

1 **Terrestrial mammal responses to habitat structure and quality of remnant riparian forests**  
2 **in an Amazonian cattle-ranching landscape**

3 Barbara Zimbres<sup>a</sup>, Carlos A. Peres<sup>b</sup>, Ricardo Bomfim Machado<sup>a</sup>

4

5 <sup>a</sup>Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade de Brasília, Brazil,  
6 70910-900

7

8 <sup>b</sup>School of Environmental Sciences, Norwich Research Park, University of East Anglia,  
9 Norwich, UK, NR4 7TJ

10

11 Corresponding author:

12 Barbara Zimbres

13 Postal address: SHIN QL 11 conjunto 6 casa 11, Brasilia-DF, Brazil 71515-765

14 Telephone number: +55 61 98148-6288

15 [babizimbres@gmail.com](mailto:babizimbres@gmail.com)

16

17

18

19 Word count: 10,387

20

21

22

23

24

25

26 **Abstract**

27 Extensive 1970-2010 deforestation in the Brazilian Amazon has generated a ~1.5 Mha  
28 fragmented region known as the ‘arc of deforestation’. Farmers and cattle ranchers throughout  
29 Brazil are legally required to set-aside riparian forest strips within their landholdings, but recent  
30 legislative changes have relaxed the minimum mandatory conditions of these riparian forests. In  
31 this context, we assessed the functional role of riparian forest remnants as landscape connectors  
32 for medium to large-bodied terrestrial mammals in a vast fragmented landscape of southern  
33 Amazonia. We selected 38 riparian forest strips and five riparian sites within continuous forest,  
34 installed four to five camera-traps along each riparian zone (199 camera-trap stations), and  
35 sampled the terrestrial mammal assemblage for 60 days per station during the dry seasons of  
36 2013 and 2014. We compared mammal use of riparian forests within both continuous and highly  
37 fragmented forests, and examined the effects of corridor width, corridor habitat structure, and  
38 landscape context on mammal species richness, composition, and functional diversity, all of  
39 which were higher in continuous forests than in riparian remnants. Functional diversity  
40 differences between corridor type was trait-independent and mediated by differences in species  
41 richness. Forest habitat degradation was associated with overall lower species richness, whereas  
42 forest specialists were more species-rich in increasingly wider corridors. Compositional shifts  
43 indicate that deforestation and forest degradation favours matrix-tolerant species with lower  
44 levels of forest habitat specificity. We show the potential landscape connectivity role for forest  
45 mammals of riparian corridors, whose width and forest degradation status are key predictors of  
46 community-wide responses. We provide evidence on the importance of these relict riparian strips  
47 to forest vertebrates, strengthening the scientific arguments that help justify the recently  
48 embattled legal requirements to maintain effective riparian corridors in Brazil.

49 **Keywords:** ecological corridors, forest degradation, functional diversity, landscape connectivity,  
50 riparian zones.

51

52 **Introduction**

53 Brazilian Amazonia retains ~28% of the world’s remaining tropical forests (FAO 2015),  
54 but has exhibited the fastest absolute tropical deforestation rates in human history (Peres et al.

55 2010). Deforestation over the last four decades has therefore created extensive fragmented forest  
56 landscapes with varying degrees of forest cover, largely within the so-called Amazonian ‘arc of  
57 deforestation’ (Fearnside 2005). This region comprises ~1.5 million km<sup>2</sup> across 248 municipal  
58 counties of southern Amazonia that are currently dominated by cattle pastures and, to a lesser  
59 extent, cropland (IBGE-SIDRA 2016). This resulted in both the fragmentation and degradation  
60 of large tracts of once continuous forest (Soares-Filho et al. 2006). Although governmental  
61 efforts in the past decade have successfully curbed much of this trend, a recent set-back in the  
62 Brazilian Forest Act, brought forward by the political pressure exerted by agribusiness lobbyists,  
63 has caused deforestation rates to rise once again across the Brazilian Amazon (Fonseca et al.  
64 2015). In particular, changes sanctioned by congress members have reduced the total and  
65 proportional amount of legally required forest set-asides within private landholdings. These  
66 changes are non-trivial, since over half of the land throughout Brazil lies within private  
67 properties (Sparovek et al. 2015), and there are few forest reserves in the public domain set-aside  
68 for biodiversity conservation throughout most of the ‘arc of deforestation’ region (Ferreira et al.  
69 2012).

70         It is therefore highly relevant to understand how biodiversity, especially taxa of  
71 conservation concern, respond to forest-pasture conversion in one of Earth’s most biodiverse  
72 regions. Medium and large-bodied terrestrial mammals can be used as ecological indicator taxa,  
73 since their response patterns to deforestation and forest degradation are highly idiosyncratic  
74 (Wiens et al. 1993), mainly because their ecology and patterns of habitat use are highly diverse.  
75 This includes small to large-bodied species of varying population densities, several trophic  
76 guilds from herbivores to carnivores, species using small to very large home ranges, and a  
77 diverse socioecological profile, ranging from solitary to large-group-living species (Eisenberg &  
78 Thorington Jr. 1973). Ecological tolerance to anthropogenic land uses is also widely variable,  
79 since some species may freely venture into the modified open-habitat matrix, while others are  
80 strict forest specialists, strongly avoiding highly degraded areas (Parry et al. 2007). This  
81 ecological and behavioural diversity likely reflects both species responses to habitat loss, and  
82 ripple effects on ecosystem functions mediated by these species, ranging from seed dispersal to  
83 top-down control of prey populations (Ahumada et al. 2011; Pavoine & Bonsall 2011).

84 Maintaining riparian corridors is one of the most widespread landscape management  
85 strategies, and by no means a new conservation tool (Beier & Noss 1998). Brazilian law requires  
86 that a minimum riparian forest remnant should be set-aside as a ‘Permanent Protection Area  
87 (APP)’ within all ~5.5 million private landholdings throughout the country to protect both  
88 hydrological functions and biodiversity (Brazil 2012). Such riparian strips are ubiquitous  
89 throughout the country, providing an obvious opportunity to maintain landscape-scale  
90 connectivity through a functioning network of ecological corridors. Relict riparian strips, even  
91 where they fail to connect two ecologically important forest patches, still play a key role in  
92 maintaining overall landscape connectivity by reducing patch isolation (Hawes et al. 2008).  
93 Moreover, riparian habitats, and consequently, riparian corridors are important biodiversity  
94 repositories (Hilty et al. 2006), and safeguard critical resources, since a large fraction of local  
95 faunas depend on access to water and riparian food sources (Naiman et al. 1993). However, the  
96 way in which different species use these connectors is far from straightforward, with many  
97 studies concluding that the importance of ecological corridors for biodiversity is highly  
98 idiosyncratic and should be considered on a case-by-case basis (Beier & Loe 1992; Wiens et al.  
99 1993).

100 Several environmental factors have been shown to affect the performance of forest  
101 corridors as a management strategy, including (1) the structural features of corridors (e.g. width,  
102 length and continuity) (Hilty et al. 2006; Hawes et al. 2008); (2) the internal quality of the  
103 vegetation, mediated by the intrusion of external disturbances such as logging activity,  
104 overgrazing by domesticated livestock (Harrison 1992; Beier & Noss 1998; Lees & Peres 2008);  
105 (3) the surrounding landscape configuration (Saunders et al., 1991; Prist et al., 2012); (4) the  
106 harshness of the matrix to any given species (Umetsu et al. 2008); and (6) the quality of forest  
107 source patches connecting corridors (Lindenmayer, 1994). The extent of a forest corridor in  
108 relation to the perceived scale of an organism should also affect corridor use for dispersal, and  
109 ultimately discriminate those species that use corridors only as landscape connectors from those  
110 that use them as integral parts of their foraging home ranges (Ricketts 2001).

