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Effects of reduced impact logging on bat biodiversity in terra firme forest of lowland Amazonia

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ABSTRACT

Timber harvest is one of the main causes of degradation of Amazonian tropical forests, where bats represent important components of biodiversity. In addition, bats may represent keystone taxa in the Neotropics, as they are primary agents of pollination and seed dispersal for many pioneer plants. We assessed the impact of low harvest (18 m³/ha), reduced impact logging (RIL) on population and community characteristics of phyllostomid bats in Amazonian terra firme forest of Brazil at 20–42 months post-harvest. Based on 103,680 net-meter-hours of netting in Tapajós National Forest, 2341 phyllostomids were captured, representing 42 species, 25 genera, and 4 broad feeding guilds. Population-level responses of common phyllostomids to RIL were minor, with 10 of 15 species evincing no change in mean abundance. Of those taxa responding to RIL (mean difference in number of individuals per site), three increased (*Artibeus concolor* [0.46 individuals], *Artibeus lituratus* [3.88], and *Glossophaga soricina* [0.71]) and two decreased (*Carollia brevicauda* [0.96] and *Carollia perspicillata* [14.04]) in abundance. Compositional (species distributions) and structural (rank distributions) aspects of bat assemblages differed between cut and control forests. More specifically, bat assemblages in cut forest had increased diversity and decreased dominance compared to control forest. Nonetheless, the proportional abundance of the five most common species, as a group, was similar in cut (86%) and control forest (88%), and frugivores dominated assemblages in both management types. Mean abundance of frugivores decreased (10.59 individuals per site) in response to RIL; however, this response was driven by decreases in *C. perspicillata*, the most abundant species in terra firme forest. Although RIL had only minor effects on biodiversity in the short-term, extrapolation to a long-term prospectus should be exercised with caution when applied to conservation or policy issues.

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1. Introduction

Timber extraction is the primary activity responsible for degradation of Neotropical forests, with other agricultural uses (e.g., nut, latex, or fruit harvest) resulting in relatively minor damage (Johns, 1997). In the tropics, timber practices range widely from clear cutting (followed by conversion to agriculture) and conventional logging, to selective logging and reduced impact logging (RIL). Because only a small portion of tropical forests are protected in natural reserves (Groombridge, 1992) and many species are not protected adequately (Andelman and Willig, 2003), management through RIL may represent sustainable use that conserves biodiversity and maintains ecosystem services (Putz, 1994; Dickinson et al., 1996). Clear cutting and conventional logging, the most destructive logging techniques, result in soil compaction, increased fire risk, reduced canopy cover, and decreased biodiversity (Veríssimo et al., 1992; Nepstad et al., 1999). Selective logging removes only a small proportion of trees and has less severe effects on the environment and biodiversity than does clear cutting, timber liquidation, or conventional logging techniques. Nonetheless, selective logging has deleterious effects on soil, nutrients, forest structure, and biodiversity (Ernst et al., 2006), and causes appreciable damage to uncut trees, especially in poorly planned operations (Johns et al., 1996; Johns, 1997). Even when only a few trees are harvested, inadequate construction of skid trails and landing sites (for storage of harvested trees) can cause severe damage to soils and forest structure. Minimizing damage from logging can be attained with carefully conceived harvest plans that follow guidelines of RIL. RIL has economic and environmental advantages over other logging practices (Johns et al., 1996; Barreto et al., 1998): it provides protection to soils, facilitates in situ regeneration of trees (i.e., seedlings, saplings), and maintains critical ecosystem processes (e.g., hydrological flow, nutrient cycling). Nonetheless, little is known about the consequences of this technique to animal populations or communities (Putz et al., 2000). An assessment of the responses of keystone taxa to RIL is necessary for a comprehensive evaluation of the potential of RIL to meet conservation goals and provide renewable timber (Azevedo-Ramos et al., 2005). Indeed, the study of taxa that provide critical ecosystem services should be a priority of management and monitoring programs in Neotropical forests (Mason and Putz, 2001; Azevedo-Ramos et al., 2005), especially from the perspective of sustainability (Dickinson et al., 1996). Demand for timber will continue to increase as human populations increase in size and disperse into wilderness areas (Nepstad et al., 1999; Asner et al., 2005). Evaluation of the effects of less destructive harvest practices (e.g., RIL) on the biota is required to better implement conservation plans and to inform natural resource policy in Neotropical forests.

In the Neotropics, bats are important agents of pollination and seed dispersal for many species of plants (Fleming and Heithaus, 1981; Galindo-González et al., 2000), and their activity promotes secondary succession of disturbed areas (Gorchov et al., 1993). Neotropical bats may be keystone taxa as well as important components of biodiversity (Kaufman and Willig, 1998). New World bats have characteristics that make them effective bioindicators; they are abundant, species rich,

ecologically diverse, widespread, responsive to disturbance, and relatively easy to sample and identify (Fenton et al., 1992; Medellín et al., 2000; Patterson et al., 2003). Responses of bats to anthropogenic disturbances (Fenton et al., 1992; Brosset et al., 1996; Cosson et al., 1999; Medellín et al., 2000; Schulze et al., 2000; Gorresen and Willig, 2004; Willig et al., 2007) and to selective logging (Ochoa, 2000; Clarke et al., 2005a,b; Peters et al., 2006) have been studied intensively in the Neotropics; however, no study has investigated the effects of RIL on Neotropical bats.

Definitive responses of fauna to conventional logging are difficult to establish because of variation among studies in experimental design (Azevedo-Ramos et al., 2005). Generally, sampling designs are not replicated within forest types, and the history, intensity, and methodologies of harvest differ among studies. Nonetheless, two general trends in response to logging are evident for Neotropical bats. Insectivorous and carnivorous phyllostomids often decrease in abundance and species richness in response to logging (Fenton et al., 1992; Brosset et al., 1996; Ochoa, 2000; Peters et al., 2006). In contrast, frugivorous and nectarivorous phyllostomids that feed primarily on fruits of successional species (e.g., *Cecropia*, *Piper*, *Solanum*) often exhibit greater abundances in forests that have been subjected to conventional or selective logging than in undisturbed forest (Fenton et al., 1992; Brosset et al., 1996; Ochoa, 2000; Peters et al., 2006).

Few studies have addressed the effects of RIL on vertebrate diversity. Recent studies suggest that effects of RIL are minimal on non-volant mammals and birds (Azevedo-Ramos et al., 2006; Wunderle et al., 2006), and that the detrimental effects of RIL are less severe than those of conventional logging techniques (Davis, 2000). To expand the taxonomic evidence concerning the effects of RIL on biodiversity, we determined the manner in which population-level and community-level characteristics of bats in a tropical rain forest responded to RIL via a replicated observational experiment that involved sampling habitats (e.g., closed canopy forest and forest gaps) in their frequency of occurrence in both undisturbed forest and forest subjected to RIL.

2. Methods

2.1. Study area

The Tapajós area of endemism, one of eight such recognized areas in Amazonia (da Silva et al., 2005), comprises 648,862 km², has lost 9.3% of forest cover, and is among the least threatened regions of the Amazon. However, this percent of forest loss is an underestimate because it does not distinguish selectively logged forest from undisturbed sites. Although 28% of the land in the Tapajós area of endemism is protected, only 0.7% of those lands are protected strictly, with the remainder designated as indigenous reserves (24.1%) or subject to sustainable use (3.5%).

Research was conducted in the Tapajós National Forest (TNF), a 560,000 ha area of lowland rainforest managed by the Instituto Brasileiro de Meio Ambiente e Recursos Naturais Renováveis. The TNF (3°21'36"S, 54°57'0"W) borders the east bank of the lower Tapajós River, near its confluence with the Amazon River, in western Pará, Brazil (Fig. 1). It is

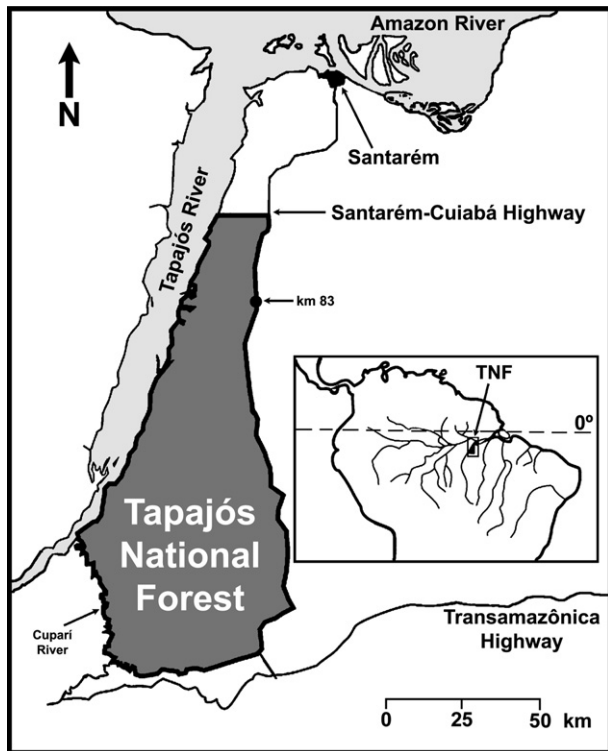


Fig. 1 – Location of Tapajós National Forest (TNF) in Pará, Brazil, showing its association with the Tapajós River, Amazon River, and Santarém-Cuiabá Highway. Insert shows the location of TNF in northern South America.

bounded by the Tapajós River, Santarém-Cuiabá Highway (BR-163), and Cupari River to the west, east, and south, respectively. Descriptions of climate, soils, and vegetation appear in Silva et al. (1985), Daly and Prance (1989), and Parrotta et al. (1995), respectively. Average rainfall is substantial (1920 mm/year), with a short drier season from August to October and most precipitation occurring from December to May. The climate is tropical, with mean monthly temperatures between 24.3 and 25.8 °C (Parrotta et al., 1995). Several forest types occur in the TNF, with terra firme forest constituting 33% of the forested lands and encompassing the entire study area. Terra firme forest occupies gently rolling terrain on poor upland soils (dystrophic yellow latosol; Silva, 1989). Canopy height ranges from 30 to 40 m, with emergent trees reaching 50 m. Typical tree species include *Bertholletia excelsa*, *Couratari* spp., *Dinizia excelsa*, *Hymenaea coubaril*, *Manilkara huberi*, *Parkia* spp., *Pithecellobium* spp., and *Tabebuia serratiolia* (Silva et al., 1985).

