

# Conservation Value of Remnant Riparian Forest Corridors of Varying Quality for Amazonian Birds and Mammals

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**Abstract:** Forest corridors are often considered the main instrument with which to offset the effects of habitat loss and fragmentation. Brazilian forestry legislation requires that all riparian zones on private landholdings be maintained as permanent reserves and sets fixed minimum widths of riparian forest buffers to be retained alongside rivers and perennial streams. We investigated the effects of corridor width and degradation status of 37 riparian forest sites (including 24 corridors connected to large source-forest patches, 8 unconnected forest corridors, and 5 control riparian zones embedded within continuous forest patches) on bird and mammal species richness in a hyper-fragmented forest landscape surrounding Alta Floresta, Mato Grosso, Brazil. We used point-count and track-sampling methodology, coupled with an intensive forest-quality assessment that combined satellite imagery and ground truthed data. Vertebrate use of corridors was highly species-specific, but broad trends emerged depending on species life histories and their sensitivity to disturbance. Narrow and/or highly disturbed riparian corridors retained only a depauperate vertebrate assemblage that was typical of deforested habitats, whereas wide, well-preserved corridors retained a nearly complete species assemblage. Restriction of livestock movement along riparian buffers and their exclusion from key areas alongside deforested streams would permit corridor regeneration and facilitate restoration of connectivity

**Keywords:** Amazonia, habitat connectivity, habitat fragmentation, habitat quality, riparian forest, tropical forest, wildlife corridors

El Valor de Conservación de Corredores Forestales Riparios Remanentes con Calidad Variable para Aves y Mamíferos Amazónicos

**Resumen:** Los corredores forestales a menudo son considerados el principal instrumento mediante el cual se atenúan los efectos de la pérdida y fragmentación del hábitat. La legislación silvícola brasileña requiere que todas las zonas riparias en terrenos privados sean mantenidas como reservas permanentes y define anchura mínima de los bosques riparios amortiguadores que deben ser retenidos a lo largo de ríos y arroyos permanentes. Investigamos los efectos de la anchura y del estatus degradación del corredor en 37 sitios forestales riparios (incluyendo 24 corredores conectados a parches forestales extensos, 8 corredores forestales no conectados y 5 zonas riparias control embebidas en parches de bosque continuos) sobre la riqueza de aves y de mamíferos en un paisaje forestal hiperfragmentado en Alta Floresta, Mato Grosso, Brasil. Utilizamos métodos de conteo por puntos y muestreo de huellas, además de una evaluación intensiva de la calidad del bosque que combinó imágenes de satélite y datos de verificación en campo. El uso de corredores por vertebrados fue altamente específico, pero emergieron patrones generales dependiendo de las historias de vida de las especies y de su sensibilidad a la perturbación. Los corredores riparios angostos y/o muy perturbados retuvieron un ensamble de vertebrados muy pobre que fue típico de hábitats deforestados, mientras que los corredores

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*amplios, bien preservados retuvieron un ensamble de especies casi completo. La restricción del movimiento de ganado a lo de los corredores y su exclusión de áreas clave a lo largo de arroyos deforestados permitiría la regeneración de corredores y facilitaría la restauración de la conectividad.*

**Palabras Clave:** Amazonia, bosque ripario, bosque tropical, calidad de hábitat, conectividad de hábitat, corredores para vida Silvestre, fragmentación de hábitat

## Introduction

The efficacy of wildlife corridors in facilitating animal movements between habitat patches remains controversial (Rosenberg et al. 1997; Beier & Noss 1998; Bennett 2003), but most forest taxa appear to respond positively to their presence. Corridors can be used by forest wildlife as movement corridors, conduits through which animals can disperse or commute between forest patches, and habitat linkages (forest habitat that supports resident populations or links populations among patches) (Rosenberg et al. 1997; Lidicker 1999). Corridors should theoretically facilitate gene flow between forest remnants and reduce rates of stochastic extinction (Fahrig & Merriam 1994) and the potential for deleterious genetic effects brought about by inbreeding depression (Brown et al. 2004).

Corridors have been delimited arbitrarily into 2 types: biodiversity conservation corridors (“biologically and strategically defined subregional space[s] selected as a unit for large-scale conservation planning and implementation”) and biological corridors (“elongated and continuous patch[es] of habitat that maintain[s] connectivity allowing the flux of individuals between 2 or more areas”) (Sanderson et al. 2003). Biodiversity conservation corridors obviously function as biological corridors but such “megacorridors” are financially and politically costly to implement. On the other hand, narrow forest corridors, which usually course along waterways, are ubiquitous in many tropical landscapes. These riparian corridors are either natural (e.g., gallery forests in tropical savannas) or anthropogenic features of the landscape (e.g., remnant riparian buffers set aside following deforestation), yet their role in biodiversity conservation remains poorly understood.

Current rates of tropical deforestation are unprecedented, and this forest loss is most acute in Brazilian Amazonia, where by 2005 the total forest area cleared had reached some 70 Mha (INPE 2006). Efforts to mitigate forest conversion have focused on the creation of vast protected areas where there is the potential to link them into reserve networks (Peres 2005; da Silva et al. 2005). Nevertheless, forest retention in a growing area of smallholdings and large private properties is also essential for the preservation of Amazonian biodiversity (Soares-Filho et al. 2006). Clearcutting operations by private landowners in Brazilian Amazonia are legally

required to set aside a riparian forest strip along rivers and perennial forest streams in the form of “permanent protection areas” (APPs). These riparian buffers are protected by Brazilian federal legislation since 1965, which designated fixed minimum widths of forest buffers alongside waterways (e.g., 30 m for streams narrower than 10 m [Código Florestal 2001]), although levels of compliance with minimum legal requirements are highly variable (Resque et al. 2004). The conservation role of APPs presumably increases in highly deforested regions, such as the “Arc of Deforestation” of southern and eastern Amazonia, which encompasses 524 municipal counties inhabited by 10,331,000 people in the states of Rondônia, Mato Grosso, Pará, Tocantins, and Maranhão.

In terms of wildlife habitat requirements, the minimum width and structural preservation status of remnant forest corridors form a contentious policy area that is yet to be investigated, but these are likely to be highly variable across different taxa depending on their relative sensitivity to edge and area effects (e.g., Spackman & Hughes 1995; Laurance & Laurance 1999). This is surprising because corridors are often accessible and relatively easy to sample, and ground truthing data can be readily related to spectral information derived from satellite imagery. Lima and Gascon (1999), who published the only study on the utility of riparian corridors to Amazonian forest wildlife, found no significant compositional differences in small-mammal and litter-frog communities between linear remnants and continuous forest. Their results suggest that corridors are important for at least these small vertebrate taxa that have small area requirements.

We addressed the biodiversity value of tropical forest corridors by investigating vertebrate-species occupancy of remnant riparian buffers in a hyper-fragmented forest landscape of southern Amazonia. We compared patterns of species richness and composition between remnant riparian buffers and adjacent riparian sites embedded in large areas of largely undisturbed continuous forest. We focused on bird and mammal species that use corridors of variable quality and traversing a matrix of actively managed cattle pastures. Specifically we examined the minimum width and structural integrity of corridors required to maintain vertebrate assemblages compared to those of continuous primary forest and whether the functional utility of corridors connected to large forest patches is higher than that of entirely isolated corridors.

