

Long-term persistence of midsized to large-bodied mammals in Amazonian landscapes under varying contexts of forest cover

Ricardo Sampaio · Albertina P. Lima · William E. Magnusson · Carlos A. Peres

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Abstract Both forest fragmentation and overhunting have profound effects on the structure of large-vertebrate assemblages in neotropical forests. However, the long-term value of habitat fragments for forest mammals remains poorly understood and few regional scale studies have replicated sampling across spatially independent landscapes. Here, we assess the species occupancy and abundance of midsized to large-bodied mammals within three neighbouring Amazonian forest landscapes varying widely in extent of forest cover. One of these consisted of forest fragments surrounded by semi-natural scrub savannahs that had been occupied by paleoindian populations for at least 7,000 years, whereas forest cover in the other two landscapes was either variegated or continuous. Data on species occurrence and abundance from diurnal and nocturnal line-transect surveys and local interviews in each landscape were used to examine the effects of forest cover and hunting pressure on mammal persistence within forest patches. The extent of forest cover was a key determinant of species persistence across the three landscapes, but populations of large-bodied species were either reduced or driven to local extinction by hunting even in the most forested and least fragmented landscape. Many game and non-game species persisted in forest isolates, even though, individually, these were likely too small to support viable populations. This study indicates that even small, long-term forest fragments may retain significant conservation value if they can be managed within the context of enhanced connectivity across wider fragmented landscapes.

Keywords Amazonian wildlife · Forest fragmentation · Hunting · Local extinction · Mammals · Forest disturbance

R. Sampaio (✉) · A. P. Lima · W. E. Magnusson
Coordenação de Pesquisas em Ecologia, Instituto Nacional de Pesquisas da Amazônia, CP 478,
Manaus, AM 69011-970, Brazil
e-mail: rcosampaio@gmail.com

C. A. Peres
School of Environmental Sciences, University of East Anglia, Norwich NR47TJ, UK

Introduction

Previously continuous tropical forest landscapes worldwide have inexorably become more fragmented, and habitat fragmentation is widely perceived as one of the key drivers of species extinctions in the humid tropics (Laurance 2008). Tropical deforestation and other land-use changes generally expose forests to potentially severe edge effects, such as fire incursions, and restrict forest cover to small patches isolated by a matrix of open habitats. In Amazonia, this is aggravated by the aggressive expansion of agricultural frontiers driven by cattle ranching and soy-bean monoculture (Soares-Filho et al. 2006), as well as large-scale forest disturbance resulting from logging. For example, between 1999 and 2002 deforestation alone generated 32,000 km of new forest edges in only four states of the Brazilian Amazon (Broadbent et al. 2008).

Studies examining the effects of habitat fragmentation on tropical forest mammals have largely concentrated on the minimum size of isolated remnants required to maintain populations of any given species (e.g. Estrada et al. 1994; Cowlshaw 1999; Chiarello 2000; Michalski and Peres 2007; Laurance et al. 2008; Galetti et al. 2009; Stone et al. 2009). However, many of these species cannot maintain viable populations within single forest fragments, which are usually too small, and the persistence of both resident and transient species is a function of landscape structure (Fahrig 2003; Debinski 2006). Studies of forest fragmentation at the patch scale tend to ignore the landscape context (Watling and Donnelly 2006) and the role of structural connectivity across the landscape (Metzger and Décamps 1997), including that provided by remnant or recreated dispersal corridors (Baum et al. 2004; Chetkiewicz et al. 2006; Lees and Peres 2009). Species assemblages within isolated forest fragments must therefore be considered within the wider landscape context (Fahrig 2003; Lees and Peres 2009).

Several neotropical forest fragmentation studies on midsized to large-bodied mammals have addressed forest fragments isolated for less than four decades (Estrada et al. 1994; Chiarello 2000; Laurance et al. 2002a; Lopes and Ferrari 2000; Ferrari et al. 2003; Martins 2005; Michalski and Peres 2007), and most of these have been based on only one survey method. However, the processes operating in recently isolated forest fragments may differ from those isolated for much longer periods (Debinski 2006). In addition, surveying a broad spectrum of nonvolant mammal species usually requires a wide variety of sampling techniques (Altrichter and Boaglio 2004; Michalski and Peres 2005).

Mammals larger than 2 kg are frequently pursued by subsistence hunters visiting forest fragments. Deforestation is correlated with human population density in Amazonia (Laurance et al. 2002b) and in many cases fragmentation facilitates physical access by hunters (Peres 2001). Hunting depresses primarily populations of large-bodied mammals both in vast tracts of continuous tropical forest (Bodmer 1995; Peres and Palacios 2007; Fa and Brown 2009) and fragmented landscapes (Cullen-Junior et al. 2000; Peres 2001). In most tropical forest countries, however, hunting is an important subsistence activity for the rural poor, complementing their animal-protein requirements (Bennett 2002; Robinson and Redford 1991).

In this study, we used semi-structured local interviews, line-transect surveys, and surveys of indirect animal signs to quantify the occupancy and abundance of mammal species across a macro-mosaic of forest landscapes of central Brazilian Amazonia. This region has supported a large human population for several millennia (Roosevelt et al. 1996), and remains subjected to intense human activity. The study region was comprised of three landscape types, including continuous primary forest within a forestry reserve, a previously continuous-forest landscape that had been severely deforested in the last 30 years, and a

fragmented landscape dominated by small forest patches that have been isolated for many centuries or even millennia. Specifically, we examine (1) the effects of habitat loss on mammal species richness and composition; (2) how the disturbance regime and characteristics of isolated forest patches other than size (e.g. tree density and hunting pressure) affect species persistence; and (3) whether the persistence of game species was more likely to be affected by habitat loss than that of non-game species.

Methods

Study site

The study was undertaken on the right bank of the lower Rio Tapajós basin, 35 km or more from the city of Santarém (2°31'S, 55°00'W; Fig. 1). The region has attracted increasing demand for soybean monoculture along the controversial BR-163 Highway, which links Santarém in Pará to Cuiabá in Mato Grosso (Fearnside 2007).