Bats were captured using three sampling designs (Saldanha, 2000). Census surveys characterized the bat fauna of undisturbed and RIL areas of the TNF. A gap-matrix study was executed as a non-manipulative experiment to define physiognomy-specific (gaps versus understory) associations of bats in RIL and undisturbed forest based on equal sampling of each type of physiognomy in each forest type (Presley et al., 2007). Incidental captures of bats in day roosts served as an ancillary method to detect species not commonly captured in mist nets. Data from all sampling protocols contributed to the checklist of species for TNF (Table 1). In contrast, only

data from census surveys were analyzed to characterize structure of the bat fauna, because this methodology was designed to examine physiognomies and associated bat faunas in proportion to their occurrence in terra firme forest.

A system of roads and trails at kilometre 83 of the Santarém-Cuiabá Highway provided access to the forest. Experimental blocks were located within a 5000 ha grid (3°21'21"S, 54°56'58"W) that was established as a demonstration for logging practices. Census surveys were conducted in two undisturbed forest or control blocks (C1 and C3) and in two RIL or cut blocks (T18 and T2). Each experimental block encompassed 100 ha (i.e., 1000 m by 1000 m). Control blocks were within the 500 ha control area and located 1–2 km from each of the cut blocks. Control blocks were bordered by undisturbed forest on three sides and by selectively logged (40 m³/ha) forest to the north. Block C3 comprised primary forest, whereas half of the area of block C1 was 20-year-old secondary forest that previously was cleared for subsistence agriculture. Cut blocks were separated from each other by 2.5 km of selectively logged forest, and were bordered by undisturbed forest on one side and selectively logged forest (40 m³/ha) on the other sides. Although timber harvest inside cut blocks was completed 20 months before initiation of surveys, timber harvest continued in adjacent blocks throughout the study. In cut blocks, trees larger than 45 cm dbh were harvested at low intensity (18.7 m³/ha). RIL uses several methods to reduce soil compaction and collateral damage to non-harvested trees, including mapping the locations of all trees >45 cm dbh to determine optimal skidder trail locations, cutting and removing vines from trees prior to felling, and directional felling of trees. In addition, RIL uses a reduced number of landing sites and pre-existing roads to further reduce damage to the forest (Pinard and Putz, 1996). *Manilkara huberi*, *M. paraensis*, *Protium pernevatum*, *Dinizia excelsa*, and *Piptadenia suaveolens* were the most commonly harvested species at TNF (Keller et al., 2004). Details about implementation of RIL techniques in Amazonia have been described elsewhere (Veríssimo et al., 1992; Vidal et al., 1997). In total, 394 (1870.49 m³) and 379 (1872.708 m³) trees were removed from blocks T2 and T18, respectively.

2.2. Field methods

Census surveys based on mist-netting were divided into three sessions: April–May 1999, November–December 1999, and April 2000 (Saldanha, 2000). Twelve sites were located in each block, with sites arranged in two parallel rows, each row containing six uniformly spaced (200 m) sites, starting and finishing on the border of each block (Fig. 2). Each night, five 12 m nets were deployed at each of four sites, for a total of 20 nets per night; nets were checked hourly. During most nights (34 nights, 66.6%), nets were opened before dusk (around 18:00 h) and closed at midnight. On other nights (17 nights, 33.4%), nets were not closed until dawn (06:00 h). Sites that had 12-h sampling periods were rotated each session. Each site was monitored once per session for a total sampling effort of two partial nights and one full night at each site. Sex, mass, age (juvenile or adult), and reproductive condition were recorded for each captured bat. Before release, bats were marked by making a small notch in the border of the pinna,

Table 1 – Checklist of bat species from Tapajós National Forest, Brazil

Family	Species code	Body mass (g)	Guild		Survey source	Range size (10 ⁶ km ²)	Roost type
Subfamily			Broad	Fine			
Species							
Emballonuridae							
<i>Centronycteris maximiliani</i>	Cma	5.5 ^b	AEI	BCAEI	C, GM	8.041	Tree ¹
<i>Diclidurus albus</i>	Dal	15.6 ^a	AEI	USAEI	C	7.917	Foliage ⁴
<i>Peropteryx kappleri</i>	Pka	9.4 ^a	AEI	USAEI	C, GM	5.532	Tree ¹
<i>Peropteryx leucoptera</i>	Ple	6.4 ^c	AEI	USAEI	C	4.432	Tree ¹
<i>Peropteryx macrotis</i>	Pma	5.4 ^a	AEI	USAEI	GM	13.200	Tree ¹
<i>Saccopteryx bilineata</i>	Sbi	9.0	AEI	BCAEI	C, GM	13.110	Tree ^{2,1}
<i>Saccopteryx gymnura</i>	Sgy	4.0 ^d	AEI	BCAEI	IR	0.408	Unknown
<i>Saccopteryx leptura</i>	Sle	4.8	AEI	BCAEI	C, GM	11.300	Tree ^{2,3}
Phyllostomidae							
Desmodontinae							
<i>Desmodus rotundus</i>	Dro	35.5	SAN	HCSGS	C, GM	19.390	Trees, caves ^{2,5}
Glossophaginae							
<i>Choeroniscus godmani</i>	Cgo	7.9 ^a	NEC	HCSGN	GM	2.402	Tree ¹⁶
<i>Choeroniscus minor</i> *	Cmi	7.7	NEC	HCSGN	C, GM	6.209	Tree ¹⁶
<i>Glossophaga soricina</i>	Gso	8.6	NEC	HCSGN	C, GM	15.640	Tree, building ³
<i>Lichonycteris obscura</i>	Lob	5.6 ^a	NEC	HCSGN	C, GM	3.695	Unknown
<i>Lonchophylla thomasi</i>	Lth	6.8	NEC	HCSGN	C, GM	7.261	Tree ¹
Phyllostominae							
<i>Chrotopterus auritus</i>	Cau	78.3	GAN	HCSGC	C, GM	9.101	Tree, cave, building ⁶
<i>Glyphonycteris sylvestris</i> *	Gsy	10.0	GAN	HCSGI	C, GM	8.110	Tree, cave ¹⁶
<i>Lampronnycteris brachyotis</i>	Lbr	10.5 ^a	GAN	HCSGO	GM	3.939	Tree, cave, building ⁷
<i>Lophostoma carrikeri</i> **	Lca	28.5	GAN	HSGSI	C, GM	4.294	Tree ^{1,8}
<i>Lophostoma silviculum</i>	Lsi	29.0	GAN	HCSGI	C, GM	14.250	Tree ^{1,9}
<i>Micronycteris hirsuta</i>	Mhi	12.4 ^a	GAN	HCSGI	C, GM	4.924	Tree ^{1,3}
<i>Micronycteris megalotis</i>	Mme	6.3 ^a	GAN	HCSGI	C, GM	13.050	Tree ^{1,3}
<i>Mimon crenulatum</i>	Mcr	12.5	GAN	HCSGI	C, GM	9.996	Tree ¹
<i>Phylloderma stenops</i>	Pst	60.1	FRG	HCSGF	C, GM	10.040	Not known
<i>Phyllostomus discolor</i>	Pdi	35.6	GAN	HCSGO	C, GM	12.030	Tree, cave ^{16,17}
<i>Phyllostomus elongatus</i>	Pel	38.7	GAN	HCSGO	C, GM	10.640	Tree ³
<i>Phyllostomus hastatus</i>	Pha	92.5 ^a	GAN	HCSGO	C	12.850	Tree, cave ^{2,1}
<i>Tonatia saurophila</i>	Tsa	26.4	GAN	HCSGI	C, GM	12.180	Tree ¹⁷
<i>Trachops cirrhosus</i>	Tci	33.1	GAN	HCSGI	C, GM	12.910	Tree, building ^{1,3}
<i>Trinycteris nicefori</i>	Tni	8.5	GAN	HCSGO	C, GM	3.417	Tree, building ^{16,17}
<i>Vampyrum spectrum</i> *	Vsp	169.4 ^a	GAN	HCSGC	C	5.269	Tree ²
Carollinae							
<i>Carollia brevicauda</i>	Cbr	14.0	FRG	HCSGF	C, GM	12.440	Tree, cave, building, foliage ¹⁶
<i>Carollia perspicillata</i>	Cpe	16.1	FRG	HCSGF	C, GM	14.770	Tree, cave, building ^{1,3}
<i>Rhinophylla fischerae</i> *	Rfi	7.6	FRG	HCSGF	C, GM	2.474	Unknown
<i>Rhinophylla pumilio</i>	Rpu	9.2	FRG	HCSGF	C, GM	8.591	Foliage ^{1,3}
Stenodermatinae							
<i>Ametrida centurio</i>	Ace	10.3 ^a	FRG	HCSGF	C, GM	3.519	Foliage ¹⁸
<i>Artibeus concolor</i> *	Aco	20.1	FRG	HCSGF	C, GM	5.337	Unknown
<i>Artibeus gnomus</i>	Agn	10.3	FRG	HCSGF	C, GM	–	Foliage ^{1,3}
<i>Artibeus jamaicensis</i>	Aja	42.2 ^a	FRG	HCSGF	C, GM	14.430	Tree, cave, building, foliage ¹⁰
<i>Artibeus lituratus</i>	Ali	72.2	FRG	HCSGF	C, GM	15.540	Foliage ²
<i>Artibeus obscurus</i> *	Aob	36.3	FRG	HCSGF	C, GM	–	Tree, foliage ^{1,3}
<i>Chiroderma trinitatum</i>	Ctr	14.4	FRG	HCSGF	GM	8.228	Caves ¹⁷
<i>Chiroderma villosum</i>	Cvi	23.2	FRG	HCSGF	C, GM	10.350	Tree, building ¹⁶
<i>Mesophylla macconnelli</i>	Mma	7.0	FRG	HCSGF	GM	8.698	Foliage ¹
<i>Platyrrhinus helleri</i>	Phe	12.2	FRG	HCSGF	C, GM	10.620	Tree, cave, building, foliage ¹¹
<i>Sturnira lilium</i>	Sli	21.6	FRG	HCSGF	C, GM	16.860	Tree,cave, building ¹²
<i>Sturnira tildae</i>	Sti	23.4	FRG	HCSGF	C, GM	9.990	Tree, building ¹⁸
<i>Uroderma bilobatum</i>	Ubi	17.1	FRG	HCSGF	C, GM	13.510	Foliage ^{1,2}
<i>Uroderma magnirostrum</i>	Uma	17.8	FRG	HCSGF	GM	8.525	Foliage ¹
<i>Vampyressa bidens</i> *	Vbi	12.1	FRG	HCSGF	C, GM	5.738	Tree ¹³

