Impacts of selective logging and agricultural clearing on forest structure, floristic composition and diversity, and timber tree regeneration in the Ituri Forest, Democratic Republic of Congo

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Abstract. Mature tropical forests at agricultural frontiers are of global conservation concern as the leading edge of global deforestation. In the Ituri Forest of DRC, as in other tropical forest areas, road creation associated with selective logging results in spontaneous human colonization, leading to the clearing of mature forest for agricultural purposes. Following 1–3 years of cultivation, farmlands are left fallow for periods that may exceed 20 years, resulting in extensive secondary forest areas impacted by both selective logging and swidden agriculture. In this study, we assessed forest structure, tree species composition and diversity and the regeneration of timber trees in secondary forest stands (5–10 and ~40 years old), selectively logged forest stands, and undisturbed forests at two sites in the Ituri region. Stem density was lower in old secondary forests (~40 years old) than in either young secondary or mature forests. Overall tree diversity did not significantly differ between forest types, but the diversity of trees ≥10 cm dbh was substantially lower in young secondary forest stands than in old secondary or mature forests. The species composition of secondary forests differed from that of mature forests, with the dominant Caesalpinoid legume species of mature forests poorly represented in secondary forests. However, in spite of prior logging, the regeneration of high value timber trees such as African mahoganies (*Khaya anthotheca* and *Entandrophragma* spp.) was at least 10 times greater in young secondary forests than in mature forests. We argue that, if properly managed and protected, secondary forests, even those impacted by both selective logging and small-scale shifting agriculture, may have high potential conservation and economic value.

Abbreviations: CEFRECOF – Centre de Formation et de Recherche en Conservation Forestière; CTFS – Center for Tropical Forest Science; DRC – Democratic Republic of Congo; ENRA – Enzyme Refiners Association; ITTO – International Tropical Timber Organization; NSERC – Natural Sciences and Engineering Research Council of Canada

Introduction

The intrusion of human populations into primary forest areas that were previously free of anthropogenic disturbance is becoming increasingly

common in all major blocks of remaining tropical forest (Witte 1992; Verissimo et al. 1995; Coomes et al. 2000; Kammesheidt 2002). Selective logging of high value timber species is generally the first stage of this process. Shifting cultivators in search of available land use roads constructed for logging operations to penetrate deep into the forest interior and clear the forest for agricultural purposes (Witte 1992; Laurance 2001). Not all farmers are traditional shifting cultivators who are familiar with the fallow systems used to restore soil fertility and protect some of the original biodiversity. The combined effects of selective logging and unsustainable farming practices in agricultural frontiers are expected to result in considerable loss of biodiversity and degradation of timber resources.

The Congo basin, in Central Africa, contains the second largest block of undisturbed, continuous tropical rain forests after the Amazon. Until recently, commercial logging was not causing excessive degradation in the region, but is considered a major threat as an increasing number of transnational logging companies seek to operate in the Congo basin (Wolfire et al. 1998). Valuable timber trees are generally present at low density in the natural forests of Central Africa and rates of extraction rarely exceed 2 trees ha^{-1} (White 1994; Malcolm and Ray 2000; Hall et al. 2003). Although such selective logging may be relatively ecologically benign (Wilkie et al. 1992; White 1994; Hall et al. 2003), the ecological and biological complexity of the forest may be profoundly disrupted if the forest is logged repeatedly (Panayotou and Ashton 1992), or if offtake rates are high enough and logged areas serve as foci for elephant disturbance (Struhsaker 1997; Struhsaker et al. 1996). In addition, the highly selective character of such timber harvesting practices can lead to severe depletion and may eventually result in the local extinction of some high value tree species.

A much greater potential impact than the direct biological and environmental damage of selective logging, however, is the opening of mature forest areas for colonization (Verissimo et al. 1995; Johns 1997; Whitmore 1999; Laurance 1999, 2001). Logging companies construct new roads in forest areas that were previously inaccessible, thereby facilitating spontaneous colonization of logged forests by agricultural colonists (Wilkie et al. 2000; Mittelman 2001). The existence of a road network facilitates entry into the forest and increases potential agricultural economic returns because of increased opportunities to transport agricultural product surpluses to local and regional markets (Southgate et al. 1991). The consequences of increases in these returns may include a substantial increase in farm sizes and shortening of the fallow period, eventually leading to large scale and severe destruction of natural forest areas. Although this pattern is widely recognized as a central conservation concern in tropical rain forests, very little data are available on the actual impacts of selective logging and subsequent swidden agriculture on forest structure, species composition and diversity, and timber tree regeneration in Central Africa. Studies in the Neotropics suggest that land use type and intensity are important factors determining

the regrowth of woody vegetation on cleared areas (Aide et al. 1995; Guariguata and Ostertag 2001). In lightly used areas, secondary forests regrown from abandoned farms rapidly recover structural characteristics and tree diversity similar to old-growth stands. Where land use is intense, such as in grazed pastures, forest recovery is seriously impeded by the presence of grasses and other herbaceous species that inhibit the establishment of woody vegetation (Guariguata et al. 1997; Smith et al. 1999; Zahawi and Augspurger 1999; Kennard 2002).

This study reports on the impacts of logging and subsequent forest clearing on forest regeneration, structure and composition in the Ituri region, northeastern Congo basin. The history of mechanized timber harvesting in the region dates back to the early 1980s, when a 52,000 ha logging concession was awarded to ENRA in 1982. Due to the collapse of local markets in the early 1990s, logging is very selective with only very large trees of highly valuable species being extracted for export. *Milicia excelsa* (Welw.) C. Berg. (Moraceae) and five species of African mahogany (*Khaya anthotheca* (Welw.) C. DC, *Entandrophragma angolense* (Welw.) C. DC, *E. cylindricum* (Sprague) Sprague, *E. candollei* Harms, and *E. utile* (Dawe and Sprague) Sprague) accounted for 87% of total volume harvested in 1999 (R. Ducarme, personal communication). High human population density in the neighboring eastern savanna regions leads to immigration of landless farmers, who take advantage of logging roads to enter the primary forest areas where land is plentiful and cheap (Witte 1992). The activities of colonists have resulted in extensive degradation of the natural forest and its conversion to farmlands. The landscape in logged forests in the Ituri region is thus dominated by regenerating secondary forest of varying ages, intermingled with patches of mature forests, active farmlands and isolated human settlements.