## Methods

### Sampling Sites

Extensive road paving and several large agricultural resettlement programs during the 1970s catalyzed massive forest clearance in southern Amazonia. The countryside around the town of Alta Floresta, Mato Grosso, Brazil (09°53'S; 56°28'W; Fig. 1) is in the central Amazonian Arc of Deforestation and is an ideal model landscape in which to study the effects of habitat fragmentation and perturbation (Peres & Michalski 2006). A complete description of the study landscape is presented elsewhere (Michalski & Peres 2005; Lees & Peres 2006).

From May to October 2005, we conducted 444 unlimited-radius point counts at 222 sampling stations in 37

riparian forest sites (6 stations/site), including 24 connected corridors, 8 unconnected corridors (isolated by >300 m from the nearest forest patch), and 5 control sites within large patches (11,030 – 144,700 ha) of undisturbed primary forest. Corridors were widely distributed throughout a ~6000-km<sup>2</sup> landscape and separated by >500 m (mean [SD] distance = 28.2 km [15.8] km; Fig. 1 & Supplementary Material).

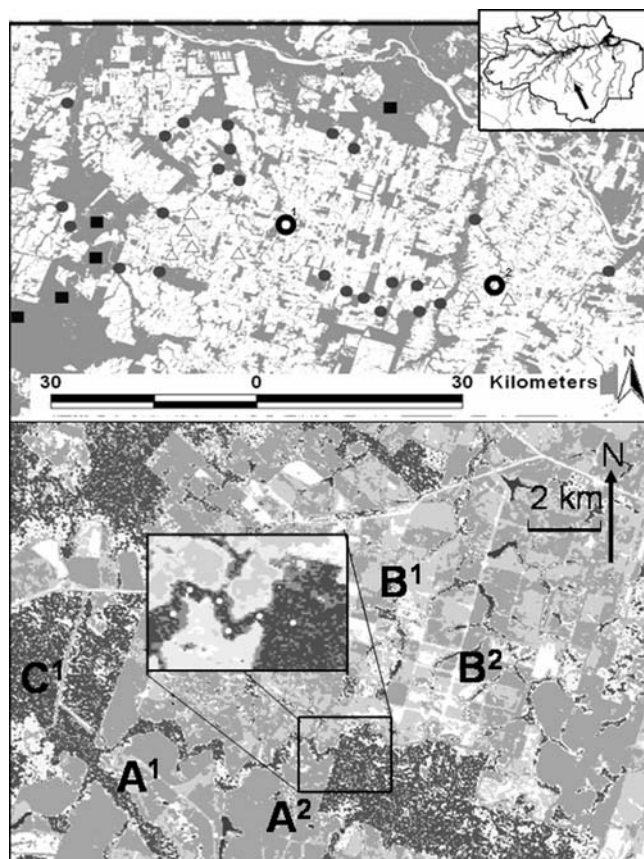
### Avian and Mammal Surveys

Each site was surveyed twice, with a 75-d interval between sampling. Six point-count sites (PC stations) were located along each riparian corridor. The first was embedded well within the source patch (>200 m from the forest edge), the second was 50 m from the patch-corridor node, and the other 4 were located 200 m to 850 m apart (Fig. 1). We considered all species except waterbirds (e.g., herons, rails), nocturnal species (e.g., owls, potoos, nightjars), and aerial insectivores (swifts and hirundines). We also assigned each bird species to 1 of 4 classes of forest habitat specificity (Stotz et al. 1996) (defined in Table 1). For a full description of the categorization scheme, a species list, and category scores see Lees and Peres (2006).

Mammal presence and absence data were recorded for diurnal primates on the basis of acoustic and visual detection events and were obtained concurrently with the avifaunal surveys during the PC sampling periods. Presence or absence of large terrestrial mammal species (ungulates, carnivores, large rodents, and armadillos) was determined through intensive searches for tracks along a 100-m riparian forest section just at the stream edge. Both the avian and mammal surveys should be regarded as conservative with respect to corridor-width effects; however, surveys in narrow (<100 m wide) and unconnected corridors were exhaustive (see Supplementary Material).

### Corridor, Patch, and Landscape Metrics

We measured corridor width perpendicular to the corridor length at each PC station with a Hip-Chain and Landsat image. We combined a ground truthed assessment of forest quality with a pixel-scale remote-sensing approach to determine the quality of forest patches. Following a 2-stage unsupervised classification of the Landsat image, we were able to unambiguously resolve 8 mutually exclusive land-cover classes ranging from closed-canopy forest to bare ground (Michalski & Peres 2005). Then we extracted landscape variables from the Landsat image with Fragstats (version 3.3, McGarigal et al. 2002) and ArcView (version 3.2, Environmental Systems Research Institute, Redlands, California). We calculated the total area of source patches connected to corridors by artificially eroding their narrowest connections, usually to corridor bottlenecks near the patch node. Erosion of connections was always carried out across the narrowest groups of 15 × 15 m pixels



**Figure 1.** Map of study area around Alta Floresta, Mato Grosso, Brazil (09°53'S; 56°28'W), showing the sites sampled in connected (solid circles) and unconnected (open triangles) forest corridors and control sites (solid squares) embedded within continuous forest sites. Forest and nonforest cover are shaded gray and white, respectively. Open circles denote urban areas and 1 is Alta Floresta and 2 is Carlinda. Rectangular insets (lower panel) show examples of connected (A) and unconnected (B) corridors and a control site in continuous forest (C).

**Table 1.** Mean structural characteristics and species richness across the 37 riparian forest (RF) sites studied in the Alta Floresta region, including 24 connected corridors (CC), 8 unconnected corridors (UC), and 5 riparian forest sites embedded within large areas of continuous forest (CF).<sup>a</sup>