The three study landscapes were located on sandy soils, but retained varying proportions of forest cover under different levels of human disturbance (Table 1). Landscape 1 (L1) is

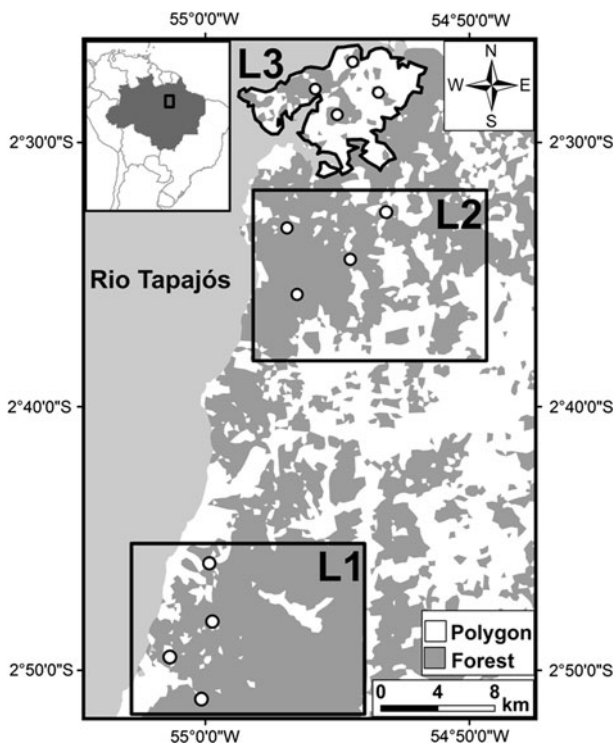


Fig. 1 Forest cover (dark gray) in the study area based on data provided by PRODES-INPE (www.obt.inpe.br/prodes). Rectangles represent the habitat configuration of the continuous forested landscape (L1) and the variegated landscape (L2); the irregular polygon represents the least forested and most fragmented forest landscape (L3). Open circles within the L1, L2 and L3 polygons represent the locations of line-transects

Table 1 The main features of the three forest landscapes (L1, L2 and L3) studied in the lower Rio Tapajós region of Brazilian Amazonia (see Fig. 1)

	L1 (FNT)	L2 (EFC)	L3 (AdC)
Landscape feature	Tapajós National Forest	Eixo Forte Communities	Alter do Chão
Geometric center (Lat/Long)	55°0′44.8″W, 2°48′7.9″S	54°53′55.2″W, 2°33′39.1″S	54°53′59.9″W, 2°7′43.6″S
Polygon size (km ²)	196	196	58
Status of forest cover	Continuous	Variiegated	Fragmented
% Forest cover (within the polygon)	84	65	30
Human population density (households/km ²)	0.8	5	1
Forest basal area (m ² /ha)	7.22	7.8	8.01 ^a
Tree density (>40 cm DBH)	1.6	1.6	1.63 ^a
Our metric of hunting pressure ^b	19	35	30 ^a
Number of transects sampled	4	4	16
Total length of transects	4.6	4.5	4.4 ^a
Diurnal and nocturnal cumulative km walked	64.74	63	61.6 ^a

^a Within L3, these variables refer to the four largest forest fragments only (see “Methods”)

^b Indicatives of hunter presence (see “Methods”)

part of a sustainable-use forestry reserve (Tapajós National Forest) and has a low human population density. Landscape 2 (L2) has an intermediate-sized population of semi-subsistence rubber-tappers, but has succumbed to increasing forest conversion to pastures in the last 30 years. Landscape 3 (L3) primarily consists of a mosaic of forest patches surrounded by a scrub savannah that is frequently subjected to anthropogenic fires. Although the origin of these forest patches remains uncertain, this entire landscape was most likely forested until ~2,000 years ago (Sanaiotti et al. 2002). The earliest record of forest fragments, however, dates to a mid nineteenth century observation by Bates (1892). This landscape has therefore been fragmented for at least 150 years and probably much longer. Vegetation changes in forest fragments of L3 may have occurred over millennia, and fires induced by paleoindian agriculture likely had a key role in the matrix transition to semi-natural savannah vegetation (Serena 1984). Although the forest type in L2 and L3 has been described as semi-deciduous (Miranda 1993), we assume that forest structure across all three landscapes is comparable since no significant difference was found in forest basal area ($P = 0.8$) and density of trees >40 cm in diameter at breast height (DBH; $P = 0.9$; see below for details on habitat sampling).

The percentage of forest cover in the three study landscapes was quantified using historical data on deforestation prior to 2006 provided by the Brazilian Amazon Satellite Monitoring Program (PRODES-INPE; see <http://www.obt.inpe.br/prodes/>). Based on the approximate boundaries of L1 and L2, we defined regular polygons of 196 km² in each of those landscapes, which incorporates all sampling points in those landscapes. However, due to the smaller extent of L3, we defined an irregular polygon of 58 km² incorporating all fragments sampled and the surrounding savannah matrix (Fig. 1). Using a GIS project with these layer files, we then calculated the proportion of closed-canopy forest cover remaining within each polygon, but excluding open water. Further details on each of these three landscapes are summarized in Table 1.

Mammal surveys

We surveyed the midsized to large-bodied mammal fauna [larger than 0.5 kg, except for two small arboreal taxa (*Mico argentatus*, *Sciurus* spp.)] using four line-transects in each of the three landscapes (Fig. 1). In the least forested and most fragmented landscape (L3), we sampled the four largest fragments, as most remaining forest patches were simply too small (Fig. 2). Transects in these four fragments were restricted to a length of 1–1.4 km, so transects in the other two landscapes (L1 and L2) were also 1 km in length. The total length of all transects in each landscape ranged from 4.4 to 4.5 km, and we ensured a minimum level of spatial independence by spacing neighbouring transects by at least 2.4 km.

In addition, we examined the effects of forest patch size, patch isolation and hunting pressure on patterns of mammal species occupancy by surveying 16 variable-sized forest fragments in L3 (Fig. 2). Because most of these fragments were smaller than 300 ha, only one transect of 0.3–1.4 km in length was placed in each forest fragment, thereby scaling our sampling effort to the patch area (Watson 2003). Transect length was therefore highly correlated with log-transformed forest patch area ($r = 0.88$), but the total census area covered by our transects corresponded to a larger proportion of the area of increasingly smaller fragments ($r = -0.83$). Wherever possible, these transects followed the major axis of each fragment.

