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How rare is too rare to harvest?
Management challenges posed by timber species occurring at low densities in the Brazilian Amazon

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ABSTRACT

Tropical forests are characterized by diverse assemblages of plant and animal species compared to temperate forests. Corollary to this general rule is that most tree species, whether valued for timber or not, occur at low densities ($<$1 adult tree ha^{-1}) or may be locally rare. In the Brazilian Amazon, many of the most highly valued timber species occur at extremely low densities yet are intensively harvested with little regard for impacts on population structures and dynamics. These include big-leaf mahogany (*Swietenia macrophylla*), ipê (*Tabebuia serratifolia* and *Tabebuia impetiginosa*), jatobá (*Hymenaea courbaril*), and freijó cinza (*Cordia goeldiana*). Brazilian forest regulations prohibit harvests of species that meet the legal definition of rare – fewer than three trees per 100 ha – but treat all species populations exceeding this density threshold equally. In this paper we simulate logging impacts on a group of timber species occurring at low densities that are widely distributed across eastern and southern Amazonia, based on field data collected at four research sites since 1997, asking: under current Brazilian forest legislation, what are the prospects for second harvests on 30-year cutting cycles given observed population structures, growth, and mortality rates? Ecologically 'rare' species constitute majorities in commercial species assemblages in all but one of the seven large-scale inventories we analyzed from sites spanning the Amazon (range 49–100% of total commercial species). Although densities of only six of 37 study species populations met the Brazilian legal definition of a rare species, timber stocks of five of the six timber species declined substantially at all sites between first and second harvests in simulations based on legally allowable harvest intensities. Reducing species-level harvest intensity by increasing minimum felling diameters or increasing seed tree retention levels improved prospects for second harvests of those populations with a relatively high proportion of submerchantable stems, but did not dramatically improve projections for populations with relatively flat diameter distributions. We argue that restrictions on logging very low-density timber tree populations, such as the current Brazilian standard, provide inadequate minimum protection for vulnerable species. Population declines, even if reduced-impact logging (RIL) is eventually adopted uniformly, can be anticipated for a large pool of high-value timber species unless harvest intensities are adapted to timber species population ecology, and silvicultural treatments are adopted to remedy poor natural stocking in logged stands.

1. Introduction

As made abundantly clear in this issue of *Forest Ecology and Management* and in forest management literature from the past 15 years, reduced-impact logging (RIL) operational systems represent state-of-the-art management for species-diverse forests across the tropics. Reducing damage to residual stands through improved felling and extraction techniques, and improving harvest efficiency through planned interventions based on detailed spatial knowledge of commercial trees, RIL offers an eco-friendly management option. Under the right conditions (e.g., no cheating with respect to minimum harvest diameter, maximum harvest intensity, off-limits streamside buffer zones, logging restrictions on steep slopes), RIL is

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potentially more profitable than conventional or predatory logging models (Barreto et al., 1998; Putz et al., 2000a; Holmes et al., 2002). Less forest structural damage means more retained commercial value in the form of surviving and future crop trees, less stand-level susceptibility to post-logging fires (Holdsworth and Uhl, 1997), and less disruption to animal, avian, and insect communities (Putz et al., 2000b; Kalif et al., 2001; Azevedo-Ramos et al., 2006)—in sum, a higher likelihood that forests will persist than under conventional logging. It follows naturally that RIL is increasingly promoted as the default industry standard by national forest legislation in countries such as Brazil and Bolivia, by international forestry policy and research organizations such as ITTO and CIFOR, and by FSC-standard certification bodies.

As an operational system, RIL's long-term impact on commercial yields depends on the rules by which forest managers must play: those federal regulations setting, for example, minimum diameter cutting limits, stand-level harvest intensity, seed tree retention rates, and densities below which timber species are considered too rare to sustainably harvest. In Brazil, forest legislation sets the minimum commercial size at 50 cm diameter (except 60 cm for big-leaf mahogany, *Swietenia macrophylla*); requires 10% retention of a given species' commercial population (20% for mahogany); and prohibits harvest of 'rare' species whose commercial density falls below three trees per 100 ha (0.03 ha^{-1}; Brasil, 2006). Best-practices management in the Brazilian Amazon couples these biological parameters with RIL harvest systems. Meanwhile industry leaders operating RIL systems in this region frequently pursue FSC-standard certification promising international consumers that green-seal forest products were sustainably managed (e.g., according to Brazilian FSC standards, management operations are expected to maintain seed trees at appropriate density and spacing to guarantee the reproduction of harvest species and to actively manage or protect species with population structures that do not favor recovery following logging; FSC, 2002).

Were they? In this article we examine whether current best-management practices for high-value timber species occurring at low to near vanishing densities in Amazonia are in fact sustainable over multiple cutting cycles. A growing body of evidence from large-scale, long-term plots monitoring post-logging forest recovery following conventional and RIL operations indicates that future harvests at fixed intervals will decline compared to first harvests (Kammesheidt et al., 2001; Phillips et al., 2004; Dauber et al., 2005; Gourlet-Fleury et al., 2005; Brienen and Zuidema, 2006; Degen et al., 2006; van Gardingen et al., 2006; Valle et al., 2007). Predicted yield declines may further mask deleterious impacts on today's high-value species as fast-growing, low-density, low-value timber species occupy growing space opened by logging, displacing preferred timbers (Alder and Silva, 2000; Schulze et al., 2005; MacPherson, 2007; Valle et al., 2007). Many of today's high-value species occur at densities generally described as 'rare' (<1 ha^{-1}) in the ecological literature (Hubbell and Foster, 1986; Pitman et al., 1999). From the perspective of forest management, what impact does species density have on sustained production? Is species density a useful biological parameter for assessing manageability, or are other life history traits such as population structure, growth and mortality rates, light requirements, and dispersal capacity more critical?

A defining characteristic of tropical forests, and one that is intimately linked to strategies for their management and conservation, is high biodiversity. For tropical tree communities, a correlate of high diversity is a preponderance of rare species (Hubbell and Foster, 1986). In forest plots spanning the tropics, researchers have found that most trees belong to a relatively small number of common species, while locally rare species account for the bulk of species richness (Hubbell and Foster, 1986; Condit et al., 1995; Pitman et al., 1999, 2001). In the CTFS pantropical large-plot network, 30–50% of species have been recorded at densities <1 ha^{-1} (Hubbell and Foster, 1986; He et al., 1997; Kenfack et al., 2007). At the landscape scale, Pitman et al. (1999) found that 88% of species registered in a network of 1-ha plots in western Amazonia occurred at average densities <1 tree ha^{-1}, though half of recorded species occurred at densities >1.5 tree ha^{-1} in at least one sample plot.

At regional scales there are a number of ways for a species to be 'rare', with different conservation implications for different patterns (Rabinowitz, 1981; Bawa and Ashton, 1991; Lepsch-Cunha et al., 1999; Pitman et al., 1999). Densities may vary widely across a species' range, meaning that while barely present in one forest it may be common in another, with this pattern discernible at local and regional scales (Schoener, 1987; Brown et al., 1995; Pitman et al., 1999). A species may be a habitat generalist, broadly distributed at low densities across a large geographic range, but with high relative abundance locally within that range. While rare in most forest stands, a species with this distribution pattern will have a large absolute population size. Another pattern for rarity is the species with a restricted geographic range, a high degree of habitat specialization within that range, and no local reservoirs of abundance. While few regional-level studies have been conducted addressing this issue, recent analyses indicate that low-density species with large geographical ranges may be more common than those with restricted ranges (Pitman et al., 1999, 2001), and that species with narrowly restricted ranges are more likely to be relatively abundant than rare at sites within that range (Kenfack et al., 2007).

Patterns of commonness and rarity extend to the pool of commercially valuable timber species in Amazonia. According to Martini et al. (1994), 89% of 305 Amazonian timber species are widely distributed across the Basin, with the remainder restricted to a specific region. A limited number of timber species are present at high densities (>1 commercial-sized tree ha^{-1}) throughout much of their range; many species are relatively abundant, or occur near this density threshold, somewhere. However, in a given forest most timber species occur at densities well below this threshold. From the conservation perspective, even very large natural ranges may not protect high-value timber species occurring generally at low to very low densities from regional depletions, as the case of big-leaf mahogany (*S. macrophylla*) clearly illustrates (Grogan and Barreto, 2005; Grogan et al., 2008).

Timber species' density patterns create an inherent conflict between economic and ecological goals of sustainable forest management in Amazonia. In a given forest stand, a subset of high-density timber species typically furnishes the majority of logged stems, yet much of the first harvest's value derives from low-density, high-value species such *S. macrophylla*, *Tabebuia impetiginosa*, *Cedrela odorata*, and *Hymenaea courbaril*. Thus species the logger businessman most prizes are precisely those presenting the most daunting management challenges. Are timber harvests destined to simplify forests by decimating populations of rare timber species while selecting for a subset of more easily managed species? Can RIL operational systems be adapted to address this ecological reality?

Here we describe community-level patterns of timber species abundance and rarity from large-scale (>200 ha) inventories at seven management and research sites spanning Brazil's Amazon region. Using long-term growth and mortality data for six heavily exploited timber species occurring at widely variable densities among four eastern sites, we simulate post-logging population recovery following legal harvests under RIL protocols during 30-year cutting cycles, and evaluate the relative impacts on recovery of species densities, diameter size class distributions, and vital rates. By adjusting simulation parameters we examine whether adaptive management could promote local persistence and recovery of species fitting the ecological definition of ‘rare’ but occurring at densities higher than the Brazilian legal definition (0.03 ha^{-1}).

2. The study species

The six timber species described here co-occur at highly variable densities across wide natural ranges in Amazonia. The six species are each from a different family or sub-family, present contrasting life history traits (Table 1), are poorly understood from ecological and management perspectives, and face increasing logging pressure as their working properties and natural beauty become recognized by international markets (Schulze et al., 2005). *Tabebuia serratifolia* (ipê) produces a dark, dense timber highly prized for residential decking in the US. *H. courbaril* (jatobá) is another heavy-wooded species increasingly exported for flooring and heavy construction. *Cordia goeldiana* (freijó cinza) and *Simarouba amara* (marupá, caxêta) yield bright, lightweight timber highly regarded in European markets for fine furniture and veneers. *Astronium lecointei* (muir-acatiara) is exploited for its colorful, ornate grains, while *Parkia pendula* (fava de bolota) produces large-diameter boles easily processed for plywood. Four species are canopy emergents, capable of attaining 35–40 m height and up to 2 m diameter (*Astronium*, *Hymenaea*, *Parkia*, and *Tabebuia*—from here we refer to the six species by generic names only). Four are light demanding as juveniles (*Cordia*, *Hymenaea*, *Simarouba*, *Tabebuia*) while one is shade-tolerant (*Astronium*); only the latter occurs at high densities as advance regeneration in unlogged forest. Two species capable of extremely rapid diameter and height growth (*Parkia*, *Simarouba*) experience, along with *Cordia*, high mortality rates in unlogged forests compared to other species. For *Simarouba* and *Cordia* this may be related to their smaller stature at maturity and the likelihood of being overtopped by larger trees. Seed weights range enormously among the six species (0.02–4.00 g), as do dispersal syndromes and background densities of seedling regeneration (Table 1).

3. Methods

3.1. Inventories

Large-scale 100%-area inventories were conducted at seven sites across eastern and southern Brazilian Amazonia covering 204–11,370 ha (Table 2). While all sites receive <2200 mm of rainfall annually and are seasonally dry during 1–6 months of the year, underlying geomorphology and soil physical and chemical properties vary widely among sites (IBGE, 2003; Schulze, 2003; Grogan and Galvão, 2006). As a consequence, forest structure ranges from tall closed evergreen canopies in eastern forests (sites A–C) to tall open evergreen forests in the southwest (F and G), low broken semi-evergreen forest in the southeast (D), and open semi-deciduous forest in Rondônia (E). All sites have been or are slated to be logged at intensities determined by commercial species mix and distance to transportation infrastructure and market centers.

