

Effects of reduced-impact logging and forest physiognomy on bat populations of lowland Amazonian forest

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Summary

1. As human population size increases, demand for natural resources will increase. Logging pressure related to increasing demands continues to threaten remote areas of Amazonian forest. A harvest protocol is required to provide renewable timber resources that meet consumer needs while minimizing negative effects on biodiversity and ecosystem services. Reduced-impact logging (RIL) may be a viable option to achieve these goals.
2. Effects of RIL ($18 \text{ m}^3 \text{ ha}^{-1}$) and forest physiognomy were assessed for populations of bats from Amazonian *terra firme* forest in Brazil at 20–42 months postharvest.
3. Based on 64 512 meter-hours of netting, 1468 bats were captured representing 47 species, 30 genera, four families and five feeding ensembles. Five species (one nectarivore and four frugivores) responded to management in a consistent manner: four were more abundant in logged forest and one was more abundant in undisturbed forest. Ten species (one nectarivore, two gleaning animalivores and seven frugivores) responded to forest physiognomy in a consistent manner: nine were more abundant in closed-canopy sites and one was more abundant in gaps. Three species (all frugivores) exhibited idiosyncratic responses to management that were contingent on physiognomy.
4. Using qualitative measures (changes in status from common to rare, or from present to absent), RIL elicited negative responses from 16 species, mostly rare taxa. After accounting for differences in total number of collected individuals, control forest harboured seven to 15 more rare species than did forest subjected to RIL.
5. *Synthesis and applications.* In the short term, RIL generally did not negatively affect populations of abundant bats. In contrast, reductions in abundance or local extirpation in response to RIL generally characterized uncommon or rare species. Arrangement of RIL sites in a matrix of undisturbed forest may allow source–sink dynamics to mitigate effects of RIL on rare or sensitive species and enhance sustainability at a regional scale.

Key-words: bats, conservation, deforestation, habitat use, population dynamics, sustainable-use forest management

Introduction

On a global scale, habitat loss associated with anthropogenic activities is increasing at an alarming rate (Soares-Filho *et al.* 2006), especially in the Neotropics, which harbours a large proportion of the world's species (Heywood & Watson 1995).

Logging pressure related to economic growth, as well as local and global timber needs, threaten pristine Neotropical forests in remote regions of Amazonia. Over the past 30 years, low-intensity logging practices (as opposed to conventional selective harvesting, timber liquidation or clear cutting) that harvest two to eight trees per hectare, have become increasingly common in the New World tropics (Clarke, Pio & Racey 2005a). Reduced-impact logging (RIL) is a modification of selective logging that implements pre- and postlogging guidelines to

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protect seedlings, saplings and small trees from injury, minimize soil damage, prevent unnecessary damage to non-target species, and protect critical ecosystem processes (e.g. hydrogeology and carbon sequestration; Putz, Dykstra & Heinrich 2000). Felling and skidding techniques used in conventional selective logging practices can kill 27 trees of ≥ 10 cm dbh for every harvested tree (Verissimo *et al.* 1992). In contrast, RIL minimizes damage to surrounding forest while extracting a reduced number (two to four trees per hectare) and volume ($5\text{--}19\text{ m}^3\text{ ha}^{-1}$) of commercially valuable trees. After logging, the forest is allowed to recover for several years before the next harvest (Fimbel, Gramal & Robinson 2001). Dykstra & Heinrich (1996) provide detailed guidelines on the implementation of RIL. The cyclical nature and low impact of these harvests on the structure and composition of the forest may minimize negative effects on biodiversity and provide a renewable resource of economic value (Grieser Johns 1997). From a conservation perspective, it is essential to determine consequences of RIL on the biota because such practices are rapidly becoming an industry standard (Clarke *et al.* 2005a).

In the Neotropics, bats are the sole or primary agents of pollination and seed dispersal for many species of plants (Fleming & Heithaus 1981; Fleming 1988; Galindo-González, Guevara & Sosa 2000). Indeed, the activities of some phyllostomid species (New World fruit-eating bats) promote secondary succession because they disperse seeds of pioneer plants differentially (Fleming 1988; Gorchoff *et al.* 1993). In the Neotropics, seed dispersal by animals is integral to the establishment and persistence of a seed bank that is representative of the local flora (Parrotta, Turnbull & Jones 1997; Wunderle 1997). Consequently, understanding the effects of logging regimes on bat populations is critical to designing a forest-management programme that maintains a high degree of natural ecosystem function in lowland Amazonian rainforests.

Bats respond to logging practices and associated habitat fragmentation in a species-specific manner (Fenton *et al.* 1992; Clarke, Rostant & Racey 2005b; Gorresen *et al.* 2005; Willig *et al.* 2007). Few studies (e.g. Ochoa 2000; Clarke *et al.* 2005a; Peters *et al.* 2006) have evaluated the effects of low-intensity logging, and no studies have evaluated effects of RIL practices on bat populations. We used comparative observational studies (non-manipulative natural experiments) to evaluate the effects of RIL on populations of phyllostomid bats in lowland Amazonian rainforest.

Methods

STUDY AREA

Research was conducted in lowland Amazonia within the Tapajós National Forest (TNF), a 560 000-ha area managed by the Instituto Brasileiro de Meio Ambiente e Recursos Naturais Renováveis. The TNF is in the Tapajós area of endemism, one of eight such recognized areas in Amazonia (da Silva, Rylands & Fonseca 2005). The Tapajós area of endemism comprises 648 862 km², has lost only 9.3% of its forest cover, and is among the least threatened regions of the Amazon. However, this estimate of forest loss does not include selectively logged areas, and thus is an underestimate of overall

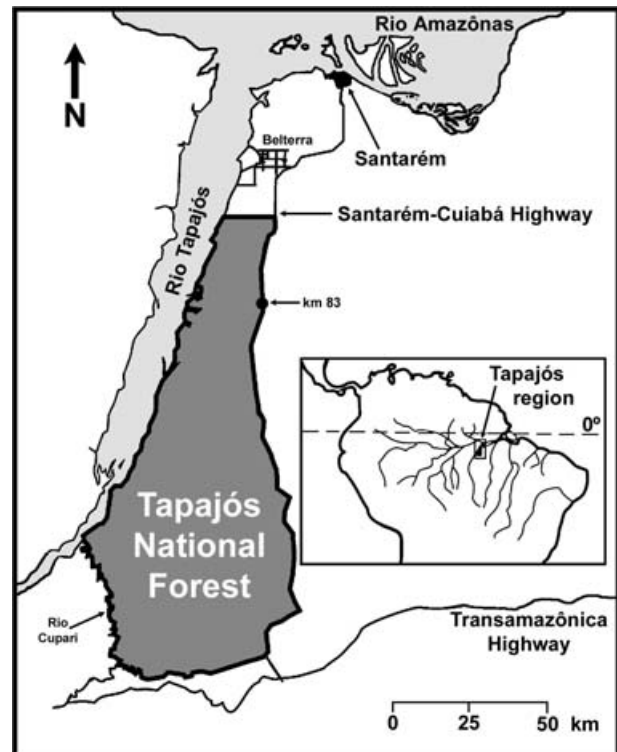


Fig. 1. Location of Tapajós National Forest ($3^{\circ}36' S$, $54^{\circ}95' W$) in Pará, Brazil. The study site was located at km 83 of the Santarém–Cuiabá highway. Modified from Wunderle, Willig & Henriques (2005).

impact. Over 28% of the Tapajós area of endemism enjoys some level of protection. However, only 0.7% of land is protected strictly, with the rest dedicated as indigenous reserves (24.1%) or subject to sustainable use (3.5%).