Mammal data

Based on interviews with local residents, which were confirmed by putative geographic range polygons available in NatureServe (Patterson et al. 2003), 39 species of midsized to

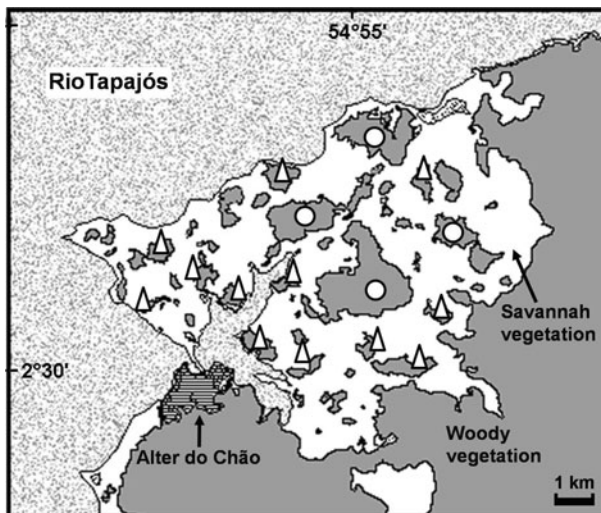


Fig. 2 Map of the 16 forest fragments isolated by scrub savannahs (L3). *Open circles* indicate the four largest fragments that were used for comparisons with the other two landscapes and *open triangles* indicate the other 12 fragments surveyed

large-bodied mammals potentially occur in the study region (Table 2). The two small cats (*Leopardus wiedii* and *Leopardus tigrinus*) could not be distinguished on the basis of sightings, tracks and other indirect evidence so we pooled the data for these species.

Species-occupancy data and identification of local game species were obtained from semi-structured interviews conducted between October and December of 2005 with 10, 25 and 30 local residents in L1, L2 and L3, respectively. Interviewees were required to be older than 45 years, to have lived within each study landscape for >30 years, and were selected on the basis of their long-term first-hand knowledge of the local midsized to large bodied nonvolant mammal fauna. We used colour plates of mammal species to establish their occurrence and to determine the time each species was last detected in each landscape.

Mammal surveys were conducted between July and November 2006. We recorded sightings or any indirect evidence (tracks, vocalizations, faeces, hair, and carcasses) during nine diurnal and five nocturnal surveys repeated at each sampling site. Both diurnal and nocturnal line-transect surveys followed the standard guidelines provided in Peres (1999). However, because transects were relatively short, all species were detected fewer than 30 times per transect, so reliable density estimates could not be obtained. Transects were surveyed in the morning (0545–1000 h) and at night (1900–2200 h) by a single observer walking quietly at 1 km/h in the morning and 0.8 km/h at night. The leaf-litter along all transects was removed prior to each survey to reduce the observer's background noise, and head torches were used to locate mammal eye-shines during nocturnal surveys, which were not conducted during the 3 days of peak full moon.

In addition, tracks were recorded during diurnal surveys within 1 m² sand track-plates placed along each transect at 50-m intervals. Tracks outside track-plates were also recorded, but only during diurnal surveys and all tracks were erased on a daily basis to prevent double-counting. To guard against possible seasonal effects, we systematically rotated census walks so that all sites were allocated the same number of repetitions in different months of the year.

Site data

Based on data from the Santarém Municipal Health Office and the IBAMA human population census of 2006, we estimated the household density (per km²) in each landscape.

An indirect logging disturbance index was estimated for different classes of large-trees (DBH ≥ 40 , ≥ 50 and ≥ 70 cm) and total basal area of large trees was estimated within a 5-m wide strip along each line transect. However paired comparisons across different tree size classes were highly correlated (Pearson correlations >0.80) so we use the density of all canopy trees (DBH ≥ 40 cm; Table 1) to conduct further analysis.

Hunting pressure was estimated using counts of any evidence of previous or ongoing hunting activity in each of the 14 surveys. Evidence of hunting included direct encounters with hunters at the time of surveys, shotgun blows detected within hearing range, spent shotgun shells, hunter 'waiting' platforms and any other residual artefacts or signs of hunters.

The patch sizes of the 16 forest fragments in L3 were calculated by Albernaz (2001) from a 2001 Landsat TM5 satellite image. According to local informants, these fragments had been stable for many years and had not changed in size since 2001.

Data analysis

We examined species-accumulation curves using rarefaction analysis for the four longest transects sampled within each landscape. We constructed the curves using Mao-Tao

Table 2 Checklist, mean body mass and known occurrence of species or species groups occurring in our three study landscapes that could be detected by our survey methodology

Species	Body mass (kg) ^b	L1 (B–A%)	L2 (B–A%)	L3 (B–A%)
Primates				
<i>Alouatta discolor</i> ^a	6.5	Present	Present	Present
<i>Ateles marginatus</i>	11	Extinct (0–50%)	Extinct (0–100%)	Extinct (30–50%)
<i>Mico argentatus</i>	>0.5	Present	Present	Present
<i>Aotus infulatus</i>	0.7	Present	Present	Present
<i>Cebus apella</i>	2.5	Present	Extinct for 20% (0–0%)	Extinct for 60% (20–10%)
<i>Saimiri sciureus</i>	0.8	Present	Present	Extinct for 20% (10–3%)
<i>Chiropotes albinasus</i>	2.3	Extinct (0–50%)	Extinct (20–20%)	Extinct for 90% (0–0%)
<i>Callicebus moloch</i>	1	Present	Present	Present
Rodentia				
<i>Coendu prehensilis</i>	5	Present	Present	Present
<i>Sciurus</i> spp.	>0.5	Present	Present	Extinct for 20% (3–0%)
<i>Cuniculus paca</i> ^a	7.5	Present	Present	Present
<i>Dasyprocta leporina</i> ^a	4	Present	Present	Present
<i>Hydrochaeris hydrochaeris</i>	50	Extinct for 50% (0–50%)	Extinct for 60% (0–0%)	Extinct for 70% (3–0%)
Artiodactyla				
<i>Mazama americana</i> ^a	36	Present	Extinct for 40% (20–20%)	Extinct for 40% (20–10%)
<i>Mazama gouazoubira</i> ^a	14.5	Present	Present	Present
<i>Pecari tajacu</i> ^a	16.2	Present	Present	Present
<i>Tayassu pecary</i>	31.4	Present	Extinct (40–40%)	Extinct (0–47%)
Perrisodactyla				
<i>Tapirus terrestris</i>	139.6	Present	Extinct (0–80%)	Extinct (3–40%)
Xenartha				
<i>Bradypus</i> spp.	4.3	Present	Present	Present
<i>Choloepus didactylus</i>	6.5	Present	Present	Present
<i>Cyclops didactylus</i>	0.4	Present	Extinct for 20% (0–0%)	Extinct for 30% (7–3%)
<i>Cabassous unicinctus</i>	3	Present	Present	Present
<i>Dasyopus kappleri</i>	10.5	Present	Extinct (20–40%)	Extinct (10–20%)
<i>Dasyopus novemcinctus</i> ^a	3.5	Present	Present	Present
<i>Priodontes maximus</i>	27	Present	Extinct (0–80%)	Extinct (20–30%)
<i>Myrmecophaga tridactyla</i>	30	Extinct for 50% (0–50%)	Extinct for 40% (0–60%)	Extinct (7–23%)
<i>Tamandua tetradactyla</i>	5.5	Present	Present	Present
Carnivora				
<i>Atelocynus microtis</i>	7	Extinct (0–0%)	Extinct (20–0%)	Extinct (0–0%)
<i>Speothos venaticus</i>	5.5	Extinct for 60% (0–0%)	Extinct for 70% (20–0%)	Extinct for 90% (0–0%)