111 Here, we assess the role of remnant riparian forests as landscape connectors for medium  
112 to large-bodied terrestrial mammals in a fragmented landscape of southern Brazilian Amazonia.  
113 In particular, we compare mammalian use of riparian forests embedded within large tracks of

114 continuous forest with those remaining as relict habitat in highly fragmented landscape contexts.  
115 We expect that community richness and functional diversity to be higher in continuous riparian  
116 forests than in remnant corridors, as well as a shift in community composition between these  
117 forest corridor types. Secondly, we quantitatively assess corridor use by the mammal  
118 assemblage, and relate richness, functional diversity, and composition patterns to corridor  
119 structure and quality, and landscape context. We hypothesize that both species richness and  
120 functional diversity will be lower, and species composition will be simplified in narrower and  
121 more isolated corridors of lower habitat quality, particularly those connected to distant and  
122 smaller source patches. This study focused on observed patterns of corridor use, resulting in  
123 direct conclusions on how intrinsic features of corridors affect their use by forest wildlife, and  
124 indirect conclusions on the role of riparian corridors in maintaining landscape connectivity.

## 125 **Materials and Methods**

### 126 1.1 Study area

127 This study was conducted across a 16,200-km<sup>2</sup> landscape encompassing three municipal  
128 counties in the northern state of Mato Grosso, southern Brazilian Amazonia: Alta Floresta  
129 (09°53'S, 56°29' W), Paranaíta (09°40'S, 56°28' W), and Carlinda (09°58'S, 55°49'W). All  
130 three counties were subjected to high deforestation rates in the past four decades, and  
131 collectively represent one of the most fragmented regions of the Amazonian 'arc of  
132 deforestation'. Prior to the onset of deforestation in 1978, this entire region consisted of a similar  
133 baseline mosaic of forest formations, including mostly upland (*terra firme*) forests and to a lesser  
134 extent seasonally flooded forests. However, only ~53% of the study landscape currently retains  
135 its original forest cover. Although human settlement patterns vary among those three counties,  
136 their anthropogenic habitat matrix is similar, and consists primarily of extensively managed  
137 livestock pastures under low cattle stocking densities (Michalski et al. 2008).

### 138 1.2 Study design

139 We selected 43 sampling sites including 38 remnant riparian forest corridors of varying  
140 width, which were embedded into a cattle pasture matrix, and five relatively homogenous  
141 pseudo-control riparian areas embedded within relatively large tracts of continuous forest in the  
142 landscape (> 5 000 ha; Fig. 1). We defined a riparian corridor structurally, as a narrow forest

143 remnant (relatively to its length) maintained along streams. All riparian sites were at least 1 000  
144 m in length and spaced apart by a minimum distance of 1,500 m. At each sampling site, we  
145 installed four to five digital camera traps (Bushnell Trophy Cam and Reconyx HC500  
146 HyperFire) along the riparian zone, which were spaced apart by 250-300 m. These two camera  
147 trap models were randomly distributed across corridors, in order to avoid model-dependent  
148 biases due to differential animal detection of cameras (Meek et al. 2014). Our observational  
149 sample size thus amounted to 199 camera-trapping stations, whereas our inferential sample size  
150 consisted of 43 independent sampling areas.

151         At least 45 camera traps were used to sample batches of 10 riparian sites simultaneously  
152 for a period of 30 consecutive days. All cameras were then translocated to a new set of between  
153 seven to ten additional sites each month, until all 43 sites had been sampled over a 5-month  
154 period. This sampling schedule was deliberately restricted to the dry season (May-October), and  
155 repeated over two consecutive years (2013 and 2014). The chronological sequence of sampling  
156 across all sites was systematically rotated between years, so that sites that had been sampled at  
157 either the onset or at the end of the dry season in the first year were sampled during the peak of  
158 the dry season in the second year. We chose to restrict sampling to the dry season due to  
159 logistical reasons, including lack of physical access during the wet season, when large portions  
160 of all riparian floodplains were inundated. All camera-trap stations were baited with sardine tins  
161 pierced with multiple holes and fixed 0.75 m above ground on trees or poles placed in front of  
162 the cameras. Because of technical problems with some cameras and exceptional cases of camera  
163 theft, sampling of some riparian corridors were restricted to only four stations, resulting in a  
164 variable exposure time between stations considering both years of study (range = 28 – 62  
165 sampling days). This difference in sampling effort was, however, subsequently taken into  
166 account in the analyses. Consecutive camera-trapping records of the same species were defined  
167 as independent if they were separated in time by a minimum interval of 24 h, since this is the  
168 time-lag within which we observed temporal correlations of conspecific records (conspecifics  
169 being recorded more often by the same camera). As to the spatial independence between  
170 cameras, we conducted our analysis using a hierarchical approach in which a random factor was  
171 included to account for the autocorrelation among cameras within corridors (see below).

### 172 1.3 Environmental variables

173 We performed a supervised classification of 43 georeferenced RapidEye scenes, with a  
174 15-m resolution, from the years 2011-2013, which were obtained from the Brazilian Ministry of  
175 Environment. All classification procedures were conducted in ENVI 5.0 (Exelis Visual  
176 Information Solutions, Boulder, Colorado) and could resolve five mutually exclusive land cover  
177 classes: 1) closed-canopy primary forest; 2) open-canopy forest (interpreted as either degraded or  
178 secondary forest); 3) shrubby vegetation; 4) managed and unmanaged cattle pastures; 5) and  
179 eucalyptus/teak plantations. Local forest patch and landscape metrics were quantified and  
180 extracted in ArcGIS 10.2.2 (ESRI 2015), and included: (1) riparian corridor width (m); (2)  
181 nonlinear distance to the nearest source forest patch (m); (3) size of source forest patch (ha); (4)  
182 the total proportion of both closed-canopy and degraded forest retained within a 1,000-m buffer  
183 around the camera-trap line while excluding the area of the corridor, which we defined as  
184 measure of corridor isolation in the landscape; and (5) proportion of degraded forest within a 50-  
185 m buffer around each camera-trap station. Riparian strip width and non-linear distances from  
186 each camera-trap station to the nearest source patch were measured manually using the classified  
187 landscape map. These measurements were averaged across sites to give a mean value for each  
188 riparian strip. The nearest source patch connected to each corridor was identified and isolated,  
189 and its total area quantified. This was done by generating the core areas within all forest patches  
190 across the entire landscape, defined as the forest interior area farther than 100m from the nearest  
191 forest edges, and subsequently buffering those core areas at the same distance, thereby producing  
192 isolated patches that excluded narrow protrusions and connections. The first four variables above  
193 were analysed as landscape metrics, whereas the proportion of degraded forest within a 50-m  
194 buffer around each station was used as a patch metric describing corridor quality.

195 We also conducted in situ habitat sampling around each camera-trap station following a  
196 plotless (point-quadrant) protocol, and quantified key features of within-corridor habitat structure  
197 and vegetation status. These variables included: 1) tree basal area density ( $\text{m}^2/\text{ha}$ ), 2) understorey  
198 density, 3) number of mauritia (*Mauritia flexuosa*) arborescent palms, 4) and degree of bovine  
199 cattle intrusion. The first two variables were measured with a point-quadrant method, in which  
200 four points centred at each camera-trap station were placed 20 m apart along a parallel line to the  
201 forest-pasture edge of the corridor. At each of those points, a circle of 10-m in radius was  
202 established and divided into four quadrants. Within each quadrant, we measured and identified  
203 the nearest tree  $\geq 20\text{cm}$  in DBH (diameter at breast height) and its distance to the central point.