Table 1 – continued

Family Subfamily Species	Species code	Body mass (g)	Guild		Survey source	Range size (10 ⁶ km ²)	Roost type
			Broad	Fine			
Vampyressa thylone	Vth	8.1	FRG	HCSGF	C, GM	5.745	Foliage ¹
Mormoopidae							
Pteronotus parnellii	Ppa	19.7	AEI	BCAEI	C, GM	6.576	Caves ¹⁴
Furipteridae							
Furipterus horrens	Fho	3.2 ^a	AEI	BCAEI	C	7.495	Tree ¹
Thyropteridae							
Thyroptera tricolor	Ttr	4.2	AEI	BCAEI	C, GM	8.641	Foliage ²
Molossidae							
Eumops auripendulus	Eau	28.5 ^a	HFI	USAEI	IR	14.460	Tree, building ¹⁵
Molossus molossus	Mmo	15.3	HFI	USAEI	IR	17.110	Building ³

Taxonomic designations follow Simmons (2005).

Body mass comes mainly from unpublished data (Willig personal data from Iquitos, Perú, no alphabetical superscript). Other sources of body masses are: ^aSmith et al. (2003), ^bReid (1997), ^cSimmons and Voss (1998) and ^dLim and Engstrom (2001a). Broad guild (Wilson, 1973; Gardner, 1977; Willig, 1986) abbreviations are: AEI, aerial insectivore; SAN, sanguinivore; NEC, nectarivore; GAN, gleaning animalivores; FRG, frugivores; HFI, high flying insectivores. Fine guild (Kalko et al., 1996; Kalko and Handley, 2001) abbreviations are: BCAEI, background cluttered space aerial insectivore; USAEI, uncluttered space aerial insectivore; HCSGC, highly cluttered space gleaning carnivores; HCSGF, highly cluttered space gleaning frugivores; HCSGI, highly cluttered space gleaning insectivores; HCSGN, highly cluttered space gleaning nectarivores; HCSGO, highly cluttered space gleaning omnivores; HCSGS, highly cluttered space gleaning sanguinivores. Range sizes obtained from Andelman and Willig (2003). Range sizes in bold indicate Amazonian endemic species (Marinho-Filho and Sazima, 1998). Source codes are: C, Census survey; GM, Gap-Matrix; IR, incidental recordings. Eight species appear in the endangered species red list (IUCN, 2006) in two categories: LRnt (lower risk near threatened) and VUA2 (vulnerable, 20% reduction is projected or suspected within the next 10 years).

Sources for roost affiliations are: ¹Kunz and Lumsden (2003), ²Lewis (1995), ³Simmons and Voss (1998), ⁴Ceballos and Medellín (1988), ⁵Greenhall et al. (1983), ⁶Medellín (1989), ⁷Medellín et al. (1985), ⁸McCarthy et al. (1992), ⁹Medellín and Arita (1989), ¹⁰Ortega and Castro-Arellano (2001), ¹¹Ferrell and Wilson (1991), ¹²Gannon et al. (1989), ¹³Lee et al. (2001), ¹⁴Herd (1983), ¹⁵Best et al. (2002), ¹⁶Handley (1976), ¹⁷Reid (1997) and ¹⁸Nowak (1999).

Roost affiliations were grouped in three categories: (1) tree, including fallen trees, logs, exfoliating bark, hollows in trees, tree boles, tree cavities, dead standing trees and ant-termite nests in trees; (2) foliage, including rolled leaves, unmodified leaves and leaf-tents; building, including culverts, bridges, ruins, and human dwellings; (3) cave, for mines and caves.

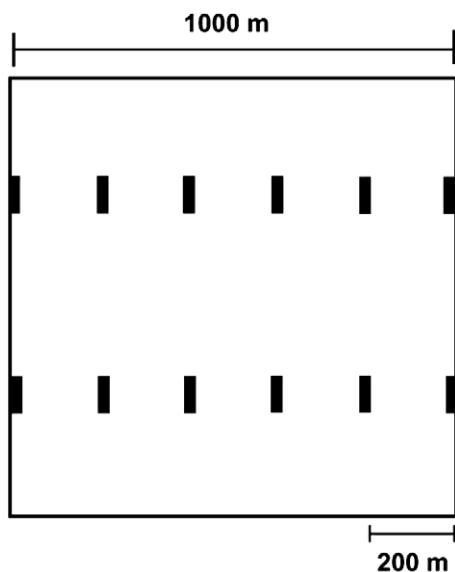


Fig. 2 – Schematic diagram showing arrangement of net sites (black bars) within a 100-ha block (large square) of terra firme forest at the Tapajós National Forest, Brazil.

facilitating the distinction of recaptures within sessions. Species identification was facilitated by taxonomic keys in Vizotto and Taddei (1973), Freeman (1981), Taddei et al. (1982),

and Linares (1987), as well as from diagnoses in Eisenberg (1989), Emmons and Feer (1997), Eisenberg and Redford (1999), Marques-Aguiar (1994), Handley (1987), and Handley and Ochoa (1997). For each species, a set of voucher specimens was prepared, preserved in 70% ethanol, and deposited in the mammal collection at the Museu Paraense Emílio Goeldi in Belém, where taxonomic identifications sensu Simmons (2005) were verified. In addition, we classified phyllostomid species according to two different schemes: broad and fine foraging guilds (names and abbreviations in Table 1). Broad guild (Wilson, 1973; Gardner, 1977; Willig, 1986) and fine guild classification schemes (Kalko et al., 1996; Kalko and Handley, 2001) were used to distinguish functional groups of species based on foraging habitat, foraging mode, and food type.

2.3. Data analysis

Inferential analyses were restricted to the Phyllostomidae to avoid inherent biases (e.g., underestimation of molossids, emballonurids, and vespertilionids) characteristic of ground-level mist-netting (Voss and Emmons, 1996; Willig et al., 2007). Moreover, analyses were restricted to data from census surveys so that the composition and abundance of species reflected the empirical distribution of physiognomies in cut and control forest. Blocks were used to account for spatial variation within cut or within control forest, and were not

replicates from a statistical point of view. Sampling sites within a block were the replicates (12 per block). To some extent, abundances of bats at sites were positively correlated because of spatial proximity, thereby reducing variances among replicates within blocks, and enhancing the likelihood of declaring significant block or treatment effects. The magnitude of this bias is unknown.

The effects of RIL were analyzed from multiple perspectives at the population and assemblage levels. We evaluated the effects of logging (i.e., cut blocks versus control blocks) on abundances of species, abundances of guilds, species richness, species composition (i.e., species distributions, SDs), assemblage structure (i.e., species rank distributions, SRDs), guild composition (guild distributions, GDs), and guild structure (guild rank distributions, GRDs).

For each of the 15 most common species and for each guild of phyllostomids, a generalized linear mixed-effects model (GLMM; Venables and Ripley, 2002) with assumption of Poisson errors, quantified the effects of management (cut versus control forest) on abundance (i.e., total number of captures). In the GLMMs, block was a model II factor that controlled for random effects due to local spatial variation and was nested within levels of management; analyses were executed using the R programming environment (R Development Core Team, 2005), with the MASS (Venables and Ripley, 2002) and nlme (Pinheiro and Bates, 2000) libraries. A Bonferroni sequential adjustment (Rice, 1989) was applied to each of three suites of analyses (i.e., 15 species, four broad guilds, and six fine guilds) to assess overall significance and to protect against elevated experiment-wise error rates.