Variable	Riparian forest type (SD)			ANOVA <sup>b</sup>		Percent variance <sup>c</sup> explained by	
	CC	UC	CF	F	p	RF type	corridor subset
Habitat							
corridor width (log <sub>10</sub> m) <sup>d</sup>	280.43 (153.68)a	164.53 (37.02)b	—	9.04	<0.001	64.22	5.98
source patch size (log <sub>10</sub> ha) <sup>d</sup>	3.37 (0.80)b	—	4.73 (0.58)b	—	<0.001	90.76	9.24
spectral forest quality	7.98 (0.76)a	6.52 (0.76)b	8.43 (0.22)b	8.67	<0.001	46.89	18.93
mean height of vertical <sup>d</sup> profiles	260.63 (31.75)a	214.12 (49.82)b	—	5.17	<0.001	28.53	26.03
tree density (stems/ha)	256.52 (83.45)	196.88 (106.65)	293.0 (86.19)	2.04	0.002	15.34	14.32
tree basal area (m <sup>2</sup> /ha)	25.83 (12.17)a	17.22 (11.42)a	36.87 (14.68)b	30.75	<0.001	26.46	19.07
nonpalm tree basal area (m <sup>2</sup> /ha)	24.26 (8.32)a	13.43 (5.68)b	36.87 (9.03)c	5.52	<0.001	38.82	14.72
understory density	5.32 (1.61)a	3.28 (1.8)b	6.8 (1.14)a	20.17	<0.001	22.84	12.47
canopy cover (%)	71.38 (24.43)a	38.22 (34.60)b	83.72 (11.93)a	6.83	<0.001	37.56	20.91
bamboo abundance	0.60 (0.83)a	1.06 (1.29)b	0.73 (1.00)	7.99	<0.001	0.0	50.98
<i>Mauritia</i> palm abundance	0.69 (0.92)a	1.81 (0.77)b	0.20 (0.21)a	9.67	<0.001	32.27	33.04
Species richness							
all birds	100.70 (21.19)a	70.62 (12.88)b	141.4 (6.38)c	6.40	<0.001	42.43	15.47
birds (S1) <sup>e</sup>	13.46 (8.60)a	2.38 (1.77)b	29.8 (6.22)c	6.49	<0.001	47.34	12.13
birds (S2) <sup>e</sup>	39.36 (13.29)a	17.87 (4.64)b	65.8 (1.92)c	10.10	<0.001	54.97	15.60
birds (S3) <sup>e</sup>	36.00 (5.17)a	30.50 (5.20)b	40.2 (2.77)a	1.89	0.003	1.97	11.81
birds (S4) <sup>e</sup>	11.79 (4.97)a	19.50 (7.72)b	5.60 (2.97)a	8.23	<0.001	48.93	16.18
all mammals	8.33 (1.49)a	5.5 (2.92)b	9.4 (1.34)a	2.90	<0.001	21.28	10.61
large terrestrial mammals	3.52 (1.39)a	2.39 (1.54)b	4.38 (1.01)a	2.97	<0.001	24.37	16.40
primates	2.62 (1.01)a	1.88 (0.64)a	3.0 (0.70)a	1.23	0.197	4.18	0.88

<sup>a</sup>Group means of variables were tested with Tukey multiple comparisons. Different letters represent significant differences at  $\alpha = 0.05$  among riparian forest types where differences among sites were significant within analysis of variance.

<sup>b</sup>The analysis of variance (ANOVA) F tests are nested ANOVAs in which the 222 point-count (PC) stations were nested within each type of remnant corridor or undisturbed control site.

<sup>c</sup>Variance component analysis was used to estimate the amount of variability contributed by each hierarchical site factor (PC station nested within corridor subsets, which were nested within corridor type).

<sup>d</sup>Comparisons between only connected and unconnected corridors.

<sup>e</sup>Habitat-sensitivity classes for birds: S1, all strict forest understory and midstory species; S2, all remaining species dependent on primary forest; S3, forest species able to tolerate secondary or highly degraded forest; S4, primarily nonforest species including scrub and open-habitat countryside species.

in the most disturbed forest-cover class such as young second growth. A forest-quality index was then computed for each PC station on the basis of the number of pixels representing each land-cover class, incorporating the nearest 10 pixels around each station. Structural forest habitat variables quantified at each PC station included stand (palm and nonpalm) basal area, mean understory density, and canopy cover. In addition we also quantified the abundance of understory bamboo (*Guadua* sp.) and Buriti palms (*Mauritia flexuosa*), intrusion by cattle, and hunting pressure (see Supplementary Material).

We took standardized digital photographs of a 100-m-wide segment (centered at each PC station) of vertical corridor profiles from 120 m perpendicular to the forest edge. We used these images to determine corridor forest quality. The images were then analyzed with Pixel Counter (A. Etchells, University of East Anglia, Norwich, United Kingdom), which counted forest (dark) pixels in one-pixel-wide columns across the image and calculated a mean and SD for each image (see Supplementary Ma-

terial). Estimates of forest height were derived by calibrating the pixel heights with measurements of corridor height with a clinometer. This provided another estimate of forest perturbation: less-disturbed corridors had a taller and more uniform canopy profile, whereas disturbed corridors were often heavily invaginated following a history of selective logging and tree mortality induced by edge effects.

### Data Analysis

Forest patch size is a key predictor of faunal diversity and explains 96% of bird (Lees & Peres 2006) and >90% of mammal (F. Michalski & C.P., unpublished data) species richness in the Alta Floresta forest fragments. Therefore we used the following strategy to examine patterns of bird and mammal species richness. First we evaluated differences between all 3 riparian forest types with one-way and nested analysis of variance (ANOVA) and variance component analyses in which measurements at each PC

station ( $n = 222$ ) were nested within each corridor (or control site) associated with variable-sized patches.

Second we modeled species richness ( $S$ ) at the 192 PC stations along all 32 connected and unconnected corridors with generalized linear mixed models (GLMMs) in which  $S$  estimates were assumed to be nested within clusters (corridors) over which the random effects varied. The GLMMs were fitted to model different forest, patch, and landscape variables that were entered as fixed effects. In different models we incorporated either corridor type or size of the source patch [ $\log_{10}(x + 1)$ ] as a fixed effect, but patch size of unconnected corridors was assumed to be zero.

Third we used analyses of covariance (ANCOVAs) to test whether the slopes of species-corridor width relationships differed significantly between connected and unconnected corridors. Fourth we evaluated species richness along connected corridors at the 6 PC stations placed at varying distances from source patch nodes by standardizing local species richness ( $S_{PCi}$ ) in relation to the source patch to which it was connected ( $S_{SP}$ ). Changes in  $S$  ( $\Delta S$ ), expressed as  $\Delta S = (S_{PCi} / S_{SP}) - 1$ , therefore, ignored differences in the total number of species retained within the 24 source patches and could be modeled with a binomial error distribution across all connected sites with GLMs. Minimum GLMM and GLM models were fitted within the R platform (Ihaka & Gentleman 1996) and selected based on a supervised information-theoretic approach with the Akaike's information criterion (AIC) (Burnham & Anderson 2002).

Finally we investigated variation in species composition among sites with nonmetric multidimensional scaling ordinations (MDS; Clarke & Green 1988) with the Bray-Curtis dissimilarity measure of presence-absence matrices and an analysis of similarity (ANOSIM; Faith et al. 1987). We used the BIO-ENV procedure within PRIMER (Carr 1996) to determine which combination of variables most influenced community composition (see Supplementary Material).

## Results

### Corridor Forest Structure

Riparian forests (RF) around Alta Floresta were highly heterogeneous both in terms of their patch metrics and preservation status whether we considered unnested comparisons or nested ANOVAs in which the 222 PC stations were nested within the 37 RF sites (Table 1). Stand basal area was significantly different among the 3 types of RF sites (one-way ANOVA;  $F = 38.2$ ,  $df = 31$ ,  $p < 0.001$ ). Remnant connected corridors retained a significantly higher structural integrity in terms of their width, basal area, canopy structure, and height (estimated by vertical pixel counts) compared with those that had lost connectivity to source patches. Corridor height differed

significantly between the taller and more structurally uniform connected corridors and the lower-stature and more degraded unconnected corridors (ANOVA;  $F = 9.6$ ,  $df = 31$ ,  $p < 0.004$ ). Across the 32 corridors, mean width was positively correlated with spectral forest quality ( $r = 0.592$ ,  $p < 0.001$ ), corridor height ( $r = 0.425$ ,  $p = 0.015$ ), nonpalm tree basal area ( $r = 0.317$ ,  $p = 0.077$ ), and canopy cover ( $r = 0.473$ ,  $p = 0.006$ ). Cattle intrusion occurred in 70% and 89% of all connected and unconnected corridor plots, respectively, although wire fences were only erected in 16% and 2% of connected and unconnected corridor plots, respectively. Cattle intrusion, however, may have been suppressed or restricted in some plots by dense stands of bamboo (*Guadua* sp.), which occurred in 24% of connected corridor plots, 40% of unconnected corridor plots, and 33% of control plots. *Mauritia* palms occurred in 42% of connected corridor plots, 90% of unconnected corridor plots, and 16% of control plots.