Disturbed and fragmented tropical forests have been increasingly recognized as being important economically, socially, and for biodiversity conservation, especially in light of the destruction of the original primary forests (Lugo 1995; Cannon et al. 1998; Fredericksen 1998; Kammesheidt 2002). The aim of this study is to compare forest structure and composition and the regeneration of major timber trees, particularly African mahoganies, between secondary forests regrown after slash-and-burn agriculture in selectively logged forests and undisturbed mature forest stands in the Ituri Forest. The combined effects of selective logging and forest clearing for agriculture in one of our study sites can be expected to result in secondary forests having low species diversity and reduced major timber tree regeneration. The specific hypotheses tested here are (1) secondary forests impacted by both selective logging and agriculture will have lower tree diversity than mature forests, (2) species composition of secondary forests will favor fast growing early successional species; however, (3) those species that are economically important, such as African mahoganies, will show reduced abundance in secondary forests as a result of prior selective logging.

Study sites

The study was conducted at two sites in the Ituri Forest, in the northeastern part of the Congo basin forest block (Democratic Republic of Congo, DRC). The first site (Mandumbi) was a 17 years old logging concession located 25 km northwest of the town of Beni (0°45′ N latitude, 29°15′ E longitude), whereas a second site was located at Epulu, in the 1,350,000 ha Okapi Wildlife Reserve. Field investigation at this site was carried out within the 5 km^2 Lenda Study Area (LSA, 1°19′ N and 28°38′ E) established by CEFRECOF. The elevation in the region from varies 750 m to ∼950 m above sea level. Mean annual rainfall in Beni is 1639 mm and 1725 mm in Epulu. A dry season occurs from December to February, during which monthly average rainfall is less than 100 mm. May and October are the wettest months of the year, with average precipitations of 186 mm and 200 mm, respectively. Annual average daily temperature at both sites is 23–25.5 °C and varies little through the year (Figure 1).

The vegetation in the region is a mixture of evergreen forest, including extensive areas of "mbau forest" dominated by *Gilbertiodendron dewevrei* (De Wild.) J. Léonard, and "mixed forests" in which no species is predominant, but other Caesalpinoid legumes, such as *Julbernardia seretii* (De Wild.) Troupin and *Cynometra alexandri* C.H. Wright, are abundant (Makana et al. 2004). At the eastern edge of the region, evergreen forests grade into a semi-deciduous forest whose canopy is dominated by light-demanding tree species that include *Entandrophragma* spp. (Meliaceae), *K. anthotheca* (Meliaceae), *Albizia* spp. (Mimosaceae) and *Canarium schweinfurthii* Engl. (Burseraceae). Evergreen mixed forest is the main vegetation type in Epulu, while semi-deciduous forest prevails at the Mandumbi site. Large-scale human activities at the Mandumbi site have resulted in extensive areas of active crop fields and secondary vegetation of various ages. Secondary forests were generally young, less than 10 years old, and were dominated by the early pioneer tree *Musanga cecropioides* R. Br. There was also an old secondary forest created by shifting agriculture fields abandoned in the 1960s at the Epulu site. However, no selective logging took place prior to forest clearing at this site.

Soils at both sites are derived from granitic or alluvial rocks and fall under the order Oxisols, which dominates most of the Congo basin rain forest block in central Africa. Their texture ranges from loamy sand to sandy clay. The soils are very acidic, with mean pH values at 20 cm averaging ∼4 in Epulu, and low in available nitrogen and phosphorus. Mean soil sand content at LSA is ∼70% (Hart 1985).

Logging activities in the Ituri region are concentrated in the relatively drier semi-deciduous forests near the transition between closed canopy forest and eastern savanna woodlands, likely due to the proximity of export routes to the Indian Ocean through Uganda and Rwanda. The forests at the savanna margin are also richer in high-value timber trees such as African mahoganies and *Milicia excelsa* than moist evergreen forests found in central and western Ituri (Makana 2004).
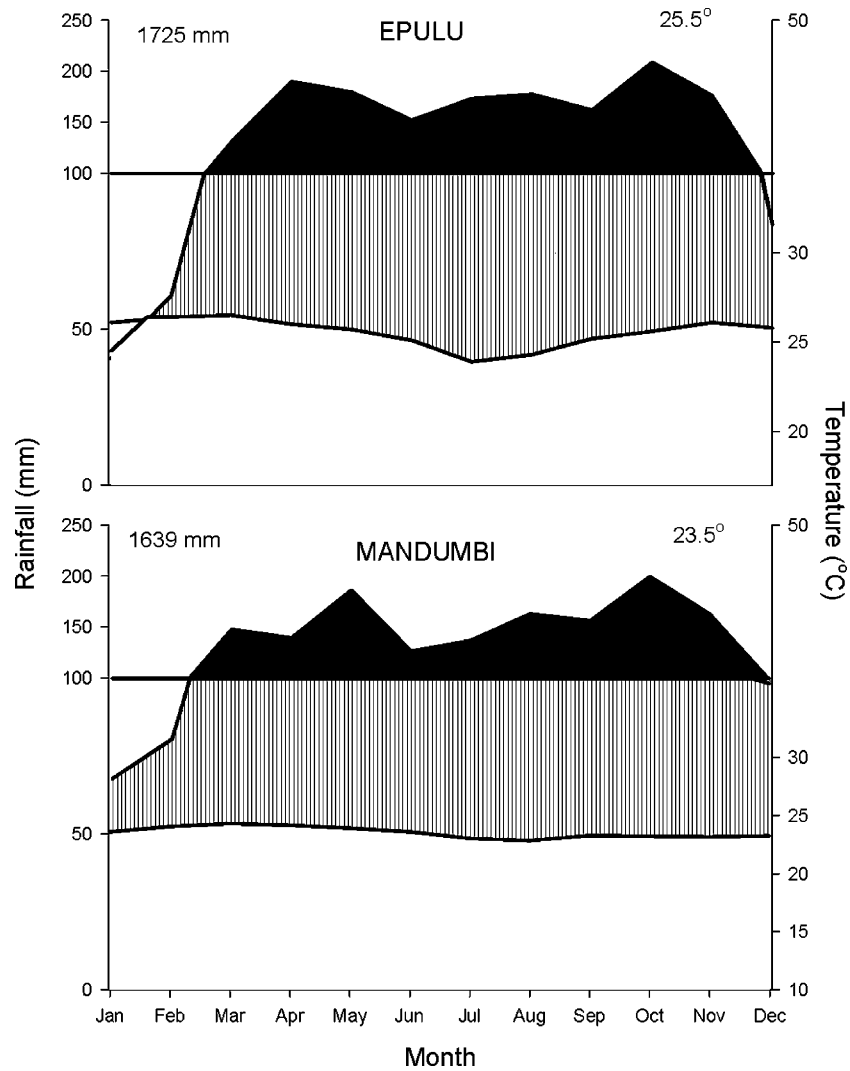
Figure 1. Climatic data of the two study sites, Epulu and Mandumbi. Data for Mandumbi came from a weather station in the town of Beni. Mean annual rainfall and mean average daily temperature are given at the top corners of each graph.