We illustrated compositional aspects of each assemblage by weighting the presence of species by abundance to quantify SDs. Effects of block and management on species composition (i.e., SD) were evaluated with an X^2 randomization test in Ecosim version 7 (Gotelli and Entsminger, 2005). This randomization test provides two advantages over conventional χ^2 analysis: results are not sensitive to small expected values and it is not necessary to specify degrees of freedom (Gotelli and Entsminger, 2005).

We quantified structural aspects of each assemblage by ranking species based on their abundances to create SRDs. Effects of block and management on SRDs was evaluated with a Kolmogorov–Smirnov test (Sokal and Rohlf, 1995) using SPSS version 11.0 for Windows (SPSS, 2001). In addition, we characterized the form of each SRD using a variety of diversity metrics including species richness (i.e., cumulative number of species), Shannon diversity (Pielou, 1975), Camargo evenness (Camargo, 1993), Berger–Parker dominance (Berger and Parker, 1970), and rarity (i.e., number of species with a relative frequency of capture less than the inverse of species richness; Camargo, 1993; Gaston, 1994). A randomization procedure was employed to determine if bat biodiversity, as represented by each index, was significantly different between cut and control forest (Solow, 1993). The absolute value of the difference between the values of a metric for cut forest and control forest (blocks combined) was used as the test statistic. All individuals, regardless of their association with cut or control forest, were pooled to create a universe from which to sample. In each iteration, individuals were assigned randomly without replacement to cut or control forest. The number of

individuals assigned to each management type was fixed and equal to empirical values (i.e., 1052 individuals to cut forest and 1289 individuals to control forest). For each randomly generated assemblage, the five diversity indices were calculated, and absolute values of differences between cut and control forest were determined. This process was repeated 10,000 times to create a null distribution. Significance was determined as the proportion of randomly generated differences that were greater than or equal to the empirical difference. All randomizations were performed in Matlab 6.0 for Windows (The Math Works Inc., 2000); script files are available from the authors.

We analyzed the effects of RIL on guild composition and structure by evaluating GDs and GRDs, respectively. We weighted each guild by its proportional abundance or by its proportional richness. Effects of block and management on GRDs were evaluated with a Kolmogorov–Smirnov test (Sokal and Rohlf, 1995), whereas effects of block and management on GDs were evaluated with an X^2 randomization test. In addition, the same suite of biodiversity indices calculated for assemblage-level analyses based on species, were calculated for assemblage-level analyses based on guilds. For all analyses, results were considered significant at $P \leq 0.05$.

3. Results

3.1. Bat species inventory

Based on 168,192 net-meter-hours (62% during census surveys and 38% during gap-matrix study), and 18 incidental captures from roosts, 4144 bats were recorded representing 55 species, 36 genera, 6 families, and 6 broad guilds (Table 1). Most of the bat fauna of TNF (46 species) was captured during the census surveys. Six additional species (*Choeroniscus godmani*, *Micronycteris brachyotis*, *Uroderma magnirostrum*, *Peropteryx macrotis*, *Mesophylla macconnelli*, and *Chiroderma trinitatum*) were captured only during the gap-matrix study and three species (*Eumops auripendulus*, *Molossus molossus*, and *Saccopteryx gymnura*) were obtained exclusively from incidental roost captures.

3.2. Census netting

During 103,680 net-meter-hours of sampling, we recorded 2460 bats representing 46 species, 32 genera, 5 families, and 5 broad guilds. Phyllostomids dominated captures (91% of species, 95% of individuals) and included 42 species, 25 genera, and 4 broad guilds. To assess the completeness of sampling in undisturbed and RIL forest, we used eight different estimators calculated by EstimateS (Colwell, 2005). Depending on the estimator, sampling detected 80.7–95.2% of the species predicted to occur in the undisturbed forest and 75.1–91.4% of the species predicted to occur in RIL forest.

3.3. Abundances of species and guilds

For 10 of the 15 most common species, abundance did not differ between cut and control forest (Table 2). Mean differences in abundance between cut and control forest characterized five species; abundances of *Artibeus concolor* (0.46 individuals per site), *Artibeus lituratus* (3.88), and *Glossophaga soricina*

Table 2 – Effect of block (B) and management (M) on the abundance (mean number of individuals per site) of each of four broad guilds, six fine guilds, and the 15 most common species of phyllostomids in Tapajós National Forest using a generalized mixed-effects model (GLMM) with an assumption of Poisson errors

	Means				GLMM		Change in mean abundance
	Cut		Control		Significance		
	T18	T2	C1	C3	B	M	
Species							
<i>Artibeus concolor</i>	0.33	1.17	0.25	0.33	0.178	0.043	+0.46
<i>Artibeus gnomus</i>	0.42	0.42	0.50	0.33	0.776	0.959	
<i>Artibeus jamaicensis</i>	1.75	2.58	1.00	1.42	0.563	0.106	
<i>Artibeus lituratus</i>	9.75	13.33	5.08	10.25	0.028	0.045	+3.88
<i>Artibeus obscurus</i>	2.92	2.33	2.25	2.25	0.801	0.515	
<i>Carollia brevicauda</i>	0.17	1.50	3.00	0.58	<0.001*	0.033	−0.96
<i>Carollia perspicillata</i>	10.08	23.67	46.33	15.50	<0.001*	<0.001*	−14.04
<i>Glossophaga soricina</i>	0.92	1.33	0.42	0.42	0.733	0.029	+0.71
<i>Lonchophylla thomasi</i>	1.75	4.00	2.83	1.17	0.038	0.245	
<i>Lophostoma silviculum</i>	0.67	0.67	0.58	1.00	0.649	0.618	
<i>Phyllostomus elongatus</i>	0.33	0.08	0.50	0.58	0.565	0.225	
<i>Rhinophylla fischeri</i>	0.33	0.67	1.17	0.42	0.147	0.222	
<i>Rhinophylla pumilio</i>	0.08	0.33	0.83	0.75	0.572	0.061	
<i>Tonatia saurophila</i>	0.50	1.33	0.67	0.50	0.146	0.146	
<i>Uroderma bilobatum</i>	0.25	0.42	0.50	0.33	0.712	0.696	
Broad guilds							
Frugivores	26.17	47.33	61.67	33.00	<0.001*	0.017	−10.59
Gleaning animalivores	2.67	3.17	3.00	4.17	0.511	0.353	
Nectarivores	3.00	5.33	3.67	1.75	0.100	0.159	
Sanguinivores	0.00	0.00	0.17	0.00	1.000	0.994	
Fine guilds							
Frugivores	26.17	47.33	61.67	33.00	<0.001*	0.017	−10.59
Carnivores	0.00	0.00	0.08	0.08	1.000	0.996	
Gleaning insectivores	1.58	2.58	1.83	2.83	0.221	0.675	
Omnivores	1.08	0.58	1.08	1.25	0.561	0.434	
Nectarivores	3.00	5.33	3.67	1.75	0.100	0.159	
Sanguinivores	0.00	0.00	0.17	0.00	1.000	0.994	

Blocks were nested within levels of management. The differences in abundance between management types (cut–control) are indicated only if significant.

Values in bold were significant ($P \leq 0.05$) before application of a Bonferroni sequential adjustment. Particular treatment effects that remained significant after application of a Bonferroni sequential adjustment to each of three suites of analyses (i.e., species, broad guilds, and fine guilds) are indicated by an asterisk.

(0.71) were greater in cut forest, whereas the abundances of *Carollia brevicauda* (0.96), and *Carollia perspicillata* (14.04) were greater in the control forest. After Bonferroni sequential adjustment, only the response to management of *C. perspicillata* was significant. Spatial variation within cut and within control forest produced added variance components in the abundances of four species (*A. lituratus*, *C. brevicauda*, *C. perspicillata*, and *Lonchophylla thomasi*) as revealed by significant block effects; only those for both species of *Carollia* remained significant after Bonferroni sequential adjustment (Table 2).

Despite significant added variance components due to blocks, mean abundances of frugivores responded negatively to RIL (10.59 fewer individuals per site); fine and broad guild composition were the same for frugivores. Abundances of all other guilds, based on broad or fine classifications, did not differ between cut and control forest (Table 2).

3.4. Assemblage structure and composition

Compositional aspects of each assemblage as portrayed by the SD were different between management types as well

as between blocks in control forest (Table 3 and Fig. 3). *C. perspicillata* was the dominant species in cut (375 individuals, 38%) and in control forest (772 individuals, 57%). It was four times more abundant than *A. lituratus*, the next most common species, in control forest, and only 10% more abundant than *A. lituratus* in cut forest (Fig. 3). In each management type, the five most common species accounted for a similar proportion (~83%) of individuals. Four of these species were medium to large sized (14–72 g) frugivores and one was a small (6.8 g) nectarivore.

Assemblage structure (i.e., SRDs) differed between cut and control forest, as well as between blocks within each management type (Table 3 and Fig. 4). Diversity indices reflect particular attributes of the shape of SRDs. Shannon diversity responded positively ($P < 0.001$) and dominance responded negatively ($P < 0.001$) to RIL. Species richness, number of rare species, and Camargo Evenness did not respond to RIL (Figs. 4 and 5).