204 This resulted in 16 trees measured per camera-trap station, or 80 trees per riparian corridor.  
205 These two measurements were then used to calculate tree basal area density for each camera-trap  
206 station. In addition, at each of the four point-quadrants, understory density was quantified using  
207 a 200-cm segmented pole held upright by one observer a while a second observer counted the  
208 number of 10-cm segments that were entirely visible from a distance of 10 m. We thus obtained  
209 four understory density measurements for each camera-trap station, or 20 measurements per  
210 corridor.

211 *M. flexuosa* palms represent an important food source for many terrestrial and arboreal  
212 frugivores, and their clusters typically indicate the presence of *vereda* habitats, which are  
213 permanently water-logged environments. From a distance of 60 m outside the corridor edge, we  
214 therefore visually counted all mauritia palms present within 100-m corridor segment, thus  
215 providing a measure of arborescent palm density. Finally, a rank variable (0 – 4) describing the  
216 degree of bovine cattle penetration (or intrusion) into the forest corridor was estimated based on  
217 direct observations of cattle tracks within a 30-m radial area around each camera-trap station, as  
218 following: (0) no evidence of cattle trampling; (1) rare; (2) occasional; (3) frequent; and (4) very  
219 severe trampling.

#### 220 1.4 Data Analysis

221 Measures of terrestrial mammal species richness and functional diversity (FD) were used  
222 to assess the effects of environmental gradients associated with each corridor on the entire  
223 mammal assemblage. Estimated species richness ( $S_{ext}$ ) was generated using an extrapolation  
224 procedure based on the Chao1 estimator (Colwell et al. 2012), which estimates the number of  
225 species expected for each sampling site (camera-trap station) at the highest level of sampling  
226 effort per station (a census and recensus of 30 days = 60 sampling days). This procedure was  
227 necessary to account for variation in sampling days due to occasional camera failure,  
228 malfunction or theft (total amount of sampling time lost due to those events amounted to 23% of  
229 an expected 286,560 camera-trap-hours under a zero-failure rate), and the variable number of  
230 stations per corridor. We considered both total species richness and the richness of forest-  
231 specialists only, here defined as strict forest species that are not known to use nonforest habitats  
232 (see our classification of degree of forest-specificity below).



233 Species life-history traits selected to generate the FD metric included: (1) group biomass,  
234 calculated by multiplying the mean adult body size by the mean group size as reported in the  
235 literature; (2) forest habitat specificity, which we classified on a 1-3 scale (1: frequently found  
236 dispersing and foraging in open habitats such as pasture; 2: not entirely restricted, but still  
237 dependent on forest habitats; 3: restricted to forest areas, and strongly avoiding open habitats),  
238 based on the literature and our own combined field experience (55 years) on the ecology of  
239 neotropical forest mammals; (3) home range size (ha); (4) a categorical measure of the main  
240 vertical locomotion strata (terrestrial, scansorial or arboreal); and (5) a trophic index, generated  
241 as a weighted mean of the energetic level of a species diet given the proportion of dietary items,  
242 as compiled by Wilman et al. (2014). The energetic levels considered for each diet category were  
243 assigned as an ordinal sequence including 1 (folivores: leaves), 2 (frugivores: fruit pulp), 3  
244 (granivores: seeds), 4 (insectivore/faunivores: invertebrates), and 5 (carnivores: vertebrates).  
245 Traits were selected that either describe their diverse ecological roles and/or relate to their  
246 ecological sensitivity to disturbance. All traits assigned to each species, and the references used  
247 to compile them are provided in the online Supporting Information (Table A1). From the overall  
248 trait matrix, we then calculated the observed functional diversity metric ( $FD_{obs}$ ) using the Gower  
249 distance and the unweighted paired-group clustering method. This was done by calculating  
250 arithmetic averages to generate a functional dendrogram from the trait matrix (Fig. A1), and  
251 computing the branch length of the standardized tree for each sampling point based on the local  
252 pool of species ( $S$ ) that we recorded (Petchey & Gaston 2002). In order to account for the high  
253 correlation between  $S$  and observed FD ( $FD_{obs}$ ), we randomized the tips of the functional tree  
254 1,000 times to generate an expected FD metric ( $FD_{exp}$ ) for each level of richness (R package  
255 *picante*, Kembel et al. 2010; and *FD*, Laliberté et al. 2014). This was calculated as:  $(FD_{obs} -$   
256  $mean\ FD_{rand}) / sd\ (FD_{rand})$ . We thus obtained a functional diversity measure that is independent of  
257 species richness, thereby indicating whether any loss in functional diversity is greater (negative  
258  $FD_{exp}$  values, suggesting non-random trait losses) or lower (positive  $FD_{exp}$  values, suggesting  
259 idiosyncratic trait losses) than expected by any reduction in species richness.

260 Differences in  $S$  and FD between riparian forest types (corridors vs. continuous forests)  
261 were examined with likelihood-ratio tests and variance component analyses, in which the 199  
262 camera-trap stations were nested within the 43 riparian forests. We fitted generalized linear  
263 mixed-models (GLMM) to examine the effects of corridor quality (proportion of degraded forest,

264 tree basal area density, understorey density, *M. flexuosa* count, and cattle intrusion rank) on total  
265 species richness, richness of forest-specialists, and  $FD_{exp}$ , with a random factor for the corridor  
266 ( $n=38$ ) in which camera-trap stations were nested ( $n=174$ ). To examine the effects of both patch  
267 and landscape variables (mean corridor width, mean distance to the nearest source patch, source  
268 patch area, and isolation) on the same mammal assemblage properties, we fitted generalized  
269 linear models (GLM) for riparian corridors as a whole. First, we ascertained that there was no  
270 strong multicollinearity ( $r < 0.6$ ) between the variables entered into the global models. We then  
271 tested for residual overdispersion of the global models, and in case this was detected,  
272 overdispersion was corrected by including an observation-level random effect (Harrison 2014).  
273 GLM models that required the overdispersion correction parameter were thus transformed into  
274 GLMM models to include the random factor. All predictors included in the models were  
275 standardized to account for the different magnitudes between variables (Table 1). We identified  
276 meaningful predictors of community measures on the basis of a model selection procedure,  
277 considering all combinations of the variables included in the global models, with the Akaike  
278 Information Criterion corrected for small sample sizes (AICc, Burnham & Anderson 2002). The  
279 relative importance of each variable was compared using their regression coefficients and  
280 unconditional standard errors generated by model-averaging.

281         Community composition was analysed using a Principal Coordinate Analysis (PCoA),  
282 which ordinated the communities based on a Bray-Curtis similarity index, and identified which  
283 variables (describing both local forest habitat quality and landscape structure) significantly  
284 affected mammal species composition, as well as identifying which species influenced  
285 community shifts the most. We therefore based our similarity index on an imperfect proxy for  
286 abundance – temporally independent camera-trapping rates – because we considered that a  
287 measure of observed incidence would be informative to elucidate patterns of corridor use, in  
288 addition to the presence/absence data. We again performed this analysis for both the entire local  
289 assemblage and forest-specialists only. Finally, to elucidate the way in which composition was  
290 changing in space, we generated metrics of  $\beta$ -diversity that describe which proportion of the  
291 dissimilarity between local assemblages is explained by either species loss (community  
292 nestedness) or by species replacement (community turnover) (Carvalho et al. 2011). All analyses  
293 were conducted within the R 3.1.2 platform (R Core Team 2014).