The TNF ($3^{\circ}36' S$, $54^{\circ}95' W$) is located on the east bank of the lower Tapajós River in western Pará, Brazil (Fig. 1). The climate is tropical, with mean monthly temperatures between 24.3 and $25.8^{\circ} C$ (Silva 1989). Rainfall is substantial (≈ 1920 mm per year), with most precipitation occurring from December to May, and a modest dry season from August to October. Several distinct moist and wet forest types occur in the TNF, with *terra firme* forest constituting 33% of forested lands and encompassing the entire study area. *Terra firme* is characterized by 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.

A system of roads and trails at km 83 of the Santarém–Cuiabá Highway provided access to forest, including four 100-ha experimental blocks. These blocks were within a 5000-ha grid established as a demonstration for logging practices in *terra firme* forest. Two control blocks were undisturbed forest and two cut blocks were subjected to RIL. Control blocks were adjacent to each other and were 1–2.3 km from cut blocks. Cut blocks were separated from each other by 2.5 km of selectively logged forest.

Timber harvest in cut blocks was completed in December 1997, 20 months before initiation of the study. In addition to minimizing damage related to felling, skidding or log processing, RIL techniques that were applied to cut blocks harvested fewer trees and a reduced volume of wood ($<19.0\text{ m}^3\text{ ha}^{-1}$) compared with forest subjected to traditional selective logging ($\approx 40\text{ m}^3\text{ ha}^{-1}$). In RIL forest, an average

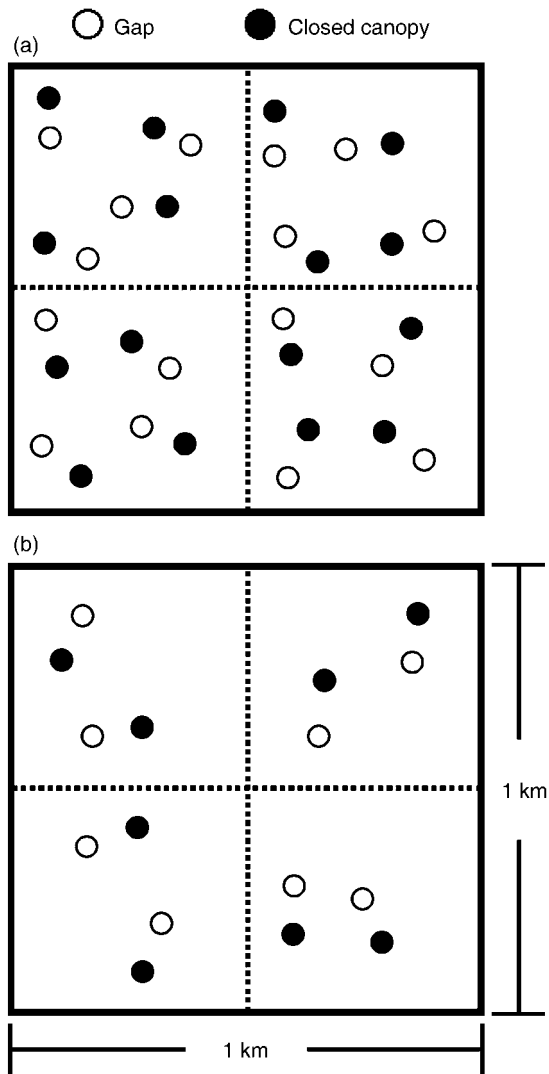


Fig. 2. Arrangement of net sites in 100-ha blocks of *terra firme* forest in Tapajós National Forest, Pará, Brazil. Each block was divided into four quadrats (delimited by dashed lines) and an equal number of sites (circles) were placed in gaps (open) and closed-canopy (solid) sites. (a) In each block of undisturbed forest, four closed canopy and four gap sites were located in each quadrat. (b) In each block of logged forest, two closed-canopy and two gap sites were located in each quadrat.

of 3.94 (18.70 m³) and 3.79 (18.73 m³) trees per hectare were removed from cut blocks. All trees harvested were >45 cm dbh. *Manilkara huberi*, *Manilkara paraensis*, *Protium pernevatum*, *Dinizia excelsa* and *Piptadenia suaveolens* were the most commonly harvested species at TNF (Keller *et al.* 2004).

SAMPLING METHODS

Two groups of understorey sites were selected based on habitat physiognomy: treefall gaps and closed canopy (henceforth gap and closed canopy, respectively). Sixteen gaps formed by natural treefalls and 16 closed-canopy sites were selected in each control block; similarly, eight gaps resulting from logging of individual trees and eight closed-canopy sites were selected in each cut block (Fig. 2). All sites were >30 m from the edge of the block. Each block was divided

into four quadrats, and an equal number of gaps and closed-canopy sites were located in each quadrat to ensure dispersion of sites throughout each block. To enhance comparable sampling of variation within quadrats, each gap was associated with a closed-canopy site (Fig. 2). Location of an associated closed-canopy site with respect to a particular gap site was random with respect to direction, and at a random distance between 25 and 50 m. Associated sites were closer to each other than they were to any other site. The size of gaps from tree harvest ($\bar{Y} = 219 \text{ m}^2 \pm 55 \text{ SE}$) in cut blocks were indistinguishable from the size of gaps that were formed naturally ($\bar{Y} = 286 \text{ m}^2 \pm 37 \text{ SE}$) in undisturbed forest (Wunderle, Henriques & Willig 2006).

Sampling was organized into four time periods: June–July 1999, August 1999, November–December 1999, and April 2000 (Saldanha 2000). During each sampling period, each site was surveyed for one night. Depending on gap size and shape, 24 m of net in various combinations and configurations of 6- and 12-m segments were used to sample bats from gaps. Matching net configurations were used in corresponding closed-canopy sites. All mist nets (four-shelf, 2.6 m tall, 35 mm mesh) were erected at ground level and checked every hour from 18.00 to 01.00 h. Depending on intersite distances, two or three pairs of gap and closed-canopy sites within the same block were surveyed each night. Order of site selection within a block was random, and sites within each block were sampled in a temporal fashion (all sites of one block were sampled before sampling in another block). In addition, block order was randomized each sampling period. Nets were closed during heavy rain. If heavy rain occurred for more than 2 h of netting on any night, data from that night were excluded from analyses, and another night of netting was scheduled to replace lost sampling effort. To minimize effects of lunar phobia (Crespo *et al.* 1972) on sampling efficacy, netting was not conducted within two nights of a full moon.