Table 2 continued

Species	Body mass (kg) ^b	L1 (B–A%)	L2 (B–A%)	L3 (B–A%)
<i>Leopardus pardalis</i>	8	Present	Present	Extinct for 20% (20–0%)
<i>Leopardus wiedii/tigrinus</i>	3.2/2.2	Present	Present	Extinct for 10% (7–0%)
<i>Panthera onca</i>	90	Present	Extinct for 40% (40–0%)	Extinct for 40% (10–3%)
<i>Puma concolor</i>	40	Present	Extinct for 60% (40–0%)	Extinct for 60% (30–7%)
<i>Puma yagouaroundi</i>	2.6	Present	Extinct for 20% (0–0%)	Extinct for 10% (3–0%)
<i>Eira barbara</i>	4	Present	Present	Present
<i>Galictis vittata</i>	3	Extinct for 50% (0–50%)	Extinct for 10%	Extinct for 40% (0–0%)
<i>Nasua nasua</i>	4	Present	Present	Present
<i>Potos flavus</i>	3	Present	Extinct for 20% (0–20%)	Extinct for 30% (0–0%)

Local extinctions were presumed when all interviewees consistently confirmed the absence of sightings or any other evidence in recent years. Percentages of interviews reporting the last sighting of any given species prior to 30 years ago (before, B) and percentage of interviews reporting one or more sightings within the last 30 years (after, A) are presented in parentheses

^a Local hunted species

^b Data from Eisenberg and Redford (1999)

indices based on the aggregate presence–absence data from each transect based on all field survey methods, excluding data from interviews. Curves were generated using the EstimateS program (Colwell 2005) on the basis of repeated surveys during the day because some species were observed during both diurnal and nocturnal surveys.

The Nestedness Temperature Calculator Program (Atmar and Patterson 1993) was used to test whether species assemblages in the most deforested landscape were comprised of non-random subsets of assemblages in more intact landscapes. This test estimates the maximum nestedness of an incidence matrix, reorganizing sites and species to minimize unexpected species occurrences. Temperature metrics evaluate the symmetry in the distribution of unexpected absences and presences, on both sides of a ‘perfect’ nestedness boundary. Lower temperatures in the incidence matrix indicate lack of symmetry, while higher temperatures indicate higher symmetry. Since “temperature” evaluates any asymmetry, it can indicate patterns that are not necessarily nested. Therefore, it is necessary to inspect the matrix to determine if the pattern represents true nestedness (Almeida-Neto et al. 2007).

We avoided high levels of collinearity between landscape and forest disturbance variables by excluding those variables that had Pearson correlations >0.80. In order to investigate the local determinants of mammal species richness, we first examined the degree to which the species-by-site matrix was independent of spatial effects within landscapes by explicitly considering the geographic position of the midpoint of each of the transects walked.

No overall spatial autocorrelation was found in the mammal species assemblages recorded along linear transects sampled in the 24 sites across the three landscapes. Spatial correlation was nevertheless detected in the richness of mammal species related to the

shortest between-transect distance class across the 24 sites and all 1-km transects (12 sites) in the three landscapes. However, no spatial correlation was found in the species richness of the 16 small forest fragments (L3). These tests were performed using the Mantel Correlogram Test available from the *ecodist* package (Goslee and Urban 2007) and the Moran Correlogram using the *pgirmess* package (R Development Core Team 2008; Giraudoux 2009).

We then performed generalized linear models (GLMs) with a LOG link function by assuming a Poisson error distribution in the response variable (species richness) and including four variables describing the 12 forest sites surveyed [(1) Landscape identity (L1, L2 and L3); (2) Proportion of forest cover within 2.4 km buffer of each transect, which represented the largest possible distance with no overlap between buffers; (3) our composite metric of hunting pressure; and (4) the forest basal area along transects]. After testing all main effects and all possible interactions among variables, we used a supervised stepwise procedure available from the MASS package (Venables and Ripley 2002), to select the most parsimonious minimum model based on the Akaike's information criterion (AIC). We used stepwise backward regression models with elimination at $P = 0.15$ to retain the best predictors of species richness. The Durbin–Watson D statistic, eigenvalues and analysis of variance were used to assess the goodness of fit of the multiple regression models. Models were fitted within the R platform (R Development Core Team 2008) and evaluated according to the deviance explained.

Results

A maximum of 38 mammal species (or taxa consisting of closely related congeners) could occur throughout our entire study region. However, all interviews with local residents indicate that white-fronted spider monkeys (*Ateles marginatus*; but see Ravetta and Ferrari 2009), white-nosed bearded saki-monkeys (*Chiropotes albinasus*) and small-eared dogs (*Atelocynus microtis*) no longer occurred in any of the three landscapes and had been likely extirpated on a regional scale. White-lipped peccary (*Tayassu pecari*), lowland tapir (*Tapirus terrestris*), greater long-nosed armadillo (*Dasybus kappleri*) and giant armadillo (*Priodontes maximus*) had long been absent from the two least forested landscapes (L2 and L3) and giant anteater (*Myrmecophaga tridactyla*) had been absent from the forest fragments in L3 (Table 2). In addition to these regional scale extinctions, only highly elusive species (*Cyclops didactylus*; *Speothus venaticus*; *Galictis vittata*) were not recorded during our line-transect surveys at any site (Table 3).