Methods

Vegetation sampling

Censuses were conducted in regenerating secondary forests and in mature forests at both Mandumbi and Epulu in nested plots. In Epulu, plots were located every 50 m along a 500-m long transect in each forest type. Transects from the

two forest types were parallel and ∼150 m apart. In Mandumbi, where small farms are intermingled with patches of mature forest fragments, plot location was dependent on the availability of appropriate secondary forest stands (e.g. secondary forests of ∼5–10 years old). Plots were spatially interspersed across forest patches, with a minimum distance of 50 m between any two adjacent plots. At both sites, secondary forest plots were located at least 20 m away from the adjacent mature forest edge. All free-standing trees ≥1 cm dbh (diameter at breast height) were identified and measured for dbh in 5 m × 5 m plots. Trees ≥10 cm dbh were identified and measured in 10 m × 10 m plots extending from each 5 m×5 m plot. For the most common tree species identifications were made directly in the field. When definitive field identification was not possible leaf samples were collected and compared to voucher specimens at CEFRECOF's herbarium in Epulu. Species names follow Lebrun and Stork (1997). In addition to botanical data, environmental information was collected at each plot. This information included soil texture, herbaceous cover, exposed mineral soil and litter depth. Soil texture was assessed according to the finger assessment of soil texture of the Ontario Institute of Pedology (1985). For the purposes of this study, soil texture was classified only in three major categories: sandy, loamy and clay soils. Herbaceous cover and the proportion of surface area made of exposed mineral soil were visually estimated and recorded as a percent of total area. Litter depth was measured by inserting a knife through the litter until it reached mineral soil, then the thickness of the litter and organic matter layer was determined to the nearest half centimeter by measuring the length of the portion of the knife that was inserted into the litter. A total of 54 plots were inventoried; 32 were at the Mandumbi site and 22 at the Epulu site.

Seedling demography

The regeneration of timber trees was assessed in each of the 54 vegetation plots described above. Seedlings (30 cm height to 0.9 cm dbh) were identified, tagged and measured for total aboveground height and collar diameter in 5 m × 5 m plots. Saplings (1–9.9 cm dbh) were identified and measured for dbh in 10 m × 10 m. Diameter and height were taken at two different times to assess growth. The first measurements were done in 2000–2001 and the second ones took place in August–October 2002. Diameter was measured to the nearest 0.01 mm using an electronic caliper for seedlings and trees < 4 cm dbh or to the nearest millimeter for individuals ≥4 cm dbh, whereas height was measured to the nearest cm using a graduated stick. Stem diameter of seedlings was measured at 10 cm from the ground.

Data analysis

For each plot, which was the experimental unit of this study, the total number of individuals, the number of species and Shannon-Wiener diversity index were

calculated for seedlings, saplings, trees ≥ 1 cm dbh, and trees ≥ 10 cm dbh. Seedling abundance was log-transformed before the analysis to homogenize variance and produce approximately normal residuals (Sokal and Rolhf 1981). ANOVA was used to assess the effects of site, forest type and their interaction on tree and seedling abundance and diversity. If a significant interaction was found, the means of site by forest type combinations were compared by a Tukey-Kramer test. Analysis of covariance served to assess the effects of forest type on the relationship between light availability and seedling relative growth rates. Multivariate analysis was used to explore the variation of floristic composition across sites and forest types. Detrended correspondence analysis (DCA) was utilized because an arch effect was observed for correspondence analysis (ter Braak 1995). Logistic regression was utilized to compare the abundance of seedlings and saplings of individual timber tree species in secondary and primary forest plots. The number of seedlings/saplings per plot was transformed into three categories: 0 for no seedling recorded, 1 for 1–4 seedlings, and 2 for > 5 seedlings.

Results

Vegetation structure

The density of trees ≥ 1 cm dbh and ≥ 10 cm dbh differed significantly between the two study sites, Mandumbi and Epulu (Table 1). On average, Mandumbi had higher tree density than Epulu for both dbh cut-offs. There was a marginally significant effect of forest type on the density of trees ≥ 1 cm dbh ($F_{1,50} = 2.5$, $p = 0.094$). In Epulu, primary forest had significantly more stems than secondary forest, whereas the density of trees ≥ 1 cm dbh was only slightly higher in primary forest compared to secondary forest in Mandumbi. Basal area was significantly higher in secondary than in primary forests for both dbh cut-offs (Table 1). Higher basal area in secondary forests was in the most part due to the presence of fast growing pioneer species. The early successional and short-lived *Musanga cecropioides* was very common in the secondary forest of Mandumbi and it represented 55% of total basal area. Some of the basal area in secondary forest stands was also accounted for by remnant trees. In Epulu, long-lived early colonizers such as *Albizia* sp., *Petersianthus macrocarpus* (P. Beauv.) Liben, and *Alstonia boonei* De Wild. made up most of basal area in secondary forest plots.

The number of stems decreased rapidly with increasing tree size (Figure 2). Trees < 10 cm dbh represented $> 80\%$ of the total number of stems in each forest type at both study sites. Although primary forest sites in Epulu had more trees ≥ 10 cm dbh than secondary forest, the overall size distribution was similar between the two forest types ($\chi^2 = 4.5$, d.f. $= 2$, $p = 0.210$). In Mandumbi, the size distribution was significantly different between the two forest types ($\chi^2 = 16.3$, d.f. $= 2$, $p < 0.001$); small trees (< 20 cm dbh) were more abun-

Table 1. Structural characteristics and diversity of mature logged and undisturbed, and secondary forest stands in northeastern Congo basin. Values of stem density are averages per hectare, and were calculated on the basis of 5 m × 5 m subplots. Species richness and Shannon's diversity index were calculated for 5 m × 5 m quadrats for trees ≥1 cm dbh and for 10 m × 10 m quadrats for trees ≥10 cm dbh. Figures are least squares means and standard errors[1].