Species identity, sex, reproductive condition, age (juvenile, subadult or adult), mass and standard morphometric measurements were recorded for each bat captured. To facilitate identification of recaptures within the same sampling period, bats were marked with a small notch in the border of one of the pinnae; notch location was unique for each time period. Recaptures from previous sampling periods were not discriminated from new captures in subsequent sampling periods. This ensured that the spatiotemporal focus of the study, the average number of individuals (new captures) per species per sampling period, was not overestimated by counting the same individual on multiple occasions within a sampling period. Accurate field identification of bats was facilitated by collecting a series of voucher specimens from the area prior to the study, but not at the sites of actual field work (Saldanha 2000). This synoptic series is deposited in the Museu Paraense Emílio Goeldi (Belém, Brazil). Nomenclature followed Simmons (2005) except in recognizing *Artibeus planirostris* instead of *A. jamaicensis* (Lim *et al.* 2004) as occurring in Amazonia. We classified bats into broad foraging ensembles (taxonomic subsets of a guild) based on published recommendations (Gardner 1977) that reflect the primary components of each species' diet. Phyllostomids captured at TNF represented four foraging ensembles (Table 1), including sanguivores, nectarivores, frugivores and gleaning animalivores (a composite of foliage-gleaning carnivores and foliage-gleaning insectivores).

Because all mist nets were placed at ground level, the presence or abundance of some taxa, particularly species in the Emballonuridae, Natalidae, Vespertilionidae and Molossidae, may be underestimated in multistrata tropical rainforests. This problem is not universal, as many species of emballonurids and vespertilionids may be captured at ground level more frequently than in elevated nets (Peters, Malcolm & Zimmerman 2006). To minimize such complications, we restricted

Table 1. Ensemble association, familial classification, and number of captured individuals in each combination of management and physiognomy for each of 39 bat species in Tapajós National Forest, Brazil. Species richness, total number of captures, and a rarity threshold are presented for each combination of management and physiognomy. Rarity thresholds are specific to each combination of management and physiognomy, and equal the abundance of phyllostomids in that combination divided by phyllostomid richness in that combination. Species with abundances greater than or equal to the rarity threshold for a particular combination of management and physiognomy were considered common and are indicated by bold numbers. Conservation status: LR:nt, lower risk, near threatened; VU A2c, vulnerable, population reduction of at least 20% projected or suspected within 10 years in areas of occupancy, extent of occurrence, or quality of habitat

Subfamily/species	Feeding ensemble	Conservation status	Control		Cut		Total
			Gap	Canopy	Gap	Canopy	
Desmodontinae							
<i>Desmodus rotundus</i>	Sanguinivore		2	2	0	0	4
Glossophaginae							
<i>Choeroniscus godmani</i>	Nectarivore		0	1	0	0	1
<i>Choeroniscus minor</i>	Nectarivore		0	3	0	0	3
<i>Glossophaga soricina</i>	Nectarivore		4	4	4	11	23
<i>Lichonycteris obscura</i>	Nectarivore		0	1	0	1	2
<i>Lonchophylla thomasi</i>	Nectarivore		5	30	5	16	56
Phyllostominae							
<i>Chrotopterus auritus</i>	Gleaning animalivore		0	3	0	0	3
<i>Glyphonycteris sylvestris</i>	Gleaning animalivore	LR:nt	0	1	0	1	2
<i>Lamproncycteris brachyotis</i>	Gleaning animalivore		1	0	0	0	1
<i>Lophostoma carrikeri</i>	Gleaning animalivore	VU A2c	1	0	0	0	1
<i>Lophostoma silvicolum</i>	Gleaning animalivore		4	14	1	11	30
<i>Micronycteris hirsute</i>	Gleaning animalivore		1	1	0	0	2
<i>Micronycteris megalotis</i>	Gleaning animalivore		2	2	0	2	6
<i>Mimon crenulatum</i>	Gleaning animalivore		0	6	0	0	6
<i>Phylloderma stenops</i>	Gleaning animalivore		1	1	0	2	4
<i>Phyllostomus discolor</i>	Gleaning animalivore		0	1	2	5	8
<i>Phyllostomus elongatus</i>	Gleaning animalivore		6	8	0	2	16
<i>Tonatia saurophila</i>	Gleaning animalivore		8	18	1	10	37
<i>Trachops cirrhosus</i>	Gleaning animalivore		2	2	0	0	4
<i>Trinycteris nicefori</i>	Gleaning animalivore		3	1	1	0	5
Carollinae							
<i>Carollia brevicauda</i>	Frugivore		11	7	15	12	45
<i>Carollia perspicillata</i>	Frugivore		152	172	71	138	533
<i>Rhinophylla fischeriae</i>	Frugivore	LR:nt	17	4	11	7	39
<i>Rhinophylla pumilio</i>	Frugivore		8	22	3	2	35
Stenodermatinae							
<i>Ametrida centurio</i>	Frugivore		2	0	0	0	2
<i>Artibeus concolor</i>	Frugivore	LR:nt	7	26	5	8	46
<i>Artibeus gnomus</i>	Frugivore		7	6	9	3	25
<i>Artibeus litratus</i>	Frugivore		57	98	13	72	240
<i>Artibeus obscurus</i>	Frugivore	LR:nt	12	64	3	30	109
<i>Artibeus planirostris</i>	Frugivore		3	10	0	3	16
<i>Chiroderma trinitatum</i>	Frugivore		0	4	0	3	7
<i>Chiroderma villosum</i>	Frugivore		0	1	0	1	2
<i>Mesophylla macconnelli</i>	Frugivore		3	1	0	0	4
<i>Platyrrhinus helleri</i>	Frugivore		0	2	3	7	12
<i>Sturnira lilium</i>	Frugivore		1	0	0	1	2
<i>Sturnira tildae</i>	Frugivore		1	3	0	0	4
<i>Uroderma bilobatum</i>	Frugivore		4	10	6	5	25
<i>Vampyressa bidens</i>	Frugivore	LR:nt	2	12	0	3	17
<i>Vampyressa thuyone</i>	Frugivore		0	2	0	0	2
Phyllostomid richness			28	35	16	25	39
Total phyllostomid abundance			327	543	153	356	1379
Rarity threshold			11.7	15.5	9.6	14.2	35.4

analyses to populations of phyllostomid bats. All sampling methods, including those for volant mammals, involve some degree of species-specific bias (capture probabilities are not the same for all taxa, especially for those with different sensing or locomotor modalities). This is particularly problematic when estimating community-level

characteristics such as species diversity or evenness, as differences in abundance or catchability among species are reflected in metrics of biodiversity that weight species presence by relative abundance. Such concerns are less critical for comparisons of intraspecific metrics such as abundance, because interspecific differences in sensing or locomotor

modalities are not germane. The important assumption when comparing abundances is that the biases associated with a sampling method are equivalent in different levels of a treatment factor (e.g. cut vs. control forest). We use the term 'abundance' to refer to the number of captures for each species because of its ease of exposition, with the understanding that variation in the number of captures at a site can be a consequence of the catchability, habitat use or density.