Inventories were conducted either for commercial purposes by logging companies following RIL protocols (stems >30 or 35 cm diameter of commercial species measured, tagged, and mapped in reference to a trail grid) or for research purposes (stems >5 cm or >20 cm diameter at varying spatial scales depending on objectives and resources). We describe community-level species density patterns for canopy trees (attaining >35 cm diameter) at four sites (A–D) where both commercial and non-commercial species were inventoried in areas ranging from 14 to 400 ha. At these and at the remaining three sites where only commercial stems were inventoried, we present density patterns in six classes (<3 per 100 ha, 3–10 per 100 ha, up to >100 per 100 ha) for stems >20 (or >30) cm diameter and >50 cm diameter (the legal minimum diameter cutting limit in Brazil), the difference representing submerchantable or future crop trees. Data are presented as number of trees per 100 ha because forest management operations in Brazilian Amazonia are typically implemented in 100-ha blocks. This unit area is easy to visualize – picture a

Table 1
Key life history traits of six study species

	Astronium lecointei	*Cordia goeldiana*	*Hymenaea courbaril*	*Parkia pendula*	*Simarouba amara*	*Tabebuia serratifolia*
Botanical family	Anacardiaceae	Boraginaceae	Caesalpinioideae	Mimosoideae	Simaroubaceae	Bignoniaceae
Wood specific gravity (g/cm^3)[a]	0.75–0.88	0.48–0.59	0.76–0.95	0.45–0.60	0.37–0.44	0.85–1.08
95th percentile diameter (cm)[b]	89 (2844)[c]	65 (1097)	118 (2534)	100 (1094)	84 (870)	105 (2250)
Max diameter (cm)[b]	187.0	100.0	185.6	151.0	124.5	286.0
Mean PAI (cm)[d]	0.42 B	0.32 A	0.42 B	0.73 C	0.71 C	0.25 A
95th percentile PAI (cm)[d]	1.10	1.03	1.15	1.72	1.63	0.72
Annual mortality unlogged forest (%)[e]	0.53 (325)	1.90 (149)	0.52 (413)	1.57 (281)	2.09 (154)	0.87 (244)
Post-logging annual mortality (%)[e]	0.88 (206)	1.77 (366)	1.43 (150)	1.56 (70)	1.43 (91)	1.48 (81)
Seedling shade tolerance[f]	Shade-tolerant	Light-demanding	Light-demanding	Moderately light-demanding	Light-demanding	Light-demanding
Density regeneration (per 100 ha)[g]	1075	28	82	88	122	25
Logging gap density (per 100 ha)[h]	555	175	212	322	63	25
Seed weight (g)[i]	0.02	0.03	4.00	0.10	0.27	0.04
Seed dispersal[j]	Wind	Wind	Animal	Animal	Animal	Wind

[a] References: Chudnoff (1984), Souza et al. (1997), Loureiro et al. (2000), and IBAMA (2006).

[b] For stems ≥ 10 cm diameter, calculated from inventories at seven sites; see Table 3 for sample sizes.

[c] Numbers in parentheses throughout table refer to number of individuals sampled.

[d] PAI = periodic annual increment, or rate of stem diameter growth. Values are for stems ≥ 5 cm diameter at four sites. See Table 3 for sample numbers. Italicized capital letters show significant differences in mean PAI among species. Species sharing the same letter code did not display significant differences ($p \geq 0.05$) in mean growth in one-way ANOVA with Tukey's multiple comparisons of means (SPSS version 10).

[e] Mean for stems ≥ 10 cm diameter in unlogged and logged forest over 6–10 years. Annual mortality rates calculated at each site using Sheil et al.'s (1995) equation, then averaged among sites, weighting by sample size.

[f] Based on monitoring of planted and naturally occurring seedlings in forest understory at five eastern Amazonian sites (Schulze, 2003).

[g] Average density of stems >50 cm height and <2 cm diameter in understory plots (Schulze, 2003).

[h] Total density of regeneration per 100 ha management block in felling gaps two years after logging; calculated from densities in 360 felling gaps, mean felling gap area, and mean number of felling gaps per 100 ha (Schulze, 2003).

[i] *Sources*: Hammond and Brown (1995), Hammond et al. (1996), Rose (2000), and Schulze (2003).

[j] *Source*: Martini et al. (1994).

Table 2
Description of inventory sites in the Brazilian Amazon

Site	Municipality, state	Location	Inventory area (ha)	Min diameter (cm)	Mean annual rainfall (mm)[a]	Dry season (months)
(A) Flona Tapajós km 83	Belterra, Pará	3°04′S, 54°15′W	400	35	2000	4–6
(B) Fazenda Agrosete	Paragominas, Pará	3°00′S, 47°20′W	210 (98)[b]	50 (10)[c]	1700	4–6
(C) Faz. Cauaxi	Goianesia, Pará	3°40′S, 48°20′W	1,200 (90)	35 (5)	2200	4–5
(D) Marajoara	Pau d'Arco, Pará	7°50′S, 50°16′W	204 (34)	20 (5)	1860	4–6
(E) Faz. Imaculada II	Chupinguaia, Rondônia	12°43′S, 61°00′W	1,015	30	1700	3
(F) Faz. São Jorge	Sena Madureira, Acre	9°25′S, 68°38′W	685	30	2100	2–3
(G) Faz. Seringal	Líbrea, Amazonas	8°44′S, 68°59′W′	11,370	30	2200	1–2

[a] Climate data sources: Silva et al. (1995), IBGE (1997, 2003), Barreto et al. (1998), Holmes et al. (2002), Schneider et al. (2002), Gerwing (2001), Keller et al. (2001), and Grogan and Galvão (2006).
[b] Numbers in parentheses refer to number of hectares subsampled for small diameter stems.
[c] Numbers in parentheses refer to smallest stem diameter sampled.

square 1 km on a side – and permits density measures to represent whole trees rather than fractions thereof (Grogan et al., 2008).

To estimate roundwood volumes we used the following single-entry equation developed for Tapajós National Forest (Silva and Carvalho, 1984):

$$V = e^{-7.62812+2.1809 \times \ln(\text{diameter})} \tag{1}$$

where diameter = diameter at 1.3 m height on the bole or above buttresses.

3.2. Study species diameter increment and mortality rates

Populations of the six study species were censused annually or bi-annually for diameter increment and mortality at sites A–D from 1993 to 1997 until 2003 to 2006, depending on site (Table 3), providing measurement intervals of 8–10 years. At each site, all size classes >5 cm diameter were included and a minimum of 100 and 15 ha were inventoried for adult and sub-adult size classes, respectively. Trees were monitored in both unlogged and logged forests. Total samples by species ranged from 150 to 567 individuals. Stems in growth studies were tagged and measured during each census at two fixed intervals (10 and 30 cm) below an aluminum nail at 160 cm height or 50 cm above buttresses; two measurements per tree per census helped control measurement error (tests of error rate on stem subsamples in different census years found means of 0.4–1 mm).

Mortality was monitored over the same time intervals for stems included in diameter increment studies as well as for additional trees not measured for growth (Table 1). Annualized mortality rates were calculated according to Sheil et al. (1995):

$$m = 1 - \left(\frac{N_1}{N_0}\right)^{1/t} \tag{2}$$

where N_0 is the number of live stems at time 0 and N_1 is the number of survivors at time t.

Observational and experimental studies of study species regeneration patterns and resource requirements in the forest understory and in logging gaps inform species descriptions and interpretation of simulation results (see below; Schulze, 2003).

3.3. Simulating study species post-logging commercial population recovery

To assess potential long-term impacts on commercial populations of current Brazilian legislation regulating forest management, we simulated post-logging recovery by the six study species at all sites by the following criteria: a minimum-felling diameter limit of 50 cm; 10% retention rate of commercial-sized trees; and simulations run over 30 years, the median interval between harvests anticipated under Brazilian forest legislation (25–35 years; Brasil, 2006).

After randomly selecting 90% of trees >50 cm diameter for harvest at all sites, surviving submerchantable and commercial-sized trees were grown over 30 years at annualized increment rates assigned randomly from the total pool of observed long-term increment rates for each species by trees in the same 10 cm diameter size class (10–20, 20–30 cm, etc.); no differences in growth rates for any species were found among sites. Because short-term post-logging growth rates may over-estimate long-term growth rates due to temporary community-level release associated with forest structural disturbance (Silva et al., 1995, 1996; Poels et al., 1998; De Graaf et al., 1999; Schulze, 2003; Vidal, 2004; Schulze et al., 2005), projections based on available data will likely over- rather than under-estimate long-term diameter growth and volume recovery (Valle et al., 2006).

Two species-specific annualized mortality rates were derived by pooling data among sites. The first, for post-logging mortality in highly disturbed forests with irregular canopies, was applied for the first 10 years of simulations (Table 1). The second, for mortality in unlogged forest, was applied during years 10–30 of simulations when forest canopies could be expected to have largely closed as noted above (Table 1). Mortality was assigned by two criteria: trees growing at the slowest increment rates (50%) to cull the weakest individuals, and trees randomly selected from the pool of survivors (50%) to account for stochastic factors causing death.

Though RIL harvesting is designed to minimize impacts on the residual stand, a certain amount of damage to submerchantable trees is unavoidable. We therefore subjected submerchantable stems to randomly assigned logging-induced mortality associated with infrastructure (especially skidding) and falling commercial

Table 3
Sample sizes and monitoring intervals for diameter increment studies of six study species at four eastern Amazonian sites

Site	*Astronium*	*Cordia*	*Hymenaea*	*Parkia*	*Simarouba*	*Tabebuia*	Monitoring interval
(A) Tapajós	181	32	61	20	47	61	1997–2005
(B) Faz. Agrosete	84	262	180	57	52	68	1993–2003
(C) Faz. Cauaxi	172	234	134	59	51	32	1997–2006
(D) Marajoara	–	–	192	121	–	–	1996–2006
Total	437	528	567	257	150	161	

trees. Based on unpublished field data (J. Zweede, personnel communication) and extensive documentation in the literature, we eliminated stems <35 cm diameter at the conservative rate of 12% (Johns et al., 1996; Holmes et al., 2002; Sist and Ferreira, 2007). Trees larger than this generally escape mortal injury during well-planned RIL operations.

Each population was resampled 1000 times to account for variation inherent to this method, with median, quartile, and 90th percentile values reported for estimated number of commercial trees and roundwood volume 30 years after the first harvest. Commercial population recovery during the first cutting cycle was assessed for all simulations in terms of percent density and timber volume recovery per 100 ha by trees >50 cm diameter compared to initial densities and volumes.

Three additional simulations adjusting harvest criteria were performed for five species (excluding *Simarouba*): (1) raising the minimum diameter cutting limit to 70 cm from 50 cm for all species except *Cordia* and retaining 10% of commercial-sized trees as before; (2) retaining 20% of commercial-sized trees after raising the minimum diameter cutting limit as in (1); (3) retaining 40% of commercial-sized trees after raising the minimum diameter cutting limit as in (1).