## 294 **Results**

295 We obtained 4 459 independent records of 25 terrestrial mammal species during a total of  
296 10 441 sampling days. Nine-banded armadillo (*Dasybus novemcinctus*), the most recorded  
297 species (1 369 independent records, 30.7%), was detected at all corridors and all but one control  
298 continuous forest sites. Other frequently detected species occurring in most surveyed sites  
299 included lowland tapir (*Tapirus terrestris*, 579 records), paca (*Cuniculus paca*, 569 records), red-  
300 rumped agouti (*Dasyprocta leporina*, 325 records), and collared-peccary (*Pecari tajacu*, 315  
301 records). The least detected species included jaguarundi (*Puma yagouaroundi*, 1 record),  
302 Brazilian porcupine (*Coendou prehensilis*, 6 records), crab-eating fox (*Cerdocyon thous*, 7  
303 records), margay (*Leopardus wiedii*, 7 records), and bush-dog (*Speothos venaticus*, 9 records).  
304 Our dataset represents the entire regional species pool, and documents all species expected to  
305 occur at this southern Amazonian landscape.

### 306 2.1 Patterns of diversity

307 Both observed and estimated species richness were significantly higher at riparian sites  
308 within continuous forests than those in remnant corridors, which were more variable (corridors:  
309  $S_{\text{obs}} = 3 - 19$  species; continuous forests:  $S_{\text{obs}} = 14 - 19$  species; Table 2). The same pattern was  
310 observed for forest-specialists only, whose observed richness ranged from 12 to 15 species in  
311 continuous forests, and from 2 to 14 in corridors. Observed functional diversity was significantly  
312 different between continuous forests and corridors, but expected FD differences between these  
313 two classes did not differ, indicating that they were independent of specific traits, and simply  
314 mediated by differences in species richness (Table 2).

315 Models explaining estimated species richness as a function of corridor quality indicated  
316 that habitat degradation and *M. flexuosa* palm abundance were both associated with lower  
317 numbers of species for both the entire community ( $\beta_{\text{degradation}} = -0.15 [-0.20 - -0.10]$ ,  $\beta_{\text{mauritia}} = -$   
318  $0.23 [-0.29 - -0.16]$ ) and for forest-specialists only ( $\beta_{\text{degradation}} = -0.18 [-0.28 - -0.09]$ ,  $\beta_{\text{mauritia}} =$   
319  $-0.23 [-0.40 - -0.16]$ ) (Fig. 2 and Fig. A2). Patch structure, as measured by corridor width,  
320 however, had a positive effect on forest-specialist species richness ( $\beta_{\text{width}} = -0.17 [0.07 - 0.27]$ ;  
321 Fig. A2), and corridors had to be at least 100-m wide to retain the same average number of  
322 forest-dependent species typical of continuous riparian areas (approx. 10 species, Table 2),

323 although the species richness in corridors of 100 – 400 m in width was widely variable (Fig. 2).  
324 Finally, we failed to detect any effect of explanatory variables on expected functional diversity  
325 (Fig. A3).

326 As a post-hoc analysis, we ran a piecewise regression between corridor width (at the  
327 scale of camera-trap stations) and species richness to assess whether this relationship was  
328 asymptotic, thereby indicating a specific width threshold supporting the most species-rich  
329 mammal assemblages. However, the relationship between riparian corridor width and species  
330 richness was monotonically positive, despite the wide variation in corridors surveyed (Table 1).  
331 We then built post-hoc generalized linear models testing the effect of the interaction between  
332 corridor width and corridor degradation on estimated species richness at both spatial scales (CT  
333 stations and whole corridors), in order to further elucidate the relationship between structural  
334 status of corridors and the community of forest-specialist species. We detected no interaction  
335 between these variables at either scale, and forest degradation was selected once again at the CT  
336 scale ( $\beta = 0.116 [0.017-0.262]$ ), and patch width was selected as influential only at the scale of  
337 entire corridors ( $\beta = -0.203 [-0.309 - -0.098]$ ). Width and degradation were negatively but not  
338 strongly correlated (Pearson's  $r = -0.50$ ).

## 339 2.2 Patterns of assemblage composition

340 Mammal assemblage composition in remnant riparian forests diverged from those in  
341 continuous forests, although they had a high degree of species overlap, suggesting that some  
342 corridors shared a similar set of species with riparian zones in continuous forests. Community  
343 composition varied strongly among camera trap stations within the same riparian forest (Fig. 3),  
344 and although there was a clear effect of overall species richness on these community-wide  
345 differences, species turnover played an even stronger role in explaining the dissimilarity (Fig. 3  
346 and 4a). Measures of habitat quality that were significantly associated with these differences  
347 included *M. flexuosa* abundance and the proportion of surrounding degraded forest for all  
348 mammal species, for which more species-rich assemblages containing mostly forest-specialists  
349 were associated with low values of forest degradation and mauritia abundance (Fig. 4).  
350 Understorey density, cattle intrusion, and mauritia abundance also affected the composition of  
351 forest-dependent mammals, for which observed dissimilarities were best explained by  
352 community nestedness, rather than species turnover. Red-rumped agouti (*D. leporina*), collared-

353 peccary (*Pecari tajacu*), and lesser anteater (*Tamandua tetradactyla*) were associated with higher  
354 understory densities, lowland tapir (*T. terrestris*) occurred more frequently in areas containing  
355 denser mauritia palm clumps, while paca (*C. paca*) was negatively associated with mauritia  
356 abundance. Also, occurrence of tapir and paca were weakly related to higher levels of cattle  
357 intrusion (Fig. 4).

358 In terms of the overall landscape structure, species replacements affected overall  
359 community dissimilarity more than did species losses, and both corridor width and corridor  
360 isolation were significantly associated with those community differences. Most species were  
361 weakly positively associated with proportion of forest cover around corridors, and pacas were  
362 associated with wider corridors. Variation in occupancy of nine-banded armadillo, tapir, and  
363 other forest-dependent species best explained species turnover in relation to corridor isolation  
364 and width. Yet the tapir and the armadillo were little affected by either variable (Fig. 4). Finally,  
365 corridor width was again significantly associated with community dissimilarity of forest-  
366 specialists, and both nestedness and species replacements explained those differences. Here, the  
367 occurrence of three rare species – jaguar (*Panthera onca*), giant armadillo (*Priodontes maximus*),  
368 and margay (*L. wiedii*) – as well as agouti (*D. leporina*) were related to wider corridors (Fig. 4).

## 369 **Discussion**

370 Riparian forest remnants present a huge potential for planning and implementing  
371 connectivity networks that can not only ensure the retention of relict forest habitat but maintain  
372 the flux of many forest species across the landscape, ultimately contributing to a healthier  
373 ecosystem functioning (Crooks & Sanjayan 2006). However, the structure of these remnant  
374 features will ultimately determine whether or not they can effectively serve their full functional  
375 connectivity role for a wide range of species. In our study region in southern Amazonia, riparian  
376 forest remnants retained within private landholdings by migrant farmers less than four decades  
377 ago ranged widely in their integrity status in terms of both corridor structure and vegetation  
378 quality. Comparisons between remnant riparian strips within cattle pastures and those embedded  
379 into large continuous tracts of forest also confirmed that wide and well-preserved remnants can  
380 function as suitable habitat and/or landscape conduits for a wide range of terrestrial vertebrates  
381 present in the landscape. There were significant differences in species diversity and species  
382 composition between remnant riparian corridors and riparian zones within continuous forests,

383 although functional diversity differences between these two classes were trait-independent.  
384 However, the high mammal community overlap between wide, high-quality riparian remnants  
385 and continuous riparian sites indicate that well-preserved corridors are the best available  
386 opportunity to maintain terrestrial mammal diversity in highly deforested landscapes. This is,  
387 however, a conservative estimate of community similarity because even our continuous “pseudo-  
388 control” sites are not exactly pristine primary forest, thereby serving as an imperfect baseline of  
389 the observed patterns. Although these continuous riparian zones were embedded within relatively  
390 large forest fragments (>5 000 ha) compared to most other forest patches remaining in the  
391 region, they do not represent the vast unbroken tracts of forests of our study region until the late  
392 1970s, and some have been subject to selective logging thereafter. Despite an imperfect baseline,  
393 however, these large patches currently operate as source patches for mammal populations,  
394 thereby strengthening the potential of remnant riparian strips as dispersal corridors for the  
395 contemporary mammal assemblage.