ANALYTICAL METHODS

For each of the 17 most common species of phyllostomid in TNF, a generalized linear mixed-effects model (GLMM; Venables & Ripley 2002) with the assumption of Poisson errors quantified the effects of management (cut vs. control forest), forest physiognomy (gap vs. closed canopy), and their interaction on abundance (average number of captures per time period at each site). In all GLMMs, management and physiognomy were model I factors, and block (a model II factor) was nested within levels of management. Because of the nesting of blocks within levels of management, factors quantifying this nesting, as well as the interaction of physiognomy and block within management, were included in each GLMM. All GLMMs were executed in the R programming environment (R Development Core Team 2005) and the MASS and nlme libraries. We were interested in population-level responses of each species to management and physiognomy, rather than overall multivariate evidence of effects on the phyllostomid assemblage. Therefore results were interpreted without application of Bonferroni sequential adjustments (BSA). Considerable controversy surrounds the use of such adjustments, and the exploratory nature of this research argues against the use of such highly conservative approaches (Moran 2003; Roback & Askins 2005). Because of conservation and forest management implications, we were more concerned with detecting responses to management and forest physiognomy than we were with the potential for type I errors. Therefore we report exact P values without application of BSA, and discuss all responses that were significant ($P \leq 0.05$) or approached significance ($0.05 < P \leq 0.10$).

Because species abundances reflect the vulnerability of a species to extinction, species rarity is a topic of increasing interest in ecology and conservation biology (Kunin & Gaston 1997; Rodrigues & Gaston 2002; Hartley & Kunin 2004). We used a statistical metric of rarity (Camargo 1992) that considers a species to be rare if its abundance is less than the average abundance (\bar{n}) of all species in an assemblage ($< N/S$, where N = total number of individuals in an assemblage and S = species richness). Because differences in the density or type of vegetation, as well as flowering or fruiting phenology, can affect local or site-specific capture rates, and because more pairs of sites (16 vs. eight) were sampled in control forest than in cut forest, we calculated \bar{n}_{ij} separately for each combination of management (i) and physiognomy (j). Subsequently, \bar{n}_{ij} was used as the rarity threshold for each respective combination of management and physiognomy: species with abundances $< \bar{n}_{ij}$ were considered to be rare and species with abundances $\geq \bar{n}_{ij}$ were considered to be common.

Qualitative comparisons (common vs. rare; present vs. absent) of species between treatments were confounded by unequal numbers of captures and unequal numbers of sites (Table 1). For example, if five species were rare in control forest but absent from cut forest, these differences could be explained by differences in quality of habitat (actual differences in species associations) as well as by differences in number of captured individuals or number of sites sampled in each management type (sampling bias). To address sampling issues, we employed rarefaction (Heck, van Belle & Simberloff 1975) to standardize the number of individuals for each comparison. Rarefaction

was based on 1000 bootstrapped samples of the number of individuals in the smaller sample. Similarly, we used an incidence-based approach (Colwell, Mao & Chang 2004) to account for differences in the number of sites between treatments as well as to estimate parametric values of richness for each combination of management and physiognomy. To compare the number of rare species in different combinations of management and physiognomy, three sets of rarefaction analyses were used to compare control forest with cut forest, control gaps with cut gaps, and control closed-canopy sites with cut closed-canopy sites. Rarefaction was conducted in MATLAB ver. 6.1 (2001) (Math Works, Inc., Novi, MI, USA) and analyses of incidence were conducted in EstimateS ver. 7.5 for Windows (Colwell 2005). We used these techniques to evaluate the influence of sampling on the ability to detect species presence in each management type, not in an attempt to estimate parametric measures of diversity. This approach established levels of confidence for the absence of species in particular habitats.

This paper is part of a series to investigate the effects of RIL on bat ecology, paralleling a suite of comparable papers that focus on birds (Henriques, Wunderle & Willig 2003; Wunderle, Willig & Henriques 2005; Wunderle *et al.* 2006). We focus on population-level responses of bats, whereas other studies (Castro-Arellano *et al.* 2007) evaluate responses by bat-feeding ensembles and assemblages.

Results

During 64 512 net meter-hours of sampling, we captured 1468 bats representing 47 species, 30 genera, four families and five broad feeding ensembles. Of those bats, phyllostomids represented 1379 captures, 39 species, 25 genera and four ensembles (Table 1). Of the 11 bat species endemic to the Amazon (Marinho-Filho & Sazima 1998), two (*Lophostoma carrikeri* and *Rhinophylla fischeriae*) were captured in TNF (Table 1). Regardless of management type, more species and individuals of phyllostomid bat were captured in closed-canopy sites than in gap sites (Table 1). These data are the product of an exceptionally intensive study of the effects of logging on bats, with more sites, greater replication and greater sampling effort at each site than that in similar contemporary studies (e.g. Ochoa 2000; Clark *et al.* 2005a, 2005b).

QUALITATIVE ASSESSMENT

Thirty of the 39 species of phyllostomids documented during the study were rare in each combination of management and physiognomy (Table 1). One species (*Lonchophylla thomasi*) was common in closed-canopy sites in both management types; three species (*Tonatia saurophila*, *Rhinophylla pumilio* and *Artibeus concolor*) were common in closed-canopy sites in control forest; one species (*Artibeus obscurus*) was common in all but gap habitats in cut forest; two species (*Carollia brevicauda* and *R. fischeriae*) were common in gaps regardless of management type; and two species (*Carollia perspicillata* and *Artibeus lituratus*) were common in all combinations of management and physiognomy.

Three species were common in both types of management, but were less abundant in cut forest. *Lonchophylla thomasi* was 19% less abundant in closed-canopy sites of cut forest compared with those of control forest, *A. lituratus* was 51% less abundant in gaps from cut forest compared with those of control forest,

and *A. obscurus* was 47 and 29% less abundant in gaps and closed-canopy sites, respectively, in cut forest compared with control forest.