Based on broad guild classification, most phyllostomids in TNF were frugivores (17 species in cut forest, 18 species in control forest) or gleaning animalivores (11 species in cut

Table 3 – Comparison of bat species distributions (SD), species rank distributions (SRD), guild distributions (GD), and guild rank distributions (GRD) between blocks within a management type, and between control and cut areas (blocks combined) of Tapajós National Forest

	Management		Cut blocks		Control blocks	
	TS	P	TS	P	TS	P
Species						
SD weighted by abundance	187.21	<0.001***	55.73	0.690*	179.94	<0.001***
SRD weighted by abundance	4.59	<0.001***	1.58	0.010	4.08	<0.001***
Broad guilds						
GD weighted by richness	1.03	1.000	1.42	0.930	1.27	0.990
GD weighted by abundance	16.81	0.019*	2.07	0.838	11.48	0.131
GRD weighted by richness	0.18	1.000	0.48	0.976	0.14	1.000
GRD weighted by abundance	1.06	0.213	0.36	0.999	0.89	0.404
Fine guilds						
GD weighted by richness	2.74	0.999	1.64	0.979	1.31	1.000
GD weighted by abundance	18.72	0.075	6.21	0.495	17.14	0.113
GRD weighted by richness	0.18	1.000	0.48	0.976	0.18	1.000
GRD weighted by abundance	1.09	0.183	0.37	0.999	0.95	0.323

Test statistics (TS) from the X^2 randomization test evaluated compositional (SD and GD) differences between assemblages, whereas the Kolmogorov-Smirnov test evaluated differences in structure (SRD and GRD) between each assemblage. Significance levels are: ***highly significant and *significant.

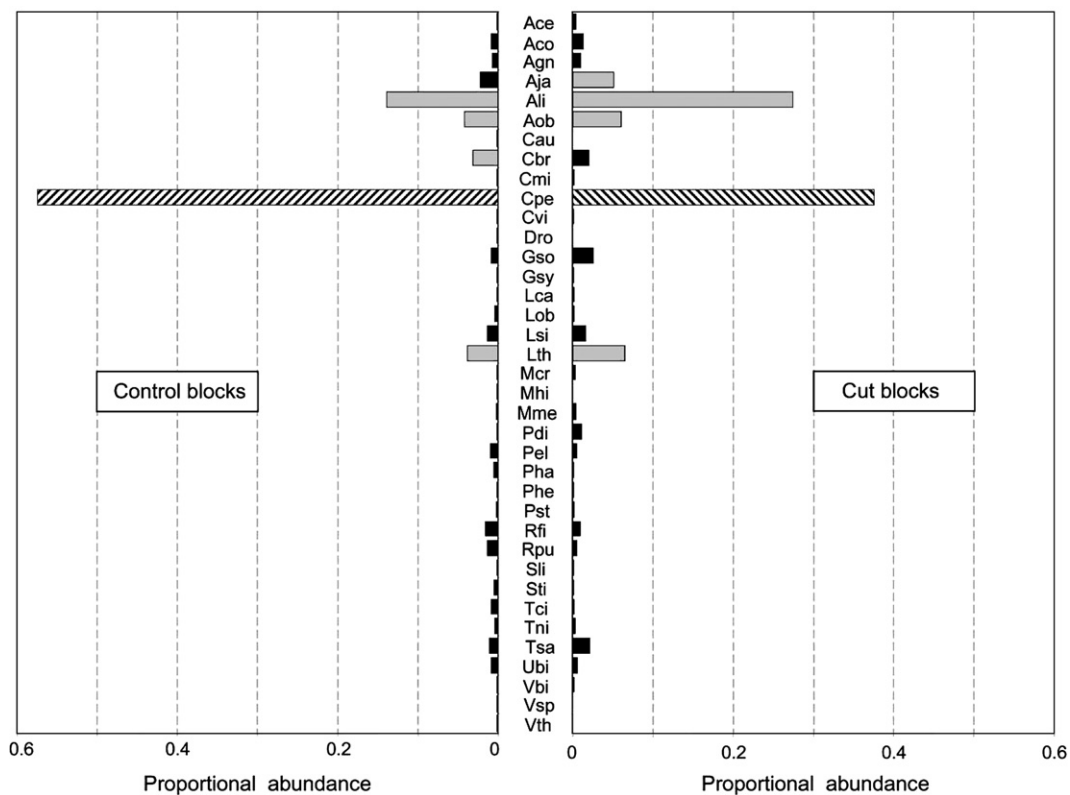


Fig. 3 – Species distributions (SD) weighted by proportional abundance for cut and control areas in Tapajós National Forest (data for blocks combined within each forest type). Striped bars represent dominant species (most abundant), gray bars represent common species (non-dominant species with a relative frequency $\geq$ inverse of species richness), and black bars represent rare species (species with a relative frequency $<$ inverse of species richness). Species codes appear in Table 1.

forest, 14 species in control forest). Only four species of nectarivores occurred in each management type, and one species of sanguivore (*Desmodus rotundus*) occurred in control forest (Fig. 6). Frugivores dominated the assemblage, accounting for

>80% of individuals in each management type (Fig. 6). Gleaning animalivores and nectarivores had comparable relative abundances (<10% of individuals) in each management type (Fig. 6). Division of species into finer guilds produced similar

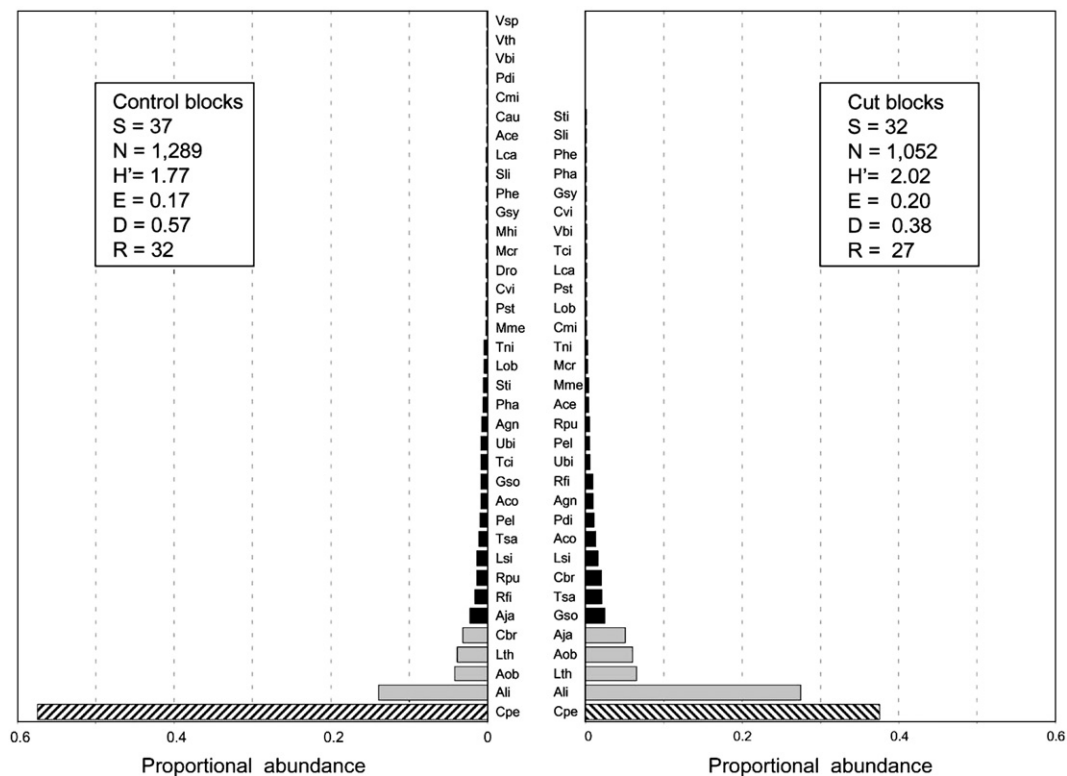


Fig. 4 – Species rank distributions (SRD) weighted by proportional abundance for control and cut areas of the Tapajós National Forest (data for blocks combined within each forest type). Striped bars represent dominant species (most abundant), gray bars represent common species (non-dominant species with a relative frequency $\geq$ inverse of species richness), and black bars represent rare species (species with a relative frequency $<$ inverse of species richness). See Table 1 for species codes. Abbreviations are: S, number of species; N, number of individuals; H' , Shannon's index of diversity (Pielou, 1975); E, Camargo's evenness index (Camargo, 1993); D, Berger–Parker dominance index (Berger and Parker, 1970); and R, number of rare species.

results, with frugivores the most species-rich group (17 and 18 species in cut and control forest, respectively) followed by gleaning insectivores (7 and 8 species in cut and control forest, respectively). Four species of nectarivores and omnivores occurred in each management type (Fig. 6). Carnivores and sanguinivores occurred only in control forest. Because the species composition of frugivores is the same in broad and fine classifications, so too are all statistical assessments.

Guild composition weighted by richness did not differ between cut and control forest based on either guild classification (Table 3 and Fig. 6). GDs weighted by abundance differed between management types for broad guilds but not fine guilds (Table 3 and Fig. 6). Regardless of classification scheme, GRDs did not differ between cut and control forest, and no added variance components characterized blocks within management (Table 3).

4. Discussion

4.1. Tapajós bat species richness

The number of species of phyllostomid bat (42) recorded from TNF is comparable to those reported for many other localities in Amazonia (Table 4). The richness of phyllostomids detected

in Amazonian forest sites ranges from 32 to 51 species; however, empirical richness is influenced by sampling effort and sampling techniques, as well as by regional biogeographic differences in the composition of species pools (Voss and Emons, 1996). As expected, sites with surveys that extended over several years (e.g., Iquitos, Peru) and sites that included mist netting in the canopy (e.g., Manaus, Brazil) recorded the greatest number of species. Maximizing the number of recorded species is a priority of many surveys of bats. In contrast, work in TNF focused on effects of RIL on bats and was restricted to a single forest type (i.e., terra firme). The TNF comprises many forest types (e.g., open palm forest, closed canopy upland forest, alluvial forest; Hernandez Filho et al., 1993); therefore, an expanded survey to include a representative sample of other habitat types likely would reveal that the TNF harbors one of the most species-rich phyllostomid bat assemblages in Amazonia.