396 As expected, the species richness of forest-specialists was higher in wider corridors.  
397 Those species are intolerant to the open habitat matrix, and are most sensitive to the multi-  
398 pronged edge effects that dominate narrow corridors (Hobbs 1992; Hilty et al. 2006). A study in  
399 Central Amazonia also concluded that the minimum width of riparian forest set-asides as  
400 required by Brazilian legislation was clearly insufficient to maintain the heterogeneity of snake  
401 assemblages, even under the less lenient Forest Act (De Fraga et al. 2011). Based on a multi-taxa  
402 assessment, it has been suggested that Amazonian forest corridors should be at least 300m wide  
403 to minimize penetration of various forms of edge effects (Laurance & Gascon 1997). For  
404 instance, maintaining forest bird communities would require riparian corridor widths of at least  
405 400 m (Lees & Peres 2008; Bueno et al. 2012). Species responses to edge-dominated habitats are  
406 likely the main predictors of how corridors are used primarily as either habitat or dispersal  
407 conduits (Lidicker 1999; Hilty et al. 2006). Edge effects can be associated with the intrusion of  
408 external disturbances from the matrix and the perception of risk by sensitive species, particularly  
409 forest specialists (Laurance & Laurance 1999; Frid & Dill 2002).

410 The synergistic effects of reduced riparian corridor width and greater isolation by  
411 additional clearing of upland forests will also favour matrix-tolerant habitat generalist species,  
412 which often venture into pasture areas. The higher species turnover in increasingly isolated

413 corridors indicates that these were used less frequently by species that rarely traverse gaps  
414 between remaining forest patches, and more frequently by those species typically exhibiting  
415 matrix movements in open habitats. This is the case of nine-banded armadillo, the most matrix-  
416 tolerant species, and by far the most frequently recorded in the study, and tapir, which can  
417 exhibit wide gap-crossing capacity despite being forest dependent. Also, as further evidence of  
418 the environmental facilitation of forest clearing for open-area species, local populations of native  
419 nonforest large herbivores, such as capybaras, are rapidly expanding in the study region  
420 (Michalski et al. 2006), probably because of greater foraging habitat availability and reduced  
421 top-down control by large felids. Capybaras (*Hydrochaeris hydrochoerus*) exploit riparian zones  
422 throughout northern Mato Grosso, possibly further exacerbating heavy grazing pressure and  
423 modifying fluvial geomorphology, ultimately suppressing corridor regeneration (BZ and CAP,  
424 pers. obs; CAP, unpubl. data). Another open-habitat specialist whose geographic range is rapidly  
425 expanding northward from the central Brazilian savannas (*cerrado*) is the crab-eating fox  
426 (*Cerdocyon thous*) (CAP, unpubl. data). We interpreted the low numbers of detections of this  
427 species as evidence of ongoing population spread, rather than indicating sensitivity to forest  
428 fragmentation.

429         Structural forest degradation is a patch-scale feature that is seldom explored, and  
430 deserves more explicit consideration (Lees & Peres 2008; Hawes et al. 2008). Mammal species  
431 richness was depressed in more degraded forest, although this was less associated with cattle  
432 intrusion than we expected. For forest specialists, cattle intrusion only explained compositional  
433 shifts, but degradation as a whole consistently affected both total species richness and  
434 composition. Recurrent cattle access to shade and water in riparian zones induced changes in  
435 understorey structure through both overgrazing below the browse-line and excessive trampling,  
436 which often modified stream geomorphology mainly via collapsed overhanging banks (Armour  
437 et al. 1991). This effect was corroborated by overall compositional changes associated with both  
438 understorey density and level of cattle intrusion, as observed for agouti and collared-peccary. On  
439 the other hand, our estimates of forest degradation generated from our supervised remote-sensing  
440 approach mainly captured forest canopy gaps, thereby representing more severe and advanced  
441 stages of degradation, which may be caused by timber extraction and occasional wildfire events  
442 (Gerwing 2002). Although cattle trampling within riparian forests may facilitate eventual canopy

443 openings through suppressed regeneration, signs of cattle use were most conspicuous during  
444 field sampling of the forest understorey and undetectable from satellite images.

445         The question of relative importance of forest corridor width vs. degradation for the entire  
446 mammal community cannot be easily addressed quantitatively, but these factors clearly operate  
447 at different scales. Corridor width affected forest-dependent species only at the scale of whole  
448 corridors, whereas forest degradation dominated the effects of forest width within corridors. This  
449 is likely related to the scale at which different species perceive their habitats: even within  
450 corridors that are wide enough to function as foraging habitat or a dispersal conduit, individual  
451 animals will still make fine-scale ranging decisions based on local forest heterogeneity.

452         Functional diversity was not affected by species absences from narrow and degraded  
453 corridors, and specific traits did not necessarily determine which species were lost first since we  
454 found no relationship between the environmental factors and the expected diversity metric. A  
455 relatively high ecological plasticity can be observed in several medium to large-bodied mammal  
456 species, for instance, by partially altering their diets, activity patterns or ranging behaviour to  
457 adjust to the effects of habitat loss and fragmentation (Onderdonk & Chapman 2000; Jepsen &  
458 Topping 2004). For example, jaguars and pumas depend on forest habitats, but can often venture  
459 out into open areas particularly at night, and were recorded in a few very narrow and highly  
460 degraded corridors. Large felids in our study region are also attracted to vulnerable cattle even in  
461 the most deforested ranches, which is facilitated by hands-off herd management (Michalski et al.  
462 2006). This pushes them farther into the dendritic network of variably connected riparian  
463 corridors. In any case, a severely deforested landscape retaining only small forest patches will  
464 ultimately support a homogenized and depauperate mammal assemblage that will likely yield  
465 reduced ecosystem functions mediated by trait-independent species loss.

466         Although mauritia palm clusters (*veredas*) provide important food sources for many  
467 ungulate and rodent species, such as the tapirs (*T. terrestris*), white-lipped peccaries (*Tayassu*  
468 *pecari*), pacas (*Cuniculus paca*) and agoutis (*D. leporina*) (Beck 2006; Endress et al. 2013), palm  
469 density had a negative effect on mammal community structure. This can be explained by the high  
470 rates of deforestation of *veredas* in the region. *Veredas* were dominated by mauritia palms, and  
471 consisted of poorly drained, waterlogged soils even during the dry season. Although palm  
472 swamps are also legally protected, the absence of a clearly-defined water course, from which to



473 measure the buffer strip width, may explain why many landowners feel entitled to convert a  
474 larger fraction of *veredas* than what would be required to meet their minimum APP legal  
475 compliance. This results in *veredas* becoming the most deforested vegetation formation  
476 throughout our study area, with pastures often encroaching right up to the stream (BZ and CAP,  
477 pers. obs.). *Vereda* corridors were therefore typically very narrow (<40m wide) and waterlogged  
478 throughout, so it is unsurprising that local movement rates under these conditions were  
479 apparently low for several species. This is corroborated by the fact that large herds of white-  
480 lipped peccaries as well as the pacas were virtually never observed using these narrow corridors,  
481 despite the high abundance of a preferred food resource.