Tonatia saurophila, *R. pumilio* and *A. concolor* were common in closed-canopy sites of control forest, but were rare in all other combinations of physiognomy and management. These species responded negatively to disturbance, but responded more strongly to logging than to natural treefalls. Reduction in abundances of *T. saurophila*, *R. pumilio* and *A. concolor* in closed-canopy sites of cut forests compared with those of control forests were 15, 86 and 53%, respectively.

Thirteen species were obtained in control forest but not in cut forest, including six gleaning animalivores (*Chrotopterus auritus*, *Lamproncyteris brachyotis*, *L. carrikeri*, *Microncyteris hirsuta*, *Mimon crenulatum* and *Trachops cirrhosus*), two nectarivores (*Choeroniscus godmani* and *Choeroniscus minor*), four frugivores (*Ametrida centurio*, *Mesophylla macconnelli*, *Sturnira tildae* and *Vampyressa thyone*), and one sanguinivore (*Desmodus rotundus*). More bats were captured in control forest (870) than in cut forest (509), and twice as many sites were sampled in control forest (64) than in cut forest (32). Both of these facts could contribute to differences in the detection of rare species in cut forest. Rarefaction analyses that standardized sample sizes to 509 individuals predicted 32.0 and 23.6 species in control and cut forest, respectively. Rarefaction analyses that standardized number of sites to 32 predicted 33.1 and 26.0 species in control and cut forest, respectively. Estimates of parametric richness (incidence-based coverage estimator) based on species incidence standardized to 32

samples predicted 44.0 and 29.6 species in control and cut forest, respectively. Differences in species richness between management types are probably caused by a larger number of rare species and not a larger number of common species. Therefore, after accounting for potential sampling effects, cut forest harboured 7–15 (observed = 13, individual rarefaction = 8.4, site rarefaction = 7.1, parametric estimate = 14.4) fewer rare species than did control forest. Similar patterns occurred in analyses within each physiognomy; gap (6–13 species) and closed canopy (3–12) sites harboured more rare species in control forest than in cut forest. Rarefaction indicated that approximately half of the difference in the number of rare species detected between management types within each physiognomy can be accounted for by differences in total abundance or number of sites sampled.

QUANTITATIVE ASSESSMENT

The effects on abundance of management, physiognomy, and their interaction were evaluated separately for each of the 17 most abundant species of phyllostomid. Sixteen of 17 species responded to management (*Glossophaga soricina*, *C. breviceauda*, *R. pumilio*, *Artibeus gnomus* and *Platyrrhinus helleri*), physiognomy (*L. thomasi*, *Lophostoma silvicolium*, *T. saurophila*, *R. fischeriae*, *R. pumilio*, *A. concolor*, *A. planirostris*, *A. obscurus*, *P. helleri* and *Vampyressa bidens*), or their interaction (*C. perspicillata*, *A. lituratus* and *Uroderma bilobatum*; Table 2; Figs 3 and 4). A significant block within management effect was observed for *C. perspicillata* and *A. lituratus*. No significant

Table 2. Significance levels (exact *P*-values) from generalized linear mixed effects models that quantify the effects of management, physiognomy, and their interaction on abundance for each of the 17 most common species of phyllostomid bat in Tapajós National Forest, Brazil. In addition, significance is presented for block effects within management and the interaction of block effects within management and physiognomy. Bold font indicates results that at least approached significance (i.e. $P \leq 0.10$)

Subfamily/species	Captures	Management	Physiognomy	Management × physiognomy	Block within management	Physiognomy × block within management
Glossophaginae						
<i>Glossophaga soricina</i>	23	0.002	0.172	0.296	0.267	0.546
<i>Lonchophylla thomasi</i>	56	0.907	<0.001	0.445	0.853	0.204
Phyllostominae						
<i>Lophostoma silvicolium</i>	30	0.274	0.010	0.246	0.415	1.000
<i>Phyllostomus elongatus</i>	16	0.874	0.345	1.000	1.000	1.000
<i>Tonatia saurophila</i>	37	0.424	0.001	0.696	0.339	0.459
Carollinae						
<i>Carollia breviceauda</i>	45	0.001	0.574	0.702	0.164	0.493
<i>Carollia perspicillata</i>	533	0.046	0.007	0.023	0.022	0.196
<i>Rhinophylla fischeriae</i>	39	0.277	0.033	0.290	0.601	0.166
<i>Rhinophylla pumilio</i>	35	0.060	0.018	0.823	0.497	0.378
Stenodermatinae						
<i>Artibeus concolor</i>	46	0.433	0.003	0.188	0.389	0.476
<i>Artibeus gnomus</i>	25	0.090	0.276	0.313	0.636	0.898
<i>Artibeus lituratus</i>	240	0.001	<0.001	0.031	<0.001	0.685
<i>Artibeus obscurus</i>	109	0.956	<0.001	0.456	0.598	0.885
<i>Artibeus planirostris</i>	16	0.477	0.002	1.000	0.141	1.000
<i>Platyrrhinus helleri</i>	12	0.023	0.003	1.000	0.940	0.182
<i>Uroderma bilobatum</i>	25	0.200	0.553	0.014	0.422	0.881
<i>Vampyressa bidens</i>	17	0.473	<0.001	1.000	0.946	1.000