Records of hunting activity detected along transects during the 14 surveys ranged from 0 to 12 (mean = 4.967 ± 3.07 , $N = 24$) and more signs of hunters were recorded in the least forested landscapes (L2 and L3), but this difference was not significant (ANOVA: $F_{2,9} = 7.98$; $P = 0.10$). On the basis of interviews with 65 local residents, the most frequently hunted game species in the study region were armadillos (*Dasybus novemcinctus* and *Cabassou unicinctus*; reported in 26.7% of all interviews), collared peccary (*Pecari tajacu*; 22.8%), brocket deer (*Mazama* spp.; 20.9%), paca (*Cuniculus paca*; 19%), agouti (*Dasyprocta leporina*; 5%) and howler monkey (*Alouatta discolor*; 4%).

Line-transect surveys in landscapes L1, L2 and L3 resulted in 275, 199 and 138 mammal (or mammal group) records, respectively. Of the 38 species expected to occur in the study region, we recorded only 26 in L1, 23 in L2, and 18 species in the four largest forest fragments surveyed in L3. However, the overall number of species detected in L3

Table 3 Number of direct or indirect observations of midsized to large-bodied mammals in the continuous (L1) and variegated forest landscapes (L2), and the four largest forest fragments (4 L3) and the 16 forest fragments isolated by savannah (16 L3) within the fragmented forest landscape (L3)

Species	L1	L2	4 L3	16 L3
Primates				
<i>Alouatta discolor</i>	18	12	17	59
<i>Ateles marginatus</i> ^a	0	0	0	0
<i>Mico argentatus</i>	18	18	11	38
<i>Aotus infulatus</i>	4	0	2	3
<i>Cebus apella</i>	5	1	0	0
<i>Saimiri sciureus</i>	8	4	1	1
<i>Callicebus moloch</i>	17	23	17	65
<i>Chiropotes albinasus</i> ^a	0	0	0	0
Rodentia				
<i>Sciurus</i> spp.	7	6	0	1
<i>Coendu prehensilis</i>	4	3	2	7
<i>Cuniculus paca</i>	23	10	4	15
<i>Dasyprocta leporina</i>	33	24	8	20
<i>Hydrochaeris hydrochaeris</i>	1	0	0	4
Artiodactyla				
<i>Mazama americana</i>	10	8	2	10
<i>Mazama gouazoubira</i>	25	19	20	61
<i>Pecari tajacu</i>	19	12	11	32
<i>Tayassu peccary</i> ^a	0	0	0	0
Perrisodactyla				
<i>Tapirus terrestris</i> ^a	0	0	0	0
Xenartha				
<i>Bradypus</i> spp.	0	0	0	2
<i>Choleopus didactylus</i>	2	1	0	0
<i>Cyclops didactylus</i>	0	0	0	0
<i>Cabassous unicinctus</i>	7	1	2	10
<i>Dasyopus kappleri</i> ^a	0	0	0	0
<i>Dasyopus novencinctus</i>	35	38	32	73
<i>Priodontes maximus</i> ^a	0	0	0	0
<i>Myrmecophaga tridactyla</i> ^a	0	0	0	0
<i>Tamandua tetradactyla</i>	7	6	4	12
Carnivora				
<i>Atelocynus microtis</i> ^a	0	0	0	0
<i>Speothus venaticus</i>	0	0	0	0
<i>Leopardus pardalis</i>	10	1	1	3
<i>Leopardus wiedii/tigrinus</i>	4	1	0	2
<i>Panthera onca</i>	3	2	1	2
<i>Puma concolor</i>	1	1	0	0
<i>Puma yagouaroundi</i>	1	0	0	0
<i>Eira barbara</i>	4	3	1	1
<i>Galictis vittata</i>	0	0	0	0

Table 3 continued

Species	L1	L2	4 L3	16 L3
<i>Nasua nasua</i>	7	3	2	6
<i>Potos flavus</i>	2	2	0	0
Total	275	199	138	427

^a Species considered to be locally extinct on the basis of interviews

increased to 22 species when all 16 forest fragments surveyed were also considered (Table 3).

Cumulative number of species encountered increased with the number of repetitions of diurnal line-transect surveys, and was highest in L1, followed by L2 and L3 (Fig. 3). The estimated numbers of species detected following nine diurnal repetitions were significantly different between L1 and L3 (ANOVA: $F_{2,9} = 7.97$; $P = 0.01$; Turkey post-hoc tests: $P_{L1,L2}$: 0.34; $P_{L1,L3}$: 0.01; $P_{L2,L3}$: 0.08).

The nestedness analysis indicated a hierarchical pattern of species composition in the 12 sites (temperature of observed matrix = 13.4° ; temperature of random matrix = $55.6^\circ \pm 6^\circ$; $P < 0.001$), where the lowest species richness was recorded in L3, which retained a nested subset of species occurring within the more forested landscapes (Fig. 4).

Mammal species richness across all 12 survey sites ranged nearly four-fold (7–24 species; mean \pm SD = 15.33 ± 4.74). The total number of species recorded differed among the three landscapes ($P = 0.02$) and none of the predictor variables other than landscape identity contributed a significant amount of additional variation. This was primarily due to differences in the proportion of forest cover in each landscape: when landscape identity was omitted from analyses, the proportion of forest cover was the only variable explaining a meaningful amount of variance in species richness ($P = 0.07$), whereas all other variables were decidedly unimportant ($P > 0.50$). In addition, landscape identity was the only variable retained in the stepwise regression model explaining species richness within each survey site ($P = 0.01$), although we caution against over-interpretation of these results due to the spatial structure of the data within each landscape.

The detection frequency of the nine most ubiquitous species at the 12 sites across the three landscapes in 14 surveys varied from 0 to 13 (mean = 4.5 ± 2.8 , $N = 108$) and was affected by both species (ANOVA: $F_8 = 12.14$, $P < 0.001$) and landscape identity (ANOVA: $F_2 = 10.38$, $P < 0.001$). There was no significant interaction between species and landscape (ANOVA: $F_{16} = 1.52$, $P = 0.12$), although some species showed strong differences between sites (e.g. *Dasyprocta leporina*), and others showed smaller differences (e.g. *Callicebus moloch* and *Dasypus novemcinctus*). Counter-intuitively, of the nine most ubiquitous species, six (*Dasypus novemcinctus*, *Mazama* spp., *Pecari tajacu*, *Cuniculus paca*, *Dasyprocta leporina*, and *Alouatta discolor*) were frequently hunted by local residents, suggesting that hunters were resorting to those species still persisting at these sites.