482 We failed to detect an effect of nonlinear distance from the source forest patch on any of  
483 the response variables examined. Given the spectrum of morpho-ecological traits in terrestrial  
484 mammals >1 kg considered here, some species exhibit large home ranges, great dispersal  
485 capacity, and high levels of tolerance to the anthropogenic matrix, thereby frequently travelling  
486 through alternative open habitat. This contributes to the degree to which different species travel  
487 long distances through riparian corridors, and endorses the importance of this management  
488 strategy in maintaining landscape connectivity, especially for matrix-intolerant species. On the  
489 other hand, the definition of focal groups for conservation is often based on which taxa are the  
490 most demanding in terms of specific landscape attributes (Lambeck 1997). We therefore  
491 highlight the fact that other vertebrate taxa may be more sensitive than medium and large-sized  
492 mammals to a number of structural corridor attributes (Lima & Gascon 1999; Lees & Peres  
493 2008; Bueno et al. 2012). However, this does not mean that mammal responses to habitat loss  
494 and degradation should be ignored, given their diverse functional roles in regulating other animal  
495 and plant populations (Ahumada et al. 2011; Pavoine & Bonsall 2011). We simply highlight that  
496 using terrestrial mammals as surrogate for other taxa may be inadequate, since requirements of  
497 different groups can range widely, and important mismatches in their priorities have been  
498 identified (Andelman & Fagan 2000; Sobral et al. 2012). We therefore advise caution in  
499 extrapolating the patterns observed here for other taxonomic groups.

### 500 3.1 Policy implications

501 Prior to legislative changes, the Brazilian Forest Act required landowners to set aside a  
502 permanent forest strip (APP) of at least 30 m on each side of rivers and perennial streams

503 narrower than 10 m. The more lenient current legislation prevents any further clearing, but  
504 bestows amnesty to landholdings up to 400 ha that failed to comply with the legislation prior to  
505 2008 in requiring a strip width of only 5-10 m on both sides of streams, depending on  
506 landholding size (Brazil 2012). These small non-complying landholdings represent the vast  
507 majority of private properties in the study region (Michalski et al. 2010) and elsewhere in the  
508 Brazilian Amazon (Godar et al. 2014). In terms of width, the amount of riparian forest protection  
509 currently required by law has already been shown to be insufficient (Lima & Gascon 1999; Lees  
510 & Peres 2008; De Fraga et al. 2011; Bueno et al. 2012), and most species, particularly forest  
511 specialists that are usually of highest conservation concern, rarely use very narrow corridors. In  
512 practice, the newly approved Forest Act condones past illegal deforestation, effectively  
513 increasing compliance rates. However, recent deforestation monitoring indicates a 53% increase  
514 in the overall annual deforestation rate for the Brazilian Amazon between 2014 and 2015  
515 (Fonseca et al. 2015).

516         Beyond discussions on minimum amounts of forest required, we have shown that low-  
517 quality riparian remnants provide limited potential for maintaining landscape connectivity (see  
518 also Harrison 1992; Lees & Peres 2008), and there was considerable variation in forest  
519 degradation rates even in wider corridors, suggesting that wide corridors will not necessarily be  
520 suitable to more sensitive species in terms of habitat quality. Indeed this conclusion is  
521 corroborated by other Amazonian studies, which found that forest disturbance was responsible  
522 for a loss of 39-54% of the conservation value of catchments covered by over 80% of primary  
523 forest (Barlow et al. 2016). Yet federal legislation in Brazil is completely lenient in terms of  
524 environmental requirements concerning the quality and integrity of private forest set-asides. The  
525 vegetation along riparian set-asides can include either primary or secondary forests in any state  
526 of regeneration, and can legally contain exotic species in up to 50% of the APP area. This can  
527 only boost degradation rates, and indeed since the new Forest Act (2012) was sanctioned, there  
528 has been a 147% increase in forest degradation across the Brazilian Amazon between 2014 and  
529 2015 alone, 85% of which in Mato Grosso (Fonseca et al. 2015).

530         Monitoring degradation using a remote-sensing approach is efficient, and landscape  
531 metrics derived from RapidEye images were related to mammal community structure. However,  
532 the riparian forests we surveyed were on average degraded by ~30%, against a background of

533 ~12% of degradation for the entire landscape. This is of course underestimated since other, less  
534 conspicuous drivers of forest degradation may be entirely invisible from satellite images (Peres  
535 et al. 2006). For instance, hunting may be widespread in the Amazon's 'arc of deforestation',  
536 even though we avoided sampling hunted areas. Therefore, it is crucial to consider the limitations  
537 of large-scale remote-sensing monitoring approaches, and address cryptic drivers of forest  
538 degradation, which will require working with local stakeholders. Our best chance to safeguard  
539 the connectivity and habitat potential of riparian forests for biodiversity relies on achieving  
540 management goals beyond those prescribed by the legislation. Two management fronts will need  
541 to be carried out: promoting the maintenance and restoration of wider corridors (at least 100-m  
542 wide), and minimizing disturbance drivers, such as selective logging, wildfires, cattle intrusion  
543 and hunting (Peres 2001; Gerwing 2002; Broadbent et al. 2008). Further information on how  
544 these specific drivers affect forest structure and composition would be beneficial for in situ  
545 assessments of forest quality and monitoring of recovery success after the exclusion of  
546 disturbance drivers.

### 547 3.2 Conclusions

548 The potential of riparian remnants as a landscape management tool goes well beyond  
549 promoting connectivity for wildlife. They ultimately contribute to the health of hydrological  
550 ecosystem services across entire regions by acting as microclimatic and biophysical buffers, and  
551 protecting water quality and stream morphology (Naiman et al. 1993). The appropriate  
552 management of these critical landscape features therefore needs to be a priority in the face of  
553 relentless tropical deforestation, and should take into account a mounting body of applied  
554 landscape ecology. Although curbing deforestation can be achieved through a system of  
555 incentives and disincentives, we suggest that maintaining or restoring forest habitat quality,  
556 which remains widely neglected by national policy in many tropical forest countries, needs to be  
557 explicitly considered. We suggest that managing highly fragmented tropical forest landscapes  
558 should be planned to maximize the width and integrity of riparian set-asides, while minimizing  
559 overall isolation within the landscape as well as identifying and controlling the drivers of further  
560 degradation of forest remnants. The first step in that direction should be to enforce landholder  
561 compliance with the legislation, but landscape-scale planning of private forest reserves should be

562 coordinated between landholdings to create a comprehensive forest remnant network that can  
563 function at both local and regional scales.

#### 564 **Acknowledgments**

565 We are grateful to the Brazilian Ministry of Education (CAPES) for funding BZ's PhD  
566 studentship. We thank the University of Brasilia for help in the purchase of camera traps, and the  
567 University of East Anglia for hosting BZ during a study visit. CNPq provided a research grant  
568 (#306392/2013-5) to RBM. We also thank IdeaWild Organization, Rufford Small Grants  
569 Foundation (#12658-1), and the National Geographic Society/Waitt Grant (#W314-14), and a  
570 CAPES grant to CAP (004-2012) for financial support for the fieldwork in Mato Grosso, Brazil.  
571 We are indebted to Danilo Fortunato for assistance in data analyses, and all landowners for  
572 granting access to their properties.

573

#### 574 **References**

575 Ahumada JA et al. 2011. Community structure and diversity of tropical forest mammals: data  
576 from a global camera trap network. *Philosophical transactions of the Royal Society of*  
577 *London. Series B, Biological sciences* **366**:2703–11.