	Epulu		Mandumbi		Significance[2]		
	PF[3] (n = 11)	SF (n = 11)	PF (n = 16)	SF (n = 16)	Site	FT	Site*FT
Trees ≥1 cm dbh							
Stem density (ha^{-1})	6473(678)^a	4509 (678)^b	7571 (601)^a	7343 (601)^a	0.004	0.094	0.182
Basal area (m^2 ha^{-1})	26.82 (5.75)^a	44.92 (5.75)^b	28.17 (4.93)^{ab}	39.16 (4.93)^b	0.683	0.009	0.510
Richness	10.9 (0.89)	11.5 (0.96)	12.9 (0.86)	12.3 (0.76)	0.072	0.683	0.796
Shannon's index	2.0 (0.14) ^{ab}	1.9 (0.14)^a	2.3 (0.13)^{ab}	2.3 (0.11)^b	0.007	0.955	0.440
Trees ≥10 cm dbh							
Stem density (ha^{-1})	427 (62)^a	356 (62)^a	636 (55)^b	721 (55)^b	<0.001	0.912	0.181
Basal area (m^2 ha^{-1})	22.63 (6.32)^a	41.94 (6.32)^b	26.49 (5.60)^{ac}	35.40 (5.41)^{ab}	0.955	0.014	0.482
Richness	3.3 (0.41)^a	3.2 (0.48)^a	4.67 (0.77)^a	1.9 (0.41)^b	0.010	0.001	<0.001
Shannon's index	1.1 (0.12)^{ab}	1.0 (0.16)^{ab}	1.6 (0.14)^a	0.8 (0.18)^b	0.450	0.010	0.027
Environmental characteristics							
Herb cover (%)	11.1 (3.97)^a	35.5 (4.64)^b	15.4 (5.81)^a	16.5 (6.0)^{ab}	0.164	0.014	0.047
Litter depth (cm)	1.2 (0.14)^a	0.9 (0.12)^a	2.7 (0.37)^b	3.8 (0.86)^b	<0.001	0.612	0.167

[1] Means with common subscripts are not significantly different according to Tukey's multiple comparison test (α = 0.05).
[2] Abundance was included as explanatory variable for ''richness'' to remove the effects of tree density on species richness.
[3] Forest type codes: PF for primary forest and SF for secondary forest. The primary forest at Mandumbi was disturbed by logging and tree harvesting for construction; it is undisturbed at Epulu. The secondary forest stands at Mandumbi were young (<10 years old), but those at Epulu were much older (~40 years old).
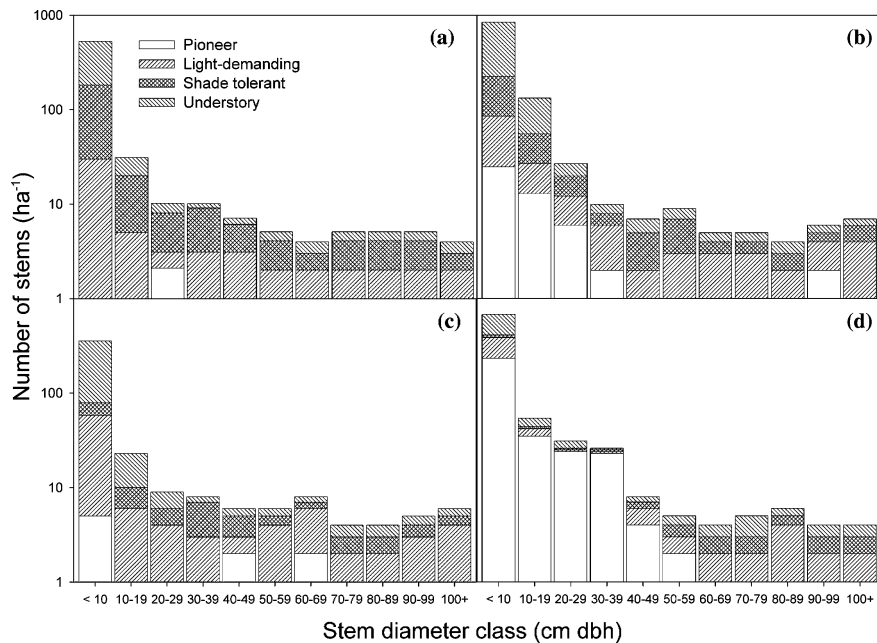
Figure 2. Whole-forest diameter distribution in 10 cm dbh intervals for (a) Epulu primary forest, (b) Mandumbi primary forest, (c) Epulu secondary forest, and (d) Mandumbi secondary forest.

dant in primary forest, whereas secondary forest had more intermediate-sized trees (20–39 cm dbh) than primary forest stands. At both sites, understory and shade tolerant trees constituted the majority of trees in primary forest stands (Figure 2a and b), whereas light demanders and pioneers were dominant in secondary forests (Figure 2c and d).

Herbaceous cover varied significantly with respect to forest type ($F_{1,50}$ = 6.6, p = 0.014). At both sites, herbaceous vegetation was more abundant in secondary forest than in primary forest, and it was dominated by species of the family Maranthaceae and Zingiberaceae. The litter layer was at least twice as thick in Mandumbi as in Epulu ($F_{1,\ 50}$ = 33.3, $p < 0.001$) but it did not vary significantly with respect to forest disturbance. No significant differences were observed in soil texture or percent of ground area in exposed mineral soil. At both sites, soil texture ranged from sandy to clay. Small areas of exposed mineral soil were recorded in seven plots, representing ∼0.17% of the total area sampled.

Species composition and diversity

A total of 159 species were recorded in the census plots, of which 121 taxa were identified to the species level, 17 to genus, 17 to family, and the remaining four

were unidentified. Overall, Mandumbi plots had 122 species, while 82 species were represented in Epulu plots. Species richness and Shannon's diversity index showed different patterns relative to tree sizes (Table 1). For trees ≥1 cm, mean number of species per plot was similar in the two sites and forest types; however, the value of Shannon's index was significantly higher in Mandumbi than in Epulu ($F_{1,50} = 8.1$, $p = 0.007$). In contrast, species richness of trees ≥10 cm dbh varied significantly according to both site and forest disturbance, while Shannon's index was only affected by forest disturbance. There were significant interactions in both diversity measures between site and forest type. In Epulu, both the mean number of species per plot and the mean value of Shannon's index were similar for primary and secondary forests. In contrast, there was a significant difference for both parameters between the two forest types in Mandumbi. The young secondary forest at the latter site was much less diverse than primary forest for trees ≥10 cm dbh (Table 1). Among the four combinations of site and forest type, richness and Shannon's diversity index of trees ≥10 cm dbh were highest for the primary forest of Mandumbi and lowest for the young secondary forest of the same site.