While the records of *Mazama gouazoubira* ($P = 0.58$), *Pecari tajacu* ($P = 0.44$), *Alouatta discolor* ($P = 0.66$) and *Dasypus novemcinctus* ($P = 0.64$) did not differ statistically between the three landscapes (Fig. 5b, c, d, g), *C. paca* was less frequently recorded in L3 (Fig. 5e), and the lack of significance (Kruskall–Wallis test: $K = 4.71$; $P = 0.10$) may be a type II error. *Mazama americana* (Kruskall–Wallis test: $K = 6.15$; $P = 0.04$)

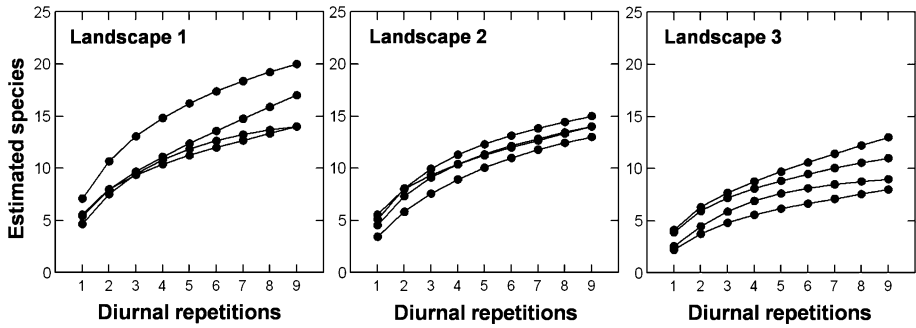


Fig. 3 Species accumulation curves estimated using the Mao-Tao index, based on nine diurnal census repetitions across the three study landscapes (see “Methods” for further details). Each curve represents one line transect

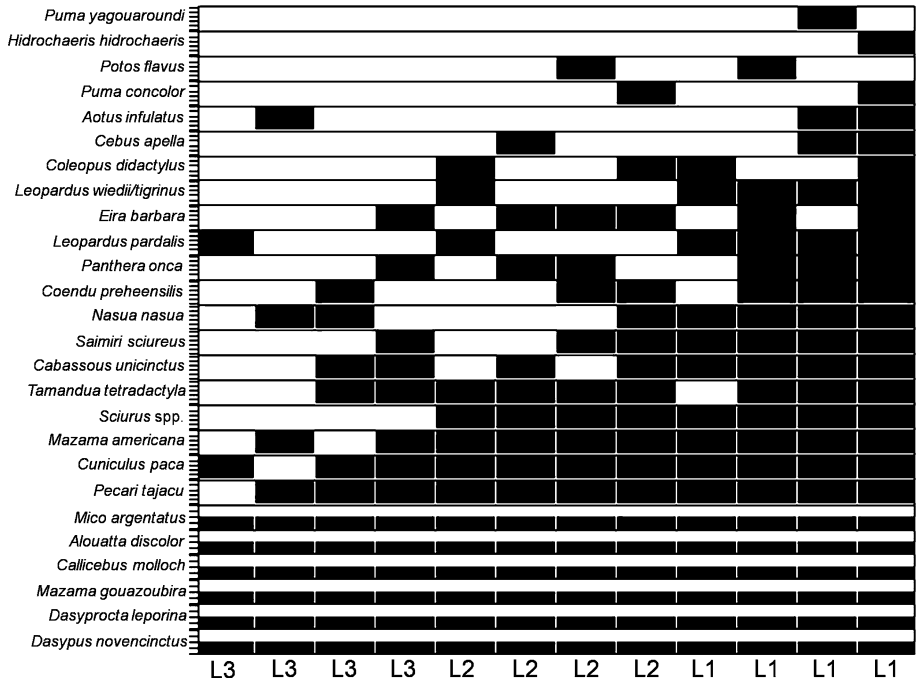


Fig. 4 Direct ordination of species occupancy in relation to the number of species detected per transect and the extent of forest cover. Landscape 1 (L1) had 84% forest cover; Landscape 2 (L2) had 65% forest cover, and Landscape 3 (L3) had 30% forest cover

and *Dasyprocta leporina* (Kruskall–Wallis test: $K = 7.54$; $P = 0.02$) were recorded at varying frequencies at the three landscapes and were more abundant in L1 (Fig. 5a, f).

The two small-bodied primates species (*Mico argentatus* and *Callicebus molloch*) were not pursued by local hunters, were frequently recorded (Fig. 5h, i), and were recorded at similar frequencies across the three landscapes ($P = 0.16$ and $P = 0.24$, respectively).