578 Andelman SJ, Fagan WF. 2000. Umbrellas and flagships: efficient conservation surrogates or  
579 expensive mistakes? *Proceedings of the National Academy of Sciences* **97**:5954–5959.

580 Armour CL, Duff DA, Elmore W. 1991. The effects of livestock grazing on riparian and stream  
581 ecosystems. *Fisheries* **16**:7–12.

582 Barlow J, Lennox GD, Ferreira J, Berenguer E, Lees AC, Nally RM, ... Gardner TA. 2016.  
583 Anthropogenic disturbance in tropical forests can double biodiversity loss from  
584 deforestation. *Nature* **535**:144-147.

585 Beck H. 2006. A review of peccary – palm interactions and their ecological ramifications across  
586 the Neotropics. *Journal of Mammalogy* **87**:519–530.

- 587 Beier P, Loe S. 1992. In my experience: a checklist for evaluating impacts to wildlife movement  
588 corridors. *Wildlife Society Bulletin* **20**:434–440.
- 589 Beier P, Noss RF. 1998. Do habitat corridors provide connectivity? *Conservation Biology*  
590 **12**:1241–1252.
- 591 Brady MJ, McAlpine CA, Possingham HP, Miller CJ, Baxter GS. 2011. Matrix is important for  
592 mammals in landscapes with small amounts of native forest habitat. *Landscape Ecology*  
593 **26**:617–628.
- 594 Brazil. 2012. Código Florestal Brasileiro. Lei 12.651/2012.  
595 [http://www.planalto.gov.br/ccivil\\_03/\\_ato2011-2014/2012/lei/l12651.htm](http://www.planalto.gov.br/ccivil_03/_ato2011-2014/2012/lei/l12651.htm)
- 596 Broadbent E, Asner G, Keller M, Knapp D, Oliveira P, Silva J. 2008. Forest fragmentation and  
597 edge effects from deforestation and selective logging in the Brazilian Amazon. *Biological*  
598 *Conservation* **141**:1745–1757.
- 599 Bueno AS, Bruno RS, Pimentel TP, Sanaiotti TM, Magnusson WE. 2012. The width of riparian  
600 habitats for understory birds in an Amazonian forest. *Ecological Applications* **22**:722–734.
- 601 Burnham KP, Anderson DR. 2002. Model selection and inference: a practical information-  
602 theoretic approach. Springer, New York.
- 603 Carvalho GH, Batalha MA, Silva IA, Cianciaruso MV, Petchey OL. 2014. Are fire, soil fertility  
604 and toxicity, water availability, plant functional diversity, and litter decomposition related in  
605 a Neotropical savanna? *Oecologia* **175**:923–935.
- 606 Colwell RK, Chao A, Gotelli NJ, Lin S-Y, Mao CX, Chazdon RL, Longino JT. 2012. Models  
607 and estimators linking individual-based and sample-based rarefaction, extrapolation and  
608 comparison of assemblages. *Journal of Plant Ecology* **5**:3–21.
- 609 Crooks KR, Sanjayan M. 2006. Connectivity conservation: maintaining connections for nature.  
610 Cambridge University Press, Cambridge.

- 611 De Fraga R, Lima AP, Magnusson WE. 2011. Mesoscale spatial ecology of a tropical snake  
612 assemblage: the width of riparian corridors in central Amazonia. *Herpetological Journal*  
613 **21**:51–57.
- 614 Eisenberg JF, Thorington Jr RW. 1973. A preliminary analysis of a neotropical mammal fauna.  
615 *Biotropica* **5**:150-161.
- 616 Endress BA, Horn CM, Gilmore MP. 2013. *Mauritia flexuosa* palm swamps: composition,  
617 structure and implications for conservation and management. *Forest Ecology and*  
618 *Management* **302**:346–353.
- 619 ESRI. 2015. ArcGIS Desktop: Release 10.2.2. Environmental Systems Research Institute,  
620 Redlands, California.
- 621 FAO. 2015. FAO 2015 Forest Resources Assessment. [http://www.fao.org/forest-resources-  
assessment/current-assessment/en/](http://www.fao.org/forest-resources-<br/>622 assessment/current-assessment/en/)
- 623 Fearnside PM. 2005. Deforestation in Brazilian Amazonia: history, rates, and consequences.  
624 *Conservation Biology* **19**:680-688.
- 625 Ferreira J, Pardini R, Metzger JP, Fonseca CR, Pompeu PS, Sparovek G, Louzada J. 2012.  
626 Towards environmentally sustainable agriculture in Brazil: challenges and opportunities for  
627 applied ecological research. *Journal of Applied Ecology* **49**:535–541.
- 628 Flynn DFB, Gogol-Prokurat M, Nogeire T, Molinari N, Richers BT, Lin BB, Simpson N,  
629 Mayfield MM, DeClerck F. 2009. Loss of functional diversity under land use intensification  
630 across multiple taxa. *Ecology Letters* **12**:22–33.
- 631 Fonseca A, Justino M, Souza Jr C, Veríssimo A. 2015. Deforestation report for the Brazilian  
632 Amazon (July 2015). Imazon, Belém, Brazil.
- 633 Frid A, Dill L. 2002. Human-caused disturbance stimuli as a form of predation risk.  
634 *Conservation Ecology* **6**:11.

- 635 Gerwing JJ. 2002. Degradation of forests through logging and fire in the eastern Brazilian  
636 Amazon. *Forest Ecology and Management* **157**:131–141.
- 637 Godar J, Gardner TA, Tizado EJ, Pacheco P. 2014. Actor-specific contributions to the  
638 deforestation slowdown in the Brazilian Amazon. *Proceedings of the National Academy of*  
639 *Sciences* **111**:15591-15596.
- 640 Harrison RL. 1992. Toward a Theory of Inter-Refuge Corridor Design. *Conservation Biology*  
641 **6**:293–295.
- 642 Harrison XA. 2014. Using observation-level random effects to model overdispersion in count  
643 data in ecology and evolution. *PeerJ* **2**:e616.
- 644 Hawes J, Barlow J, Gardner TA, Peres CA. 2008. The value of forest strips for understorey birds  
645 in an Amazonian plantation landscape. *Biological Conservation* **141**:2262–2278.
- 646 Hilty JA, Lidicker WZ, Merenlender AM. 2006. *Corridor ecology: the science and practice of*  
647 *linking landscapes for biodiversity conservation*. Island Press, Washington D.C.
- 648 Hobbs RJ. 1992. The Role of Corridors in Conservation: Solution or Bandwagon? *Trends in*  
649 *ecology & evolution* **7**:389–392.
- 650 IBGE/SIDRA. 2016. Instituto Brasileiro de Geografia e Estatística/Sistema de Recuperação  
651 Automática. <http://www.sidra.ibge.gov.br/>
- 652 Jepsen JU, Topping CJ. 2004. Modelling roe deer (*Capreolus capreolus*) in a gradient of forest  
653 fragmentation: behavioural plasticity and choice of cover. *Canadian Journal of Zoology*  
654 **82**:1528-1541.
- 655 Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP,  
656 Webb CO. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*  
657 **26**:1463-1464.
- 658 Laliberté E, Legendre P. 2010. A distance-based framework for measuring functional diversity  
659 from multiple traits. *Ecology* **91**:299-305.