### Bird Assemblages

We recorded 17,999 detections of 365 bird species during 444 point counts. Mean corridor width was a significant predictor of bird species richness per corridor ( $R^2 = 0.393$ ,  $p < 0.001$ ,  $n = 32$ ). There was a critical width threshold of  $\sim 400$  m beyond which species accumulation did not increase significantly (Fig. 2). Other highly significant predictors included spectral forest quality ( $R^2 = 0.473$ ,  $p < 0.001$ ) and the distance from the nearest of the 2 major urban centers (Alta Floresta or Carlinda) ( $R^2 = 0.372$ ,  $p < 0.001$ ). Less important but still significant determinants of bird species richness included nonpalm basal area ( $R^2 = 0.242$ ,  $p = 0.002$ ), mean corridor height ( $R^2 = 0.111$ ,  $p = 0.035$ ), and canopy cover ( $R^2 = 0.157$ ,  $p = 0.014$ ).

Bird species were widely variable in their persistence in the 3 types of riparian forests. Some taxa (e.g., Red-bellied Macaw [*Orthopsittaca manilata*] and other psittacids) were nearly ubiquitous across all sites and were more abundant in unconnected corridors because of the higher abundance of *Mauritia* palms, one of their key food plants. Likewise, some riverine specialist passerines (e.g., Silvered Antbird [*Sclateria naevia*]) were frequently encountered in all 3 riparian forest types and were only absent in the most degraded sites. Levels of species richness in control sites were far higher than in either corridor types, and more species occurred in connected than in unconnected corridors. Some species conspicuously absent from unconnected corridors were common in connected corridors (e.g., Black-tailed Trogon [*Trogon melanurus*]), whereas others were common in control sites and rare or absent in both corridor types (e.g., Cinereous Antshrike [*Thamnomanes caesius*]).

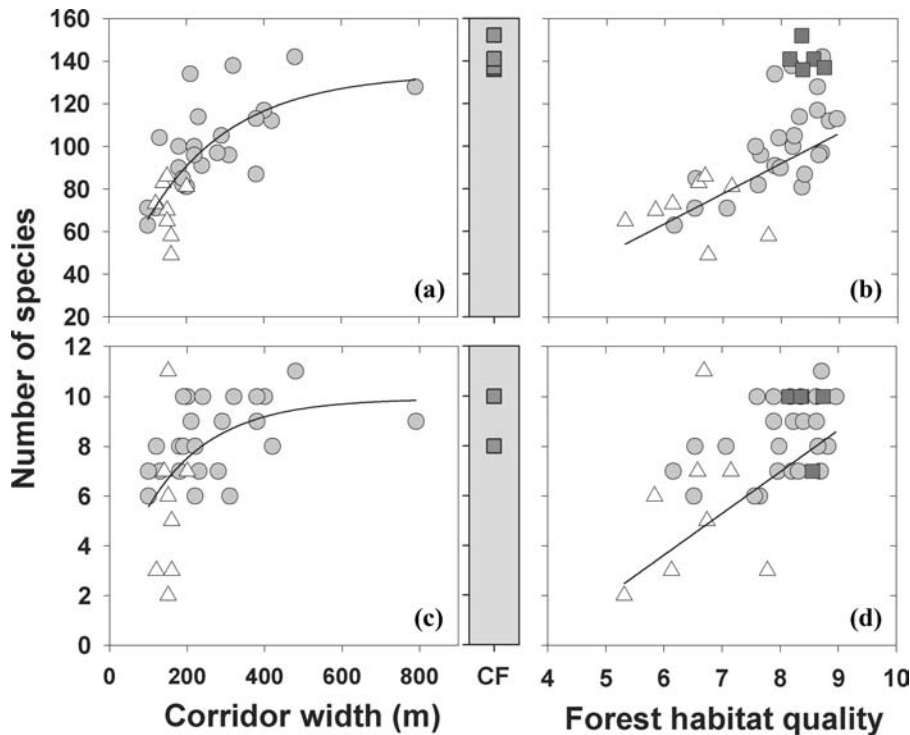


Figure 2. Relationships between vertebrate species richness and mean corridor width and forest quality for riparian forest corridors that are either connected (shaded circles) or unconnected (open triangles) to large forest patches and control sites within continuous forest patches (CF, dark-shaded squares): (a, b) birds and (c, d) mammals.

Bird species richness was affected by different patch and landscape characteristics in connected and unconnected corridors and control sites, but responses were highly species-specific. The most significant positive predictors of the number of primary forest-sensitive species (classes 1–2) retained in riparian corridors were (in order of importance) corridor width, size of source patch, and forest basal area (Table 2; Fig. 3), whereas *Mauritia* palm abundance and cattle intrusion had a negative effect. Conversely the less-sensitive species (classes 3–4) were negatively affected by forest canopy cover, but positively affected by *Mauritia* palm abundance and source patch size. Forest-sensitive species responded to bamboo abundance and corridor height and width, whereas less-sensitive species were more likely to occur in sites of low forest quality, which contained a more heterogeneous vertical profile. For the riparian sites within large forest patches, canopy cover was the only significant variable retained for the most sensitive species, and there were more less-sensitive species in low-quality patches.

In connected corridors only, a higher fraction of the species richness in adjacent source patches was lost with increasing distance from these patches ( $p = 0.020$ ), but  $\Delta S$  was also significantly depressed at narrow corridor sites ( $p < 0.001$ ), which contained lower canopy cover ( $p = 0.002$ ) and a spectral index of poorer quality ( $p = 0.042$ ), particularly where cattle intrusion had regularly taken place ( $p = 0.016$ ). This species decay along corridors was very pronounced within 50 m of the patch node, but was more gradual with increasing distance from the source patch (Fig. 4).

According to the BIO-ENV analysis, the most important grouping of variables predicting community structure among all 37 sites were corridor width, spectral forest quality, *Mauritia* palm abundance, and cattle intrusion ( $R = 0.544$ ). Excluding the 5 control sites, spectral forest quality and bamboo and *Mauritia* abundance were the most important combination of variables ( $R = 0.402$ ). Unconnected corridors and narrow connected corridors retained far fewer species than wide, connected corridors and control riparian areas, and MDS scores indicated they were more dissimilar from one another in assemblage composition (Fig. 5). Similarly, community composition differed significantly among all riparian sites (overall ANOSIM  $R = 0.501$ ,  $p < 0.05$ ) and between the 3 riparian types (overall ANOSIM  $R = 0.319$ ,  $p < 0.05$ ).