Five bat species (*D. rotundus*, *Chrotopterus auritus*, *Micronycteris hirsuta*, *Vampyrus spectrum*, and *Vampyressa thuyone*) were recorded exclusively from control forest, whereas no species was recorded exclusively from cut forest (Fig. 3). Although effects of passive sampling related to differences in sample size (control forest $N = 1289$; cut forest $N = 1052$) may account for some of these differences in detected species, it is unlikely that all of the species detected in only one management type

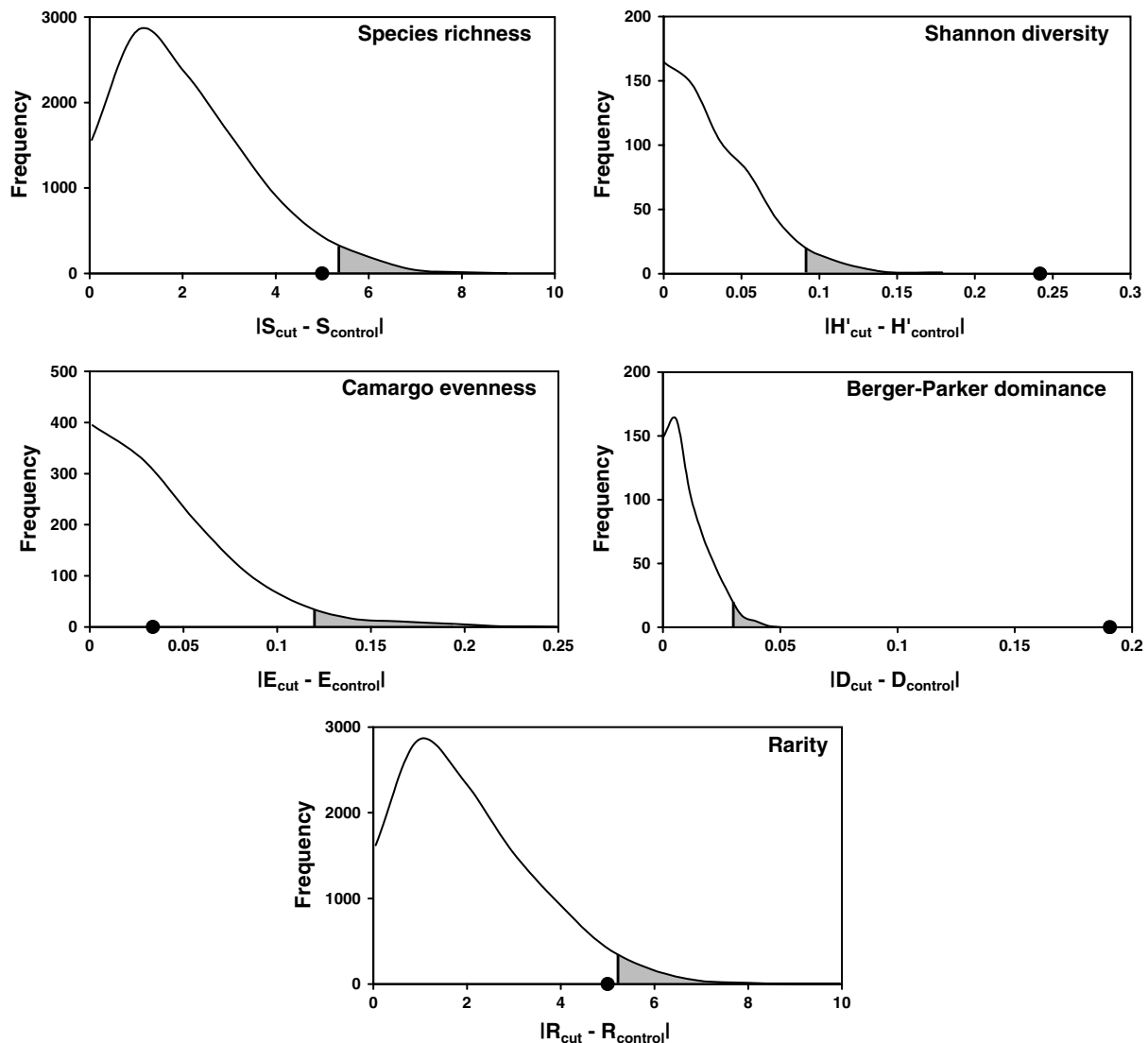


Fig. 5 – Graphical representations of the outcome of simulation analyses (10,000 iterations) showing the distribution of the test statistic (i.e., absolute value of differences between simulated index for cut forest and control forest) and its empirical value (●), separately, for species richness (S), Shannon diversity (H'), Camargo evenness (E), Berger–Parker dominance (D), and rarity (R). The area of each simulated distribution that represents the rejection region ($\alpha = 0.05$) is grey.

would be found in control forest exclusively (i.e., based on the binomial distribution, the probability that all seven individuals representing these species would occur in control forest is quite low, $P = 0.008 [0.5^7]$). Consequently, at least some of the rare species in control forest were absent from areas subject to RIL for reasons other than chance.

We recorded eight of the 17 species of Amazonian phyllostomids that occur on The World Conservation Union Red List of Threatened Species (IUCN, 2006). Two (*Lophostoma carrikeri* and *Rhinophylla fischeriae*) are Amazonian endemics (Marinho-Filho and Sazima, 1998) and six (*Glyphoncteris sylvestris*, *V. spectrum*, *Choeroniscus minor*, *A. concolor*, *Artibeus obscurus*, and *Vampyressa bidens*) are non-endemics. Three Amazonian Red List species were sufficiently abundant for population-level analyses; *A. obscurus* and *R. fischeriae* did not respond to RIL, whereas *A. concolor* increased in abundance in response to RIL. Four of five Red List species that were rare (*L. carrikeri*, *G. sylvestris*, *C. minor*, and *V. bidens*) were captured in cut and

control forest, but *V. spectrum* was captured only in control forest. Over the short-term, RIL did not appreciably reduce the abundance or locally extirpate phyllostomid bats with Red List status.

4.2. Effects of RIL

Population-level responses of bats in TNF were idiosyncratic (Table 2). Populations of most species in TNF were not affected by RIL. Nonetheless, mean abundances of some species that specialize on nectar (i.e., *G. soricina*) or fruits of *Cecropia* (i.e., *A. concolor* and *A. lituratus*) responded positively to RIL. In contrast, abundances of some species that specialize on fruits of *Piper* (i.e., *C. brevicauda* and *C. perspicillata*) responded negatively to RIL. The species-specific nature of responses of bats to RIL are consistent with responses to other anthropogenic activities in the Neotropics, although responses to RIL were less pronounced than to conventional logging practices,

