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# Disturbance-Mediated Mammal Persistence and Abundance-Area Relationships in Amazonian Forest Fragments

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**Abstract:** Few researchers have investigated the synergistic effects of tropical forest fragmentation and disturbance on species persistence and abundance. We examined effects of both forest-patch metrics and forest disturbance in determining richness and abundance of midsized to large-bodied mammal species in a highly fragmented Amazonian forest landscape. Twenty-one forest fragments, ranging from 2 to 14,480 ha, and two continuous forest sites were sampled based on sightings, tracks, line-transect censuses, armadillo burrow censuses, and camera trapping. Patch occupancy of 37 species recorded ranged from 4% to all forest sites surveyed. Forest fragment size was the strongest predictor of species persistence, explaining 90% of the variation in species richness. Information-theoretic analysis confirmed that fragment area was the most important explanatory variable for the overall species richness and abundance of mammal species, followed by surface fires, which affected the abundance of seven species. Large mammal species were typically absent from fragments <100 ha, whereas some ubiquitous species were favored by fragmentation, exhibiting hyperabundance in small patches. Our findings highlight the importance of large (>10,000 ha), relatively undisturbed forest patches to maximize persistence and maintain baseline abundances of Neotropical forest mammal species.

**Keywords:** Amazonian forest, forest disturbance, forest fragmentation, mammal abundance, species abundance, species richness

Persistencia y Relaciones Abundancia-Área de Mamíferos en Condiciones de Perturbación en Fragmentos de la Selva Amazónica

**Resumen:** Pocos autores han investigado los efectos sinérgicos de la fragmentación y perturbación de bosques tropicales sobre la persistencia y abundancia de especies. Examinamos los efectos tanto de medidas de parche de bosque como de perturbación sobre la determinación de la riqueza y abundancia de mamíferos medianos a grandes en un paisaje Amazónico altamente fragmentado. Veintiún fragmentos de bosque, entre 2 y 14,480 ha, y dos sitios con bosque continuo fueron muestreados con base en avistamientos, censos en transectos, censos en madrigueras de armadillos y trampas fotográficas. La ocupación de parches por 37 especies registradas varió entre 4% hasta todos los sitios forestales muestreados. El tamaño del fragmento de bosque fue el mejor predictor de la persistencia de las especies, explicando 90% de la variación en la riqueza de especies. Los análisis informático-teóricos confirmaron que el área del fragmento fue la variable explicativa más importante para la riqueza y abundancia de especies de mamíferos, seguida por incendios, que afectaron la abundancia de 7 especies. Las especies de mamíferos mayores típicamente estuvieron ausentes en fragmentos <100 ha, mientras que las especies ubicuas fueron favorecidas por la fragmentación, exhibiendo hiperabundancia en fragmentos pequeños. Nuestros hallazgos resaltan la importancia de parches de bosque extensos (>10,000 ha), relativamente no perturbados, para maximizar la persistencia y mantener la abundancia de especies de mamíferos forestales neotropicales.

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**Palabras Clave:** abundancia de mamíferos, fragmentación de bosques, perturbación de bosques, riqueza de especies, selva Amazónica

## Introduction

Habitat fragmentation is one of the most serious threats to biological diversity worldwide and can be defined as a process during which a large habitat tract is converted into several smaller, increasingly isolated patches (Fahrig 2003). Erosion of species diversity has been associated primarily with the size of habitat remnants and their degree of isolation (MacArthur & Wilson 1967). The larger the remaining forest area, the higher the original number of species included and the lower the subsequent extinction rate (Terborgh & Winter 1980). Nevertheless, fragmented forest landscapes often consist of a complex patchwork of varying habitat quality, where rural people harvest timber and nontimber resources from forest remnants long after they have become isolated (Peres & Michalski 2006). These remnants thus continue to be degraded by different forms of anthropogenic disturbance, including logging (Nepstad et al. 1999), surface fires (Cochrane & Laurance 2002), and hunting (Peres 2001), all of which may interact additively or synergistically with area effects, on which much of the habitat fragmentation literature has focused.

Although the relationship between mammal abundance and habitat fragment size has been examined in temperate forests (Dooley & Bowers 1998), few researchers have addressed tropical mammals (Bowers & Matter 1997). Results of several studies show a decrease in species diversity in tropical forest fragments for small mammals and bats (Granjon et al. 1996; Schulze et al. 2000; Pardini et al. 2005). Population densities may increase in small fragments for some mammal species (Matthiae & Stearns 1981; Chiarello 2000), but this response could be restricted to habitat generalists that benefit from highly disturbed or edge habitats or tolerate the surrounding habitat matrix (Fonseca & Robinson 1990; Malcolm 1997). In any case the persistence of populations stranded in habitat fragments is inextricably linked to their postisolation demography, with local extinction events primarily penalizing intrinsically rare species or those declining in the aftermath of fragmentation (Newmark 1991).

The responses of medium- to large-bodied mammals to both habitat disturbance and fragmentation remain poorly understood. Large carnivore populations are often extirpated from small, isolated habitat patches owing to low densities, large spatial requirements, and potential conflicts with humans (Noss et al. 1996; Crooks 2002), and those still persisting may be too small to ensure long-term viability (Woodroffe & Ginsberg 1998).

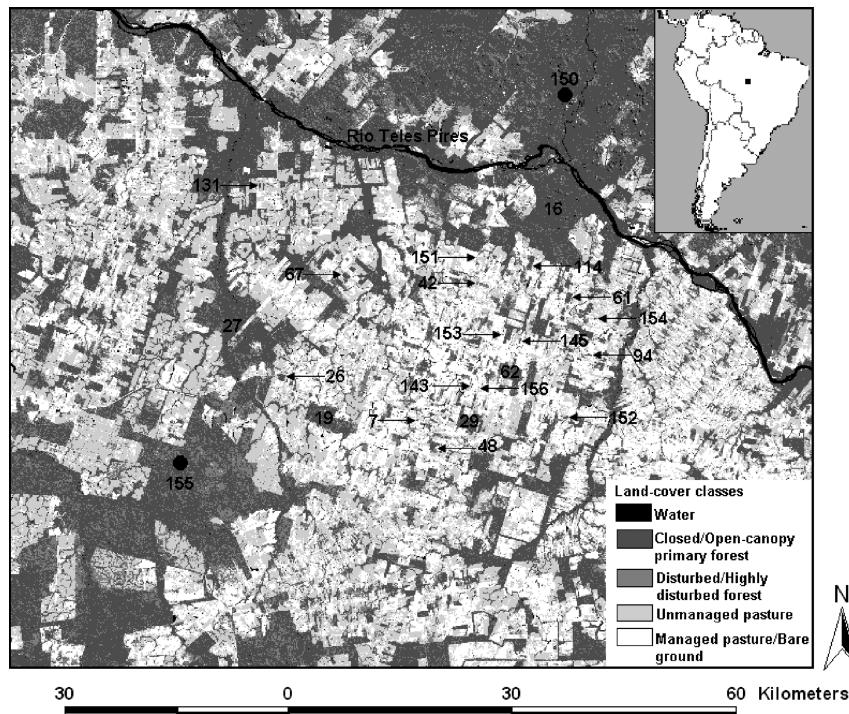
Many large mammals decline in abundance or disappear in Neotropical forest remnants (Rylands & Keuroghlian 1988; Chiarello 2000; Laurance et al. 2002). This trend is likely conservative because most studies have been conducted in protected fragments, which are atypical of most tropical forest landscapes that remain exposed to anthropogenic disturbance.