3.4. Effect of defective stems on simulations

We did not adjust harvest simulations to account for trees with stem hollows (Phillips et al., 2004; van Gardingen et al., 2006; Valle et al., 2006, 2007). Trees with large hollows are often left standing under RIL protocols in Amazonia due to low quantities of salvageable sawnwood and concerns about limiting canopy openings. Although hollow and defect rates have been poorly studied and show variation among sites and species, inventory and felling data from two of our four study sites have shown hollow and defects rates of around 25–40% at the first harvest (Barreto et al., 1998; Holmes et al., 2002; J. Zweede, unpublished; E. Vidal, unpublished). Hollow rates for commercial-sized trees at the second harvest are expected to be lower than at the first, as harvest trees will on average be smaller and younger in the second harvest (Valle et al., 2006, 2007; MacPherson, 2007). However, obvious defect rates (i.e., excluding cryptic hollows) of 12–37% were found in submerchantable populations at the four sites used for models (Valle et al., 2006; J. Zweede, unpublished; Schulze, unpublished). It is unclear whether loggers actually do reject hollow trees of high-value species like *Tabebuia* and *Cordia*, or log them hoping that some portion of the bole will be salvageable—a common practice for big-leaf mahogany (Grogan et al., 2008). In the absence of rigorous auditing of seed tree quality, many loggers complying with seed tree retention rules do so by designating hollow or otherwise undesirable trees for retention. Thus most or all of the trees retained in the initial harvest, and projected to account for 0–72% (mean 30.9 ± 20.8%) of species' second-harvest volume in our simulations, may be defective. Given these uncertainties, we opted for the simplicity of models that assume sound trees in both harvests. We acknowledge that the total volume of both the first and second harvests is likely overestimated for all populations, but are confident that the ratios we report are relatively immune to this bias, as subtractions of defective trees from each harvest projection will largely cancel each other.

4. Results

4.1. Patterns of commonness and rarity

4.1.1. The community versus commercial species

Within the community of tree species attaining the forest canopy and >35 cm diameter, only 3–9% of species exceeded densities of 100 trees per 100 ha ($1\ \mathrm{ha}^{-1}$) among four eastern Amazonian sites where community-level inventory data was available (Table 4, sites A–D). At three of four sites 61–67% of species occurred at densities <10 per 100 ha. At site D, where overall community diversity was much lower than at other sites, 36% of species occurred at densities below this threshold. Commercial species density patterns largely mirrored those of the community, with 3–13% of species exceeding 100 trees per 100 ha (equivalent to 3–5 species per site) and 50–54% of species occurring at densities <10 trees per 100 ha (30% at site D).

Table 4

Percentage of species in six stem density classes (number of stems per 100 ha) at seven sites in Brazilian Amazonia

(1) Density class	Site: A. Tapajós		Site: B. Faz. Agrosete		Site: C. Faz. Cauaxi		Site: D. Marajoara		Site: E. Faz. Imaculada		Site: F. Faz. São Jorge		Site: G. Faz. Seringal	
	All spp.	Comm.	All spp.	Comm.	All spp.	Comm.	All spp.	Comm.	All spp.	Comm.	All spp.	Comm.	All spp.	Comm.
>100	3.1%	5.1%	4.3%	5.4%	5.3%	2.7%	9.1%	13.3%	–	–	–	–	–	–
50–100	5.5%	11.1%	4.8%	10.9%	6.9%	10.6%	18.2%	16.7%	–	–	–	–	–	–
25–50	11.3%	6.1%	9.1%	15.2%	8.9%	13.3%	11.4%	26.7%	–	–	–	–	–	–
10–25	16.0%	23.2%	15.3%	18.5%	18.2%	22.1%	25.0%	13.3%	–	–	–	–	–	–
3–10	22.7%	23.2%	25.4%	20.7%	27.9%	26.5%	36.4%	13.3%	–	–	–	–	–	–
<3	41.4%	31.3%	41.1%	29.3%	32.8%	24.8%	NA	16.7%	–	–	–	–	–	–
# species	326	99	209	92	247	113	88	30	–	–	–	–	–	–
# hectares	400	400	75	98	150	1200	14	204	–	–	–	–	–	–

(2) Density class	Site: A. Tapajós		Site: B. Faz. Agrosete		Site: C. Faz. Cauaxi		Site: D. Marajoara		Site: E. Faz. Imaculada		Site: F. Faz. São Jorge		Site: G. Faz. Seringal	
	≥20 cm	≥50 cm	≥20 cm	≥50 cm	≥20 cm	≥50 cm	≥20 cm	≥50 cm	≥20 cm	≥50 cm	≥20 cm	≥50 cm	≥20 cm	≥50 cm
>100	–	3.0%	18.5%	1.1%	25.0%	0.9%	13.3%	3.3%	7.5%	0.0%	13.6%	0.0%	0.0%	0.0%
50–100	–	3.0%	17.4%	8.7%	21.4%	2.7%	36.7%	16.7%	10.0%	10.0%	13.6%	4.5%	0.0%	0.0%
25–50	–	12.1%	16.3%	8.7%	25.0%	11.5%	16.7%	16.7%	22.5%	12.5%	18.2%	22.7%	5.5%	5.5%
10–25	–	15.2%	20.7%	18.5%	21.4%	19.5%	16.7%	13.3%	17.5%	27.5%	40.9%	31.8%	25.5%	12.7%
3–10	–	23.2%	10.9%	17.4%	7.1%	29.2%	13.3%	30.0%	22.5%	15.0%	13.6%	31.8%	21.8%	25.5%
<3	–	43.4%	16.3%	45.7%	0.0%	36.3%	3.3%	20.0%	20.0%	35.0%	13.6%	22.7%	47.3%	56.4%
# species	–	99	92	92	28	113	30	30	40	40	25	25	55	55
# hectares	400	98	90	1200	204	1015	685	11,370						

(1) All species vs. commercial species for those attaining canopy status and >35 cm diameter; data unavailable for sites E–G. (2) Density patterns for commercial species, all stems >20 cm diameter vs. commercial stems >50 cm diameter; data unavailable for stems <35 cm diameter at site A.

4.1.2. Commercial species' density patterns across sites

Inventories registered the highest numbers of commercial species in northeastern Amazonia (Table 4, sites A–C: 92–113 species) because forests were the most highly diverse in this region, and because transportation infrastructure and markets are the most highly developed in the northeast (Lentini et al., 2005). Despite differences in total number of commercial species, proportions of species by density class were broadly consistent among sites (Table 4). Considering stems >20 cm diameter, that is, including submerchantable size classes, from 8% to 25% of commercial species occurred at densities >100 stems per 100 ha, excluding site G in the far southwest (Amazonas) where commercial species registered at extremely low densities. Seven to 43% of commercial species occurred at densities <10 stems per 100 ha (again excluding site G). However, timber species appear a great deal 'rarer' when we consider only commercial size classes (>50 cm diameter): from 0% to 3% of species occurred at densities >100 stems per 100 ha, while 50–66% of species densities were <10 stems per 100 ha (81% at site G). At least one fifth of timber species met the Brazilian legal definition of rare (<3 commercial-sized trees per 100 ha) at all sites. Fifty-six percent of timber species at site G occurred at densities too low to legally harvest.

4.1.3. Site-level commercial species density patterns

The six study species were widely distributed across Amazonian sites at highly variable local densities (Table 5). Three species (*Cordia*, *Hymenaea*, *Tabebuia*) occurred at densities >100 stems per 100 ha at a single site when including submerchantable trees (>20 cm diameter); no species attained this density for commercial-sized trees (>50 cm diameter). All six species were relatively abundant at some sites, especially in the northeast (sites A–C), but occurred at extremely low densities (<10 stems per 100 ha) or were absent at other sites, especially in the southwest (sites E–G). All species except *Hymenaea* were legally 'rare' or absent as commercial-sized trees at one or more sites. Site-level populations of the two smaller-statured species, *Cordia* and *Simarouba*, tended to be dominated by submerchantable trees (e.g., sites B–D; but see sites A and E) as relatively few adult trees grew larger than the minimum diameter cutting limit. Sampled populations of two large-statured species, *Hymenaea* and *Tabebuia*, tended to be dominated by commercial stems with fewer submerchantable trees present (e.g., sites A, E, and G), though this was not true at all sites (sites B, D, and F for *Tabebuia*).

Similar trends and variability were found for 18 additional timber species widely distributed across the Amazon (Table 5). Most were absent from one or more sites, with a number of species restricted either to northeastern or southwestern sites. At northeastern sites, several light-demanding species occurred at higher densities at site B where forest structure was more broken or vine-tangled compared to floristically and edaphically similar forests at sites A and C. Many widely distributed species were absent from the transitional southeastern site D where the forest canopy was low and highly irregular; there, however, light-demanding pioneer and emergent species such as *Jacaranda copaifera*, *Cedrelinga catenaeformis*, and *Trattinickia burseraefolia* were found at exceptionally high densities.

4.1.4. Within-site commercial species density patterns

Within a given site, species densities may fluctuate dramatically from one harvest block (typically 100 ha) to another, that is, at the meso-scale (*sensu* Clark et al., 1998). At site C, inventory data for six study species from 13 harvest blocks show densities for trees >35 cm diameter ranging from 0 to 104 stems per 100-ha block (Table 6). Among other species, block-level density ranged as wide as 2–271 stems per 100 ha (*Trattinickia rhoifolia*, Table 6). Of

Table 5

Density patterns of selected commercial species at seven sites across Brazilian Amazonia, for stems >20 cm diameter (sub merchantable + commercial) and for stems >50 cm diameter (commercial only), as number of stems per 100 ha

	Species	Site: A. Tapajós		Site: B. Faz. Agrosete		Site: C. Faz. Cauaxi		Site: D. Marajoara		Site: E. Faz. Imaculada		Site: F. Faz. São Jorge		Site: G. Faz. Seringal	
		≥20 cm	≥50 cm	≥20 cm	≥50 cm	≥20 cm	≥50 cm	≥20 cm	≥50 cm	≥20 cm	≥50 cm	≥20 cm	≥50 cm	≥20 cm	≥50 cm
(1)	*Astronium lecointei*	51	36	61	25	61	32	–[a]	–	1	1	58	24	21	14
	Cordia goeldiana	14	7	231	31	70	24	–	–	3	2	–	–	6	2
	Hymenaea courbaril	17	14	128	68	48	25	92	61	31	25	5	4	15	13
	Parkia pendula	8	7	35	10	15	9	87	50	6	5	–	–	5	4
	Simarouba amara	15	7	39	4	24	7	21	3	33	22	–	–	3	2
	Tabebuia serratifolia	34	24	50	18	14	6	40	9	114	85	67	12	4	2
(2)	*Amburana acreana*	–		–	–	–	–	–	–	28	19	45	29	10	9
	Apuleia molaris/leiocarpa[b]	–		–	–	≪1	–	47	34	60	53	25	19	15	14
	Bagassa guianensis	NA[c]	8	26	17	18	9	–	–	16	11	NA	2	3	2
	Caryocar villosum	NA	15	46	25	34	16	–	–	42	25	NA	27	13	12
	Cedrela odorata	NA	8	14	3	NA	2	5	≪1	10	6	22	10	13	9
	Cedrelinga catenaeformis	NA	1	–	–	–	–	75	56	≪1	≪1	–	–	2	2
	Ceiba pentandra	–	–	–	–	NA	6	16	7	8	8	NA	53	31	27
	Copaifera duckei	NA	7	69	41	34	18	54	10	3	3	10	9	7	7
	Dinizia excelsa	–	–	2	2	40	33	–	–	3	2	–	–	3	2
	Dipteryx odorata	NA	11	41	25	5	4	–	–	4	3	44	37	16	16
	Euxylophora paraensis	–	–	–	–	24	19	–	–	–	–	–	–	2	1
	Hymenolobium cf. heterocarpum	–	–	–	–	–	–	27	5	–	–	–	–	–	–
	Hymenolobium petraeum	NA	1	3	1	NA	1	–	–	–	–	–	–	–	–
	Jacaranda copaia	NA	42	92	10	24	5	873	428	41	26	–	–	1	1
	Tabebuia impetiginosa	20	15	29	21	14	3	–	–	–	–	17	3	–	–
	Trattinickia burseraefolia	–	–	–	–	–	–	416	145	–	–	–	–	–	–
	Trattinickia rhoifolia	NA	10	106	2	65	30	–	-	–	–	–	–	–	–
	Virola michelii	NA	32	218	4	142	16	–	–	–	–	–	–	–	–

(1) This study's six species. (2) Eighteen additional widely distributed commercial species.