### Mammal Assemblages

We detected 794 tracks of 22 species of non primate mammals and 226 sightings of 5 primate species. Corridor width was a significant predictor of mammal species richness (all species combined:  $R^2 = 0.192$ ,  $p < 0.012$ ,  $n = 32$ ; large terrestrial mammals:  $R^2 = 0.147$ ,  $p < 0.017$ ), but not of primates alone ( $R^2 = 0.076$ ,  $p < 0.127$ ). The quality of the forest habitat was also a significant predictor of mammal species richness ( $R^2 = 0.312$ ,  $p = 0.001$ ). Less important, but still significant, determinants included mean corridor height ( $R^2 = 0.132$ ,  $p = 0.023$ ) and canopy cover ( $R^2 = 0.161$ ,  $p = 0.013$ ).

As with birds, responses to corridors were highly species-specific (Table 2). Some species (e.g., small

**Table 2.** Minimum, generalized linear mixed models (GLMMs) of bird and mammal species richness in 24 connected and 8 unconnected corridors, accounting for point-count (PC) sites nested within clusters (corridors).<sup>a</sup>

Variable	Birds						Mammals					
	all (358 species)		primary- forest specialists (207 species)		edge and second-growth tolerant (151 species)		all (18 species)		large (13 species)		primates (5 species)	
	$\beta$	p	$\beta$	p	$\beta$	p	$\beta$	p	$\beta$	p	$\beta$	p
Intercept	-5.051	0.550	-25.531	<0.001	22.828	<0.001	-1.634	0.248	-0.960	0.432	-0.262	0.563
Corridor width (m)	1.623	0.020	13.944	<0.001	-1.575	0.524	1.599	0.012	0.945	0.086		
Patch size (ha) <sup>b</sup>	0.113	0.059	1.497	0.019	0.251	0.519	0.188	0.048	0.203	0.030		
Mean height <sup>c</sup>	0.009	0.509	0.002	0.842	0.010	0.241	0.004	0.107	0.002	0.180	0.001	0.258
Spectral forest quality			0.546	0.352	-0.671	0.158					0.070	0.221
Tree basal area (m/ha)			0.087	0.060			0.022	0.041	0.026	0.004		
Understory density											0.037	0.104
Canopy cover (%)			0.026	0.198	-0.036	0.021						
Bamboo abundance	1.099	0.092	0.641	0.207			0.277	0.014	0.330	<0.001		
<i>Mauritia</i> palms	-1.129	0.109	-1.239	0.024								
Cattle intrusion	-1.460	0.415	-0.622	0.650			-0.597	0.063	-0.380	0.149	-0.216	0.169
Hunting score											0.117	0.201

<sup>a</sup>Coefficients ( $\beta$ ) and their respective p values are listed for all variables retained in the best models; blank cells indicate excluded variables (variables not included in the best models).

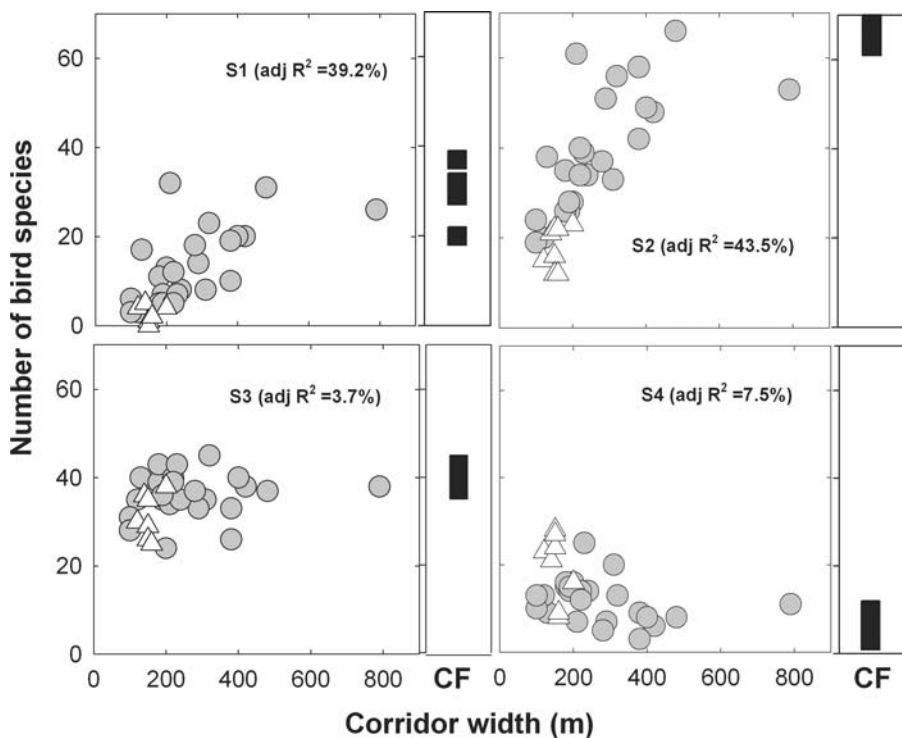
<sup>b</sup>Log<sub>10</sub> transformed.

<sup>c</sup>Mean height (in pixels) of corridor vertical profiles based on digital photographs (see text).

armadillos, *Dasypus* spp.) were ubiquitous, whereas others (e.g., *Capybara* [*Hydrochoerus hydrochaeris*]) were encountered more frequently in corridors than in control sites. Nevertheless, encounter rates for most species were lower in corridors than in control sites. Some species were common in control sites and connected corridors

but rarer in unconnected corridors (e.g., paca [*Agouti paca*]), whereas others were conspicuously absent from both corridor types (e.g., spider monkey [*Ateles* sp.]).

Mammal species richness was affected by different predictor variables across the 3 types of sites. In connected corridors, source patch size was the most important



**Figure 3.** Relationships between species richness and corridor width for 4 functional groups of bird species with varying degrees of habitat sensitivity (sensitivity classes; S1, all strict forest understory and midstory species; S2, all remaining species dependent on primary forest; S3, forest species able to tolerate secondary or highly degraded forest; S4, primarily nonforest species including scrub and open-habitat countryside species). Open triangles, gray circles, and black squares indicate unconnected corridors, connected corridors, and control riparian sites, respectively.