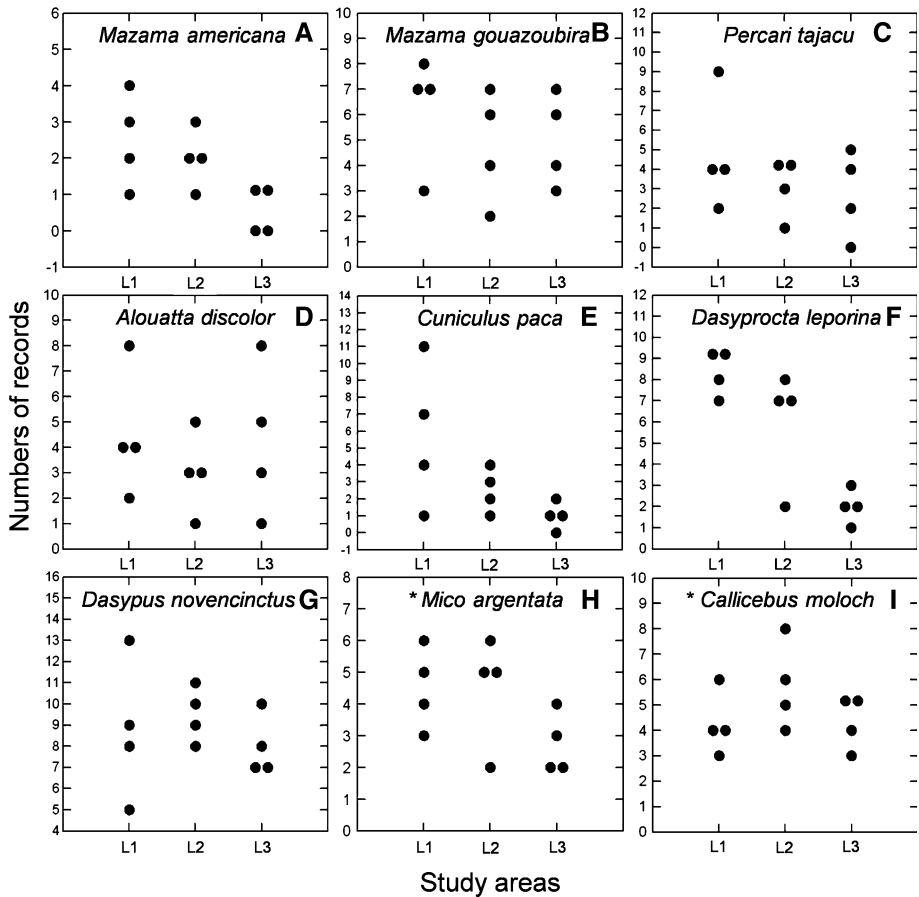


Fig. 5 Variation in the frequency of encounters during surveys for the nine most frequently recorded mammal species in each line transect within Landscape 1 (L1), Landscape 2 (L2) and Landscape 3 (L3). Asterisks indicate those species that were not reported as hunted by subsistence hunters in the local communities interviewed

Species persistence in long-term forest isolates

Although species richness in forest fragments was low compared to forest-dominated landscapes (Fig. 6), we recorded 22 midsized to large-bodied mammal species across all 16 remnants surveyed in L3 (Table 3). Forest patch size alone was a poor predictor of the number of species detected within each patch ($R^2 = 0.02$, $P = 0.57$, Fig. 6), perhaps because the largest fragment was only 361 ha. In addition, forest patch size, hunting pressure, and forest basal area considered simultaneously had no significant effect on species richness ($R^2 = 0.20$; $P = 0.43$).

Seven species that were locally reported as persistently hunted in forest fragments (*D. novencinctus*, *P. tajacu*, *M. americana*, *M. gouazoubira*, *C. paca*, *D. leporina* and *A. discolor*) were recorded more frequently than other species (Table 3). Multiple-regression models indicated that forest patch size, tree density and hunting intensity did not

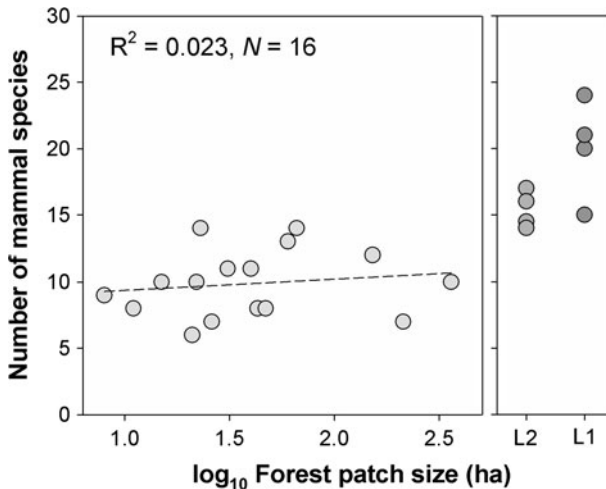


Fig. 6 Species–area relationship for all forest fragments surveyed around Alter-do-Chão (L3), and the number of species recorded along transects in the Eixo Forte area (L2) and Tapajós National Forest (L1). There was no significant relationship between patch size and estimated number of species ($P = 0.57$; $R^2 = 0.0234$; $N = 16$)

significantly affect the abundance of *M. americana* ($P = 0.97$), *M. gouazoubira* ($P = 0.16$), *P. tajacu* ($P = 0.69$), *C. paca* ($P = 0.84$), *D. leporina* ($P = 0.53$) or *A. discolor* ($P = 0.19$). The model for *D. novemcinctus* showed a small probability associated with the null hypothesis ($P = 0.07$). However, patch size ($P = 0.12$), tree density ($P = 0.46$), and hunting intensity ($P = 0.61$) did not contribute significantly to the model.

Discussion

Despite controversy over the effects of forest fragmentation (Debinski and Holt 2000), studies of many taxa have found strong evidence of lower species richness in smaller forest fragments (Fahrig 2003; Henle et al. 2004; Fisher and Lindenmayer 2007). This is, however, insufficient to indicate that small forest fragments have low conservation value (Turner and Corlett 1996). Until recently, there had been few attempts to replicate forest fragmentation studies at the landscape scale (Fahrig 2003), and few community-wide mammal studies have addressed large tropical forest landscapes, likely due to logistical difficulties in replicating multiple sampling methods (but see Michalski and Peres 2007).

Midsized, generalist species are relatively common in isolated neotropical forest fragments and are often more abundant in small patches than in continuous forest (Chiarello 2000; Lopes and Ferrari 2000; Peres 2001; Ferrari et al. 2003; Michalski and Peres 2007). However, the degree of isolation and habitat loss that these species can tolerate in the long term is poorly understood. In this study, we compared three landscapes retaining different proportions of forest cover, given that habitat loss at the landscape, and possibly at the regional scale, would most likely reduce the number of species, as predicted by Fahrig (2003). However, this may be primarily attributed to hunting pressure, rather than remaining forest cover per se. According to local residents of the local communities in the

Eixo Forte (L2) and at Alter-do-Chão (L3), several large terrestrial (e.g. *Tapirus terrestris*, *Tayassu pecari*, *Prionotes maximus*, *Dasybus kappleri*, *Myrmecophaga tridactyla*) and large arboreal mammals (e.g. *Chiropotes albinasus* and *Ateles marginatus*) had already been driven to local extinction at these sites over 30 years ago. Moreover, the low frequency of recent encounters with some species by local people in the continuous forest landscape (L1) suggests that this is primarily related to hunting rather than to the direct or indirect effects of habitat loss.

Local extinction of large mammals, as documented here, is consistent with studies elsewhere in Amazonia (Lopes and Ferrari 2000; Peres 2001; Ferrari et al. 2003; Michalski and Peres 2007). Area- and harvest-sensitive species require large areas of effectively protected forests to maintain viable populations in long term, as it remains unclear whether realistic management plans can ensure sustainable offtakes for those species. On the other hand, little can be stated about the effects of forest loss on elusive, cryptic, or otherwise infrequently recorded species, such as some carnivores and sloths because they are naturally rare and virtually undetectable during short-term surveys.