The southern Brazilian Amazon was subjected to massive deforestation rates during the 1970s–1980s, generating several types of landscape structure with thousands of forest fragments that are widely variable in size and degree of connectivity (Oliveira-Filho & Metzger 2006) and human disturbance (Souza et al. 2005). The postisolation history of most forest remnants in this region is often marked by recurrent habitat disturbance, including canopy damage by logging and wildfires (Peres & Michalski 2006). We examined the synergistic effects of habitat fragmentation and anthropogenic disturbance on mammal species in a large number of forest fragments. We predict that mammal assemblages in forest fragments subjected to high levels of disturbance (e.g., logging, wildfires, and hunting) would be simplified compared with undisturbed continuous forest sites. To test this hypothesis, we conducted mammal surveys in 21 forest fragments and 2 continuous forest sites subjected to a variable history of disturbance and evaluated their responses at two levels: (1) patterns of species persistence and its relationship with forest area and (2) patterns of species persistence and abundance and their relationships with forest area and disturbance at each site. Finally, for a subset of species, we considered how forest-patch area alone might explain their abundances and whether these species were sensitive to the fragmentation process or exhibited hyperabundance in small fragments.

## Methods

### Study Landscape

The Amazonian region of Alta Floresta, Mato Grosso, Brazil ( $09^{\circ}53'S$ ,  $56^{\circ}28'W$ ; Fig. 1), has been subjected to high deforestation rates since the 1970s that has resulted in a highly fragmented landscape (Peres & Michalski 2006). We examined a Landsat scene (227/67) to select forest patches of particular sizes and degrees of isolation, within a 50-km radius of the urban center. To avoid possible confounding effects of patch size and disturbance, we selected forest patches within the same size class that had been exposed to different levels of forest disturbance.



**Figure 1.** Location of the study region in Alta Floresta, northern Mato Grosso, Brazil. The 21 surveyed forest patches (numbered arrows) and 2 continuous forest sites used as controls (solid circles) are shown. Key forest site numbers correspond to those listed in Table 1.

We maximized the spatial independence between sites by establishing a minimum edge-to-edge distance  $>1$  km (mean [SD] = 24.7 km [13.3], range = 1.2–67.3 km,  $n = 253$  comparisons). All 21 forest patches (mean size [SD] = 1,416 ha [3,834], range = 2–14,480 ha) selected were almost or entirely isolated from continuous forest and surrounded by a matrix of managed cattle pasture. These were compared with two continuous, undisturbed, primary-forest control sites located on either bank of the Teles Pires River (Fig. 1).

#### Mammal Surveys

Terrestrial and arboreal mammals were surveyed in all forest sites in June–December 2003 and June–December 2004 with labor-intensive in situ sampling techniques (line-transect census, counts of armadillo burrows, and camera trapping). Additional indirect and direct evidence was also used to complement the presence-absence matrix. Population abundance was estimated with the most appropriate sampling technique for each species as following.

#### LINE-TRANSECT CENSUS

We used a standardized line-transect protocol (Peres 1999) to survey all sites. At least three observers simultaneously walked at least three transects (mean velocity  $\sim 1250$  m/hour) (Table 1). All censuses took place in rainless weather in the morning (06:30–09:30) or afternoon (14:30–17:30).

In censusing small fragments we used parallel transects mean (SD) = 68.8 m (36.7) (range = 33–185 m) apart

and repeated surveys on nonconsecutive days at least nine times within a 30-day period (mean [SD] = 11.8 walks [2.6], range = 9–16). Censuses at all other sites were repeated at least 10 times within a 30-day period. In midsized (15–106 ha) and large fragments (141–1763 ha), we used parallel transects spaced mean (SD) = 176.5 (83.2) (range = 75–347 m) and 626.1 m (183.9) (range = 407–933 m) apart, respectively. In very large fragments ( $>10,000$  ha) and control sites, we used the Peres (1999) standardized protocol. Any confounding effects of seasonality were minimized by systematically rotating our monthly census schedule of sites in different size classes and levels of disturbance. In total, our census effort covered 1739.6 km, including 841.8 km and 897.8 km in forest patches  $<10,000$  ha and  $>10,000$  ha, respectively.

To minimize possible detectability bias related to fragment size, all visual and acoustic detection events with perpendicular distance (PD)  $\geq 50$  m were excluded from the analysis. We excluded species restricted to the north bank of the Teles Pires River (e.g., white-nosed bearded saki [*Chiropotes albinasus*]), and detection data were pooled for parapatric congeners in the same functional group occurring on opposite banks of this river (e.g., marmosets, howler monkeys, and spider monkeys). (Scientific names omitted in the text are provided in Table 2.)

#### ARMADILLO SURVEYS

Two observers censused only once (mean velocity  $\sim 900$  m/hour) armadillo burrows ( $\geq 50$  cm depth) encountered along each transect at all sites. On an encounter

**Table 1.** Sampling effort and patch metrics profile of the 23 forest sites surveyed in Alta Floresta region of southern Amazonia.\*

Sites	Transect	Length	Area	TDLT	TCT	TABC	Dist	IA
151	4	0.621	2.4	5.30	61.95	0.62	0.8	8
156	3	0.578	4.1	6.36	57.65	0.58	14.8	20
143	4	0.579	4.6	6.37	62.13	0.58	15.2	24
153	3	0.472	4.7	7.55	61.78	0.47	6.8	27
7	4	0.938	6.6	8.32	63.84	0.94	13.0	20
154	4	0.554	7.3	7.76	64.79	0.55	4.9	16
42	4	1.344	14.9	14.41	61.48	1.34	3.1	18
145	6	1.206	16.0	20.18	63.19	1.21	8.2	26
94	4	0.985	21.5	17.24	63.35	0.99	9.6	25
131	4	0.969	24.5	24.05	68.33	0.97	0.7	8
152	3	1.401	25.7	15.41	30.87	1.40	18.5	25
26	3	2.767	86.9	59.45	97.43	2.77	0.3	6
67	3	2.264	98.2	56.20	103.35	2.26	5.3	18
61	3	2.166	106.2	57.28	92.55	2.17	2.8	16
114	3	2.135	141.3	51.24	94.33	2.14	1.1	8
48	3	2.682	211.7	85.49	93.66	2.68	12.3	24
29	3	4.970	787.2	114.78	225.50	4.97	17.0	12
62	3	5.630	899.8	127.38	233.38	5.63	10.8	20
19	3	8.89	1,763.3	157.06	305.88	8.89	5.7	16
27	3	10.95	11,034.7	247.45	314.41	10.95	0	0
16	3	10.90	14,480.5	211.45	295.63	10.90	0	0
150	4	10.375	144,805.0	228.60	283.11	10.38	0	0
155	3	10.50	144,805.0	210.31	287.67	10.50	0	0