[a] Species not present in inventory.

[b] Apuleia = molaris in southeast Amazonia, leiocarpa in southwest Amazonia.

[c] NA = inventory data for this size class not available.

Table 6

Density patterns (number of stems per 100 ha) of selected commercial species within management blocks[a] at Faz. Cauaxi (site C), for stems >35 cm diameter (the minimum diameter inventoried)

	Species	A	B	C	D	E	F	G	H	I	*J*[b]	*K*	*L*	*M*	Minimum	Maximum	Median
(1)	*Astronium lecointei*	50	32	43	38	42	48	41	55	54	35	46	10	47	10	55	43
	Cordia goeldiana	77	48	13	104	75	12	73	30	65	0	0	1	27	0	104	30
	Hymenaea courbaril	37	43	34	29	29	34	32	37	28	13	46	9	24	9	46	32
	Parkia pendula	14	14	9	0	11	24	9	6	15	13	8	14	8	0	24	11
	Simarouba amara	6	1	1	17	6	16	13	19	2	7	7	10	6	1	19	7
	Tabebuia serratifolia	4	1	0	12	11	6	15	4	5	0	12	0	5	0	15	5
(2)	*Apuleia molaris*	0	0	0	0	0	0	3	1	0	0	0	0	0	0	3	0
	Bagassa guianensis	12	16	10	12	12	18	15	9	5	0	5	1	23	0	23	12
	Bombax paraensis	29	15	5	0	17	0	0	0	0	7	16	6	23	0	29	6
	Caryocar villosum	31	25	20	10	37	12	23	20	12	4	34	7	13	4	37	20
	Cedrela odorata	0	2	4	1	7	4	4	1	1	0	0	1	1	0	7	1
	Chrysophyllum lucentifolium	104	131	36	132	156	140	150	117	117	7	40	3	38	3	156	117
	Copaifera duckei	29	26	26	39	23	26	20	20	25	17	28	7	17	7	39	25
	Dinizia excelsa	23	32	47	14	29	40	32	29	12	72	38	54	28	12	72	32
	Dipteryx odorata	5	3	2	4	9	8	6	3	5	4	8	4	4	2	9	4
	Euxylophora paraensis	0	0	0	0	2	0	0	4	13	16	38	77	155	0	155	2
	Hymenolobium petraeum	12	3	5	1	4	8	1	4	1	4	0	6	1	0	12	4
	Jacaranda copaia	20	14	7	13	26	8	16	17	23	5	9	1	18	1	26	14
	Sacoglottis guianensis	5	7	0	78	9	108	133	67	102	21	78	0	61	0	133	61
	Tabebuia impetiginosa	3	3	4	5	14	4	5	5	2	0	3	0	0	0	14	3
	Trattinickia rhoifolia	18	12	53	232	18	14	271	101	2	14	10	7	3	2	271	14
	Virola michelii	115	87	32	76	81	50	43	52	73	28	40	11	15	11	115	50

(1) This study's six species. (2) Sixteen additional commercial species.

[a] Most harvest blocks covered 100 ha, but ranged from 50 to 115 ha.

[b] Italicized harvest block codes indicate blocks with dissected and/or low-lying terrain. Remaining nine blocks were sited on plateaus.

113 commercial species inventoried at site C, 88 were present at densities <3 trees per 100 ha in at least one harvest block, even though only 27 species (29.3%) occurred at an average density below this threshold across all plots. Conversely, 41 species occurred at densities as high as 50 stems per 100 ha in one or more harvest blocks, though only 15 species occurred at or above this density on average.

Meso-scale fluctuations in species densities at least in part reflect habitat associations. For example, *Euxylophora paraensis* attained high densities at site C only in low-lying or heavily dissected terrain predominating in only four of 13 harvest blocks (Table 6B); by contrast, many species were scarce on this type of terrain. However, much of the variation in species densities was not obviously related to environmental variation among harvest blocks. Similar habitat-mediated distribution patterns at the meso-scale were observed at site D (Schulze, unpublished data).

4.2. Study species life history characteristics

4.2.1. Size class frequency distributions

Just as study species' density patterns varied widely among sites across Amazonia, their submerchantable and commercial population structures also proved extremely variable among sites, though with observable tendencies (Fig. 1). In general, higher density populations of the study species were more likely to have relatively abundant submerchantable stems, and where locally rare, species' population structures tended to be amodal, with approximately equal representation among size classes.

The most shade-tolerant species, *Astronium*, had the highest densities of pole-sized (5–20 cm diameter) stems where these size classes were inventoried, and displayed steeply declining density with increasing size classes up to 30 cm diameter (to 50 cm diameter at some sites). This pattern loosely fits the 'balanced' negative exponential or classic reverse-J distribution. Size class distributions of *Astronium* canopy trees (stems >30–40 cm diameter) were relatively flat or slightly peaking between 40 and 60 cm diameter before declining as trees grew larger than 100 cm diameter.

Parkia, a fast-growing species with higher seedling shade tolerance than the remaining four light-demanding species, had size class frequency distributions similar to *Astronium* at eastern sites, with consistently high relative densities of pole-sized trees and relatively flat frequency distributions of larger stem size classes (canopy trees). At southwestern sites, *Parkia* population structures approximated unimodality, though higher minimum inventory diameters at southwestern sites (E–G) make interpretation for this and other study species difficult.

For the remaining four light-demanding species, population structures were highly variable among sites. *Cordia* and *Simarouba* populations declined steeply in density >60–70 cm diameter, with few adults attaining large diameters. Coupled with diameter increment data (see below), this indicates that these two species are relatively short-lived compared to other study species. It follows that *Cordia* and *Simarouba* populations had substantially more submerchantable stems (<50 cm diameter) than commercial-sized trees, with up to 92% of stems >10 cm below the minimum-felling diameter.

Size class frequency distributions of *Hymenaea* and *Tabebuia*, two light-demanding emergent species, were highly variable among sites, taking amodal, unimodal, and approximately reverse-J forms. Among the four species attaining very large adult sizes (>120 cm diameter), *Hymenaea* and *Tabebuia* had the lowest proportion of observed populations in submerchantable size classes (means: 52% and 57%, respectively, vs. 65% for *Astronium* at fully inventoried sites where all three occurred).

4.2.2. Diameter increment rates

For all six study species, sample-wide mean periodic annual diameter increment (PAI) was well below 1 cm yr^{-1} (Table 1). Based on PAI, the study species sorted into fast-growing (*Parkia*, *Simarouba*), slow-growing (*Cordia*, *Tabebuia*) and intermediate (*Astronium*, *Hymenaea*) pairs. However, for all species virtually every size class displayed a wide range of PAI values (Fig. 2), and maximum increment rates by size class far exceeded mean values. This contrast was particularly acute for *Cordia*, a species capable of

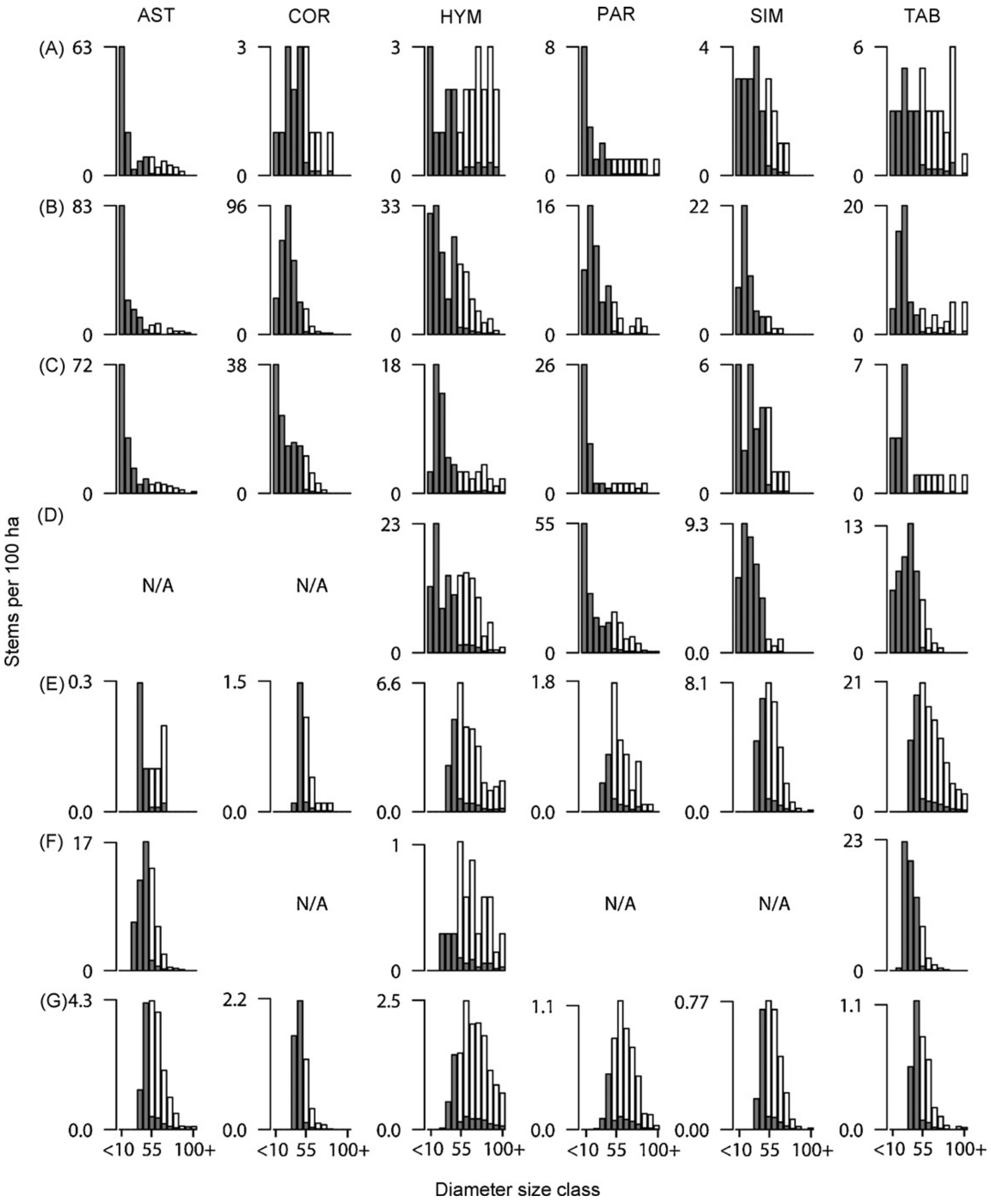

Fig. 1. Size class frequency distributions for six species by 10 cm size classes at seven sites in the Brazilian Amazon. Panel letters (A–G, left side) correspond to sites listed in Tables 2–5. The smallest size class shown is 5–10 cm diameter; largest is 120+ cm diameter. Gray columns indicate live trees; white columns (full or partial) show logged trees (90% of stems >50 cm diameter). Note variable ***Y***-axis scales (stems per 100 ha). AST = ***Astronium lecointei***, COR = ***Cordia goeldiana***, HYM = ***Hymenaea courbaril***, PAR = ***Parkia pendula***, SIM = ***Simarouba amara***, and TAB = ***Tabebuia serratifolia***.

sustained diameter increment of 1.5 cm yr^{-1}, but with few trees actually growing near maximum rates. For all species except *Tabebuia*, 95th percentile diameter increment rates were $\geq$1 cm yr^{-1}, and approached 2 cm yr^{-1} for *Parkia* and *Simarouba*.