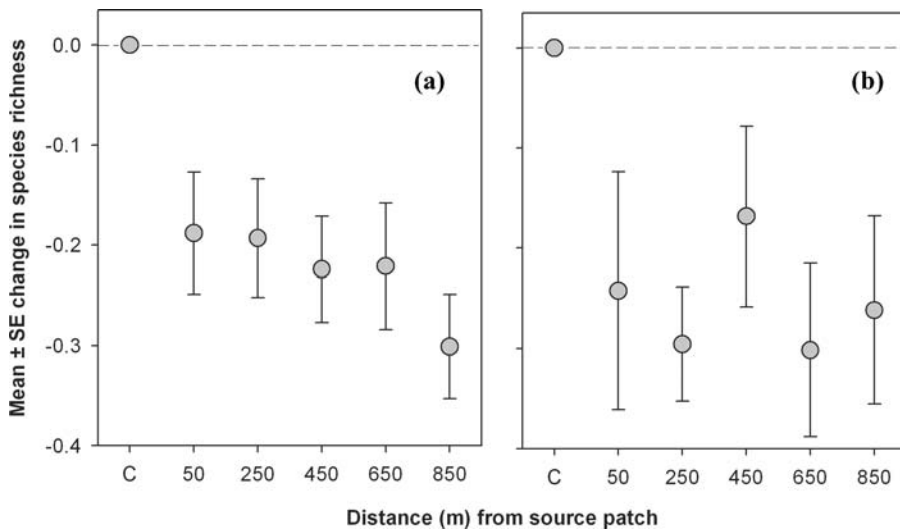


Figure 4. Changes in species richness ( $\Delta S$ ) for (a) birds and (b) mammals along connected corridors as a function of distance from their respective source-forest patch nodes.

predictor, followed by corridor width, corridor height, canopy cover, bamboo abundance, and hunting pressure. In unconnected corridors, the only 2 variables retained in the GLMs were *Mauritia* palm abundance and SD of corridor height. Few variables had a strong effect on the control sites, but those retained in the GLMs included nonpalm basal area and understory density (Table 2).

For the BIO-ENV analyses, the most important grouping of variables predicting mammal community composition across all 37 sites were patch size, spectral forest quality, distance to the nearest urban center, bamboo abundance, and presence of cattle ( $R = 0.368$ ). Excluding the 5 control sites, patch size, distance to urban center, understory density, bamboo abundance, and spectral forest quality were the most important combination of variables ( $R = 0.343$ ). The MDS scores showed a more diffuse scatter of control sites, although the same broad trend of increasing similarity in assemblage composition of large patches and control sites was apparent (Fig. 5). Community composition did not differ significantly among all riparian

sites (overall ANOSIM  $R = 0.115$ ,  $p = 0.28$ ) but was significantly different among the 3 sampled riparian types (overall ANOSIM  $R = 0.509$ ,  $p < 0.001$ ).

## Discussion

Our results show that many forest bird and mammal species in southern Amazonia use riparian forest corridors and that narrow remnant corridors fail to provide suitable habitat for many forest vertebrate species. Narrow, unconnected corridors typically retained only one-third of the bird and one-quarter of the mammal species richness found in riparian forests within large forest patches. Although corridor width was the most important determinant of species richness, there was a strong interaction between width and degree of forest perturbation, with wider corridors usually associated with a more intact canopy structure. Yet narrow riparian corridors are a predominant feature of many deforested landscapes in the humid tropics, including the expanding Arc of

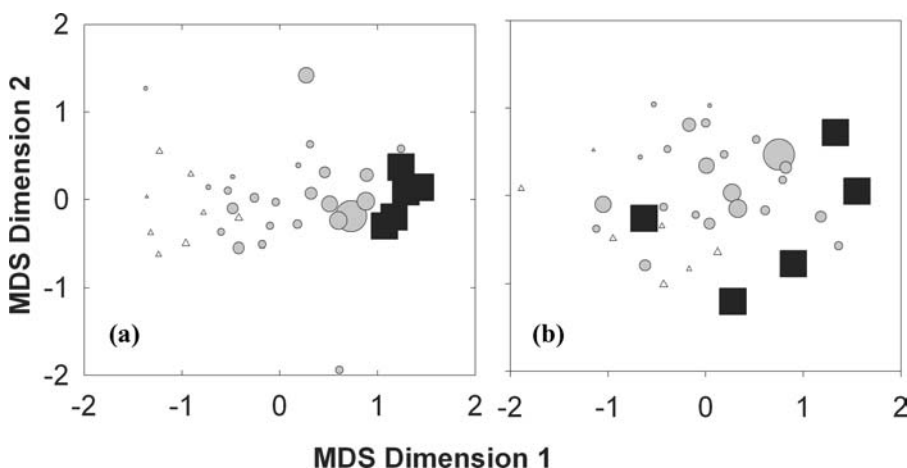


Figure 5. Vertebrate assemblage composition as a function of forest corridor width for patch size for (a) birds (stress = 0.15) and (b) mammals (stress = 0.2). Open triangles, gray circles, and black squares indicate unconnected corridors, connected corridors, and control riparian sites, respectively. Circle size is proportional to forest corridor width and control patch size, which was the significant predictor of the variation in multidimensional scaling (MDS).



Deforestation of Amazonia (Resque et al. 2004). There is no evidence to suggest that differences in tree species and faunal composition among sites were due to preexisting differences in forest and soil types (see Peres & Michalski 2006; Michalski et al. 2007). An overwhelming proportion of changes in species composition among sites is therefore assumed to result from differences in patch and landscape characteristics.

### Patterns of Corridor Occupancy

Narrow corridors (<200 m wide) were more vulnerable to edge effects than wider corridor and control forest sites and contained no core forest habitat. This renders narrow corridors more vulnerable to edge effects (Ferreira & Laurance 1997; Cochrane & Laurance 2002), which can be exacerbated by timber extraction, often leading to structural collapse of the corridor (Fig. 2). The persistence within riparian corridors of some medium-to-high sensitivity riparian specialists, such as Long-billed Woodcreepers (*Nasica longirostris*), is encouraging. Nevertheless, these species likely maintained narrow linear territories along forest streams even within undisturbed areas and therefore could have their area requirements met in sufficiently wide (>200 m) and well-preserved corridors. Likewise, even unconnected corridors retained sensitive riparian specialists such as Silvered Antbirds and the endemic Glossy Antshrike (*Sakesphorus luctuosus*).

Conversely, other species and functional groups were rarely recorded in any corridor type. This may be partly due to species-specific requirements for upland forest but is perhaps more likely related to area effects and edge intolerance (Laurance & Bierregaard 1997). The absence of Cinereous Antshrikes from many connected and all unconnected corridors suggests that narrow corridors do not satisfy the area requirements for understory mixed-species flocks, although unaffiliated dispersing individuals could theoretically move between patches through connected corridors. Similarly, terrestrial insectivores such as the Black-faced Anthrush (*Formicarius analis*) and Ringed Antpiper (*Corythopsis torquatus*) were uncommon in connected and absent in unconnected corridors, perhaps due to terrestrial mammal overabundance resulting in increased rates of nest predation for these species (Stratford & Stouffer 1999). Canopy flocks were, however, recorded much more frequently than understory flocks in both connected and unconnected corridors. These flocks are more vagile and less sensitive to fragmentation (Maldonado-Coelho & Marini 2004), so it is unsurprising that they occurred over a greater range of corridor widths.