\*Key to column heads: sites, forest site numbers correspond to those in Fig. 1; transect, number of transects in each forest site; length, accumulated length of the transects in each forest site; area, forest area ( $\log_{10}$  ha); TDLTC, total diurnal line-transect census effort (km) at each forest site; TCT, total camera-trapping census effort (trap days); TABC, total armadillo-burrow censuses (km); dist, distance (km) from forest sites to continuous forest or patches  $>10,000$  ha; IA, isolate age in years.

with a burrow, we recorded the most likely species, measurements (see McDonough et al. 2000), PD from the transect, and burrow activity. Burrows exhibiting fresh digging were classified as active, whereas those filled or covered with leaves or well-developed spider webs were classified as inactive. Size of the forest patch had no effect on the ratio of active to inactive burrows (GLM<sub>[binomial error]</sub>,  $p = 0.97$ ), and burrow density in both classes was highly correlated ( $r = 0.741$ ,  $p_{\text{bonf.}} = 0.001$ ). To minimize detectability bias related to undergrowth cover, burrows with PD  $>5$  m were excluded from the analysis. Burrows of at least three species (giant armadillo, six-banded armadillo, and southern naked-tailed armadillo) could be clearly distinguished by their characteristics (Carter & Encarnação 1983). There were also clear differences in burrow diameter between greater long-nosed armadillo and the much smaller nine-banded armadillo. In total, we measured 719 burrows along 83.9 km of transects (mean [SD] = 31.3 [27.7], range = 4–99 burrows per site).

#### CAMERA TRAPPING

To detect nocturnal and secretive mammal species, we deployed CamTrakker phototrap (Camtrakker, Watkinsville, Georgia) baited with a scent lure (Hawbaker's Wild Cat Lure 2, Minnesota Trapline Products, Pennock, Minnesota) (Sanderson 2004). We uniformly distributed phototraps across the entire fragment on a

hexagonal grid to minimize variation in density of phototrap stations ( $\sim 500$  m apart). Fewer traps were placed in small fragments, but even the smallest site was sampled by two cameras (mean [SD] = 4.2 [3.1] phototraps/site). When sampling fragments, one or more cameras were also placed along the edge to allow detection of edge species. Cameras were placed 30–40 cm above ground, deployed for 30 days, and checked every 3–4 days to renew scent bait, batteries, and film as necessary.

Based on the photographs, we determined the occurrence of species at each phototrap station and divided the number of occurrences per species by the total exposure time (in days) at each site. Consecutive photos of the same species were defined as independent occurrences if individuals could be unambiguously distinguished or if the interval between photos was  $>30$  minutes. We obtained 1167 independent photos in 3086 trap days (mean [SD] = 134.2 [100.2], range = 30.9–314.4 trap days/site).

#### FOREST-PATCH METRICS

Landscape variables were extracted from a Landsat image (12/06/2004) with Fragstats (version 3.3) (McGarigal & Marks 1995) and ArcView (version 3.2). Following an unsupervised classification, eight land cover classes were resolved (closed-canopy forest, open-canopy primary forest, disturbed forest, highly disturbed forest, managed pasture, unmanaged pasture, bare ground, and open water).

Table 2. Model weights and parameter (slope) estimates from information-theoretic analysis of the number of mammal species and abundance of 26 species in all 23 forest sites surveyed.

Group/species	Common name	Census method <sup>a</sup>	Forest area (log to ha)		Isolate age (years)		Hunting pressure <sup>e</sup>		Burn severity <sup>e</sup>		Logging intensity <sup>e</sup>	
			$\sum w_i^e$	Slope ( $\pm SE$ ) <sup>d</sup>	$\sum w_i$	Slope ( $\pm SE$ )	$\sum w_i$	Slope ( $\pm SE$ )	$\sum w_i$	Slope ( $\pm SE$ )	$\sum w_i$	Slope ( $\pm SE$ )
Species richness		ALL	11	1,000	5,117 ± 0.550	0.180	0.338		0.300		0.181	
Primates												
<i>Aotus</i> spp. <sup>f</sup>	howler monkey	DLT	19	0.218	0.223	0.217	0.777	0.144 ± 0.082	0.228			
<i>Ateles</i> spp. <sup>g</sup>	spider monkey	DLT	22	0.613	0.116 ± 0.106	0.321	0.350		0.383	0.229		
<i>Callicebus</i>	titi monkey	DLT	11	1,000	-0.432 ± 0.084	0.700	-0.018 ± 0.011	0.188	0.178	0.226		
<i>moloch</i>												
<i>Mico</i> spp. <sup>b</sup>	marmoset	DLT	20	0.228	0.275	0.257	0.258		0.676	-0.106 ± 0.083		
<i>Cebus apella</i>	brown capuchin monkey	DLT	20	0.311	0.278	0.280	0.348		0.306			
Xenarthrans												
<i>Myrmecophaga</i>	giant anteater	CT	12	0.998	0.004 ± 0.001	0.169	0.359		0.255		0.484	
<i>Tridactyla</i>	collared anteater	CT	17	0.288	0.865	0.002 ± 0.001	0.406		0.508	-0.008 ± 0.009	0.882	0.018 ± 0.008
<i>Tamandua</i>												
<i>Tetradactyla</i>												
<i>Cabassous</i>	southern naked-tailed armadillo	BC	20	0.400	0.383	0.257	0.258		0.258		0.267	
<i>Unicinctus</i>	nine-banded armadillo	BC	2	0.998	-0.171 ± 0.030	0.960	-0.015 ± 0.005	0.129	0.998	0.225 ± 0.041	0.873	-0.145 ± 0.036
<i>Dasyurus</i>	greater long-nosed armadillo	BC	12	0.966	0.553 ± 0.150	0.230	0.179		0.198		0.273	
<i>novemcinctus</i>	six-banded armadillo	BC	21	0.382	0.228	0.399	0.361		0.399		0.279	
<i>Dasyus</i>	giant armadillo	BC	12	0.992	0.531 ± 0.141	0.169	0.255		0.723	0.314 ± 0.191	0.198	
<i>kyphéri</i>												
<i>Euphractus</i>												
<i>sexinctus</i>												
<i>Priodontes</i>												
<i>maximus</i>												
Marsupials												
<i>Didelphis</i>	common opossum	CT	20	0.392	0.356	0.300	0.263		0.285			
<i>marsupialis</i>												
Rodents												
<i>Sciurus aestuans</i>	guianan squirrel	DLT	20	0.531	0.033 ± 0.037	0.323	0.266		0.242	0.258		
<i>Dasyprocta</i>	red-rumped agouti	DLT	20	0.237	0.250	0.254	0.314		0.314	0.528	-0.059 ± 0.066	
<i>agouti</i>												
<i>Agouti pacá</i>	paca	CT	21	0.622	0.012 ± 0.010	0.278	0.329		0.216	0.248		

continued

Table 2. (continued)