The study species demonstrated three stem diameter-related increment patterns: high mean increment rates by poles and sub-adults and then steadily declining rates through adult size classes (*Cordia*); low increment rates by poles and sub-adults, with growth rates peaking by submerchantable adult size classes (30–50 cm diameter) and subsequently declining (*Astronium*, *Hymenaea*); and low growth rates by small stems with relatively uniform growth across adult size classes (*Parkia*, *Tabebuia*). Although increment rates by *Simarouba* stems 5–10 cm diameter were low, rates declined from 10 cm through adult size classes in a manner similar to *Cordia*.

4.2.3. Mortality rates

Species mortality rates in unlogged forests mirrored differences in life history characteristics. Those with lightweight wood, high potential diameter increment rates, and presumably shorter life-spans – *Cordia*, *Parkia*, *Simarouba* – experienced relatively high annual mortality rates (1.57–2.09%, Table 1) compared to community-wide annual mortality rates of approximately 1% (Schulze and Zweede, 2006; Sist and Ferreira, 2007). Annual

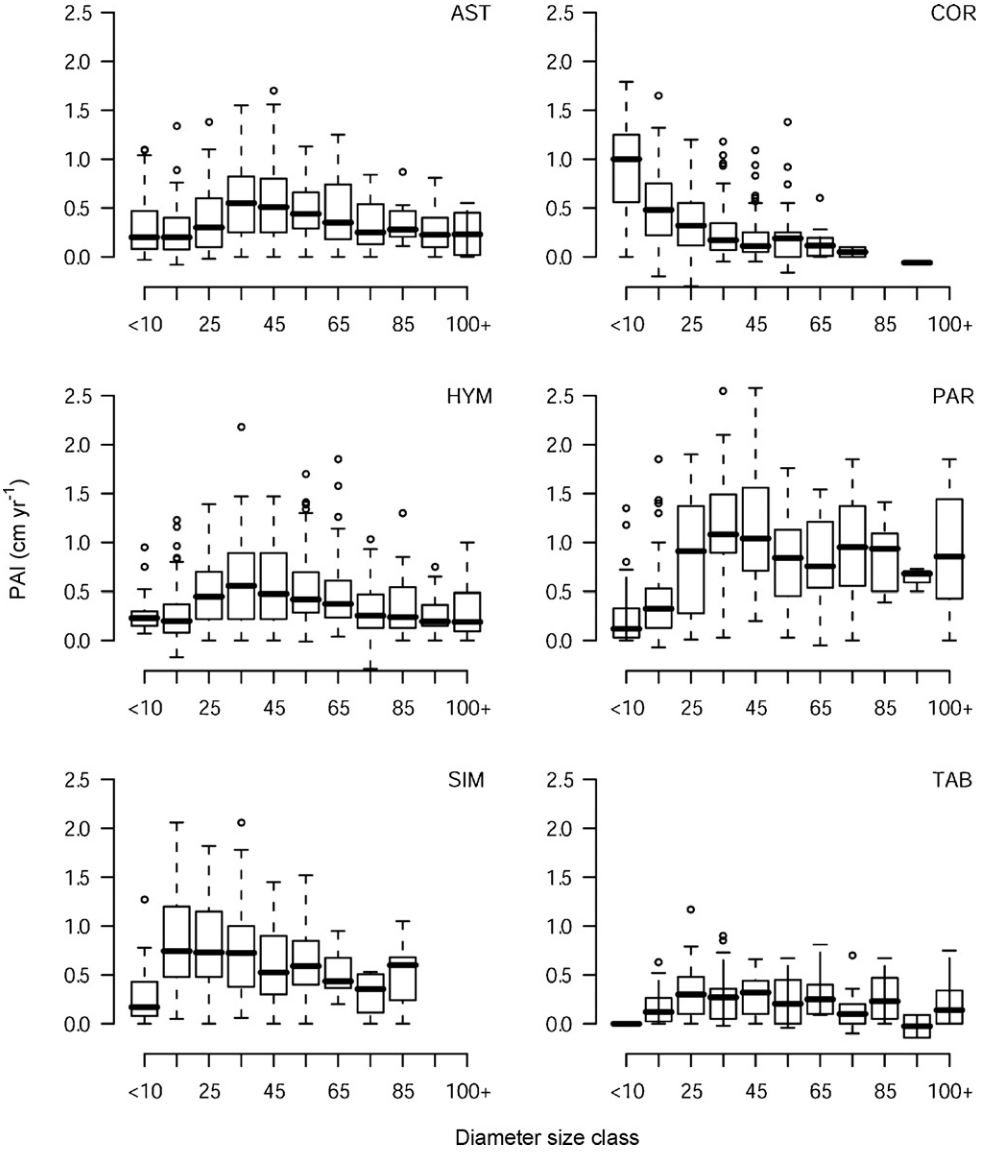

Fig. 2. Observed diameter increment rates (periodic annual increment, PAI, in cm yr^{-1}) for six species by 10 cm size class, showing pooled data from four sites (A–D, Table 2). Boxplots show median values (solid horizontal line), 50th percentile values (box outline), 90th percentile values (whiskers), and outlier values (open circles). AST = ***Astronium lecointei***, COR = ***Cordia goeldiana***, HYM = ***Hymenaea courbaril***, PAR = ***Parkia pendula***, SIM = ***Simarouba amara***, and TAB = ***Tabebuia serratifolia***.

mortality rates for the three species with moderate to high-density wood and lower potential growth rates – *Astronium*, *Hymenaea*, *Tabebuia* – were <1% (0.52–0.87%). All six species experienced accelerated annual mortality during the 3 years following logging (Schulze, 2003), but over longer post-logging intervals examined here (6–10 years), differences between mortality in unlogged and logged stands narrowed or even reversed. Longer-term post-logging mortality rates by the three fast-growing species (1.56–1.77%, Table 1) were essentially equivalent to rates in unlogged forests, reflecting perhaps a trade-off between high light and mortality for these species. The other three slower-growing species experienced accelerated post-logging mortality rates during the longer sampling periods reported here.

4.3. Simulated commercial population recovery

Simulations of species-level post-logging commercial population recovery during the first 30-year cutting cycle following Brazilian harvest regulations and RIL are summarized in Fig. 3. Projected median second-harvest commercial densities and volumes were 40–50% of pre-harvest values or lower for five of six study species (*Astronium*, *Cordia*, *Hymenaea*, *Parkia*, *Tabebuia*), with exceptions noted below. Volume recovery tended to be lower than stem density because recruits to the commercial size class during the 30-year period were small compared to many mature trees logged during the first harvest. In 13 of 22 simulations (*Astronium* and *Cordia* did not occur at site D), volume recovery was <40% of starting values. Exceptions among these five species included *Parkia* at site B (109% recovery) and *Tabebuia* at site D (84% recovery). In both cases, submerchantable stems dominated pre-logging populations. *Cordia* recovered 52–64% of starting densities and 47–56% of starting volumes at sites B and C, again courtesy of robust submerchantable populations at the time of logging.

The one species whose commercial populations recovered to nearly 100% or more of starting densities and volumes was the fast-growing *Simarouba*, which additionally had few stems larger than the minimum-felling diameter of 50 cm at any site (Fig. 1). At two sites where initial *Simarouba* densities were very low (Table 4: B and D), projected second-harvest volumes far exceeded first harvests. At site D where initial densities were too low to legally

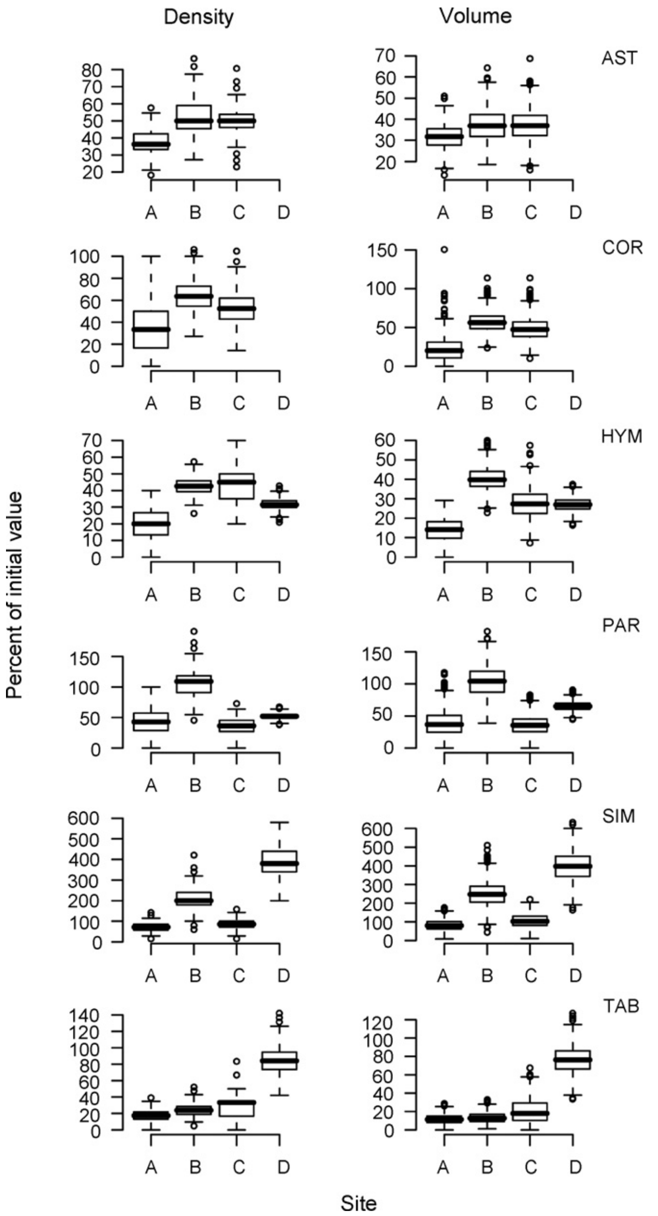

Fig. 3. Simulated recovery of six species as % of initial commercial density (left-side charts) and volume (right-side charts) at four sites (A–D, Table 2) under Brazilian legal standards for forest management. Box plots show median simulated values (solid horizontal line), 50th percentile values (box outline), 90th percentile values (whiskers), and outlier values (open circles). ***Astronium*** and ***Cordia*** did not occur at site D.

harvest (<3 stems per 100 ha), submerchantable stocks were nevertheless quite high compared to commercial-sized trees, resulting in exuberant population recovery (~400%).

For every study species, fullest recovery within 30-year simulations was made by populations with the highest pre-logging ratio of submerchantable to commercial-sized stems. This can be most clearly seen for *Tabebuia*: populations at two of three northeastern sites (A and C) were skewed towards large adult stems, while at the transitional southeastern site D this species rarely attained diameters >80–90 cm and most inventoried trees were submerchantable. Even without accounting for species differences, the proportion of submerchantable stems was highly correlated with volume recovery in the 22 simulated population responses (Spearman's $\rho = 0.652$, $p = 0.001$).

Diameter increment rates of future crop trees also influenced simulation results. For example, despite similar population structures at three sites where *Cordia* and *Simarouba* occurred together (Fig. 1A–C), mean growth rates were twice as fast by *Simarouba*. While fast-growing *Simarouba* and *Parkia* were able to recruit to commercial size during 30 years from starting diameters as small as 10 cm, recruitment by slower-growing *Hymenaea* and *Tabebuia* was restricted to larger submerchantable size classes (30–50 cm diameter with exceptions).