Responses by mammal species were similarly idiosyncratic. Species occurrence in unconnected corridors may be inextricably tied to matrix tolerance as much as area requirements. Observations of ungulates such as tapir and collared peccaries regularly crossing and often forag-

ing in the non-forest matrix may explain their use of unconnected corridors. Nevertheless, more area-demanding species such as the large-herd living white-lipped peccaries (*Tayassu pecari*), which require home ranges an order of magnitude larger than those of collared peccaries (*Pecari tajacu*) (Keuroghlian et al. 2004), were never recorded in isolated corridors. Carnivores differed significantly in their use of the 3 riparian forest types, which may reflect differences in hunting pressure and prey availability as much as matrix tolerance. Tayras (*Eira barbara*) were encountered with equal frequency in all 3 riparian types. Small cats (*Leopardus* sp. and *Puma yagouaroundi*) were encountered at similar rates in connected corridors and controls but infrequently in unconnected corridors, whereas signs of large cats (*Puma concolor* and *Panthera onca*) were also rare in unconnected corridors, uncommon in connected corridors, and regularly encountered in control sites. The two most frequently encountered primate species in unconnected corridors—brown capuchins (*Cebus apella*) and dusky titi-monkeys (*Callicebus moloch*)—were also least affected by fragmentation in the region because of their exceptional tolerance to habitat disturbance (Michalski & Peres 2005). Hunting pressure did not significantly affect large mammal species richness in corridors perhaps because hunters in Alta Floresta could afford to be highly selective because of the high availability of bovine meat.

Castellón and Sieving (2006) used radiotelemetry and translocations to study landscape use by Chucao Tapaculos (*Sceloporus rubecula*) and concluded that corridor protection or restoration and habitat management in the nonforest matrix may be equally feasible alternatives for maintaining connectivity between forest patches. Nevertheless, in the Alta Floresta region <30% of the avifauna used the open-habitat matrix (S. Mahood & A.C.L., unpublished data), which suggests that corridor protection where possible is preferable to matrix management. Because our rapid surveys were biased against transient birds that do not hold a territory and thus are unlikely to vocalize, our results emphasize bird species capable of using corridors as part of their year-round home range, which in some cases included part of the source patch. This is consistent with the abrupt collapse in species richness at short distances from source patches (Fig. 4).

Although corridors provide functional connectivity between patches, they may act as population sinks, with overspill from source patches followed by poor survivorship within corridors (Henein & Meriam 1990; Crooks & Sanjayan 2006). For example, narrow forest-dividing corridors act as ecological traps (Gates & Gysel 1978) for forest-interior Neotropical migrants that do not avoid forest margins and experience higher levels of nest parasitism and nest predation (Rich et al. 1994). Although narrow corridors may function as both sinks and traps, they are certainly preferable to no corridors, considering

the low tolerance for open habitats of many forest species and their potential use of linear forest strips.

Unlike birds most terrestrial mammals detected during corridor surveys were likely transient individuals because the track surveys were not biased against transient individuals. For instance, we regularly sighted some species moving along the entire length of the sampled corridor while the avian survey was being conducted (e.g., collared peccary herds). Corridor sites also provided important food sources. *Mauritia* palms occurred in all unconnected corridors and most connected corridors, the fruits of which are a key food resource for both ungulates and primates.

### Policy Implications

Permanent protection areas (APPs) may be critical for biodiversity conservation in Brazil, depending on the landscape-scale density of the hydrographic network. Forest remnants that buffer otherwise deforested riparian areas are ubiquitous in the Alta Floresta landscape, amounting to a mean density of 259 m of rivers and perennial streams per square kilometers. At present, however, there is considerable local variation between the legally required minimum width, according to Brazilian legislation (Law 7.803 of 18.7.1989), and the actual width of forest buffers retained as APPs. The minimum width of 30 m for streams narrower than 10 m (82% of our sampled corridors) is wholly insufficient compared with the critical-width threshold of ~400 m our results indicate. Buffers  $\geq 50$  m wide are legally required for streams 10–50 m wide (Código Florestal 2001). As of 2005, only 14% of a random set of 100 connected (mean width [SD] = 260 [320] m) and none of 100 unconnected corridors (90 [55] m) that we measured throughout the Alta Floresta region met this threshold value (Supplementary Material). Hence, the usually narrow and heavily degraded riparian buffers remaining in our study region, which are typical of other deforested regions of Brazil, are of limited use in terms of biodiversity conservation.

Riparian corridors provide many other ecosystem services to both landowners and wildlife. Many smallholders and cattle ranches acknowledged the hydrological value of forest strips adjacent to watercourses used by livestock as drinking sites. Understory overbrowsing by cattle, however, had severe negative effects on terrestrial bird species because it prevented forest regeneration, which is essential to restore structural and functional connectivity of corridors. Restricting livestock movement along riparian buffers with fences and excluding livestock from key areas alongside deforested streams would allow secondary succession and facilitate connectivity restoration (Crooks & Sanjyan 2006). We recommend that riparian strips should be  $>400$  m wide (200 m on either side of the stream) wherever possible, particularly along streams

wider than 10 m if appropriate habitat is to be provided for all bird and mammal species sampled.

Overcrowding of species and edge effects are reduced as corridor width increases, and wider corridors accommodate greater spatial heterogeneity. This provides a broader range of microhabitats that is often correlated with increased species richness (Lindenmayer & Nix 1993; Bierregaard et al. 2001). Capturing this habitat heterogeneity is critical because of autecological differences among species; for example, some bamboo or tall unflooded forest habitat specialists are not well adept at dispersing through unfavorable habitats (Stratford & Stouffer 1999). If society wishes to maintain bird and mammal species richness in fragmented forests in this area, we recommend an urgent revision of the currently outdated Brazilian forest legislation, which should require the retention of wider and less-disturbed forest corridors along watercourses. The persistence of riparian forests and their associated faunal communities in deforested landscapes will, however, require a combination of effective enforcement of existing legislation via ground personnel and satellite monitoring systems, educational initiatives, and financial incentives to private landowners.

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### Supplementary Material

Supplementary information on the methods (site selection; avian and mammal surveys; corridor, patch, and landscape metrics; and data analysis) and 3 additional figures (photograph of the Alta Floresta landscape, sample corridor profiles, and frequency distribution of corridor widths) are available as part of the on-line article from <http://www.blackwellsynergy.com/>. The authors are 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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## **Supplementary Information: Methods.**

### **Sampling site selection**

Corridor locations were selected from a georeferenced 2004 Landsat enhanced thematic mapper (ETM) image (scene 227/67: 12 July 2004) on the basis of their minimum length (>1,700 m), degree of perturbation, nature of the surrounding habitat matrix, and size of connecting forest patches. As a precondition, forest fragments connected to corridors (hereafter, source patches) had to be >200 ha (mean [SE] = 15,563 [8,170 ha],  $n= 24$ ), which captured >50% of the total forest bird species richness in the Alta Floresta region (Lees & Peres 2006). All sites were accessible by river or roads within a 50-km radius of Alta Floresta. Global positioning system coordinates were obtained in situ and were used to plot the location of each sampling site.

### **Avian surveys**

Prior to the study, one observer (A.C.L.) had amassed >200 field days in the Alta Floresta region in addition to several months in the laboratory reinforcing his knowledge of all the region's avian taxa by sight and sound. He relied on commercially available and private recordings of bird calls made by professional ornithologists. Owing to the short-term nature of this sampling protocol the total number of species in large corridors should be regarded as conservative, as some low-density and rare forest interior species may have been missed.