Group/species	Common name	Census method <sup>a</sup>	Forest area (log <sub>10</sub> ha)		Isolate age (years)		Hunting pressure <sup>e</sup>		Burn severity <sup>f</sup>		Logging intensity <sup>g</sup>	
			$\sum w_i^f$	Slope ( $\pm SE$ ) <sup>d</sup>	$\sum w_i$	Slope ( $\pm SE$ )	$\sum w_i$	Slope ( $\pm SE$ )	$\sum w_i$	Slope ( $\pm SE$ )	$\sum w_i$	Slope ( $\pm SE$ )
Carnivores												
<i>Nasua nasua</i>	coati	DLT	22	0.715 0.045 ± 0.032	0.287	0.483	0.238	0.269	0.218	0.218	0.221	
<i>Lutra longicaudis</i>	Neotropical river otter	DLT	12	0.972 0.004 ± 0.001	0.207	0.196	0.196	0.218	0.218	0.218	0.221	
<i>Eira barbara</i>	tayra	DLT	19	0.213	0.255	0.291	0.815	-0.047 ± 0.026	0.400	0.366	0.386	
<i>Leopardus pardalis</i>	ocelot	CT	22	0.575 0.007 ± 0.007	0.246	0.296	0.296	0.366	0.366	0.386	0.386	
<i>Panthera onca</i>	jaguar	DLT	12	0.994 0.004 ± 0.001	0.555	-0.000 ± 0.000	0.232	0.308	0.308	0.308	0.248	
Ungulates												
<i>Tapirus terrestris</i>	lowland tapir	CT	11	0.978 0.016 ± 0.004	0.218	0.177	0.177	0.175	0.175	0.175	0.184	
<i>Pecari tajacu</i>	collared peccary	DLT	12	0.987 0.127 ± 0.034	0.249	0.210	0.210	0.719	0.073 ± 0.046	0.175	0.175	
<i>Tayassu pecari</i>	white-lipped peccary	DLT	11	0.999 0.278 ± 0.056	0.178	0.554	-0.103 ± 0.129	0.536	0.091 ± 0.090	0.536	0.179	
<i>Mazama gouazoubira</i>	gray brocket deer	DLT	12	0.984 0.036 ± 0.011	0.179	0.442	0.442	0.490	0.490	0.490	0.195	
<i>Mazama americana</i>	red brocket deer	DLT	16	0.873 0.031 ± 0.012	0.247	0.245	0.245	0.233	0.233	0.233	0.194	

<sup>a</sup>Key: ALL, overall mammal species richness based on all sampling techniques, including line-transect censuses, armadillo burrow censuses, and camera trapping; DLT, diurnal line-transect census, expressed as individuals/10 km<sup>2</sup>; CT, camera trapping, expressed as photos/10 trap days; BC, armadillo burrow censuses, expressed as burrows/km<sup>2</sup>.

<sup>b</sup>Confidence set of models with the sum of the Akaike weight ( $w_i$ ) from largest to smallest  $\geq 0.950$ .

<sup>c</sup>The  $\sum w_i$  (Akaike weight) for all models with a given variable.

<sup>d</sup>Slope for variables with  $\sum w_i > 0.5$ .

<sup>e</sup>PCA 1.

<sup>f</sup>Includes red howler monkeys (*Alouatta seniculus*) and red-handed boulder monkeys (*A. belzebul*) on the left and right bank of the Teles Pires River, respectively.

<sup>g</sup>Includes Atelis marginatus on the right bank of the Teles Pires River and a yet undescribed color morph congener on the left bank.

<sup>h</sup>Includes black-tailed marmoset (*Callithrix jacchus*) and Smeathlage's marmoset (*Mico emiliae*) on the left and right bank of the Teles Pires River, respectively.

The image was registered and georeferenced with a positional error of  $<10$  m.

Five of 21 patches surveyed were not completely isolated from surrounding patches or small remnants of forest. We therefore artificially eroded the narrowest, most disturbed forest cover connections (mean width [SE] = 55.6 m [8.2],  $n = 12$ ) following Michalski and Peres (2005). For each patch we measured size (based on all forest types) and edge-to-edge distance between each site. For control sites embedded within continuous forests, we assigned an arbitrary forest-area value of one logarithmic magnitude greater than our largest fragment.

We obtained isolation age for all patches surveyed (mean [SD] = 16.0 [8.3] years, range = 0–27 years) from 11 biannual Landsat images (1984–2004). When forest patches had already been isolated in the earliest image, we used interviews to determine their isolation age, defined as the number of years since a forest patch had been disconnected from the continuous forest or from another patch  $>10,000$  ha. Isolation age was scored as zero for control sites or patches  $>10,000$  ha.

### Within-Patch Disturbance

Data on the intensity and extent of disturbance within each site were based on site inspections and information obtained from local interviews (Michalski & Peres 2005; Peres & Michalski 2006) to determine the history of logging intensity (four variables), burn severity (four variables), and hunting pressure (five variables). We then conducted three principal-components analyses (PCAs) to characterize these three disturbance variables and used the scores of the first axis in subsequent analyses. The PCA 1 scores of each variable were then used for the information-theoretic and the BIOENV analyses. Further details on how we described different disturbance variables and on data-reduction methods used to quantify logging intensity, burn severity, and hunting pressure are available (see Supplementary Material).

### Data Analysis

We analyzed line-transect census data in terms of single animal (or group) detections per 10 km walked. Estimates of armadillo burrow density were derived in Distance (version 4.0) (Thomas et al. 2002). Phototrapping abundance data were analyzed in terms of the number of independent photos of each species per 10 trap days, calculated for each forest site based on total exposure time. We obtained abundance data for 26 mammal species with the most appropriate sampling technique for each species (Table 2).

We used repeated-measures analysis of variance (ANOVA), with forest size as a categorical main effect (classes: 1, fragments  $<10$  ha; 2, fragments between 10 and 26 ha; 3, fragments between 86 and 212 ha; 4, fragments between 780 and 1800 ha; 5, fragments  $>11,000$  ha

and continuous forest sites) to test for possible detection probability differences among forest sizes for line-transect censuses and camera-trapping data. To assess species-area relationships between forest-patch area ( $\log_{10}$ ) and number of mammal species detected with all techniques, we performed linear regression models for all 21 forest patches ( $r^2$  values reported are the adjusted  $r^2$ ). Because fragment sizes were highly variable, there were inevitable between-site differences in cumulative census effort that could cause potential biases in our sampling and analyses. Nevertheless, we used a resampling approach to examine species-area relationships on the basis of a standardized census effort at all sites in terms of species richness per 10 detection events. This was based on a jackknife procedure (Simon & Bruce 1991) that resampled 5000-m subsamples of census walks at each of the 23 forest sites with 1000 iterations. We then plotted mean (SD) richness values against the forest-patch area ( $\log_{10}$ ). Twenty-four of 37 species were detected through line-transect census, and relative abundance for 15 of the 26 species for which we could reliably estimate abundance was estimated with this sampling technique, which was especially critical for arboreal species.

We calculated the proportion of area sampled at each site by each technique based on the total length of transects multiplied by a 50-m width on either side of the transect for line-transect census; a 5-m width for armadillo burrow censuses; and a 100-m radius for camera traps.

We examined the Jaccard dissimilarity of species composition for all pairwise comparisons between any two forest sites and tested for spatial autocorrelation. We computed a Mantel test statistic between the straight-line distances between sites and the Jaccard dissimilarity matrix for all comparisons, with  $p$  values calculated based on 5000 randomizations.