4.4. Effect of minimum harvest diameter and seed tree retention rate on commercial population recovery

Repeated post-logging simulations under steadily more restrictive harvest regulations yielded better recovery during the first 30-year cutting cycle by five of six species (Fig. 4; *Simarouba*'s response under current regulations was robust enough to exclude it from further simulations). Volume recovery increased steadily with harvest restrictions in all populations of *Astronium* and *Hymenaea*, though commercial volume recovery by *Hymenaea* approached 100% at only two sites (B and D) under the most restrictive scenarios. In contrast, most populations of *Cordia* and *Tabebuia* displayed little to no increase in volume recovery except under the most restrictive scenario (raising the minimum-felling diameter from 50 to 70 cm for *Tabebuia*, and retention rate from 10% to 40% for both species). *Tabebuia*'s exceptional recovery under adjusted regulations at site D is anticipated by the fact that this species rarely exceeds 70 cm diameter in this southeastern region. Similarly in the case of *Parkia*, simply increasing the minimum-felling diameter had a pronounced effect on volume recovery for populations at sites B and D where proportions of submerchantable stems were highest; the additional measure of increasing commercial tree retention to 40% was necessary to promote volume recovery at levels necessary for a comparable second harvest from the remaining two populations. In sum, *Parkia* was the one species for which the most restrictive combination of harvest parameters led to uniformly high recovery of harvested volume. Only two of 14 populations of the remaining four species showed 100% recovery under this scenario.

As restrictions on harvests increase, first-harvest volumes and profits decline. Raising the minimum-felling diameter to 70 cm decreased first-harvest volume by an average of 25% for populations of the four species tested (*Simarouba* and *Cordia* excluded for reasons given above). Median first-harvest volumes declined to 65% and 55% of potential volume under current regulations as commercial tree retention rates of 20% and 40%, respectively, were added to the 70 cm minimum-felling diameter in simulations. Second-harvest volumes in the more restrictive scenarios increased as a proportion of the first harvest. However, in all but two cases (minimum-felling diameter 70 cm and 10% retention for *Parkia* at sites A and C), the sum of first- plus second-harvest volumes was higher under current regulations than under any of the more restrictive scenarios (median combined harvest volume declined from 89% to 73% of potential volume under current regulations as restrictions increased). When the value of second harvests is appropriately discounted (ca. 9%; MacPherson, 2007), the financial costs of more sustainable harvest practices become even more pronounced (total net present value of two harvests under increased restrictions was 78–53% of that under current regulations).

5. Discussion

Insofar as tree species occurring at vanishingly low densities across local and regional landscapes are unlikely to attract

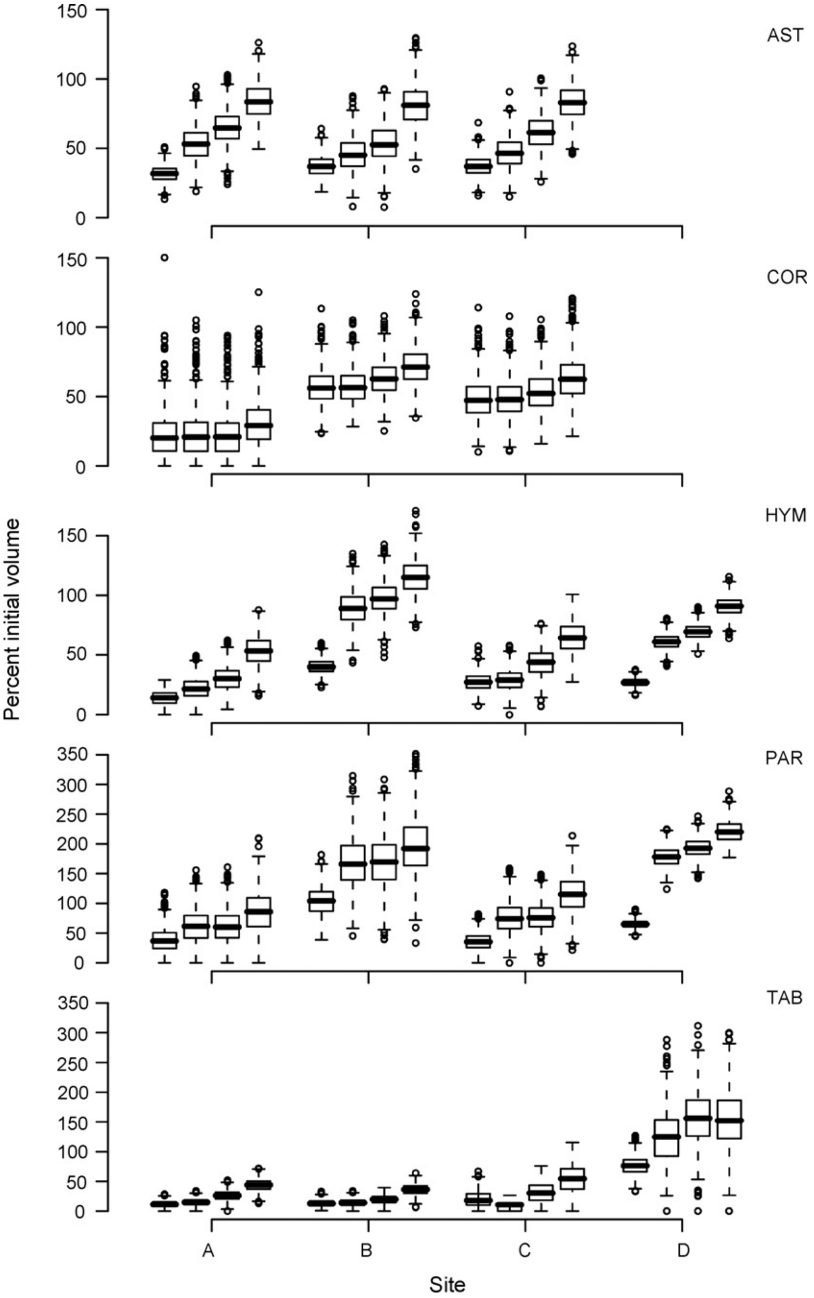

Fig. 4. Simulated recovery of five species (excluding ***Simarouba***) as % of initial commercial volume at four sites (A–D, Table 2) under progressively more restrictive harvest regulations (boxplots, ordered left to right for scenarios 1, 2, 3 and 4 at each site): (1) current legal framework as in Fig. 3; (2) raise minimum-felling diameter from 50 to 70 cm for all species except ***Cordia***, retention rate 10%; (3) as in (2) with retention rate 20%; (4) as in 2 with retention rate 40%. See Fig. 3 for species names and details on boxplots.

widespread commercial attention, timber species are unlikely to represent a strictly random subset of the forest community. Our data demonstrate this. From the logger's perspective, however, 50% or more of commercial species at a given site in Amazonia typically appear 'rare' indeed in commercial inventories (<10 stems per 100 ha). For the purposes of sustaining species populations and commercial volumes beyond the first harvest, does density matter? Current Brazilian management regulations designating three commercial stems per 100 ha as the minimum harvestable density indicate that it does. Our findings suggest that density alone tells us little about sustainability in the absence of basic understanding of species- and site-specific population structure, growth, and mortality rates, among other life history traits.

As an example, consider populations of *Simarouba* and *Tabebuia* at site C (Table 5). While occurring at roughly equivalent but extremely low commercial densities (7 vs. 6 stems >50 cm diameter per 100 ha, respectively), *Simarouba*'s submerchantable population density exceeds *Tabebuia*'s by a healthy margin (17 vs. 8 stems per 100 ha). Projected commercial population recovery during the 30-year cutting cycle at this site by these two species – median values of 86% versus 33% of initial densities and 103% versus 18% of initial volumes, respectively (Fig. 3) – indicates that *Simarouba* may persist after logging at current, if low, densities, while *Tabebuia* may be imperiled by current logging standards, even under RIL protocols. In fact, if spatial operational scales are large enough and timber prices are high enough, density may not be a critical life history characteristic at all.

5.1. Life history traits shaping future yields

5.1.1. Population structure

Forest managers generally expect that species populations with abundant stocks of seedlings, saplings, poles and submerchantable adults relative to commercial trees will recover initial commercial densities and volumes following RIL harvests, irrespective of overall landscape-scale density. In simulations described here, pre-logging size class distributions were the single most important factor in determining post-logging recovery. Only species populations with <30% of inventoried trees attaining commercial size recovered sufficiently during the first 30-year cutting cycle to permit equivalent second harvests under current Brazilian regulations for minimum-felling diameter (50 cm) and commercial tree retention rate (10%). Since few study species populations were structured in this way, we predict that in most cases commercial recovery will not occur for these species under current best-management practices in Amazonia, again irrespective of meso-scale densities.

Raising the minimum diameter felling limit adjusts the ratio of submerchantable to commercial stems, potentially addressing this issue. However, raising the minimum from 50 to 70 cm diameter in simulations failed to shift this ratio sufficiently for most species populations examined, even when raising retention rates to 20% and 40%.

5.1.2. Diameter increment (growth) and mortality rates

Coupled with differences in size class distributions among the six study species, diameter increment and mortality rates strongly influenced simulated post-logging recovery. The fast-growing species *Simarouba* and *Parkia* consistently recovered higher volume than slow-growing *Tabebuia*. Two species with similar population structures, *Simarouba* and *Cordia*, demonstrated quite different recovery rates due to relatively low median growth rates by the latter. Species with widely variable growth rates within size classes demonstrated the most variable simulated recoveries—see especially the impact on simulations of exceptionally large differences between median and potential PAI across size classes for *Cordia*. Much of the variation in growth rates among individuals of a given species may be explained by stem condition (e.g., crown damage) and local growth environment (soil fertility, crown illumination, and liana loads), factors that vary as widely among residual populations in logged forest as in undisturbed stands (Clark and Clark, 1990, 1999; Silva et al., 1995; Grogan, 2001; Schulze, 2003; Vidal, 2004; Dauber et al., 2005).

Variable mortality rates among the study species also influenced simulations. While fast growth by *Simarouba* and *Parkia* more than compensated for relatively high mortality rates, *Cordia*'s high mortality rate magnified the negative effect of slow growth, yielding more pessimistic commercial recovery projections than expected from population structures. Mortality also contributed to variance in simulations; in particular, the stochastic component of mortality when applied to small populations of adults with a wide range in diameters led to large variations in volume recovery among simulation runs (e.g., compare *Parkia* and *Hymenaea* adult densities and simulation results at site A vs. site D in Figs. 1 and 3).

5.2. Post-RIL recovery by low-density species

5.2.1. Short-term prospects for sustained yields

Our results illustrate severe limitations to the current one-size-fits-all approach to yield regulation in Amazonia. Most of the study species, and likewise most high-value hardwood species in Amazonia, will not furnish sustained yields under current regulations and RIL protocols. Static minimum-felling diameter and commercial retention rules cannot be reconciled with marked differences in timber species life histories and the need for management that is adaptive to local population structure and relative densities of timber species. These shortcomings cut both ways: small-statured species with populations characterized by abundant submerchantable stems and high growth rates could likely support harvests of smaller diameter stems (e.g., *Simarouba*). Guidelines for minimum-felling diameter limits and commercial tree retention rates must account for population structures and recovery potential if sustained production of high-quality hardwood of varying working properties is to remain a goal of forest management in Amazonia.