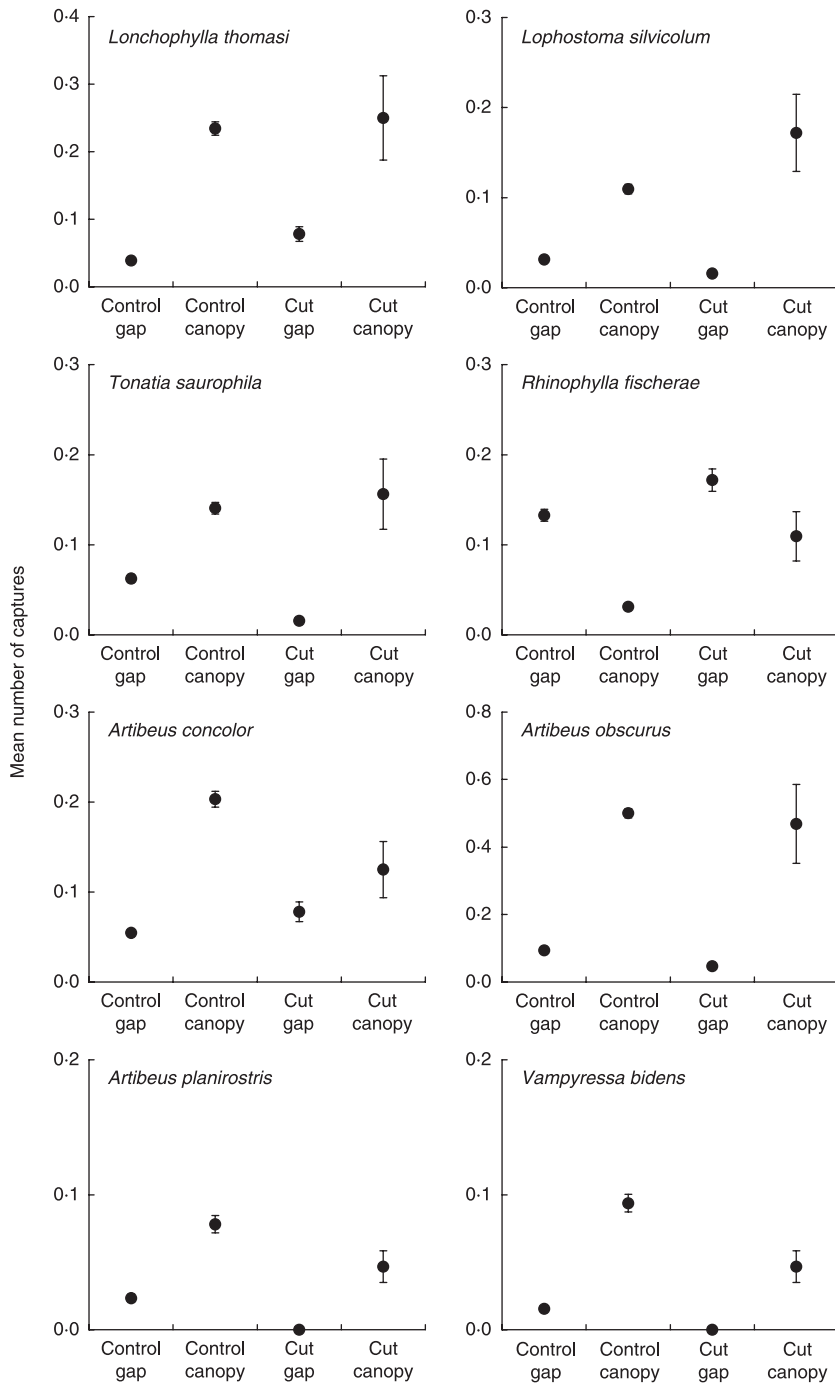


Fig. 3. Mean number of captures (± 1 SE) per sampling period per site in each combination of management and physiognomy for each of eight species of phyllostomid bat that responded to physiognomy in a consistent fashion.

responses were observed for the interaction of block within management and physiognomy (Table 2). Because sample sizes were the same for analyses of each species, significance involving management characterized 47% of species, and significance involving physiognomy characterized 76% of species, it is unlikely that power was compromised by experimental design. Rather, cases of non-significance arose when treatment effects were relatively small compared with associated variability.

Nine (*L. thomasi*, *L. silvicolum*, *T. saurophila*, *R. pumilio*, *A. concolor*, *A. planirostris*, *A. obscurus*, *P. helleri* and *V. bidens*) of the 10 species that responded to physiognomy in a con-

sistent manner were more abundant in closed-canopy sites than in gaps (Figs 3 and 4). In contrast, *R. fischeriae* was more abundant in gaps than in closed-canopy sites. Regardless of physiognomy, *R. pumilio* was more abundant in control forest than in cut forest, whereas *G. soricina*, *C. brevicauda*, *A. gnomus* and *P. helleri* were more abundant in cut than in control forest. *Rhinophylla pumilio* experienced a substantial (61%) reduction in abundance in response to RIL. Similarly, species that responded positively to RIL evinced substantially dramatic increases in abundance (107% in the case of *A. gnomus* to 966% in the case of *P. helleri*).

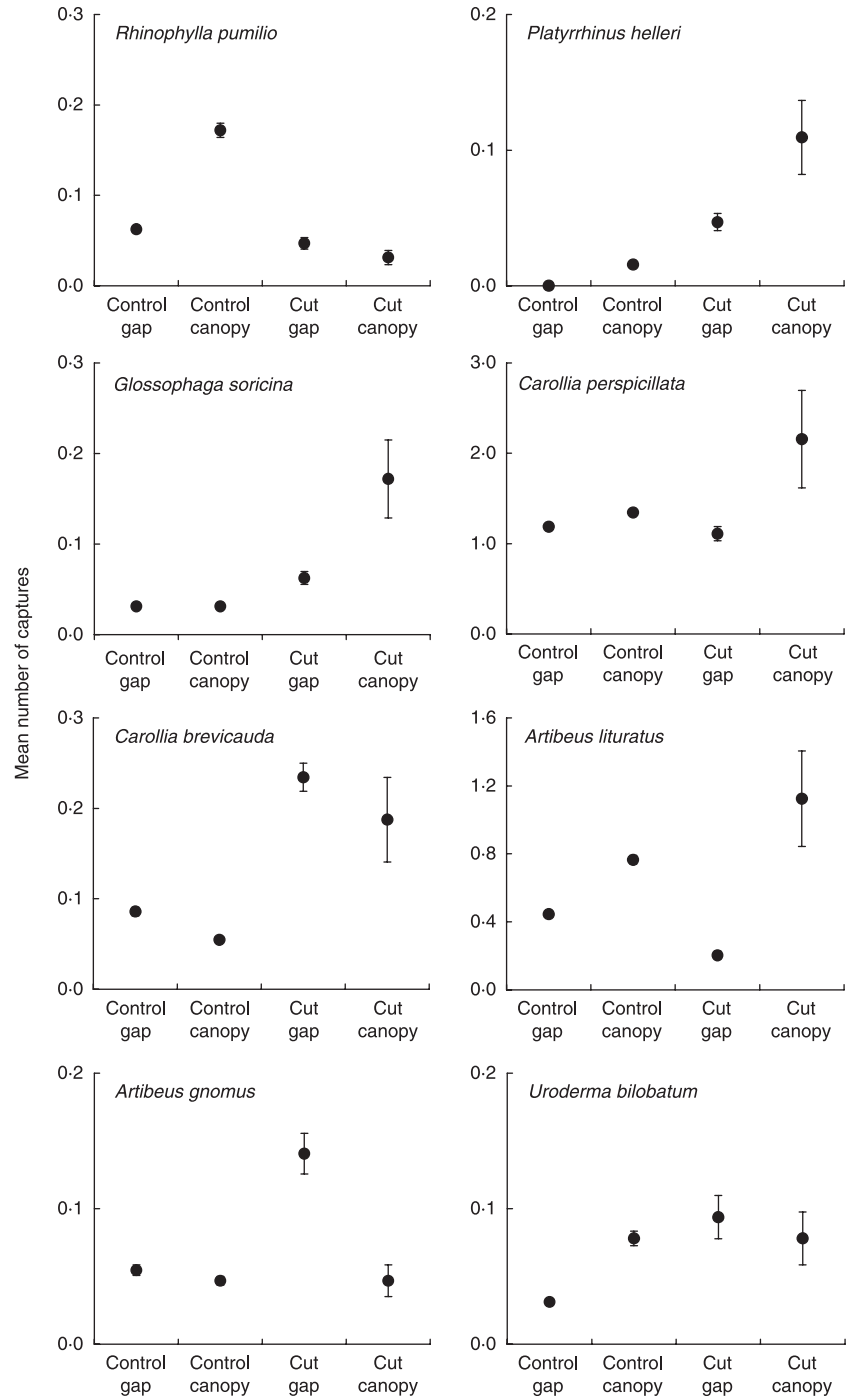


Fig. 4. Mean number of captures (± 1 SE) per sampling period per site in each combination of management and physiognomy for each of eight species of phyllostomid bat that responded to management in a consistent manner (left column, bottom three rows); that responded to both management and physiognomy in a consistent manner (top row); or that responded to physiognomy in a management-specific fashion (right column, bottom three rows).