Using an information-theoretic analysis described by Burnham and Anderson (2002), we modeled the data based on the second-order Akaike's information criterion corrected for small sample size ( $AIC_c$ ). All possible subsets of the five predictor variables (controlled for multicollinearity—Pearson's correlation  $r < 0.70$ ), including forest area, isolate age, PCA 1 of logging intensity, PCA 1 of burn severity, and PCA 1 of hunting pressure, amounting to 31 models, were modeled with generalized linear models in which total number of species and species abundance were dependent variables. The information-theoretic approach enables comparisons of competing models by evaluating the relative support in the observed data for each model that can also be ranked and weighted, providing a quantitative measure of relative support for each competing hypothesis (Johnson & Omland 2004).

We evaluated models based on their information content, as measured by  $AIC_c$  and Akaike weights ( $w_i$ ) to determine the probability of the best approximating model (Burnham & Anderson 2002). Multimodel inference from these information-theoretic analyses demonstrated how

forest size, isolate age, and disturbance variables interacted to affect persistence and abundance of mammal species in our study area. We included in our analyses all the possible candidate models; therefore, all variables were on equal footing to calculate relative variable weights (Burnham & Anderson 2002). A reduced subset of models for a 95% confidence set, based on the sum of Akaike weights from largest to smallest that resulted in the sum of  $\geq 0.95$ , was used to calculate slopes and unbiased standard errors (Burnham & Anderson 2002).

We performed nonmetric multidimensional scaling (NMDS) ordinations (Clarke 1993) based on the Jaccard similarity matrix of mammal-species occupancy of all forest patches surveyed; the Bray-Curtis similarity matrix weighted by the mean number of encounters per standardized census effort; and the Bray-Curtis similarity matrix weighted by species-specific encounter rates. Finally, the relationship between the species-specific encounter rates by site matrix and the five predictor variables (forest area, isolate age, PCA 1 of logging intensity, PCA 1 of burn severity, and PCA 1 of hunting pressure) were examined with the BIOENV procedure (Clarke & Ainsworth 1993), which searches for combinations of predictor variables that produce a similarity matrix of sites most correlated with the similarity matrix based on mammal abundance.

## Results

### Species Persistence and Area Effect

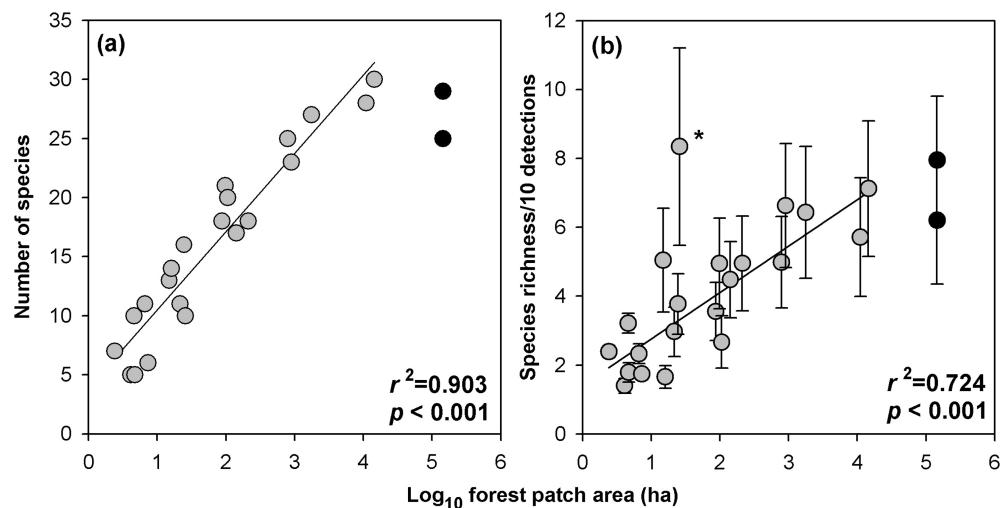
Forest fragments on average contained 16 of 37 mammal species (SD 7.7, range 5–30,  $n = 21$ ), whereas the two

continuous forest sites contained 25–29 species. There was a significant spatial autocorrelation in composition of mammal species across all sites (Mantel test,  $r = 0.645$ ,  $p < 0.001$ ), suggesting that forest sites farther apart were more dissimilar.

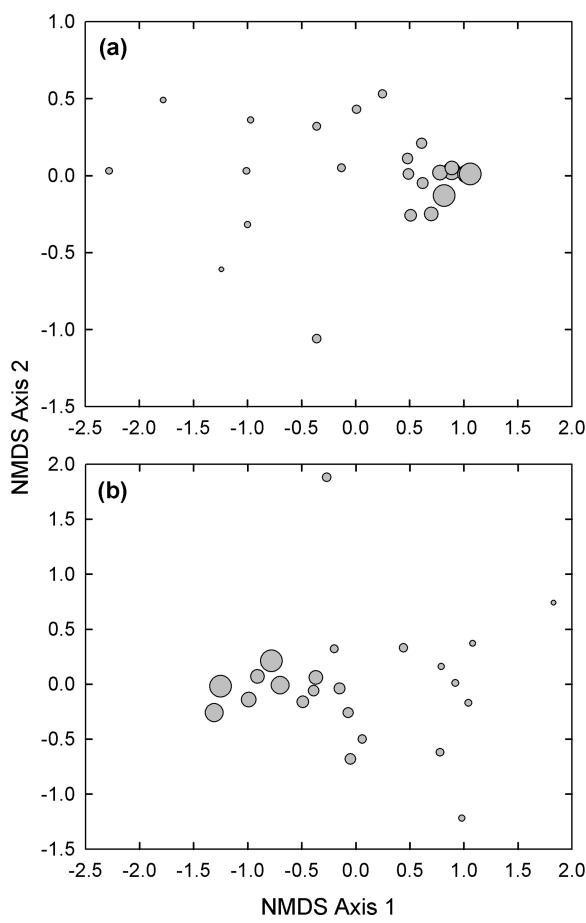
There was no effect of forest size on mammal detection probability for line-transect censuses ( $r^2 = 0.333$ ,  $F_{4,18} = 2,251$ ,  $p = 0.104$ ) or for camera trapping ( $r^2 = 0.120$ ,  $F_{4,18} = 0.613$ ,  $p = 0.658$ ). Nevertheless, it was difficult to compare results across species because no single sampling technique could be used to survey persistence and abundance of all mammal species.

Mammal species varied widely in patch occupancy rates, ranging from ubiquitous species occurring at all sites (e.g., titi monkeys) to species restricted to <4% of the sites (e.g., greater grison [*Galictis vittata*]; crab-eating racoon [*Procyon cancrivorus*]).