5.2.2. Sustaining harvests over the long term

Simulations of species response to logging through a single cutting cycle, from first to second harvest, cannot provide a full picture of population recovery in a polycyclic management system in which a complete rotation – replacement of adults in the initial harvest by regeneration from seed – is expected to take 60 or more years. They do, however, illustrate the beginning of commercial depletion of study species that we expect will be exacerbated during successive cutting cycles. Previous research on study species regeneration in unlogged and logged forests (Schulze, 2003, 2008) has documented insufficient regeneration and recruitment rates in logging gaps and other disturbed areas within logged forest by light-demanding species such as *Hymenaea*, *Parkia*, and *Tabebuia* to replace harvested adults. In the forest understory, seedling and sapling densities of all species described in this study except *Astronium* were low, growth rates were slow, and mortality rates were high, suggesting that few crop trees of the future will emerge from the relatively undisturbed forest matrix (areas not directly impacted by felling, skidding or road-building). Other researchers have documented poor regeneration of commercial stems after logging (Dickinson and Whigham, 1999; Fredericksen and Mostacedo, 2000; Grogan et al., 2003); an estimated 80% of commercial species in Bolivian forests are not regenerating at levels sufficient to replace themselves (Mostacedo and Fredericksen, 1999). These patterns indicate that third-harvest scenarios under RIL without silviculture are likely to be worse than second-harvest scenarios for the study species, and indeed for most high-value timber species in Brazilian Amazonia. This is consistent with findings from stand-level models, which project a shift in harvest composition over time from shared dominance by both light-demanding and shade-tolerant hardwoods in the first harvest to a preponderance of aggressive gap colonizers with lightweight wood in second, third, and all subsequent harvests (Alder and Silva, 2000; Phillips et al., 2004; van Gardingen et al., 2006; MacPherson, 2007; Valle et al., 2007). Long-term projections of species recovery under multiple cutting cycles will require information on reproduction and regeneration in relation to adult density. However, low post-logging regeneration rates observed for most species in this study severely limit prospects for long-term population recovery under log-and-leave management practices.

5.2.3. Silviculture's essential role

Because many trees in logged populations are growing well below maximum potential rates and because trees are responsive to changes in light and liana loads (De Graaf et al., 1999; Pérez-Salicrup and Barker, 2000; Gerwing, 2001; Grauel and Puz, 2004), liberation of future crop trees from competition with lianas and non-commercial trees may be the second greatest opportunity – after limiting damage to future crop trees during harvest under RIL protocols – for forest managers to increase growth rates by surviving trees during the interval between harvests. Experiments with post-harvest liberation, either through stand-level reductions in basal area (Finegan and Camacho, 1999; De Graaf et al., 1999; Oliveira, 2005) or treatments targeted at individual future crop trees (Penã-Claros et al., 2003 cited in Dauber et al., 2005; Wadsworth and Zweede, 2006) have shown strong positive effects on growth. Over the first several years following treatment in these experiments, increases in mean growth of liberated commercial trees relative to those in untreated plots ranged from 20% to 200–300%. However, positive effects of a given liberation treatment may not last for more than 10 years (De Graaf et al., 1999). Species populations in our study would appear amenable to post-harvest liberation, with *Cordia* especially showing a large difference between mean and potential growth rates. In addition, silvicultural treatments to enhance regeneration may be critical to management of timber species populations over a full rotation.

5.3. Clarifying the role of density in harvest regulations

5.3.1. Defining 'rare'

Based on findings presented here, we suggest that the current legal definition of rare timber species in Brazil (0.03 ha^{-1}) is flawed for a number of reasons. First, commercial density only loosely correlates with overall adult and sub-adult densities, as demonstrated, for example, by *Simarouba* and *Tabebuia* in this study. Second, population structure and vital rates are better predictors of potential recovery after logging at local scales than density. Third, the current rare species density threshold has been assigned to all species in the absence of information on biological thresholds below which genetic exchange, reproduction, regeneration and population persistence break down.

The limited literature on tropical tree pollination, genetic exchange, and reproductive success at varying adult densities and nearest neighbor distances suggests that there must be a density below which every tree species faces local biological extinction. What that density is remains a universal mystery. For this reason the rare species density threshold should be set at a conservative level until biologically meaningful definitions can be determined—for example, thresholds based on species' minimum reproductive size rather than the minimum log diameter preferred by sawmills. In this regard, we believe that the Bolivian rare density threshold of <10 stems >20 cm diameter per 100 ha (Fredericksen et al., 2001) provides a greater safety margin for maintaining minimum reproductive populations of timber species than the current Brazilian rule. A question remains: at what scale should rare species restrictions be enforced? High variability at the scale of the harvest block indicates that densities should be averaged over a larger area, yet regional estimates are far too coarse to be useful. We suggest that average densities at the scale of a forest property or management concession provide the most useful description of local rarity.

Our findings highlight the distinction between regulations meant to protect rare species and those intended to ensure sustained yields. While restrictions on logging rare species might avert biological collapse of local and regional populations, they cannot be counted on to avert declining commercial yields of high-value timber species. In our view, adjusting harvest regulations to account for timber species population structures and post-logging recovery potential is of far greater importance to the goals of sustained production and timber species conservation. Indeed, an approach to yield regulation based on species biology rather than market demands would likely render the rare species question moot.

5.3.2. Enforcement of the rare species rule

Because so many species occur at densities approaching the current Brazilian limit on harvesting, not to mention the more conservative threshold we propose above, there will always be strong incentives for logging companies to harvest rare high-value trees (e.g., the lone 140 cm diameter *Tabebuia* tree worth thousands of dollars) while avoiding sanctions by giving the appearance of compliance. In the Brazilian Amazon, there is a long history of manipulating forest inventories to obtain authorization for harvest volumes (total or of a particularly valuable species) that could not be justified under management plans with accurate inventories. This strategy can be employed to sidestep not only the rare species rule but any harvest regulation, including the population-based approach we advocate. Only systematic field-based audits of logging company inventories can prevent or at least limit illegal harvest practices.

6. Conclusion

Government and third-party regulators must decide whether depletion of timber species populations, particularly those of high-value hardwoods that are unlikely to be produced in plantations or substituted by other species or products, is consistent with management objectives. This is especially true in public forests, where the government is ostensibly managing for the greatest common good rather than short-term profits of logging contractors. A modified rule to restrict harvests of rare species could reduce the risk of timber species' extirpation from forests managed under RIL protocols, but only improved harvest regulations and silviculture can guarantee sustained yields of high-value hardwood timber species. While the opportunity costs of lower initial harvest intensity and up-front investment in silvicultural treatments do not necessarily render logging operations unprofitable (Fredericksen and Pariona, 2002; De Graaf et al., 2003; Vidal, 2004; Dauber et al., 2005; MacPherson, 2007; Schulze, 2008), they will reduce profit margins enough that loggers will have strong economic incentives to resist them under current regulatory and market conditions. In addition to improved understanding of and approaches to timber species silviculture, moving beyond RIL will require improved harvest regulations and their effective enforcement; concrete policy measures to address the competitive imbalance between forest management and unsustainable forest degradation and deforestation; and new incentives that provide immediate financial returns on investments in silviculture and management for sustained production of high-value timber.

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References

Alder, D., Silva, J.N.M., 2000. An empirical cohort model for the management of terra firme forests in the Brazilian Amazon. For. Ecol. Manage. 130, 141–157.

Azevedo-Ramos, C., Carvalho Jr., O., Amaral, B.D., 2006. Short-term effects of reduced-impact logging on eastern Amazon fauna. For. Ecol. Manage. 232, 26–35.

Barreto, P., Amaral, P., Vidal, E., Uhl, C., 1998. Costs and benefits of forest management for timber production in eastern Amazonia. For. Ecol. Manage. 108, 9–26.

Bawa, K.S., Ashton, P.S., 1991. Conservation of rare trees in tropical rain forests: a genetic perspective. In: Falk, D.A., Holsinger, K.E. (Eds.), Genetics and Conservation of Rare Plants. Oxford University Press, New York, NY, USA, pp. 62–74.

Brasil, 2006. Instrução Normativa n. 05, de 11 de dezembro de 2006. Dispõe sobre os procedimentos técnicos para elaboração, apresentação, execução e avaliação técnica de Planos de Manejo Florestal Sustentável - PMFSs nas florestas primitivas da Amazônia Legal. Ministério do Meio Ambiente & Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA). Available at: http://ibama2.ibama.gov.br.

Brienen, R.J.W., Zuidema, P.A., 2006. The use of tree rings in tropical forest management: projecting timber yields of four Bolivian tree species. For. Ecol. Manage. 226, 256–267.

Brown, J.H., Mehlman, D.W., Stevens, G.C., 1995. Spatial variation in abundance. Ecology 76, 2028–2043.

Chudnoff, M., 1984. Tropical Timbers of the World. USDA Forest Service Agricultural Handbook No. 607. Madison, WI, USA.

Clark, D.B., Clark, D.A., 1990. Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest. J. Trop. Ecol. 6, 321–331.

Clark, D.A., Clark, D.B., 1999. Assessing the growth of tropical rain forest trees: issues for forest modeling and management. Ecol. Appl. 9, 981–987.

Clark, D.B., Clark, D.A., Read, J.M., 1998. Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. J. Ecol. 86, 101–112.

Condit, R., Hubbell, S.P., Foster, R.B., 1995. Research in large, long-term tropical forest plots. Trends Ecol. Evol. 10, 18–22.

Dauber, E., Fredericksen, T.S., Peña-Claros, M., 2005. Sustainability of timber harvesting in Bolivian tropical forests. For. Ecol. Manage. 214, 294–304.

De Graaf, N.R., Poels, R.L.H., Van Rompaey, R.S.A.R., 1999. Effect of silvicultural treatment on growth and mortality of rainforest in Surinam over long periods. For. Ecol. Manage. 124, 123–135.

De Graaf, N.R., Filius, A.M., Huesca Santos, A.R., 2003. Financial analysis of sustained forest management for timber: perspectives for application of the CELOS management system in Brazilian Amazonia. For. Ecol. Manage. 177, 287–299.

Degen, B., Blanc, L., Caron, H., Maggia, L., Kremer, A., Gourlet-Fleury, S., 2006. Impact of selective logging on genetic composition and demographic structure of four tropical tree species. Biol. Conserv. 131, 386–401.

Dickinson, M.B., Whigham, D.F., 1999. Regeneration of mahogany (*Swietenia macrophylla*) in the Yucatan. Int. For. J. 1, 35–39.

Finegan, B., Camacho, M., 1999. Stand dynamics in a logged and silviculturally treated Costa Rican rain forest. For. Ecol. Manage. 121, 177–189.

Fredericksen, T.S., Mostacedo, B., 2000. Regeneration of sawtimber species following selective logging in a Bolivian tropical forest. For. Ecol. Manage. 131, 47–55.

Fredericksen, T.S., Pariona, W., 2002. Effects of skidder disturbance on commercial tree regeneration in logging gaps in a Bolivian tropical humid forest. For. Ecol. Manage. 171, 223–230.

Fredericksen, T., Contreras, F., Pariona, W., 2001. Guía de Silvicultura para Bosques Tropicales de Bolivia. Proyecto BOLFOR, Santa Cruz, Bolivia, 81 pp.

FSC (Forest Stewardship Council), 2002. Certification standards of the FSC Forest Stewardship Council for forest management on 'terra firme' in the Brazilian Amazon. Accessed March 24 2004. http://www.fsc.org.

Gerwing, J.J., 2001. Testing liana cutting and controlled burning as silvicultural treatments for a logged forest in the eastern Amazon. Ecol. Appl. 38, 1264–1276.

Gourlet-Fleury, S., Comu, G., Jesel, S., Dessard, H., Jourget, J.G., Blanc, L., Picard, N., 2005. Using models to predict recovery and assess tree species vulnerability in logged tropical forests: a case study from French Guiana. For. Ecol. Manage. 209, 69–86.

Grauel, W.T., Puz, F.E., 2004. Effects of lianas on growth and regeneration of *Prioria copaifera* in Darien, Panama. For. Ecol. Manage. 190, 99–108.

Grogan, J.E., 2001. Bigleaf mahogany (*Swietenia macrophylla* King) in southeast Pará, Brazil: a life history study with management guidelines for sustained production from natural forest. Ph.D. Dissertation. Yale University, New Haven, CT, USA.