The species accumulation curves in Figure 3 are far from asymptotic, indicating that the area sampled was too small to estimate the total number
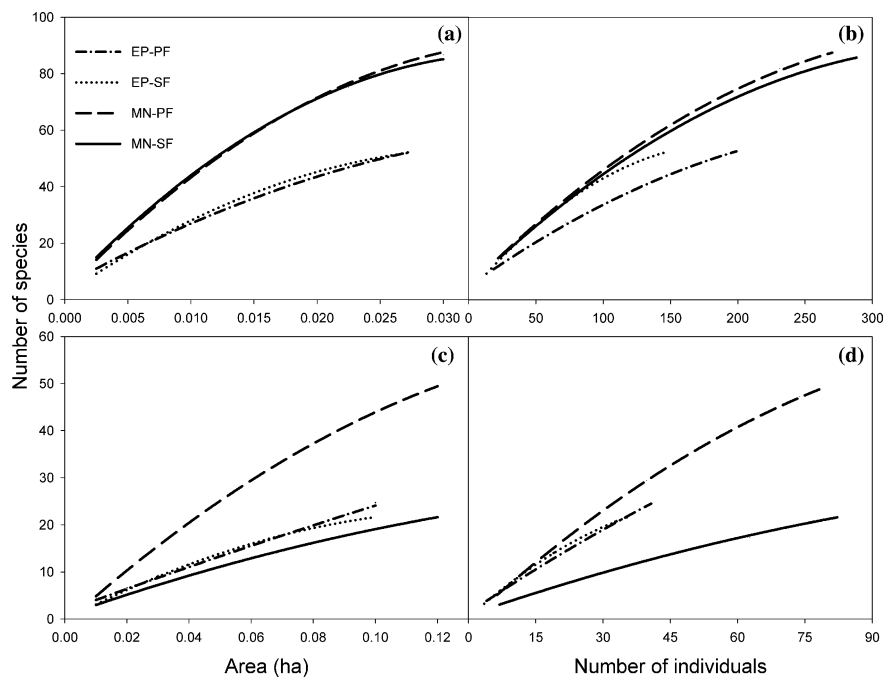

Figure 3. Species-area relationships for (a) all trees ≥1 cm dbh and (c) trees ≥10 cm dbh. Species–individual curves for (b) all trees above 1 cm dbh and (d) trees ≥10 cm dbh. EP = Epulu and MN = Mandumbi, PF = primary forest and SF = secondary forest.
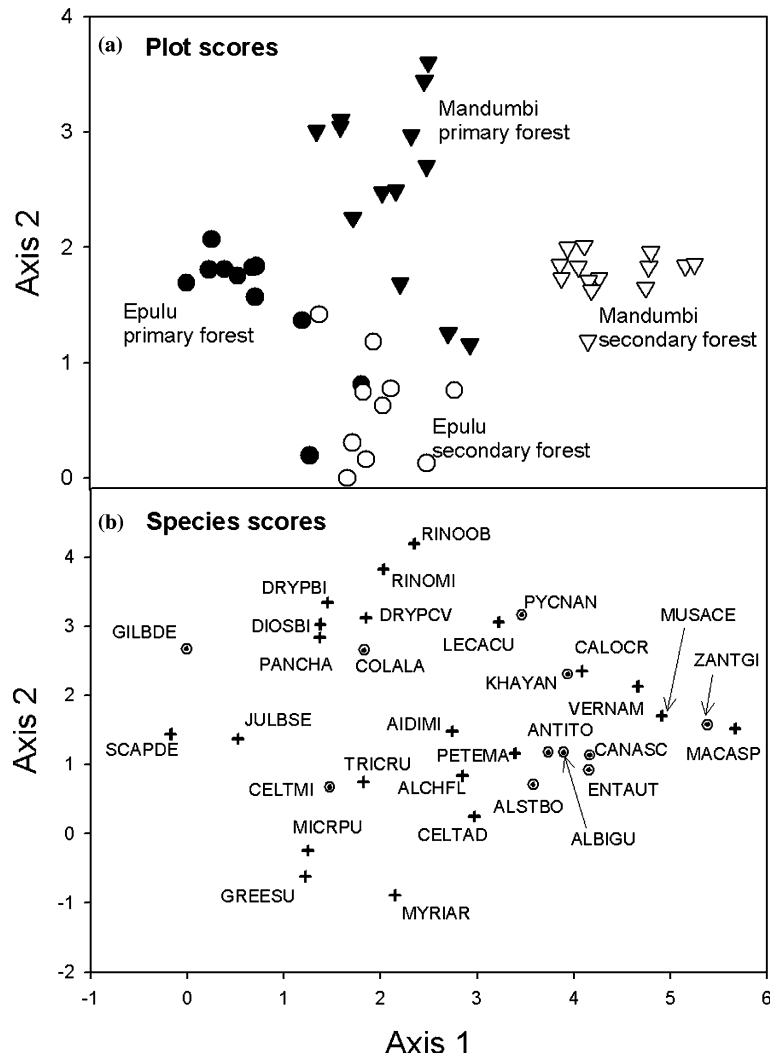
Figure 4. Axes 1 and 2 from a detrended correspondence analysis on tree species represented by at least 8 individuals in the plots: (a) plot scores (triangles represent Mandumbi site and circles Epulu site, filled symbols are for primary forest plots and open symbols for secondary forest sites) and (b) species scores (symbols with circles represent commercial timber species). Species codes as in Table 2.

of species in the studied communities. At each site, species–area curves were similar between primary and secondary forests for trees ≥1 cm dbh. The rate of species accumulation was different between primary and secondary forests in Mandumbi for trees ≥10 cm dbh, while it was quite similar between the two forest types in Epulu (Figure 3c and d). In Mandumbi, the rate of

species accumulation for trees ≥10 cm dbh was much higher in primary forest than in secondary forest.

Variation in tree species composition

The two sites and forest types shared most of their common species (Table 2). Overall, Epulu and Mandumbi shared 14 of their 20 most abundant species, while primary and secondary forests had 18 of their top 20 species in common at each site. In spite of sharing the majority of the most common species, there was no significant positive correlation of ranked abundances of these species between sites or forest types. Epulu and Mandumbi showed a significant negative correlation among abundance ranks (Spearman's $r_S = -0.549$, $p = 0.012$), as did primary and secondary forests ($r_S = -0.739$, $p < 0.001$). The most abundant species in Epulu, *Scaphopetalum dewevrei* Wildem. and Th. Dur., was totally absent from Mandumbi plots. Moreover, two of the most common species in the latter site (*Musanga cecropioides* and *Rinorea oblongifolia* Marquand) were not represented in Epulu plots. In addition, two species of African mahogany (*E. utile* and *K. anthotheca*) were much more abundant in Mandumbi than in Epulu (Table 2).

Pair-wise comparisons of species abundances for site-forest type combinations showed that the young secondary forest of Mandumbi had significant negative correlation with primary forests of both sites ($r_s = -0.743$, $p < 0.001$ and $r_s = -0.797$, $p < 0.001$ for Mandumbi and Epulu respectively). No significant correlation was found between the old secondary forest of Epulu and the primary forest of either site. Thus, the composition of the young secondary forest in Mandumbi was significantly different from that of primary forests at both sites, while that of the old secondary forest at Epulu was not.