There was a clear, linear species-area relationship for mammals. Forest-patch area alone explained 90.3% of the total variation in the number of species persisting for all survey techniques (Fig. 2a). Following our resampling procedure, patch area still explained 72.4% of the variation in mean species richness per 10 detection events (Fig. 2b). The only clear outlier in this relationship was an overhunted and isolated “empty” 25-ha fragment (site 152), where only seven detection events of five species overinflated species richness per detection ratios. Moreover, the proportional area censused by each of the three techniques was inversely related to forest size (line-transect census:  $r_s = -0.945$ ,  $p < 0.001$ ; burrow census:  $r_s = -0.990$ ,  $p < 0.001$ ; camera trapping:  $r_s = -0.923$ ,  $p < 0.001$ ,  $n = 23$ ).



**Figure 2.** Relationship between forest patch area and mammal species richness based on (a) in situ survey techniques, including line-transect censuses, armadillo-burrow counts, and camera trapping and (b) the mean (SD) number of species per 10 detection events, based on a jackknife resampling procedure applied to standard subsamples of 5000 m of line-transect census data with 1000 iterations. The 21 forest patches and two continuous forest sites surveyed are indicated by shaded and solid circles, respectively. The point marked with an asterisk (\*) was excluded from the regression due to the small number of detections ( $n = 7$ ).



**Figure 3.** Nonmetric multidimensional scaling (NMDS) ordination based on the (a) Jaccard similarity matrix of mammal species occupancy of all forest patches surveyed with all census techniques and (b) Bray-Curtis similarity matrix weighted by the overall species-specific encounter rates. Stress values are 0.07 and 0.11, respectively. Circles are scaled according to the size of forest-patch area (expressed as  $\log_{10}$  ha).

Considering all possible pairwise comparisons between sites, Jaccard similarity coefficients of mammal species occupancy based on all sampling techniques were on average 0.56 (SD 0.19) (range 0.18–0.98,  $n = 253$ ). Bray-Curtis similarity based on a standardized line-transect census effort were on average 84.63 (SD 10.39) (range 58.17–99.97,  $n = 253$ ). Bray-Curtis similarity of abundance estimates based on overall encounter rates obtained during line-transect censuses were on average 41.07 (SD 19.44) (range 1.91–79.06,  $n = 253$ ).

The NMDS ordinations based on the similarity matrices of the species occupancy, and overall abundance showed that mammal assemblage structure of large patches and continuous forests were more similar to one another than those of small- to medium-sized patches (Figs. 3a & 3b). This was consistent with results from another NMDS plot

**Table 3.** Relationship between environmental variables and mammal abundance based on results of BIOENV analysis with up to five predictor variables that best explained patterns of abundance.

Number of variables	$S_w^a$	Variables chosen <sup>b</sup>
1	0.283	forest area
2	0.221	burn severity forest area
2	0.183	forest area isolate age
2	0.173	forest area hunting pressure
3	0.167	burn severity forest area isolate age
2	0.156	forest area logging intensity
3	0.148	burn severity forest area hunting pressure
3	0.140	forest area isolate age logging intensity
3	0.133	burn severity forest area logging intensity
4	0.122	burn severity forest area hunting pressure isolate age

<sup>a</sup>Spearman rank correlation coefficient based on the best 10 results.

<sup>b</sup>Key: forest area,  $\log_{10}$  ha; isolate age in years; hunting pressure, PCA 1 of hunting pressure; burn severity, PCA 1 of burn severity; logging intensity, PCA 1 of logging intensity.

based on the similarity matrix of the mean number of encounters per standardized line-transect census effort (stress value 0.01). Indeed, the wide positional scatter of small-sized fragments in the NMDS plots indicated poor congruence in the patterns of species composition and abundance in patches <80 ha. The BIOENV procedure applied to the abundance matrix resulted in a maximum correlation with any patch or disturbance variables of 0.283, again with forest area best explaining multivariate patterns of mammal abundance across all forest sites (Table 3).

#### Area and Disturbance Effects on Species Persistence and Abundance

There was a negative relationship between forest-patch area and the aggregate abundance of all mammal species quantified with line-transect censuses ( $r^2 = 0.100$ ,  $p = 0.089$ ,  $n = 21$ ) and armadillo burrow counts ( $r^2 = 0.178$ ,  $p = 0.032$ ,  $n = 21$ ), but not with camera traps ( $r^2 = 0.0$ ,  $p = 0.764$ ,  $n = 21$ ). Abundance responses of individual species to the size of the forest patch were highly variable. Several species of primates (howler, spider,

titi, and capuchin monkeys), xenarthrans (nine-banded, six-banded, and southern naked-tailed armadillos, and collared anteater), and marsupials (common opossum) showed clear negative abundance-area relationships, being more abundant in small forest patches. On the other hand, large-bodied xenarthrans (giant anteater and giant armadillo) and ungulates (excepting collared peccaries) clearly showed positive abundance-area relationships. These species were often locally extinct in patches  $<100$  ha but became increasingly more abundant in larger patches (Fig. 4).

The 95% confidence set of models for overall species richness and abundance of 26 mammal species ranged from 2 to 22 models, with all possible models always included in the candidate models (Table 2). These results suggest that patterns of species persistence and abundance responded to interactions between patch metrics and patch disturbance in our study area. Because we used all possible candidate models, we calculated an unbiased Akaike weight for each variable based on the sum of the weights of all models incorporating any given variable.

Fragment area was clearly the most important explanatory variable for the overall species richness and abundance of 26 mammal species (Table 2). Fragment area was weighted  $>0.95$  for overall species richness and abundance of 11 mammal species and  $>0.80$  for the abundance of red brocket deer. Isolate age and burn severity were weighted  $>0.95$  only for abundance of nine-banded armadillos and  $>0.80$  for abundances of collared anteaters and tayras. Logging intensity was weighed  $>0.80$  only for abundances of giant anteaters and nine-banded armadillos. Despite the strong effect of fragment area, all other variables had an intermediate weight (0.4–0.8) for at least the abundance of some species.

Slope estimates from the information-theoretic analyses were used to describe how patch and disturbance variables affected mammal species richness and abundance (Table 2). For example, forest area increased the total number of species by 5.117 (SE 0.550) and the abundance of giant armadillos by 0.531 (0.141), but decreased the abundance of titi monkeys and nine-banded armadillos by 0.432 (0.084) and 0.171 (0.030), respectively. Isolate age increased the abundance of collared anteaters by 0.002 (0.001), but decreased the abundance of titi monkeys by 0.018 (0.011). The burn severity increased the abundance of howler monkeys, collared peccaries, and white-lipped peccaries by 0.144 (0.082), 0.073 (0.046), and 0.091 (0.090), respectively, but decreased the abundance of collared anteaters and tayras by 0.008 (0.009) and 0.047 (0.026), respectively. The degree of logging intensity increased the abundance of only collared anteaters (0.018 [0.008]), whereas levels of hunting pressure decreased the abundance of only white-lipped peccaries (0.103 [0.129]).

## Discussion

### Effects of Forest-Patch Size

As we predicted Amazonian mammal assemblages in small forest fragments subjected to higher levels of disturbance were less species rich; however, their composition was less predictable than those of larger fragments, which retained a larger complement of the original mammal fauna. This finding suggests lower rates of local extinction, higher rates of immigration, or both. Fragment area alone was the strongest predictor of faunal integrity, explaining up to 90% of the variation in species richness. Unsurprisingly, most species were missing from small forest patches, a pattern consistent with other tropical and temperate studies (Terborgh et al. 2001; Crooks 2002; Laurance et al. 2002).