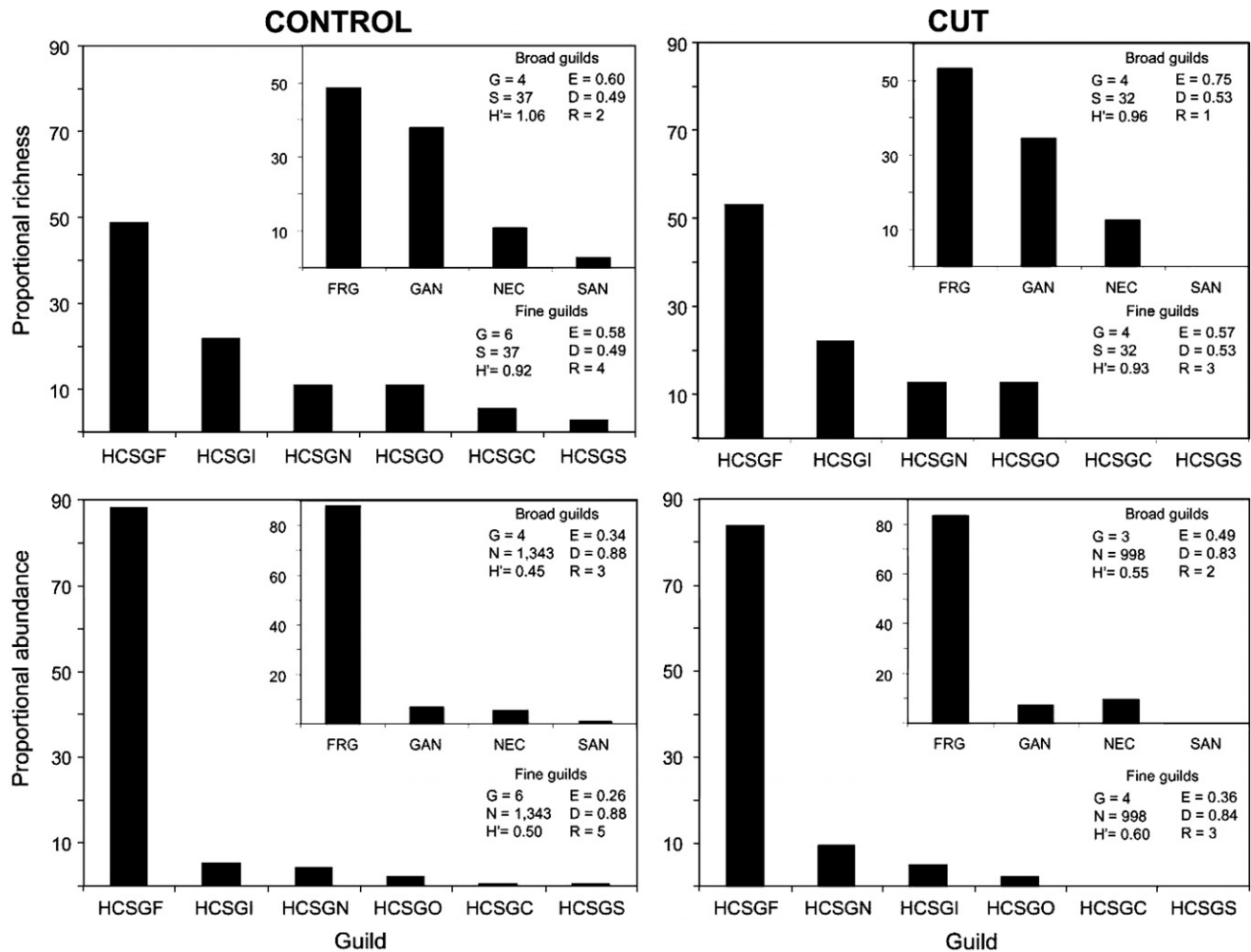


Fig. 6 – Guild richness (upper row) and guild abundance (lower row) distributions for control and cut areas in Tapajós National Forest (data for blocks combined within each forest type). Inset and larger charts correspond to data for broad guilds and fine guilds, respectively. Guild codes appear in Table 1. Abbreviations are: G, number of guilds; S, number of species; H', Shannon's index of diversity (Pielou, 1975); E, Camargo's evenness index (Camargo, 1993); D, Berger–Parker dominance index (Berger and Parker, 1970); R, number of rare guilds; N, number of individuals.

selective logging, or agricultural-related habitat conversion (Fenton et al., 1992; Bernard et al., 2001; Aguirre et al., 2003; Gorresen and Willig, 2004; Presley et al., 2007; Willig et al., 2007). In general, frugivores and nectarivores increase in abundance in disturbed areas regardless of whether the disturbance was of natural or anthropogenic origin (Fenton et al., 1992; Ochoa, 2000). Early successional and understory plants produce fruits and flowers on which these bats feed. Indeed, increases in fruit and nectar production associated with gap creation may stimulate four-fold increases in abundance of some species of frugivorous bat (Brosset et al., 1996). In contrast, specialized insectivores and vertebrate predators in the Neotropics (i.e., gleaning animalivores) typically respond negatively to any type of disturbance (Fenton et al., 1992; Brosset et al., 1996; Ochoa, 2000). As such, the negative responses of some frugivores and absence of negative responses by gleaning animalivores (e.g., *Lophostoma silvicolu*, *Phyllostomus elongatus*, and *Tonatia saurophila*) in TNF are remarkable and enigmatic. Indeed, these results suggest that RIL applied at the scale and extent of that in the demonstra-

tion forestry grid at TNF may have minimal effect on bats and the ecosystem services they provide.

Both of the species (*C. brevicauda* and *C. perspicillata*) whose mean abundances significantly decreased in response to RIL were among the most common species of frugivore in the TNF. At least in part, this “management effect” may be a legacy of previous anthropogenic disturbance that occurred about 20 years prior to the study in one of the control blocks (C1). More specifically, the mean abundances of these two species were three to five times higher in C1 than in C3, and the mean abundance in C3 was intermediate to that in the two cut blocks (Table 2). In addition, the significant response associated with the dominant taxon, *C. perspicillata*, drives the significant effects for frugivores based on fine or broad guild classifications. Thus, the appearance of a management effect is a consequence of elevated abundances in only one of the control blocks. This further corroborates the minimal negative impact of RIL on bat abundances, and suggests that at least for generalist frugivores, a mix of primary and successional forest may enhance abundances.

Table 4 – Species richness of phyllostomid bats at 17 Amazonian forest sites based on published records

Site	Country	Subfamily ^a						Individuals	Sample ^b	Years	Source
		Des	Glo	Phy	Car	Ste	Total				
Cuzco Amazonico	Peru	1	3	9	4	15	32	–	Het	2	Voss and Emmons (1996)
Ilha de Maraca	Brazil	1	3	15	2	13	34	315	Het ^M	1	Robinson (1998)
Cunucunumana	Venezuela	1	4	10	3	17	35	–	Het	<1	Voss and Emmons (1996)
Xingu	Brazil	2	4	13	3	14	36	–	Het	<1	Voss and Emmons (1996)
Piste St. Elie	Fr. Guiana	1	5	17	2	15	40	–	–	–	Lim and Engstrom (2001a)
Balta	Peru	1	5	11	4	19	40	–	Het	3	Voss and Emmons (1996)
Imataca reserve	Venezuela	1	4	15	3	17	40	–	Het ^M	–	Ochoa (2000)
Tapajós	Brazil	1	5	16	4	16	42	4144	Hom	2	Present study
Jenaro Herrera	Peru	1	5	15	5	19	45	2489	Het	4	Ascorra et al. (1993)
Yasuni	Ecuador	2	5	15	5	18	45	–	–	1	Lim and Engstrom (2001a)
Manu	Peru	2	5	14	4	21	46	–	Het	21	Voss and Emmons (1996)
Arataye	Fr. Guiana	1	6	18	3	18	46	–	Het	17	Voss and Emmons (1996)
Allpahuayo-Mishana	Peru	1	4	13	5	24	47	1937	Het	3	Hice et al. (2004)
BDFFP, Manaus ^c	Brazil	2	5	22	3	16	48	7700	Het ^{CN}	4	Sampaio et al. (2003)
Iwokrama forest	Guyana	1	5	21	3	18	48	2117	Het	1	Lim and Engstrom (2001b)
Paracou	Fr. Guiana	2	5	25	2	15	49	3126	Het ^{CN}	4	Simmons and Voss (1998)
Iquitos	Peru	1	4	17	5	24	51	14,673	Het	4	Willig et al. (2007)

Data from this study are bold.

a Phyllostomid subfamilies: Des, Desmodontinae; Glo, Glossophaginae; Phy, Phyllostominae; Car, Carollinae; Ste, Stenodermatinae.

b Sample refers to attributes of the sampling domain: Het, Heterogenous habitat sampled; Hom, homogeneous habitat sampled; Het^{CN}, Heterogenous habitat sampled and use of canopy nets; Het^M, Heterogenous habitat sampled complemented by museum records.

c Biological Dynamics of Forest Fragments Project in Manaus, Brazil.

In eastern Amazonia, non-volant mammal communities were not affected by RIL (Azevedo-Ramos et al., 2006). In contrast, arachnids exhibited site-specific changes in richness, abundance, and species composition (Azevedo-Ramos et al., 2006). More specifically, many families of arachnids not present in undisturbed forest were found after RIL, whereas abundances of other families declined. Ants exhibited similar responses, with many new genera of ants found after implementation of RIL, creating a more species-rich and even assemblage of ants in RIL forest than in undisturbed forest (Azevedo-Ramos et al., 2006). Nonetheless, responses by all taxa were considered minor as variation within sites pre- and post-logging was greater than variation among sites. Bird communities in Tapajós National Forest evinced only minor responses to RIL (Wunderle et al., 2006). Bird species richness and composition were not affected by RIL, although abundances of nectarivores and frugivores increased in response to post-harvest increases in fruit and flower production (Wunderle et al., 2006). Responses of birds, ants, and arachnids suggest that RIL may increase habitat heterogeneity by making some niches more prevalent in RIL forest than is in typical undisturbed forest. In addition, negative effects on mean abundances of species that specialize on undisturbed forest may represent a reduction in carrying capacity related to a decrease in the relative cover of their habitat. Consequently, careful implementation of RIL may increase biodiversity of some taxa via increased habitat heterogeneity while having a negligible effect on other species.

In addition to altering food availability, physical modification of the forest via removal of large trees during RIL may induce changes in bat populations by reducing the number and types of available roosts (Kunz and Lumsden, 2003). Effects of roost-site reduction have not been addressed quantitatively in the Neotropics; however, roost-site availability (i.e., the

number and types of roosts) influences bat community composition and structure on Caribbean islands (Rodriguez-Duran and Kunz, 2001) and in the Nearctic (Kunz and Lumsden, 2003). About 72% of the bat species from the TNF use roosts associated with large trees such as fallen logs, exfoliating bark, tree hollows, tree boles, dead standing trees, and ant or termite nests (Table 1). Therefore, selection of large trees (i.e., trees with dbh >45 cm) for harvest within RIL protocols may decrease roost availability for many species. However, RIL allows harvest of fewer trees than alternative methods, which should result in slight reductions of roost availability. The density of trees in TNF averages 55 individuals/ha with dbh >35 cm (Keller et al., 2001); removal of <4 trees/ha represents a minor (7%) reduction in tree density in terra firme forest.