The patterns of variation in floristic composition observed from correlation analysis were corroborated by the results of multivariate analysis. The first axis of a detrended correspondence analysis (DCA), which explained 12.9% of the total variation in the species data, appeared to be related to the composition of canopy flora and it separated primary and secondary forests at each site. For each site, secondary forests had higher scores of axis 1 than primary forests. The separation between primary and secondary forests on axis 1 was more distinct for Mandumbi than Epulu forests (Figure 4a). The second axis (7.6% of the total variation) also distinguished between primary and secondary forests of each site, but seemed to be more related to the composition of understory vegetation. Primary forests had higher scores than secondary forests on the second DCA axis. Primary forests of both sites and the old secondary forest in Epulu overlapped on both DCA axes. Mandumbi primary forest and Epulu secondary forest were indistinguishable on the first axis, but the former had higher scores of axis 2 than the latter.

Table 2. Abundance of the 20 most common tree species for stems ≥1 cm dbh in primary forests (PF) and secondary forests (SF) at two study sites (Epulu and Mandumbi) in northeastern Congo Basin. Figures are number of trees per hectare.

Species name	Code	Status	EPULU		MANDUMBI	
			PF	SF	PF	SF
Scaphopetalum dewevrei De Wild. and T. Durand	SCAPDE	Understory	1782	109	0	0
Gilbertiodendron dewevrei (De Wild.) J. Léonard	GILBDE	Canopy	764	0	833	0
Julbernardia seretii (De Wild.) Troupin	JULBSE	Canopy	800	109	401	48
Alchornea floribunda Müll. Arg.	ALCHFL	Understory	145	182	668	175
Rinorea oblongifolia (C.H. Wright) Marquand ex Chipp	RINOOB	Understory	0	0	1012	110
Diospyros bipendensis Gürke	DIOSBI	Understory	327	109	467	150
Celtis mildbraedii Engl.	CELTMI	Canopy	255	618	67	99
Khaya anthotheca (Welw.) C. DC.	KHAYAN	Canopy	36	73	167	724
Trichilia rubescens Oliv.	TRICRU	Understory	109	545	166	174
Pancovia harmsiana Gilg	PANCHA	Understory	327	0	401	98
Myrianthus preussii Engl.	MYRPR	Understory	100	440	33	101
Cynometra alexandri C.H. Wright	CYNOAL	Canopy	218	400	0	0
Musanga cecropioides R. Br.	MUSACE	Canopy	0	0	0	653
Albizia gummifera (J.F. Gmel.) C.A. Sm.	ALBIGU	Canopy	0	109	68	399
Greenwayodendron suaveolens (Engl. and Diels) Verdc.	GREESU	Understory	327	72	66	0
Pycnanthus angolensis (Welw.) Warb.	PYCNAN	Canopy	0	0	264	224
Antiaris toxicaria Lesch.	ANTITO	Canopy	73	36	67	275
Cola lateritia K. Schum	COLALA	Canopy	110	37	233	48
Entandrophragma utile (Dawe and Sprague) Sprague	ENTAUT	Canopy	0	40	65	301
Microdesmis puberula Hook. F. ex Planch.	MICRPU	Understory	182	218	0	0

Table 3. Abundance of seedlings and saplings of commercial timber tree species in primary forest (PF) and secondary forest (SF) in northeastern Congo basin. Abundances are averages of the number of stems per hectare, and were calculated on the basis of 5 m × 5 m quadrats for seedlings and of 10 m × 10 m quadrats for saplings. Significance levels for the difference in regeneration abundance between primary and secondary forests as follows: ns $p > 0.05$, * $p < 0.05$, ** $p < 0.01$.

Species name	Shade tolerance guild[1]	Seedlings ha^{-1}			Saplings ha^{-1}		
		PF	SF	Difference	PF	SF	Difference
Khaya anthotheca (Welw.) C.DC.	NPLD	237	4978	**	28	120	**
Entandrophragma cylindricum (Sprague) Sprague	NPLD	356	370	ns	31	4	ns
Entandrophragma angolense (Welw.) C. DC.	NPLD	30	978	**	14	52	*
Entandrophragma utile (Dawe and Sprague) Sprague	NPLD	0	89	–	4	40	ns
Lovoa trichilioides Harms	NPLD	30	0	–	10	24	ns
Guarea cedrata (A. Chev.) Pellegr.	Tolerant	89	59	ns	7	0	–
Albizia gummifera (J.F. Gmel.) C.A. Sm.	NPLD	607	119	ns	31	60	ns
Tieghemella africana Pierre	NPLD	59	59	ns	21	20	ns
Gilbertiodendron dewevrei (De Wild.) J. Léonard	Tolerant	5956	30	**	162	0	–
Zanthoxylum gilletii (De Wild.) P.G. Waterman	NPLD	0	0	–	7	20	ns
Nauclea diderrichii (De Wild.) E.M.A. Petit	Pioneer	0	30	–	0	24	–
Canarium schweinfurthii Engl.	Pioneer	0	0	–	4	32	ns
Alstonia boonei De Wild.	Pioneer	0	0	–	0	32	–
Klainedoxa gabonensis Pierre ex Engl.	NPLD	0	0	–	7	8	ns
TOTAL		7364	6712		326	436	

[1]NLPD: non-pioneer light demander (Hawthorne 1993)

A greater proportion of common species were associated with Mandumbi forests than Epulu forests (Figure 4b). Most of Epulu primary forest plots and Mandumbi secondary forest plots were more than 3 standard deviations apart on the first axis. This suggests that the two communities share few of their most common canopy species. Examination of Figure 4 reveals that the floristic composition of the primary forest in Mandumbi was more similar to those of the primary and old secondary forests in Epulu than to that of the young secondary forest at the same site.

Regeneration of timber species

The abundance of seedlings of commercial timber trees differed significantly between primary and secondary forest forests ($F_{1,44} = 8.0$, $p < 0.001$), and there was also a significant site by forest type interaction ($F_{1,44} = 7.9$, $p = 0.008$). The difference in seedling abundance with respect to forest type was entirely due to the extremely low abundance of timber tree seedlings in the secondary forest of Epulu, which averaged ~ 15 times less seedlings than any other combination of site and forest type. The number of seedlings in the mature and undisturbed forest of Epulu was similar to that of the logged or secondary forests of Mandumbi. The abundance of saplings of timber species did not vary significantly according to forest type. Although Mandumbi forests had consistently higher densities of saplings than Epulu forests, the difference was significant only at $p < 0.1$.