The density of several species declined in increasingly larger forest patches. Hyperabundance in small patches was typical of species subsidized by edge and/or matrix habitats or those apparently benefiting from density compensation or release from top predators. Nevertheless, even those species associated with overcrowding in some small patches could succumb to local extinctions in other small patches (Fig. 4), indicating high variance in persistence and abundance.

Differences in mammal species composition among forest fragments were unlikely due to preexisting differences in soil types and floristics (sampled in 60 quarter-hectare forest plots: Michalski et al. 2007). Before 1976 the entire study region consisted of undisturbed terra firma forest of similar physiognomy (Oliveira-Filho & Metzger 2006), and we assumed that all mammal species we found were probably widespread throughout the study area. Nevertheless, the moderate spatial autocorrelation in assemblage similarity is probably explained by the nonrandom location of different-sized fragments (Fig. 1), with smaller fragments located nearer the regional urban center, which retains fewer large mammal species. We therefore cannot attribute most of the spatial variation in species composition to preisolation landscape structure.

If present, howler monkeys and other arboreal folivores were consistently more abundant in small forest patches (cf. Terborgh et al. 2001). For example, titi monkeys persisted in even the smallest forest fragments, often attaining higher population densities in more disturbed forest, which explains their negative abundance-area relationship. Spider monkeys also exhibited hyperabundance when they were able to persist in small fragments. Brown capuchins are habitat generalists capable of crossing severely degraded forest and large gaps of pastures (Michalski & Peres 2005). Groups in small fragments were often subsidized by exotic fruit trees in the matrix, such as mango (*Mangifera indica*) and jackfruit (*Artocarpus heterophyllus*). A population of approximately 30 brown

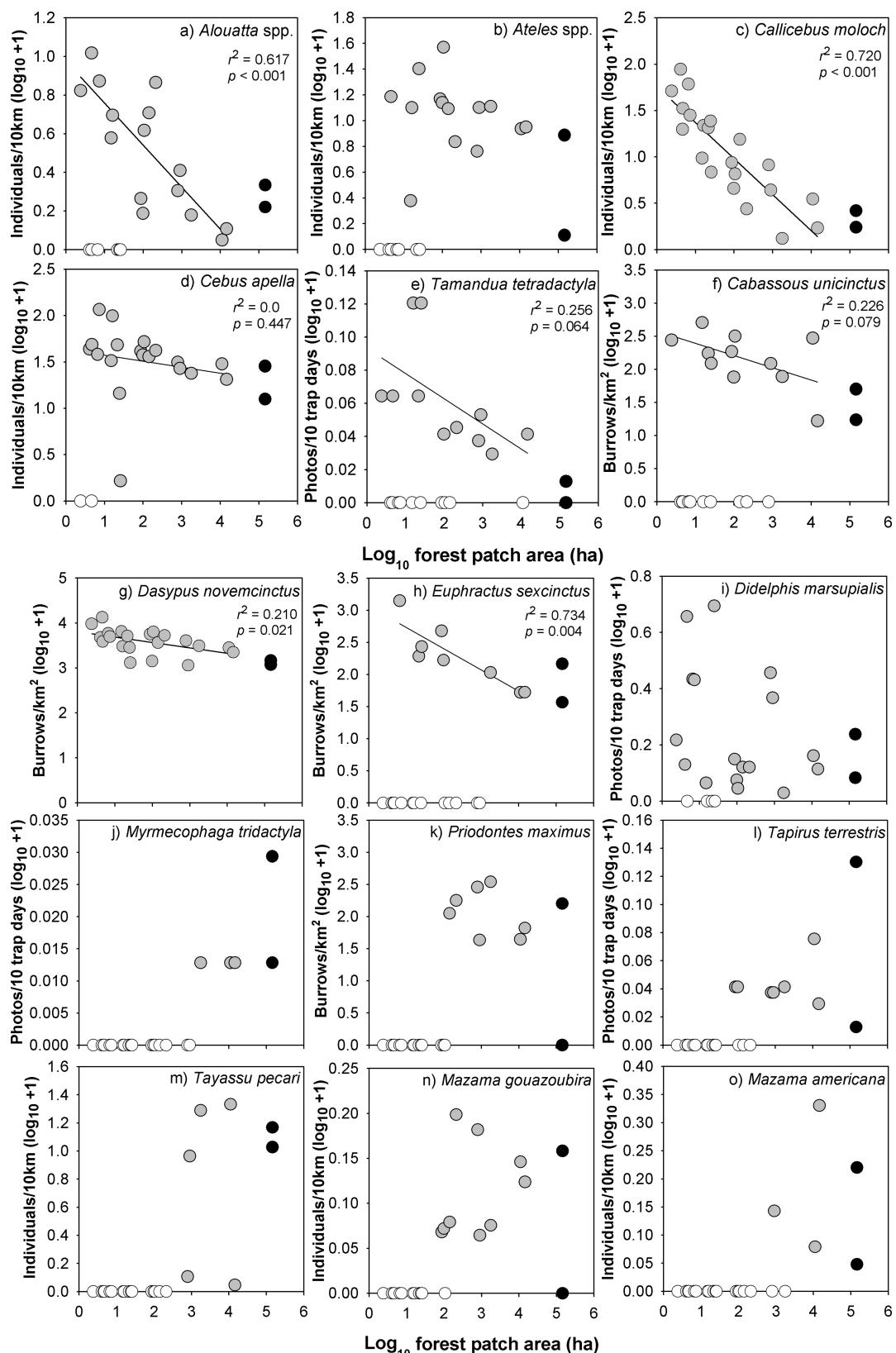


Figure 4. Relationships between forest-patch area and mammal population abundance for species showing either negative (a-i) or positive (j-o) area responses (see also Table 2), based on only those sites where a given species occurred. Open circles indicate forest fragments within which a given species was absent, shaded circles indicate occupied fragments, and solid circles indicate continuous forest sites.

capuchins—subsidized by food refuse and small livestock from neighboring households—has survived for over 25 years in an isolated 18-ha urban forest fragment in Alta Floresta (Spanga 2004).

All xenarthrans were capable of crossing, if not foraging, in the surrounding pasture matrix and, with the exception of the three largest species (giant anteater, greater long-nosed, and giant armadillo), exhibited higher densities in smaller fragments. Nine-banded armadillos were one of the most ubiquitous species, occurring in all sites surveyed. Likewise, this was one of the most common species in highly disturbed Peruvian agroforests (Naughton-Treves et al. 2003). Small fragments were often heavily disturbed, predator-free environments, which may have inflated the abundance of this species.

The abundance of common opossums, the only marsupial species surveyed, declined in increasingly larger patches. This is a notorious edge and disturbance-tolerant species that typically prospers in modified habitats (Malcolm 1997; Daily et al. 2003), attaining hyperabundance in small fragments (Fonseca & Robinson 1990). Red-rumped agoutis were also more abundant in small patches; patch area was negatively related to their population density where they occurred. Indeed, agoutis can exploit secondary forest and survive even in highly disturbed habitats (Naughton-Treves et al. 2003). Tayra, the only fragmentation-tolerant carnivore species considered in detail, could subsist in agricultural mosaics retaining some forest cover. In sum, all ubiquitous species with negative abundance-area relationships were matrix tolerant to at least some degree and often commuted between forest patches through the open-habitat matrix.