Of the infrequently recorded species in this study, *Cebus apella* and *Sciurus* spp. often persist in recently isolated forest fragments (Chiarello 2000; Ferrari et al. 2003; Michalski and Peres 2007), but these species and an arboreal procyonid (*Potos flavus*) were not recorded in forest fragments isolated by semi-natural savannah. However, local residents reported these species to occur in small fragments, so they are likely able to persist in this fragmented landscape as transient species, thereby requiring matrix movements through the scrub savannah to access multiple forests patches. Some non-game species that were recorded using any of our sampling methods in all three landscapes appear to be sensitive to human perturbation. *Saimiri sciureus*, *Aotus infulatus*, *Coendu prehensilis*, *Tamandua tetradactyla*, *Cabassous unicinctus*, *Eira barbara* and *Nasua nasua* were most abundant in continuous forest (L1) and were only rarely recorded during surveys and interviews in the other landscapes. It is unclear whether these species maintain resident populations at low densities in the forest fragments, or if our records merely represent dispersal movements from neighbouring areas of continuous forest. Recent fragmentation may create conditions that may be favourable in the short term, but cannot be maintained in long-term isolates such as those in Alter-do-Chão. Therefore, extreme caution should be taken when predicting the long-term effects of fragmentation from patterns of occupancy in recent fragments (Debinski 2006).

Although we caution in comparing the three landscapes due to the limited sampling and the spatial patterns of the surveys sites, mammal species richness was clearly highest in L1 and lowest in L3, and the depauperate species assemblages could be considered a nested subset of the more species-rich sites. It is probable that several persistent species could form a meta-population in fragmented areas (Hanski and Ovaskainen 2000) and some individuals could disperse from forested areas, as occasionally reported by local people. The persistence of Amazonian vertebrate species depends on their intrinsic dispersal capability and the connectivity among disturbed sites (Dale et al. 1994).

Forest cover had varying effects on different mammal species. Some species were relatively common in all three landscapes, including primates (*Alouatta discolor*, *C. moloch* and *M. argentata*), ungulates (*Mazama* spp., *P. tajacu*), large rodents (*D. leporina*, *C. paca*) and xenarthrans (*D. novemcinctus*), even though some terrestrial mammals (*M. americana*, *D. leporina* and *C. paca*) occurred at higher abundances in continuous forest. These species are known to be highly resilient to hunting pressure (Bodmer et al. 1997; Peres 2000), and comprise an important source of protein for local residents because sustainable harvests can be maintained even in large forest fragments (Peres 2001). Except for *C. paca*, the seven

top-ranking game species killed by local residents exhibit relatively high reproductive rates (Robinson and Redford 1991) and are apparently less sensitive to hunting pressure in both continuous forest (Bodmer et al. 1997; Peres 2000) and forest fragments (Cullen-Junior et al. 2000; Lopes and Ferrari 2000; Peres 2001). These species are also highly tolerant of disturbed forest habitat and edge-dominated forest fragments (Chiarello 2000; Peres 2001; Michalski and Peres 2007). Thus, the persistence of these species is best explained by their life history traits, rather than the characteristics of the three landscapes or any given forest fragment.

Andr n (1994) indicated an exponential effect of forest fragmentation on species distributions in landscapes retaining less than 30% of habitat cover. However, the permeability of the matrix can affect connectivity among habitat patches (Laurance 1991) and the relationship between the proportion of habitat remaining and matrix connectivity needs further investigation (Metzger and D camps 1997). Brown (1971) suggests that the relationship between species richness and forest fragment size can be affected by the post-isolation “relaxation” time (e.g. Ferraz et al. 2007). Long-lived taxa that are sensitive to habitat loss have a greater probability of being recorded in larger forest fragments several years or even decades following isolation; however, these populations may eventually succumb to local extinctions. In addition, negative indirect effects of forest fragmentation can operate strongly over time, as has been shown for birds (Feeley and Terborgh 2008). Although our most disturbed landscape (L3) retained less than 30% of forest cover, and local variables including patch size had no effect on patch-scale species richness, many species persisted in the most fragmented and least forested landscape (L3) despite the fact that most fragments were typically small (<152 ha). It is unlikely that even the largest fragments within this landscape could sustain viable populations of any of the species if individuals could not traverse the savannah matrix.

The historically fragmented landscape (Alter-do-Ch o; L3) and the variegated landscape (Eixo Forte; L2) remain entirely unprotected, but still retained about 70% (L1) and 88% (L2) of the regional midsized to large-bodied mammal fauna. In Alter-do-Ch o, this is despite a long history of persistent hunting pressure which dates back to one of the earliest prehistoric pottery excavated in the Western Hemisphere, namely the climax of the Tapaj  Indian Chiefdom which was centered in this region some 7,000 years ago (Roosevelt et al. 1991).

This study can be interpreted as a window into possible future scenarios for landscape transformation in Amazonia or elsewhere in the humid tropics. Large protected areas are critical for conserving the world’s tropical biota, but these alone will not be able to safeguard all species. The future of many species of indigenous plants and animals is closely tied to land use in human-dominated landscapes (Peres et al. 2010). Some 37% of Brazilian Amazonia is already protected to varying degrees, which may be sufficient to safeguard virtually all mammal species (Azevedo-Ramos et al. 2006). Brazilian forestry legislation [Law No. 4.771 of 1965; updated in 2001 (MP 2.166-67)] requires that protected areas should be set aside within 80% of the total area of private landholdings in the Amazon, but this minimum target is under severe political pressure from the agricultural sector in Brazil. In addition, Brazilian wildlife legislation prohibiting hunting (Law No. 5.197 of 1967) may or may not be enforced. Should these legal provisions be effective in maintaining the structural connectivity of the landscapes and providing source areas for game populations, it is likely that most or all of the midsized to large-bodied mammal species would persist within privately owned landscapes around large protected areas. Given this perspective, compliance with existing forestry legislation, and implementation of effective game management plans and more sustainable patterns of land-use, including

agro-forestry, can greatly facilitate the persistence of forest biodiversity in increasingly human-dominated tropical forest landscapes.

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