amazonia and all four species are found in terra firme forest. If this apparent endemism is real, then species richness of Lecythidaceae in central Amazonia is considerably enhanced by mechanisms not yet understood.

At the present time there are 205 known

species of Neotropical Lecythidaceae (Prance and Mori 1979; Mori and Prance 1990; Mori 1992a; Mori and Lepsch-Cunha 1995). Consequently, protection of the 100 ha Lecythidaceae plot at Reserve 1501 would include 17.6 percent of all known species of Neotropical Lecythidaceae. This figure, however, will decrease as other areas become better known and as undescribed species of Lecythidaceae from other areas are published.

To protect the thirty-eight species of Lecythidaceae in the plot, much larger tracts of forest are needed to ensure that the minimal population sizes essential for maintaining each of the species are included in proposed reserves. For example, it is evident that *Bertholletia excelsa,* with only one individual in the 100 ha, could not be protected in reserves as small as the Lecythidaceae plot at Reserve 1501. Nonetheless, well-placed reserves of adequate size (thousands of hectares) in central Amazonia based on knowledge of overall species distributions and minimal population sizes of the species of Lecythidaceae can go a long way toward protecting the species richness of this family. It is difficult to extrapolate to other families, however, because other families may differ as to where they reach their greatest species richness. The Lecythidaceae, for example, have high species richness in central Amazonia, whereas the Moraceae may be more species rich in western Amazonia (Ducke and Black 1954)—that is, a reserve designed to protect the greatest number of species of Lecythidaceae will not always protect the greatest number of species of Moraceae. Moreover, reserves should not be designated based on species richness alone without also considering higher taxa and ecosystem diversities as well, so that a reserve of some thousands of hectares that would be effective for trees in the Lecythidaceae would be far too small to preserve large, territory-demanding carnivores.

To be able to address the causes of change in forest stand characteristics as a result of forest fragmentation and climate change, it is necessary to possess baseline data from undisturbed forests. Although we know that fire has had an impact within the Lecythidaceae plot (Bassini and Becker 1990; Piperno and Becker 1996), these fires probably took place 6,000-400 yr before the Pleistocene, and therefore fire's impact on present frequency, density, dominance, and species richness of Lecythidaceae may no longer be obvious. Piperno and Becker (1996), using data from soil phytoliths, provided evidence that the Lecythidaceae plot has been under continuous forest cover since at least 4,500 BP and has never been cleared for swidden agriculture.

The largest individuals of Lecythidaceae in the plot are probably less than 400 years old. Trees of *Bertholletia excelsa* in the 140–150 cm DBH class have been estimated by radiocarbon dating to be only 270 years old (P. Camargo et al. 1994). The lone *B. excelsa* in our plot is 115 cm DBH and therefore probably became established after the last significant fire swept the plot. Lecythidaceae are exceedingly vulnerable to fire such that forests regenerated from old slash-and-burn fields usually have few individuals and species of the family (Prance 1975). Smaller, more localized, disturbances such as normal gap formation (Denslow 1980), tree mortality resulting from periodic flooding (Mori and Becker 1991), and blowdowns caused by excessive winds (Nelson 1994; Nelson, Kapos, et al. 1994) frequently occur, but their influence is similar in all central Amazonian terra firme forests. We therefore conclude that the values of frequency, density, dominance, and species richness of Lecythidaceae presented here are typical for central Amazonian terra firme forest and therefore can be used as baseline data to monitor changes in forest composition resulting from forest fragmentation or climatic change in this area.

Species-area curves have attracted the attention of botanists for many years because they indicate how well a sample represents overall species richness in a given area (e.g., Arrenhius 1921; Gleason 1922, 1925; Preston 1948) and have been the focus of a relatively recent review (McGuinness 1984). The species-area curves we present (fig. 6.1) have the advantage of being based on a known universe of the organisms being sampled—i.e., the number of species of Lecythidaceae at least 10 cm DBH in a 100 ha plot on terra firme in central Amazonian Brazil. Because all species of Lecythidaceae in this part of the world attain diameters greater than 10 cm DBH, the species we have tabulated probably represent all of the species of Lecythidaceae actually found in the plot. Exceptions would be the presence of different species that have not yet reached 10 cm DBH or our failure to recognize a species as belonging to the Lecythidaceae. We suggest that similar, contiguous 100 ha plots in this part of Amazonia will yield similar species-areas curves for Lecythidaceae and perhaps even be representative of the species-area curves of other, ecologically similar, families of trees.