The remaining two rodents, three xenarthrans, four carnivores, and five ungulates we considered ranged from slightly to highly patch-area sensitive. Although Guianan squirrels and pacas appeared to be slightly area sensitive, both species could not be adequately censused, and their abundances in small forest patches were likely underestimated. The paca is often found in highly disturbed areas (Naughton-Treves et al. 2003). Giant anteaters are susceptible to fire and persecution by dogs because of their flammable fur and sluggishness (F. M., personal observation), and rarely survive in disturbed fragmented habitats.

Area-sensitive carnivore species included coatis, Neotropical river otters, ocelots, and jaguars. Coatis can cross large gaps of unforested habitat, but family groups of 5–40 individuals (mean [SD] = 4.21 [2.87] group size,  $n = 24$ ) likely require forest patches  $>80$  ha to sustain a breeding population. This may explain the slightly positive abundance-area relationship of this species, even though it occurred in 39% of all sites. Neotropical river otters showed higher abundance in controls and fragments  $>900$  ha, and were frequently absent from human-disturbed areas (cf. Roobitaille & Laurance 2002). Ocelots showed only marginally higher abundances in increasingly larger fragments, probably because they can expand

their home ranges in fragmented landscapes to encompass sufficient forest habitat. Jaguars were restricted to large remnants of relatively undisturbed forest, which is consistent with their habitat requirements including dense forest cover and a sufficient natural prey base (Hoogesteijn & Mondolfi 1992; Michalski et al. 2006).

Most ungulates showed higher population abundances in larger forest patches. White-lipped peccaries live in large herds, thereby requiring extensive tracts of forest (Kiltie & Terborgh 1983), yet we found a herd of only 21 individuals persisting in a 900-ha forest patch for at least 20 years, confirming cases of long-term persistence in Atlantic forest fragments of 2000–2178 ha (Cullen et al. 2000; Keuroghlian et al. 2004). In contrast, the smaller-bodied and small-herd-living collared peccary is more tolerant of second-growth mosaics (Peres 2001) and was found in patches as small as 87 ha.

### Patch-Level Effects of Disturbance

Population densities of medium- to large-bodied mammals were also affected by internal disturbance of forest patches, which interacted with area and edge effects. Isolation age, hunting pressure, burn severity, and logging intensity were all important determinants of the abundance of at least some species.

Patch isolation age was an important determinant of population abundance of four species, with a positive effect only for collared anteaters and a negative effect on titi monkeys, nine-banded armadillos, and jaguars. These relationships may, however, have been confounded by patch size because recently isolated fragments farther from the Alta Floresta urban center were often large. Nevertheless, the negative effects of postisolation time on edge-tolerant species, such as titi monkeys and nine-banded armadillos, were still significant once the effects of patch size were controlled for by extracting the residuals from the relationship between isolation age and forest-patch size. The positive effect of isolation on collared anteater abundance was unsurprising because this species copes well with degraded forest habitats (Rodrigues et al. 2001).

There was a negative effect of game harvest on white-lipped peccary abundance. Nevertheless, most large mammal species in this region are not persecuted by hunters, perhaps because of the high supply of animal protein ( $\sim 17$  cattle/person; Michalski et al. 2006), so hunting pressure was not a significant effect for any other mammal species. Moreover, because our forest sites were on average 16 years old, species-persistence patterns may still reflect preequilibrium conditions because the relaxation time since isolation was likely insufficient for several long-lived taxa (e.g., Ferraz et al. 2003). Unhunted to lightly hunted sites retained the highest abundances of white-lipped peccaries, which is consistent with local

extinctions and declines of this species in hunted forest fragments (Cullen et al. 2000; Peres 2001).

Logging intensity was negatively related to abundances of marmosets, nine-banded armadillos, and red-rumped agoutis. Positive relationships with logging intensity were found only for collared anteaters, which can cope with regenerating second-growth and degraded forest habitats (Rodrigues et al. 2001). Although our measure of logging intensity had a negative effect on the abundance of only three species, further timber extraction in new cutting cycles will continue to remove key food sources, increase the density of tree-fall gaps, and desiccate a greater understory fuel load, which will render forest fragments more prone to recurrent fires (Nepstad et al. 1999; Cochrane & Laurance 2002), thereby affecting a larger fraction of the mammal fauna.

Finally, surface fire disturbance was a key variable predicting population abundance of seven species. Unburned or lightly burned forest sites retained larger populations of collared anteaters and tayras. Conversely, sites subjected to more severe, recurrent fires favored the abundance of howler monkeys, nine-banded armadillos, giant armadillos, collared peccaries, and white-lipped peccaries. In the medium term, recurrent fires can increase forest productivity of understory vegetation for terrestrial mammals and high-quality foliage for arboreal folivores and other species taking advantage of the rapid regeneration pulse (Barlow & Peres 2004). Nevertheless, even low-intensity burns can induce high rates of sapling and tree mortality and low rates of seedling recruitment that will eventually degrade forest habitat for many forest specialists.

### Conservation Implications

Our results show that nonrandom collapses in the forest mammal fauna in a fragmented landscape in the Brazilian Amazon is a function of both habitat patch size and the post isolation history of human-induced patch disturbance. Threats such as selective logging, forest fires, and hunting can all amplify the concurrently operating area and edge effects on many vertebrate species stranded in forest fragments (Peres 2001; Michalski & Peres 2005; Peres & Michalski 2006). Furthermore, species persistence patterns may reflect preequilibrium conditions because the relaxation time since isolation for many forest patches has so far likely been insufficient for several long-lived taxa (Ferraz et al. 2003). Hence, many relict, small populations persisting in small fragments may eventually become extinct. Despite the overcrowding of many small fragments, population sizes of several large-bodied, wide-ranging, or rare species were almost certainly unviable in the long run. Nevertheless, the clear species richness and abundance responses to forest-patch area and different sources of disturbance give us confidence that most species responded rapidly to habitat loss.

In particular, our results highlight the conservation importance of retaining large tracts of relatively undisturbed primary forest to the original forest fauna. Although the persistence of full mammal assemblages will require sufficiently large forest remnants ( $>10,000$  ha), smaller patches were still important to a number of matrix-tolerant or less spatially demanding species of lesser conservation concern. Nevertheless, current levels of anthropogenic disturbance can substantially inflate spatial requirements of isolated populations, and privately owned fragments that were safeguarded from extractive activities were more likely to retain more complete species assemblages. In the long term, securing relatively undisturbed and well-connected forest remnants will be essential to prevent the erosion of the Neotropical forest mammal fauna in fragmented landscapes.

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### Supplementary Material

Mammal species surveyed in the Alta Floresta region for this study (Appendix S1) and supplemental information on the methods used to characterize levels of anthropogenic disturbances at the forest sites surveyed (Appendix S2) are available as part of the on-line article from <http://www.blackwell-synergy.com/>. The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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