Each species that responded to management in a physiognomy-specific fashion exhibited a unique response (Fig. 4). *Carollia perspicillata* was most abundant in closed-canopy sites of cut forest, and exhibited indistinguishable abundances in all other combinations of management and physiognomy. *Uroderma bilobatum* was least abundant in gaps of control forest and exhibited indistinguishable abundances in all other combinations of management and physiognomy. *Artibeus lituratus* was always more abundant in closed-canopy sites than in gaps; however, the magnitude of difference in abundances between physiognomies was greater in cut than in control forest (Fig. 4).

Discussion

Conservation strategies must optimally configure land-use to sustain natural populations and maintain the composition of local communities and regional assemblages, while accommodating the needs of society (Martínez-Garza & Howe 2003; Cuarón 2005). To create a sustainable and renewable resource, while minimizing impacts on biodiversity, conservation biologists and government agencies have endorsed harvest techniques (e.g. RIL) that minimize damage to surrounding forest that is associated with logging (Fearnside 2005). It is unlikely that a moratorium on logging will be

considered, especially in the developing world. As such, it is imperative that conservation biologists identify viable options for sustainable use of forest that cause minimal impact on biodiversity. Otherwise, policy-makers will make decisions based on purely economic concerns, without a balanced view tempered by conservation science.

Timber harvest affects bats by altering the composition and structure of vegetation, availability of food resources, numbers or types of refuges and roosts, and microclimate and disturbance regimes of ecosystems (Soriano & Ochoa 2001). The severity of the effects of disturbance on bats, including that associated with RIL, may manifest as changes in species abundances that ultimately modify patterns of presence and absence or alter species composition (Clarke *et al.* 2005a, 2005b; Gorresen *et al.* 2005; Peters *et al.* 2006). Conservation concerns associated with RIL can be summarized as three demographic responses: (1) common species remain common but decrease in abundance in logged forest; (2) common species suffer reductions in abundance and become rare in logged forest; or (3) rare species are locally absent from logged forest. From a population perspective, the first signals concern but suggests that RIL may be a sustainable practice as long as the extent and fragmentation of forest do not increase dramatically in the future. The second response represents a more acute danger, as locally rare species are more susceptible to stochastic extinction events. Finally, the absence of species from logged forest is a conservation concern in its own right. Reduced-impact logging induced reductions in abundance from 19 of 39 species of phyllostomid in the TNF, including three type 1, three type 2 and 13 type 3 responses. Clearly, RIL had a deleterious effect on the abundance of many rare species of phyllostomid; however, a more comprehensive consideration of problems related to sampling rare, elusive and nocturnal animals is warranted (Thompson 2004) before arriving at an incontrovertible conclusion.

SPECIES-SPECIFIC RESPONSES

Patterns of response by bat populations to disturbance and succession are related to species-specific aspects of foraging ecology (Clarke *et al.* 2005a, 2005b; Gorresen *et al.* 2005; Peters *et al.* 2006). In general, many frugivores and nectarivores exploit food resources provided by pioneer and successional plants (e.g. *Cecropia*, *Piper* and *Solanum*) and respond positively to small-scale disturbance (Fleming 1988; Gorchov *et al.* 1993; Soriano & Ochoa 2001). In contrast, disturbance often has a negative effect on the abundance of gleaning animalivores, as documented here, and in Mexico (Fenton *et al.* 1992), Paraguay (Gorresen *et al.* 2005), Peru (Willig *et al.* 2007), Trinidad (Clarke *et al.* 2005b) and Venezuela (Ochoa 2000). Reductions in abundances of gleaning animalivores in areas with low levels of disturbance, like those observed in the TNF, may be caused by decreases in food resources or roost availability (Soriano & Ochoa 2001). Because gleaning animalivores capture prey directly from the surface of foliage, reduced abundance (or richness) of gleaning animalivores in disturbed areas with reduced vegetative cover is explicable. However, vegetation on

which prey may be located remains abundant in areas of RIL in TNF. Different species of gleaning animalivores use different types of roosts (e.g. tree hollows, leaves, culverts, buildings) in various habitats (Kalko *et al.* 1999; Bernard & Fenton 2003). For gleaning animalivores in French Guiana, roosts of five species were exclusively in large trees of primary forest, whereas roosts of three species were in culverts under dirt roads that were surrounded by secondary forest (Simmons & Voss 1998). Reduced-impact logging preferentially removes large, economically valuable trees, which may be preferred roosting locations for some species of gleaning animalivore. However, the density of trees with dbh > 35 cm in TNF averages 55 individuals ha⁻¹ (Keller, Palace & Hurtt 2001). Therefore removal of fewer than four trees per hectare represents only a 7% reduction in the number of large trees, indicating that a substantial proportion that provide roosting habitat remain post-RIL.

Thirteen species were captured exclusively in control forest, whereas no species was captured exclusively in cut forest (Table 1). Reasons for the reduction in number of rare species in response to RIL are elusive. Natural treefall gaps differ in age and degree of regeneration, whereas gaps created by logging activity in this study represented a single successional cohort (Wunderle *et al.* 2006). In addition, the increase in canopy openness associated with the creation of a larger number of gaps of similar age than those occurring naturally may affect the use of associated closed-canopy forest by some bat species, representing a conservation concern. Reduced-impact logging requires an extended period (≈20 years) between harvests; nonetheless, repeated removal of 10% of the largest trees from the forest may alter gap-phase dynamics by creating a number of cohorts of gaps of similar ages with few natural treefalls between harvests. Loss of roosting habitat related to removal of large trees is an unlikely explanation for differences in species occurrence between cut and undisturbed forest, as RIL in TNF reduced the number of trees with dbh > 35 cm by only 7% (Keller *et al.* 2001). That similar reductions in the number of rare species in cut forest were observed in gap sites and in closed-canopy sites suggests that ambient disturbances associated with logging activity itself may cause some species to abandon forests during logging activity. Our data were collected 20–42 months postharvest, which may not have been sufficient time for some species that abandon areas in response to logging activity to immigrate back into RIL forest. The absence of rare species post-RIL may represent a temporary state that is reversible if undisturbed tracts of forest are located within proximity of forest subjected to logging.