Two species were particularly abundant in the seedling and sapling populations. *Khaya anthotheca* was the most abundant timber species in the secondary forest of Mandumbi, averaging densities of ~ 8350 seedlings and 190 saplings ha^{-1}. In Epulu, *K. anthoteca* was totally absent from the seedling population and occurred only at a density of 73 saplings ha^{-1}. *G. dewevrei* dominated the seedling and sapling populations in primary forests of both sites. Mean densities of *G. dewevrei* seedlings and saplings in primary forests were ~ 6000 and 162 individuals ha^{-1}, respectively. While *K. anthoteca* was also well represented among the seedling and sapling populations of primary forests, *G. dewevrei* seedlings were very rare in secondary forests (~ 30 individuals ha^{-1}) and no saplings of this species were recorded in secondary forest (Table 3).

Mahogany regeneration

Seedlings of four species of African mahogany (*K. anthoteca*, *Entandrophragma angolense*, *E. cylindricum* and *E. utile*) were much more abundant in secondary forests (10,775 ± 3776 ha^{-1}) than in primary forests (1050 ± 336 ha^{-1}) at

Mandumbi. No seedlings of these species were found in any of the forest plots in Epulu. The abundance of mahogany saplings (1–9.9 cm dbh) was also higher in secondary forests than in primary forests at both sites, 331 (125) vs. 113 (39) stems ha^{-1} in Mandumbi and 27 (14) vs. 9 (9) stems ha^{-1} in Epulu. To determine environmental factors that affect the regeneration of African mahogany tree species in the region, the abundance of mahogany regeneration was compared between primary and secondary forests and the relationships between the abundance of the regeneration and recorded environmental variables was tested through regression analysis and analysis of variance. This analysis was limited to data from Mandumbi because mahogany regeneration in Epulu was negligible.

The abundance of the regeneration of African mahogany species varied significantly according to forest type ($F_{1,44} = 17$, $p < 0.001$) and soil texture ($F_{1,44} = 2.43$, $p = 0.038$). There were at least ten times more seedlings of these species in secondary forests than in primary forests at Mandumbi (Table 3). Loamy and sandy soils supported a higher density of seedlings and saplings of mahogany than did clay-textured soils. Simple regression analysis showed that two factors were significantly associated with mahogany regeneration. The abundance of *M. cecropioides*, an early pioneer tree species, and litter depth were positively associated with mahogany regeneration ($r^2 = 0.431$, $p < 0.001$ and $r^2 = 0.158$, $p = 0.022$ respectively). Herb cover was marginally negatively associated with the abundance of mahogany regeneration ($r^2 = 0.099$, $p = 0.075$).

A simultaneous test of all factors and their interactions through multiple regression (stepwise selection) revealed that only the abundance of *M. cecropioides* and the interaction between the latter factor and herb cover were significant ($p < 0.001$ for both variables). This model explained 61.4% of the variation in the abundance of mahogany regeneration in Mandumbi. Litter depth was not maintained in the model likely due to its strong positive correlation with the abundance of *M. cecropioides* ($r = 0.525$, $p = 0.002$).

Discussion

Secondary forests and the conservation of tree diversity

It was expected that the combination of selective logging and agricultural clearing would result in the degradation and impoverishment of natural forests. Secondary forests are generally seen as having much lower conservation value than mature forests. They generally have fewer tree species, are dominated by widespread pioneer trees, and have a simpler structure (Garcia-Montiel and Scatena 1994; Guariguata et al. 1997; Whitmore 1999; Aide et al. 2000). The return of secondary forests to the complex and species-rich primary forest conditions can be very slow, partly due to the limited availability of seeds of primary forest tree species (Holl et al. 2000; Wijdeven and Kuzee 2000). However, human-induced disturbances in tropical forests span a wide gradient,

depending on land-use type and intensity. Forest clearing for traditional slash-and-burn agriculture, such as practiced in our study sites, occupies the lower end of severe forest disturbance as compared to clearing for large commercial pastures or oil palm plantations (Lawrence et al. 1998; Mesquita et al. 2001).

This study shows that secondary forests growing after the initial clearing of primary forests for shifting cultivation in the Ituri harbor surprisingly high levels of tree species diversity for small stem sizes. Overall diversity measures of trees ≥1 cm dbh were similar between secondary and primary forest stands. Two factors that may account for the observed diversity patterns in the secondary and primary forest stands include edge effects and the dominance of primary forest stands by *G. dewevrei*. The proximity of many secondary forest plots to primary forest stands will likely result in increased diversity in these plots due to potentially high seed input from mature forests (Mesquita et al. 2001; Kennard 2002). On the other hand, most mature forest plots especially at Epulu were located in forest stands dominated by *G. dewevrei*, which are known to have very low diversity at small spatial scales (Hart et al. 1989; Makana et al. 2004). The diversity of larger trees (i.e. ≥10 cm dbh) was, however, significantly lower in young secondary forest stands (< 10 years old). However, notwithstanding the similarity in overall tree diversity, the floristic compositions of the two forest types were very different. The flora of secondary forests was particularly depauperate in common species characteristic of old-growth forests in the region, particularly *G. dewevrei* and *J. seretii*, and understory specialists such as *S. dewevrei, Drypetes* spp., *Rinorea* spp., and *Pancovia harmsiana* Gilg. In this respect, our results corroborate those of other studies on tropical forest succession (Brown and Lugo 1990; Guariguata et al. 1997; Aide et al. 2000). For example, Aide et al. (2000) noted that a 40-year old secondary forest derived from abandoned pasture had comparable tree diversity to adjacent mature forest, whereas the floristic composition was substantially different.

Stem density and basal area increased very rapidly after farm abandonment with higher basal areas observed in 10-year old secondary forests than in adjacent primary forest. However, most of the basal area in the young secondary forest of Mandumbi was accounted for by the presence of the early pioneer tree *M. cecropioides*, which does not persist beyond the senescence of the initial cohort, which may result in a reduction in the basal area of those stands when the initial cohort of that species dies out. Similar trends have been observed elsewhere in tropical forest succession (Aide et al. 2000). Our result are consistent with other findings suggesting that many structural characteristics of secondary forest stands in the tropics can reach levels encountered in mature forest stands quite early during succession (Brown and Lugo 1990; DeWalt et al. 2003). The rapid forest recovery observed in this study may be the result of light land-use intensity and high seed fall into abandoned fields due to the relatively small sizes of farms and the presence of remnant trees that attract seed dispersers.