Sensitivity to roost removal likely is species-specific. For example, *Furipterus horrens* roosts almost exclusively in fallen logs (Reid, 1997), whereas species such as *C. brevicauda* and *Artibeus jamaicensis* use a wide variety of roost sites (Handley, 1976; Ortega and Castro-Arellano, 2001). Changes in the abundance of available forage, in concert with changes in the abundance and types of available roost sites, may alter SDs in forest subjected to any logging. Careful examination of species-specific responses may reveal thresholds beyond which roosting habitat is too sparse for populations to persist. Unfortunately, preferences for roosting habitat are unavailable for many if not most Neotropical bat species (Kunz and Lumsden, 2003; Aguirre et al., 2003). Consequently, effects of long-term application of RIL on roost availability are unknown and worthy of future investigation. Careful monitoring may provide insights into potential modifications of RIL techniques that would enable more species of bat to maintain stable population sizes. Installation of artificial roosts, such as bat houses, may be a viable

option to mitigate logging related losses of natural cavities; however, the efficacy of artificial bat houses requires additional study to determine if such practices represent sound management technique in the Neotropics (Kunz and Lumsden, 2003).

Guidelines to help protect populations of keystone species include maintenance of high densities of seed trees (i.e., older, larger trees), protection of riparian areas, establishment of protected areas within timber harvest stands, and reduction of disturbance to standing and fallen dead trees (Mason and Putz, 2001). All of these guidelines can be incorporated successfully into established RIL protocols to meet goals of conservation and sustainability.

Population-level responses of species combine to create a bat assemblage in cut forest that has fewer rare species, increased Shannon diversity, and decreased dominance, compared to the assemblage in control forest (Figs. 4 and 5). Nonetheless, assemblage composition is similar between management types: the four most abundant species are the same regardless of management type, only one common species (*C. brevicauda*) in control forest is rare in cut forest, and only one rare species (*A. jamaicensis*) in control forest is common in cut forest (Fig. 4). Variation in mean abundance of the two most abundant species (*C. perspicillata* and *A. lituratus*) account for much of the significant differences in assemblage structure between cut and control forest. In control forest, *C. perspicillata* was highly dominant, with a mean abundance that was more than four times greater than that of the second most dominant species, *A. lituratus*. In cut forest, *C. perspicillata* and *A. lituratus* were co-dominant; *C. perspicillata* mean abundance was less than 1.5 times that of *A. lituratus*. Consequently, differences in the degree of dominance of *C. perspicillata* over *A. lituratus* (the only two species that responded significantly and appreciably to RIL) accounts for differences in assemblage diversity (i.e., increased Shannon diversity, and decreased Berger–Parker dominance) associated with RIL.

Regardless of guild classification scheme, RIL had little effect on guild abundances, guild composition, or guild structure (Tables 2 and 3 and Fig. 6). The decrease in mean abundance of fine and broad guild frugivores in cut forest resulted primarily from a large decrease in the abundance of *C. perspicillata*. Nonetheless, *C. perspicillata* remained the most abundant bat in RIL forest. Moreover, frugivores remained highly dominant in RIL forest (Fig. 6). In general, responses of bat assemblage composition and structure to RIL were modest, and change did not involve common species becoming rare or locally extinct. In addition, foraging guild structure and composition was not affected by RIL (Table 3). Taken together, these results suggest that RIL may have only small effects on ecosystem services provided by phyllostomid bats, at least in the short-term.

4.3. Patch dynamics and the enigmatic responses of *Carollia*

Abundances of *C. perspicillata* and *C. brevicauda* increased in response to RIL in a gap-matrix study (Presley et al., 2007) but decreased in response to RIL in the census study (Table 2), representing an enigma. These incongruous results may be best understood in the context of alterations of the

patch-dynamic characteristics (Pickett and White, 1985; Willig and McGinley, 1999) of forest subject to RIL (Fig. 7). Such results may arise because logging activities and subsequent forest regeneration creates complex patterns of local emigration and immigration of *Carollia* spp., which are usually associated with early successional forest patches. Timber harvest practices create gap cohorts of homogeneous age, thus altering patch dynamics of the forest and inducing changes in α , β , and γ diversity. A spatial redistribution of individuals during secondary succession potentially resolves this conflict, with areas of cut forest harboring fewer individuals with a more patchy dispersion compared to areas of control forest. More specifically, we hypothesize that *C. perspicillata* and *C. brevicauda* emigrate out of cut forest during logging activities because of disturbance and associated stress. After cessation of logging activity, they immigrate into cut forest and concentrate in or near gaps that are in early stages of regeneration

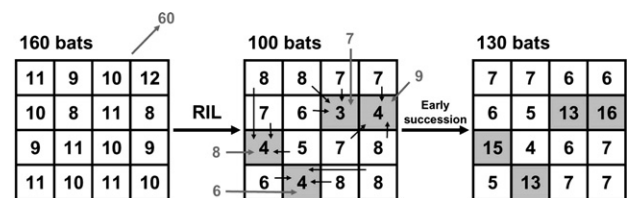


Fig. 7 – The enigmatic demographic responses of *Carollia* to reduced impact logging (RIL) may be related to spatially explicit components of patch dynamics and movement by bats during disturbance as well as during subsequent secondary succession. Each of three large squares represents the same block of forest at different times, with the 16 smaller squares representing spatially defined areas of the block (gray shading designates areas in which a tree was removed by RIL). The black numbers represent the abundance of *Carollia* within the spatially defined areas. Gray numbers represent the magnitude of change in abundance in a block based on immigration (gray arrow pointing into the block) or emigration (gray arrow pointing out of the block). Each black arrow represents the net movement of one individual within the block. Disturbances from RIL, and its associated stress, result in a net loss of individuals (60) from all portions of a block, but especially those areas from which a tree was harvested (small gray squares). From a spatial perspective, the immediate response to RIL is that gaps support fewer individuals than does matrix (3.75 versus 7.08). Within a short time after disturbance, early successional plant species colonize anthropogenically produced gaps, resulting in resource-rich patches of food for *Carollia*. These resources are hot spots that attract individuals from other areas of the block, resulting in further reduction in abundance. At the same time, these hot spots attract individuals from outside the block, further accentuating the difference between gap (14.26) and non-gap (6.08) areas, and increasing the overall abundance in the block (from 100 to 130 individuals). In this scenario, anthropogenically produced gaps enhance the abundance of *Carollia* at small spatial scales, even though RIL forest in general contains fewer individuals than does undisturbed forest.

because of abundant food resources associated with early successional plants. As a result, these bat species would be less abundant in cut forest than in control forest (consistent with the census study), but occur in greater densities in or near gaps in cut forest than in or near gaps in control forest (consistent with the gap-matrix study). This spatial distribution of individuals likely is a temporary state that prevails as long as resources such as flowers and fruits are concentrated in the unusually large cohort of RIL-generated gaps and may not reflect a long-term effect of RIL. In the absence of additional logging, differences in densities and distributions of *Carollia* spp. between cut and control forest should become less distinct over time as the forest regenerates. Nonetheless, this cautions that cyclic tree removal associated with RIL could exacerbate the modest changes in bat assemblages detected here.

4.4. Conclusions and future directions

Short-term responses of phyllostomids to RIL, even when significant, were of negligible magnitude in TNF. This is remarkable in that analyses were liberal and predisposed to detect differences between treatments because of potential for reduced variances within blocks related to spatial correlation. Most species evinced no or only small population-level responses. Moreover, only two of the five populations with a significant response to RIL decreased in abundance. Although five species of rare bat from control forest were absent from cut forest, all were locally rare and likely represent temporary local extirpations. A management design that imbeds RIL sites in a matrix of undisturbed forest, especially one that is expansive, should allow rescue effects (Brown and Kodric-Brown, 1977) to reduce the likelihood of local extinction.

Reduced abundance of a species may signal a temporary reduction in carrying capacity, local migratory responses, or a more serious negative response to RIL that forebodes local extirpation. Of particular concern is loss of species that provide ecosystem services (e.g., frugivorous or nectarivorous bats) that could modify forest dynamics and successional trajectories (McConkey and Drake, 2006). The ultimate consequence of poor survivorship of keystone taxa could be long-term degradation of forest that is incapable of providing renewable timber resources, thereby defeating the goal of RIL.

This study was conducted between 2 and 4 years post-harvest and consequently represents only short-term responses to RIL. Compared to other logging techniques, the short-term impact of RIL on bat populations, assemblages, and guilds was small, suggesting that RIL is a viable and potentially integral option for sustainable forest management. However, extrapolation of short-term consequences to a long-term prospectus is tenuous, and caution must be exercised in interpreting results in the context of conservation, management, or policy. Studies over longer periods of time or studies that include forest that was subjected previously to logging and is in various stages of regeneration (e.g., Clarke et al., 2005b) provide greater insight into long-term implications of modern logging protocols. The selective harvest of trees in the Brazilian Amazon has increased in recent times, and likely will continue to increase (Asner et al., 2005). Consequently, long-term

effects should be quantified to ascertain long-term consequences to biodiversity, as well as to ecosystem functionality and services.

Evaluation of the long-term effects of RIL on keystone species is a crucial issue for evaluating sustainable use and conservation goals that are part of the expanded system of Brazil National Forests (Verissimo et al., 2002). Indeed, the efficacy of RIL may be tested in the near future: a conservation initiative recently enacted in Pará, Brazil only allows the use of sustainable logging and agricultural practices in seven areas in northern Amazonia that cover 15 million ha (<http://news-vote.bbc.co.uk/mpapps/pagetools/print/news.bbc.co.uk/2/hi/science/nature/6205802.stm>). Because logging must be deemed sustainable to be executed within these expanded areas of conservation, clarification of the impacts of logging practices such as RIL on biodiversity is vital to the success of this new initiative and others like it.

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ERRATUM

Please correct an error on page 274, Section 3.2, Line 4 so that it reads:
“37 species” rather than “42 species”.

This discrepancy was unable to be corrected while the manuscript was in proof. We apologize for any inconvenience.