Fifteen minutes were spent systematically recording all bird species seen or heard within the boundaries of the source patch or corridor at each point-count (PC) station, thereby including typical matrix (i.e., nonforest) taxa. Sampling periods began a few minutes before dawn and ended when all 6 PC stations had been completed (within 3 hours, 05:30 – 08:30). To avoid systematic detection bias related to time of day, the first survey proceeded from each source patch outward along the corridor (PC station 1 → 6) whilst the second survey started at the farthest PC station and terminated at the source patch (6 → 1). We considered all species except waterbirds (e.g., herons, rails), nocturnal species (e.g., owls, potoos, nightjars), and aerial insectivores (swifts and hirundines).

### **Mammal surveys**

Differences in forest-habitat availability along corridors of varying width were controlled for by also searching for any other evidence (tracks, feces, scrapes, digs, and holes) of different mammal species along a random 10 x 50 m plot located within 100 m of each PC station. Searches for tracks and other indirect signs were carried out in the second round of sampling during the latter half of the dry season, when receding water levels facilitated access to the river and stream banks and exposed more of the clay substrate. Track identification was carried

out by a skilled field assistant, who had been a hunter in the Alta Floresta region for 28 years. Positive species-level identification was not possible from tracks of some closely related taxa (e.g., two species of small felids), so these data were subsequently pooled. We excluded detections of some species that were either too rare (e.g., giant anteater [*Myrmecophaga tridactyla*]) or incompletely sampled because of small sizes or strong habitat preference (e.g., common opossum [*Didelphis marsupialis*] and giant otter [*Pteronura brasiliensis*]). By walking the length of the corridor between PC stations it was possible to unambiguously confirm the presence or absence of primate groups; however, nonvocal primates in small groups could have been missed in wide corridors (>100 m).

### **Corridor, patch, and landscape metrics**

We calculated stand basal area based on six 0.1-ha (10 x 100 m) forest plots sampled per corridor within which all trees  $\geq 20$  cm diameter at breast height (DBH) were measured. In total, we measured the DBH of all (5,667) trees in 215 plots. We were unable to sample 7 plots because of access difficulties (e.g., high water levels). Basal area estimates were calculated for both arborescent palms and nonpalm trees. Estimates of mean understory density were based on two perpendicular readings per PC station of the number of 10-cm bands that were more than 95% visible on a 200-cm pole placed 10m away by a second observer. Estimates of forest canopy cover at each PC station were based on a spherical densiometer, although this may have underestimated canopy cover in the most disturbed sites.

We ranked abundance of understory bamboo (*Guadua* sp.) and Buriti palms (*Mauritia flexuosa*) on a 0–5 scale (where 0 = no palms and 5 = monodominant palm forest). Intrusion by cattle (recorded indirectly from tracks and dung piles) and presence or absence of fencing was

recorded at every PC station. Hunting pressure was quantified based on evidence encountered *in situ* (e.g., discarded shotgun shells, trap stations, hunter trails) and interviews with local landowners and was ranked on a 1–3 scale (where 1 = low and 3 = high hunting pressure).

### **Data analysis**

The BIO-ENV procedure correlates Bray-Curtis dissimilarity matrices of community composition with Euclidean dissimilarity matrices of habitat variables. This was done for all 37 sites with mean corridor width, source patch size, spectral forest quality, distance to the nearest urban area, palm and nonpalm basal area, canopy cover, understory density, hunting pressure, bamboo cover, *Mauritia* palm abundance, fencing, and cattle as environmental variables. We repeated this analysis without the five control sites and including two additional variables describing corridor structure (mean height and SD of vertical profiles based on our analysis of cross-sectional digital photographs of all corridor sites sampled).

### **Supplementary Figures**

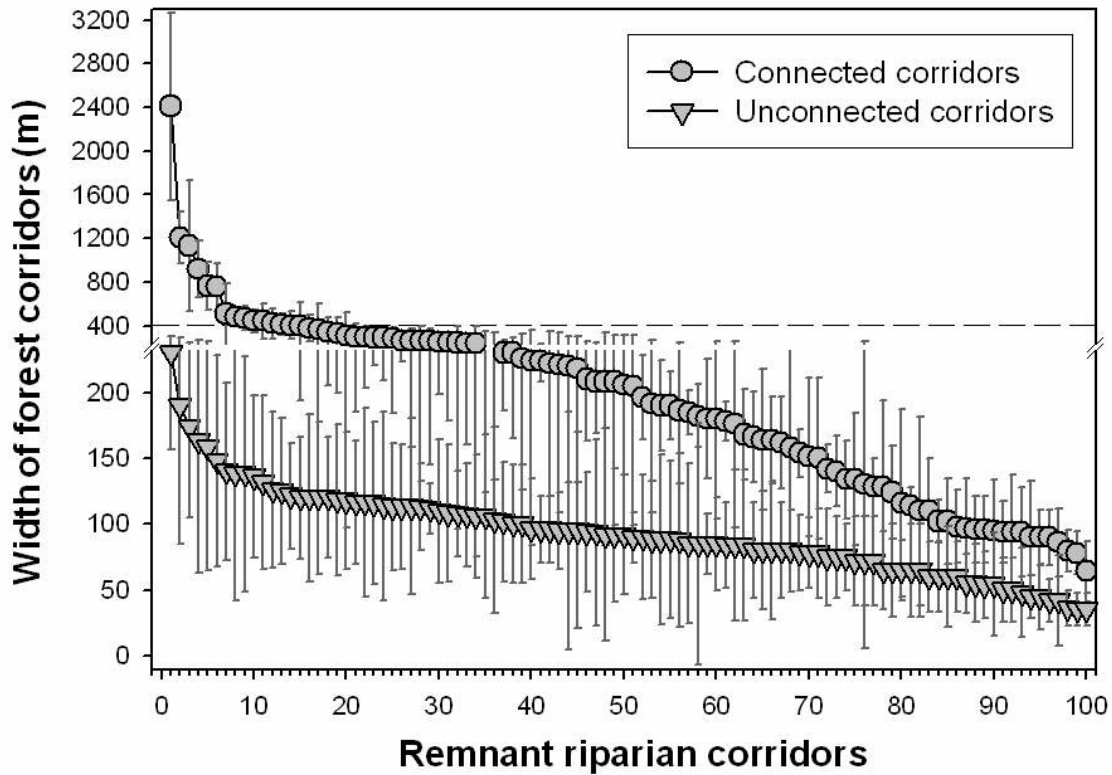


**Figure S1.** Aerial photo illustrating the typical structure of the Alta Floresta fragmented forest landscape, including numerous forest patches of various sizes and shapes that may be connected by forest corridors of varying width and quality and are surrounded by a largely uniform matrix of managed cattle pastures.





**Figure S2.** Examples of typical vertical profiles of 100-m cross-sections of forest corridors sampled in the Alta Floresta region of southern Brazilian Amazonia. Digital photos analyzed using a purpose-configured image software (see text) included (a) a relatively intact site (b) a moderately disturbed site and (c) a severely degraded site (for further details on our image analysis technique, contact the authors).



**Figure S3.** Frequency distribution of corridor width of a randomly selected sub-sample of 100 connected corridors (shaded circles) and 100 unconnected corridors (shaded triangles) within the 33,660 km<sup>2</sup> study area included in a 2004 Landsat ETM image (scene 227/67: 12/06/04). Each corridor was measured six times, perpendicularly to its main longitudinal axis, using equidistant points at least 100 m apart.