Forest disturbance and the regeneration of major timber trees

A pattern of reduced abundance of timber tree regeneration in selectively logged forests has been frequently observed in the tropical forests of Africa and Latin America (Verissimo et al. 1995; Struhsaker 1997; Mwima et al. 2001; Hall et al. 2003). Low seed availability due to the removal of most large reproductive trees (Plumptre 1995; Makana and Thomas 2004), small sizes of canopy openings created by single-tree removal, high seed and seedling predation, and the rapid invasion of logging gaps by lianas and herbaceous vegetation (Struhsaker 1997; Fredericksen 1998) are commonly blamed for this lack of timber tree regeneration after selective logging. On the other hand, several studies have reported good regeneration of Neotropical mahogany (*Swietenia macrophylla* King) following severe disturbances such as hurricane, fire, flooding or agricultural clearing (Lamb 1966; Snook 1996; Gullison et al. 1996; Mostacedo and Fredericksen 1999; Negreros-Castillo et al. 2003). Our results support the hypothesis that African mahoganies, like their Neotropical counterpart, regenerate well after severe disturbances (i.e. forest clearing for agriculture) that destroy most of the existing vegetation. Secondary forests regrowing on areas that were previously selectively logged and cleared for agricultural purposes had at least 10 times more seedlings of African mahoganies than unlogged mature forests. The positive effects of forest clearing on tree regeneration were not limited to mahoganies; other light demanding timber trees such as *Albizia gummifera* C. A. Smith*, Canarium schweinfurthii* Engl., and *Zanthoxylum gillettii* (De Wild.) Waterman also showed better seedling recruitment in secondary vegetation than in mature forests.

Good regeneration of timber trees in the secondary forest stands of this study may be the result of traditional shifting cultivation practices in the Ituri region. Mature individuals of valuable tree species (fruit trees, timber or medicinal species) are commonly left alive during forest clearing for agricultural purposes. These "remnant" trees likely dispersed seeds in abandoned farms while competition from existing vegetation was low, leading to abundant regeneration of major timber trees such as African mahoganies (Carrière et al. 2000). Slash-and-burn agriculture, which mimics hurricanes followed by wildfires, is now considered as one of the silvicultural treatments that favor the establishment of mahogany in the Neotropics (Negreros-Castillo et al. 2003). In the Peruvian Amazon, Smith et al. (1999) reported a high representation of valuable timber trees in secondary forests regrown after farm abandonment. Twenty of the 22 most important timber trees in the region were present as poles (> 10 m height) in old secondary forests.

The regeneration of African mahogany species was much more abundant in Mandumbi than in Epulu. Mandumbi is located at the margin of closed canopy forest and eastern savanna woodlands, and it has semi-deciduous vegetation, whereas the vegetation at Epulu (located in central Ituri basin) is primarily evergreen. Although African mahogany species are widely distributed across tropical Africa, their local abundance can be influenced by climate

(rainfall), soil conditions (moisture and nutrients), historic events, and disturbances (Bongers et al. 1999). Most African mahoganies have been described as belonging to the deciduous or semi-deciduous forests (Hall and Swaine 1981). The relatively drier and semi-deciduous forests of the eastern fringe of the Ituri basin probably offer more favorable conditions for the regeneration and growth of African mahoganies than the evergreen forests of Epulu. Densities of commercial size trees ($\geq$ 80 cm dbh) were ~5 times higher in Mandumbi than in Epulu (J.-R. Makana, unpublished data). Low density of adult trees may therefore partly explain the poor regeneration of *K. anthotheca* and *Entandrophragma* spp in Epulu, due to limited seed availability (Plumptre 1995; Makana and Thomas 2004).

Implications for conservation and management

Natural forests in the Ituri region host an impressive diversity of tree and animal species which has led to the designation of the Ituri forest as a refugium during late Quaternary climate fluctuations (Grubb 1982; Hart et al. 1996). The Ituri forest contains large mammal species including the endemic Okapi, forest elephant, leopard, buffalo, as well as 13 species of anthropoid primates, seven species of forest antelopes (duikers), and many other species of mammals, birds and reptiles (Hart 1986; Thomas 1991; Hart et al. 1986; Plumptre 1996). This abundant and diverse wildlife assemblage has coexisted with small communities of horticulturalists in the Ituri for centuries (Wilkie and Finn 1990). While the presence of small areas of secondary vegetation derived from swidden agriculture may benefit some mammal populations (Short 1983; Thomas 1991), the creation of large areas of secondary forests poses a threat to most mature forest dwelling species such as forest ungulates, okapi, leopard, and others. These species, especially forest ungulates, are the main source of dietary protein for local populations (Hart and Hart 1986). Therefore maintaining large tracks of undisturbed primary forest is essential to the conservation of animal diversity and to the well-being of local hunter–gatherer communities.

   Forest recovery on abandoned agricultural lands is possible through natural regeneration. It is shown here that some aspects of forest structure and the diversity of small trees can be rapidly restored to levels comparable to those of mature forests. However, forest recovery is possible only if secondary forests are protected from repeated clearing because the return of the species composition of secondary vegetation to assemblage similar to that of old-growth forests may require over 100 years due to limited seed availability and dispersal, and slow growth of mature forest tree species. Small-sized clearings, moderate land use intensity (long fallow periods), and a fine scaled landscape mosaic may speed up the return of secondary forests to mature forest species

composition. Human intervention in the recovery process may be desirable. Makana and Thomas (2004) showed that the addition of seeds in light-gaps greatly increased seedling recruitment in the study site. Thus, seed supplementation and/or enrichment planting can be valuable interventions for the rapid return of secondary forests to the complex and species-rich mature forest conditions.

Our results are consistent with the generalization that tropical secondary forest resulting from farm abandonment may provide a favorable environment for the regeneration of high value timber trees (Negreros-Castillo et al. 2003). The high abundance of African mahoganies' regeneration and the enhanced performance of their seedlings in secondary forest stands suggest that these species require sufficient light availability to regenerate well. Therefore, successful regeneration of African mahoganies may depend on the adoption of forestry practices that provide for larger clearings, followed by post-harvest silvicultural treatments to control competing vegetation (see Fredericksen and Putz 2003; Negreros-Castillo et al. 2003). It has been shown here that young secondary forests, growing on areas that were both selectively logged and cleared for agricultural purposes, have both high tree species diversity and abundant regeneration of valuable timber trees. This potentially favorable situation offers a window of opportunity to reconcile social and ecological demands on tropical forests. Planned and controlled clearing of selectively logged forests for shifting cultivation can have the potential create favorable conditions for African mahogany regeneration as well as to provide for the needs of local communities that depend on the forest, while still conserving a high portion of the original biodiversity through appropriate fallow systems and protection of primary forest stands as a source of propagules.

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