The most striking lesson to be relearned from our species-area curves of Lecythidaceae is that the species richness sampled increases rapidly for small sample sizes and slowly for large sample sizes. Therefore, it is relatively easy to sample most common species of Lecythidaceae in a given area in central Amazonia with a small sample size, but very difficult to sample all species, even with a large sample. A sample of a single hectare yields a mean species richness of 17.3 spp./ha, a two-hectare sample 23.2 spp./ha, a five-hectare sample 30.0 spp./ha, a twenty-hectare sample 35.6 spp./ha, and a fifty-hectare sample 37.2 spp./ha (table 6.3). All thirty-eight species, obviously, are inventoried with 100 percent probability only when all 100 ha are sampled. Since botanists began doing quantitative inventories in Amazonia (Black, Dobzhansky, and Pavan 1950) it has been apparent that species continue to accumulate with increased sample size. This is especially true if the samples are not taken from contiguous plots (Black, Dobzhansky, and C. Pavan 1950)—a phenomenon that probably reflects the complicated geological history of Amazonia as well as its extreme habitat richness (Tuomisto 1995).

In designing ecological and biodiversity studies, it is extremely important to establish what questions are to be asked and then determine how large a sample size is needed to answer those questions. For example, because we wanted to know exactly what species of Lecythidaceae were present in our 100 ha plot, as well as establish their ecological relationships, the entire plot was sampled. In our 10,000-sample experiment, the probability of sampling all thirty-eight species of Lecythidaceae with a 50 ha sample is only 0.3544 (table 6.3), indicating that considerably more time, effort, and money are needed to sample all species of Lecythidaceae present even in an area as small as 100 ha.

If the purpose of an ecological study is to determine density, dominance, and total number of species present without defining what all of the species are, then much smaller sample sizes can be used. For example, suppose that the goal of a study is to determine the number of species of Lecythidaceae present in a 100 ha plot of central Amazonian terra firme forest without providing the names of all of the species. One can then extrapolate from a much smaller sample size of 10 ha because, based on our data, 87 percent of all species present have already been sampled. Use of our data, however, will not be valid for forests outside central Amazonia, for forests on different soils, or for forests under markedly different disturbance regimes.

Because there are limited resources available for doing systematic and ecological studies in Amazonia, it is important that "oversampling" be eliminated from projects at the proposal stage. Oversampling not only taxes the resources of those undertaking a project, it also affects the systematics community asked to identify and archive the voucher collections needed to document ecological studies. Therefore, before undertaking ecological and biodiversity studies in Amazonia, the costs involving specialist determination and specimen handling and storage must be considered (Mori 1992b).

Conservation Lessons

1. The Lecythidaceae is one of the dominant tree families of undisturbed terra firme forests in central Amazonian Brazil, accounting for 6.8 to 8.2 percent of the species and 8.4 to 13.4 percent of the individual trees at least 10 cm DBH. Therefore this family, along with other dominant families, such as Sapotaceae and Burseraceae, is useful for monitoring changes in forest composition resulting from human disturbance and climatic change.
2. Species of Lecythidaceae are found in all 100 hectares of the 100 ha plot. An average hectare harbors 77.9 ± 19.9 (mean ± SD) individuals, a basal area of 3.76 ± 0.86 m^2 (mean ± SD), and 17.3 ± 2.6 (mean ± SD) species of Lecythidaceae. Marked deviations from these values indicate major disturbance—for example, fire—in the relatively recent past.
3. Species richness is so high in central Amazonia that it is difficult to sample all species present in hectare plots. Because of the expense of sampling in such species-rich areas, the number of hectares surveyed should be designed to answer the ecological and conservation questions addressed. Excessive sampling drains financial and human resources without adding information.
4. The current composition of Lecythidaceae in the 100 ha plot indicates that it has not undergone major disturbance within the past 400 years, and therefore large-scale fires, massive blowdowns, extreme flooding, and so forth have probably not had a direct influence on current stand composition. Nevertheless, this plot has experienced large-scale fires in the distant past and is subject to the continual smaller-scale disturbances common to Amazonian forests. Because this plot is representative of central Amazonian forests, it and the surrounding forest at Reserve 1501 merit protection as a biological reserve.
5. Central Amazonia is home to a greater number of species of Lecythidaceae than anywhere else in the world, and, in general, central Amazonia is a center of diversity of woody plant families. The presence of high species richness of trees and lianas justifies the establishment of large biological reserves throughout central Amazonia.

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