Grogan, J., Barreto, P., 2005. Big-leaf mahogany on CITES Appendix II: big challenge, big opportunity. Conserv. Biol. 19, 973–976.

Grogan, J., Galvão, J., 2006. Physiographic and floristic gradients across topography in transitional seasonally dry evergreen forests of southeast Pará, Brazil. Acta Amaz. 36, 483–496.

Grogan, J., Galvão, J., Simões, L., Veríssimo, A., 2003. Regeneration of big-leaf mahogany in closed and logged forests of southeastern Pará, Brazil. In: Lugo, A., Figueroa Colón, J.C., Alayón, M. (Eds.), Big-Leaf Mahogany: Genetics, Ecology, and Management. Springer-Verlag, New York, NY, USA, pp. 193–208.

Grogan, J., Jennings, S., Landis, R.M., Schulze, M., Baima, A.M.V., do Lopes, J.C.A., Norghauer, J.M., Oliveira, L.R., Pantoja, F., Pinto, D., Silva, J.N.M., Vidal, E., Zimmerman, B., 2008. What loggers leave behind: impacts on big-leaf mahogany (*Swietenia macrophylla*) commercial populations and potential for post-logging recovery in the Brazilian Amazon. For. Ecol. Manage. 255, 269–281.

Hammond, D.S., Brown, V.K., 1995. Seed size of woody plants in relation to disturbance, dispersal, and soil type in wet neotropical forests. Ecology 76, 2544–2561.

Hammond, D.S., Gourlet-Fleury, S., van der Hout, P., ter Steege, H., Brown, V.K., 1996. A compilation of known Guianan timber trees and the significance of their dispersal mode, seed size and taxonomic affinity to tropical rain forest management. For. Ecol. Manage. 83, 99–116.

He, F., Legendre, P., LaFrankie, J.V., 1997. Spatial pattern of diversity in a tropical rain forest in Malaysia. J. Biogeogr. 23, 57–74.

Holdsworth, A.R., Uhl, C., 1997. Fire in eastern Amazonian logged rain forest and the potential for fire reduction. Ecol. Appl. 7, 713–725.

Holmes, T.P., Blate, G.M., Zweede, J.C., Pereira, R., Barreto, P., Boltz, F., Bauch, R., 2002. Financial and ecological indicators of reduced impact logging performance in the eastern Amazon. For. Ecol. Manage. 163, 93–110.

Hubbell, S.P., Foster, R.B., 1986. Commonness and rarity in a neotropical forest: implications for tropical tree conservation. In: Soulé, M.E. (Ed.), Conservation Biology: Science of Scarcity and Diversity. Sinauer Associates, Sunderland, MA, USA, pp. 205–231.

IBAMA (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis), 2006. Database of Brazilian Tropical Woods. Labratório de Produtos Florestais, IBAMA, Brasilia, DF, Brazil. Online at: http://www.ibama.gov.br/lpf/madeira (accessed on November 1, 2006).

IBGE (Instituto Brasileiro de Geografia e Estatística), 1997. Diagnostico Ambiental da Amazônia Legal. Rio de Janeiro, RJ, Brazil.

IBGE, 2003. Base Cartográfica Integrada Digital do Brasil ao Milionésimo. Rio de Janeiro, RJ, Brazil. Online at: http://www.ibge.gov.br (accessed on November 3 2005).

Johns, J.S., Barreto, P., Uhl, C., 1996. Logging damage during planned and unplanned logging operations in the eastern Amazon. For. Ecol. Manage. 89, 59–77.

Kalif, K.A.B., Malcher, S.A.O., Azevedo-Ramos, C., Moutinho, P., 2001. The effect of logging on the ground-foraging ant community in eastern Amazonia. Stud. Neotrop. Fauna Environ. 36, 215–219.

Kammesheidt, L., Köhler, P., Huth, A., 2001. Sustainable timber harvesting in Venezuela: a modelling approach. J. Appl. Ecol. 38, 756–770.

Keller, M., Palace, M., Hurtt, G., 2001. Biomass estimation in the Tapajós National Forest, Brazil: examination of sampling and allometric uncertainties. For. Ecol. Manage. 154, 371–382.

Kenfack, D., Thomas, D.W., Chuyong, G.B., Condit, R., 2007. Rarity and abundance in a diverse African forest. Biodivers. Conserv. 16, 2045–2074.

Lentini, M., Pereira, D., Celentano, D., Pereira, R., 2005. Fatos Florestais da Amazônia. IMAZON, Belém, PA, Brazil.

Lepsch-Cunha, N., Kageyama, P.Y., Vencovsky, R., 1999. Genetic diversity of *Couratari multiflora* and *Couratari guianensis* (Lecythidaceae): consequences of two types of rarity in central Amazonia. Biodivers. Conserv. 8, 1205–1218.

Loureiro, A.A., Freitas, J.A., Loureiro Ramos, K.B., Freitas, C.A.A., 2000. Essências Madeireiras da Amazonia, vol. 4. MCT/INPA-CPPF, Manaus, AM, Brazil.

MacPherson, A.J., 2007. Following the rules: a bioeconomic policy simulation of a Brazilian forest concession. Ph.D. Dissertation. University of Florida, Gainesville, FL, USA.

Martini, A.M.Z., Rosa, N.A., Uhl, C., 1994. An attempt to predict which Amazonian tree species may be threatened by logging activities. Environ. Conserv. 21, 152–162.

Mostacedo, B.C., Fredericksen, T.S., 1999. Regeneration status of important tropical forest tree species in Bolivia: assessment and recommendations. For. Ecol. Manage. 124, 263–273.

Oliveira, L.C., 2005. Efeito da exploração da madeira e de diferentes intensidades de desbaste sobre a dinámica da vegetação de uma area de 136 ha na Floresta Nacional Tapajós. Ph.D. Dissertation. Escola Superior de Agricultura "Luiz de Queiroz", Universidade de São Paulo, Piracicaba, SP, Brazil.

Pérez-Salicrup, D.R., Barker, M.G., 2000. Effect of liana cutting on water potential and growth of adult *Senna multijuga* (Caesalpinioideae) trees in a Bolivian tropical forest. Oecologia 124, 469–475.

Phillips, P.D., Azevedo, C.P., Degen, B., Thompson, I.S., Silva, J.N.M., van Gardingen, P.R., 2004. An individually-based spatially explicit simulation model for strategic forest management planning in the eastern Amazon. Ecol. Model. 173, 335–354.

Pitman, N.C.A., Terborgh, J.W., Silman, M.R., Núñez, P., 1999. Tree species distributions in an upper Amazonian forest. Ecology 80, 2651–2661.

Pitman, N.C.A., Terborgh, J.W., Silman, M.R., Núñez, P., Neill, D.A., Cerón, C.E., Palacios, W.A., Aulestia, M., 2001. Dominance and distribution of tree species in upper Amazonian terra firma forests. Ecology 82, 2101–2117.

Poels, R.L.H., de Graaf, N.R., Wirjosentono, J., 1998. Growth and Mortality of Trees After Various Experimental Silvicultural Treatments for Natural Regeneration in Suriname. Sub-Department of Forestry, Agricultural University, Wageningen, Wageningen, Netherlands.

Putz, F.E., Dykstra, D.P., Heinrich, R., 2000a. Why poor logging practices persist in the tropics. Conserv. Biol. 14, 951–956.

Putz, F.E., Redford, K.H., Robinson, J.G., Fimbel, R., Blate, G.M., 2000b. Biodiversity conservation in the context of tropical forest management. In: Environmental Paper 76, Biodiversity Series, Impact Studies, World Bank, Washington, DC, USA.

Rabinowitz, D., 1981. Seven forms of rarity. In: Synge, H. (Ed.), The Biology of Rare Plant Conservation. John Wiley, Chichester, UK, pp. 205–217.

Rose, S.A., 2000. Seeds, seedlings and gaps—size matters. A study in the tropical rain forest of Guyana. Ph.D. Thesis. Utrecht University, Tropenbos—Guyana Series 9. Ipskamp, Enschede.

Schneider, R., Arima, E., Veríssimo, A., Souza Jr., C., Barreto, P., 2002. Sustainable Amazon: limitations and opportunities for rural development. World Bank Technical Paper N515, Environment Series. Washington, DC, USA. Online at: http://www.amazonia.org.br/arquivos/13523.pdf (accessed February 21 2006).

Schoener, T.W., 1987. The geographical distribution of rarity. Oecologia 74, 161–173.

Schulze, M., 2003. Ecology and behavior of nine timber tree species in Pará, Brazil: links between species life history and forest conservation and management. Ph.D. Dissertation. The Pennsylvania State University, University Park, PA, USA.

Schulze, M., 2008. Management of tree regeneration in logging gaps as a potential component of reduced-impact logging in the eastern Amazon. For. Ecol. Manage. 255, 866–879.

Schulze, M., Zweede, J., 2006. Canopy dynamics in unlogged and logged forest stands in the eastern Amazon. For. Ecol. Manage. 236, 56–64.

Schulze, M., Vidal, E., Grogan, J., Zweede, J., Zarin, D., 2005. Madeiras nobres em perigo: práticas e leis atuais de manejo florestal não garantem a exploração sustentável. Ciência Hoje 36, 66–69.

Sheil, D., Burslem, D.F.R.P., Alder, D., 1995. The interpretation and misinterpretation of mortality rate measures. J. Ecol. 83, 331–333.

Silva, J.N.M., Carvalho, M.S.P., 1984. Equações de volume para uma floresta secundária no planalto do Tapajós Belterra-Pará. Bol. Pesq. Flor. 8 (9), 1–15.

Silva, J., Carvalho, J., Lopes, J.C., Almeida, B., Costa, D., Oliveira, L., Vanclay, J., Skovsgaard, J., 1995. Growth and yield of a tropical rain forest in the Brazilian Amazon 13 years after logging. For. Ecol. Manage. 71, 267–274.

Silva, J.N.M., Carvalho, J.O.P., Lopes, J.C.A., Oliveira, R.P., Oliveira, L.C., 1996. Growth and yield studies in the Tapajós region, Central Brazilian Amazon. Common. For. Rev. 75, 325–329.

Sist, P., Ferreira, F.N., 2007. Sustainability of reduced-impact logging in the eastern Amazon. For. Ecol. Manage. 243, 199–209.

Souza, M.H., Maagliano, M.M., Camargos, J.A.A., 1997. Madeiras Tropicais Brasileiras—Brazilian Tropical Woods. IBAMA-DITEC, Laboratorio de Productos Florestais, Brasília, DF, Brazil.

Valle, D., Schulze, M., Vidal, E., Grogan, J., Sales, M., 2006. Identifying bias in stand-level growth and yield estimations: a case study in eastern Brazilian Amazonia. For. Ecol. Manage. 236, 127–135.

Valle, D., Phillips, P., Schulze, M., Sales, M., Vidal, E., Grogan, J., 2007. Adaptation of a spatially explicit individual-based growth and yield model and long-term comparison between reduced-impact and conventional logging in eastern Amazonia, Brazil. For. Ecol. Manage. 243, 187–198.

van Gardingen, P.R., Valle, D., Thompson, I., 2006. Evaluation of yield regulation options for primary forest in Tapajós National Forest, Brazil. For. Ecol. Manage. 231, 184–195.

Vidal, E., 2004. Dinâmica de florestas manejadas e sob exploração convencional na Amazônia Oriental. Ph.D. Dissertation. Escola de Engenharia de São Carlos/ Universidade de São Paulo, São Carlos, SP, Brazil.

Wadsworth, F.H., Zweede, J.C., 2006. Liberation: acceptable production of tropical forest timber. For. Ecol. Manage. 233, 45–51.