QUANTITATIVE RESPONSES TO RIL

Of the species that were sufficiently abundant to analyse using quantitative methods, the effects of management were not particularly dramatic. Regardless of physiognomy, four species (*G. soricina*, *C. brevicauda*, *A. gnomus* and *P. helleri*) were more abundant in cut than in control forest, and one species (*R. pumilio*) was more abundant in control than in cut forest. In contrast, 12 species exhibited negative responses (Table 2;

Figs 2 and 3) to gaps regardless of management (nine species) or in a management-specific fashion (three species). All but two (*L. silvicolum* and *T. saurophila*) specialize on fruits or flowers of successional plants. The negative effect of gap formation was unexpected for these species. Analysis of plant foliage density in gaps and closed-canopy sites (Wunderle *et al.* 2006) showed that percentage vegetative cover was greater in gaps than in closed-canopy sites for all height categories ≤ 6 m (the heights where mist nets were located). In contrast, vegetation cover was greater in closed-canopy sites than in gaps for all height categories > 6 m. Differences in characteristics of vegetation between forest physiognomies may influence flight patterns and microhabitat use by bats. For example, gaps with abundant fruit and flowers that attract bats also may have dense vegetation that prevents bats from flying close to the ground (where nets were located), which would reduce capture rates in such gaps. However, when flying through the understorey of closed-canopy forest *en route* to gaps, bats may fly closer to the ground (below dense subcanopy vegetation and where the nets are located) because it is the least obstructed path to travel. This dynamic may explain why species that are generally associated with disturbance (e.g. *Carollia* spp., *Glossophaga* spp.) were captured more often in the understorey of closed-canopy sites than in gaps. Indeed, capture of bats may reflect the use of habitats for roosting (Kalko *et al.* 1999; Bernard & Fenton 2003), for foraging, or as a corridor for flight, and may not necessarily reflect habitat preference or specialization.

SPECIES OF SPECIAL CONCERN

We captured six species that currently occupy The World Conservation Union (IUCN) Red List of threatened species (Table 1). *Glyphonycteris sylvestris* and *L. carrikeri* were rare; however, *R. fischeriae*, *A. concolor*, *A. obscurus*, and *V. bidens* were sufficiently abundant to evaluate quantitatively the effects of management and physiognomy on abundances (Table 2). Each of these four species responded consistently to physiognomy (Fig. 3), with three species more abundant in closed-canopy sites than in gaps, and one species (*R. fischeriae*) more abundant in gaps than in closed-canopy sites. None responded to management. That *R. fischeriae*, an Amazonian endemic, was more abundant in gaps (natural and man-made) than in closed-canopy sites suggests that gaps provide critical habitat for this restricted-range species. Nonetheless, because logging activity increases the proportion of the forest that is gap habitat, and because most of the threatened species avoided gaps, dramatic increases in gap prevalence may adversely affect these populations and make them more prone to local extinction.

FUTURE PROSPECTS AND CONSERVATION RECOMMENDATIONS

Phyllostomids are the sole or primary seed dispersers or pollinators for many early successional plants, therefore a significant reduction in the populations of these bats could dramatically affect forest regeneration and succession. In

general, RIL did not reduce abundances of common frugivorous or nectarivorous phyllostomids, and sometimes increased their abundance. Clearly, increases in abundance do not represent conservation concern for the focal species *per se*. However, the indirect consequences of such changes in abundance are unknown with respect to the suite of competitive, predator-prey and mutualistic interactions that involve those species. In general, common phyllostomids can thrive in areas of limited human activity, such as in areas of RIL, at least in the short term.

In contrast to the situation for common phyllostomids, many rare phyllostomids responded negatively to RIL. The fact that 1/3 of rare phyllostomids captured in control forest were not recorded from RIL forest is a significant conservation concern. Moreover, several species exhibited negative responses (reduced abundances) to logging, even though they remained in RIL forest. These responses (local absence and reduction of abundance) by rare species may represent short-term responses to RIL. High vagility of bats and close proximity of undisturbed forest that supports these rare species may facilitate rescue effects that mitigate negative consequences of RIL. As a product of short-term responses of phyllostomid populations to RIL, species richness decreases and levels of dominance by a few super-abundant species increase. Alterations in species abundance distributions may signal possible concern for long-term sustainability of co-adapted assemblages. Nonetheless, caution must be exercised in interpreting short-term results in the context of long-term conservation, management or policy issues.

Results of a study on the effects of low-intensity logging on bats in south-eastern Amazonia (Peters *et al.* 2006) suggested that low-intensity logging may not have high conservation value. This conclusion was based on changes in bat species composition in response to logging, more specifically the presence and absence of rare species, rather than by significantly reduced abundance in cut areas or by changes in species richness. Although changes in species composition are worthy of conservation concern, inadequate sampling may contribute to the conclusion that low-intensity logging is ineffective at maintaining biodiversity. Of 49 species captured, 11 were captured only in logged forest and 14 were captured only in unlogged forest. Six of these species were represented by two individuals and 15 were represented by one individual. Greater sampling effort, or elimination of rare species from analyses of composition based on factor analyses, may alter interpretation of the effects of low-intensity logging in this case.

Although RIL may be a viable option to provide a renewable resource with minimal negative consequences, the spatial arrangement of logging sites must be designed with care to minimize effects on regional biota. The 5000-ha grid that defined our study area was associated with a largely undisturbed, protected forest. This may reduce the impact of RIL on bats in TNF forest via rescue effects. Thus the impact of RIL may be context-dependent, and RIL may be sustainable from perspectives of biodiversity and ecosystem services only if large tracts of forest remain undisturbed in the vicinity of logged forest. Such a scenario is unlikely in the long term; regions such as the Tapajós watershed may experience $> 2/3$

reduction of forest cover in the next 50 years (Soares-Filho *et al.* 2006). Moreover, the sustainable use of RIL in the Amazon requires appreciable monitoring and control by managers at local, state and federal levels. Because of the cyclic nature of RIL, as well as the temporal and spatial scale required to manage biodiversity in the Amazon successfully, a considerable commitment of resources is required to support a long-term monitoring programme of the biota to ensure that regional extinctions are avoided, biodiversity is preserved, and ecosystem services are managed in a sustainable manner. The efficacy of RIL may be tested in the near future. A conservation initiative, recently enacted in Pará, Brazil, prevents the use of unsustainable 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>). Logging practices deemed to be sustainable will be permitted within the conservation areas. Clarification of the impacts of sustainable logging practices such as RIL on biodiversity is vital to the success of this new initiative, and others like it.

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