- 660 Lambeck RJ. 1997. Focal Species: A Multi-Species Umbrella for Nature Conservation.  
661 Conservation Biology **11**:849–856.
- 662 Laurance SG, Laurance WF. 1999. Tropical wildlife corridors: use of linear rainforest remnants  
663 by arboreal mammals. Biological Conservation **91**:231–239.
- 664 Laurance WF, Gascon C. 1997. How to Creatively Fragment a Landscape. Conservation Biology  
665 **11**:577–579.
- 666 Lees AC, Peres CA. 2008. Conservation value of remnant riparian forest corridors of varying  
667 quality for amazonian birds and mammals. Conservation Biology **22**:439–449.
- 668 Lidicker WZ. 1999. Response of mammals to habitat edges: a landscape perspective **14**:331.
- 669 Lima M, Gascon C. 1999. The conservation value of linear forest remnants in central Amazonia.  
670 Biological Conservation **91**:241–247.
- 671 Lindenmayer DB. 1994. Wildlife corridors and the mitigation of logging impacts on fauna in  
672 wood-production forests in southeastern Australia: a review. Wildlife Research **21**:323-340.
- 673 Meek P, Ballard GA, Fleming PJS, Schaefer M., Williams W, Falzon G. 2014 Camera Traps Can  
674 Be Heard and Seen by Animals. PLoS ONE 9: e110832.
- 675 Michalski F, Boulhosa RLP, Faria A, Peres CA. 2006. Human–wildlife conflicts in a fragmented  
676 Amazonian forest landscape: determinants of large felid depredation on livestock. Animal  
677 Conservation **9**:179–188.
- 678 Michalski F, Metzger JP, Peres CA. 2010. Rural property size drives patterns of upland and  
679 riparian forest retention in a tropical deforestation frontier. Global Environmental Change  
680 **20**:705–712.
- 681 Michalski F, Peres CA, Lake IR. 2008. Deforestation dynamics in a fragmented region of  
682 southern Amazonia: evaluation and future scenarios. Environmental Conservation **35**:93–  
683 103.



- 684 Naiman RJ., Decamps H, Pollock M. 1993. The role of riparian corridors in maintaining regional  
685 biodiversity. *Ecological Applications* **3**:209–212.
- 686 Onderdonk DA, Chapman CA. 2000. Coping with forest fragmentation: the primates of Kibale  
687 National Park, Uganda. *International Journal of Primatology* **21**:587–611.
- 688 Parry L, Barlow J, Peres CA. 2007. Large-vertebrate assemblages of primary and secondary  
689 forests in the Brazilian Amazon. *Journal of Tropical Ecology* **23**:653-662.
- 690 Pavoine S, Bonsall MB. 2011. Measuring biodiversity to explain community assembly: a unified  
691 approach. *Biological Reviews* **86**:792–812.
- 692 Peres CA. 2001. Synergistic effects of subsistence hunting and habitat fragmentation on  
693 Amazonian forest vertebrates. *Conservation Biology* **15**:1490-1505.
- 694 Peres CA, Barlow J, Laurance WF. 2006. Detecting anthropogenic disturbance in tropical  
695 forests. *Trends in Ecology & Evolution* **21**:227-229.
- 696 Peres CA, Gardner TA, Barlow J, Zuanon J, Michalski F, Lees AC, Vieira ICG, Moreira FMS,  
697 Feeley KJ. 2010. Biodiversity conservation in human-modified Amazonian forest  
698 landscapes. *Biological Conservation* **143**:2314–2327.
- 699 Petchey OL, Gaston KJ. 2002. Functional diversity (FD), species richness, and community  
700 composition. *Ecology Letters* **5**:402–411
- 701 Prist PR, Michalski F, Metzger JP. 2012. How deforestation pattern in the Amazon influences  
702 vertebrate richness and community composition. *Landscape Ecology* **27**:799–812.
- 703 R Development Core Team. 2014. R: a language and environmental for statistical computing. R  
704 Foundation for Statistical Computing, Vienna, Austria. <http://cranr-project.org>
- 705 Ricketts TH. 2001. The matrix matters: effective isolation in fragmented landscapes. *The*  
706 *American Naturalist* **158**:87-99.

- 707 Saunders DA, Hobbs RJ, Margules CR. 1991. Biological Consequences of Ecosystem  
708 Fragmentation: A Review. *Conservation Biology* **5**:18–32.
- 709 Soares-Filho BS, Nepstad DC, Curran LM, Cerqueira GC, Garcia RA, Ramos CA, Voll E,  
710 McDonald A, Lefebvre P, Schlesinger P. 2006. Modelling conservation in the Amazon  
711 basin. *Nature* **440**:520–523.
- 712 Sobral FL, Jardim L, Lemes P, Machado N, Loyola R, Cianciaruso MV. 2012. Spatial  
713 conservation priorities for top predators reveal mismatches among taxonomic, phylogenetic  
714 and functional diversity. *Natureza & Conservação* **12**:150–155.
- 715 Soler LDS, Escada MIS, Verburg PH. 2009. Quantifying deforestation and secondary forest  
716 determinants for different spatial extents in an Amazonian colonization frontier (Rondonia).  
717 *Applied Geography* **29**:182–193.
- 718 Sparovek G, Barretto AGDOP, Matsumoto M, Berndes G. 2015. Effects of governance on  
719 availability of land for agriculture and conservation in Brazil. *Environmental Science and*  
720 *Technology* **49**:10285-10293.
- 721 Umetsu F, Metzger JP, Pardini R. 2008. Importance of estimating matrix quality for modeling  
722 species distribution in complex tropical landscapes: a test with Atlantic forest small  
723 mammals. *Ecography* **31**:359–370.
- 724 Wiens JA, Stenseth NC, Van Horne B, Ims RA. 1993. Ecological mechanisms and landscape  
725 ecology. *Oikos* **66**:369–380.
- 726 Wilman H, Belmaker J, Jennifer S, de la Rosa C, Rivadeneira MM, Jetz W. 2014. EltonTraits  
727 1.0: Species-level foraging attributes of the world’s birds and mammals. *Ecology* **95**:2027.
- 728 Wright SJ, Stoner KE, Beckman N, Corlett RT, Dirzo R, Muller-Landau HC, Nuñez-Iturri G,  
729 Peres CA, Wang BC. 2007. The plight of large animals in tropical forests and the  
730 consequences for plant regeneration. *Biotropica* **39**:289–291.

731

732 **Tables**

733

734 **Table 1.** Independent variables tested as predictors of mammal community patterns in the  
 735 analyses. Variables are grouped into descriptors of internal forest quality, and landscape and  
 736 patch structure.

Variable	Mean [Range]
<i>Landscape structure</i>	
Corridor width (m)	215.4 [40.1–1316.8]
Distance to source patch (m)	1201.3 [125–8572]
Source patch area (ha)	6703 [89.5–54538]
Total forest proportion <sup>a</sup>	0.31 [0.13–0.51]
<i>Forest quality</i>	
Tree basal area (m <sup>2</sup> /ha)	35.8 [1.9–145.5]
Understory density	0.54 [0.01–0.99]
<i>Mauritia flexuosa</i> count	5.6 [0–81]
Cattle intrusion	1 [0–4]
Degraded forest proportion <sup>b</sup>	20.4 [0.0–100.0]

737 <sup>a</sup>Total forest proportion refers to the proportion of forest within a 1-km buffer around the  
 738 corridor, excluding the area of the corridor.

739 <sup>b</sup>Degraded forest proportion refers to the proportion of forest classified as degraded or secondary  
 740 within a 50-m buffer around each camera trap station.

741

742

743

744

745

746 **Table 2.** Mean [SD] observed and estimated measures of diversity considered in the study,  
 747 including likelihood ratio comparisons between remnant riparian forest (RF) corridors and those  
 748 within continuous forest areas (significant differences shown in bold).

Variable	Corridor	Continuous forest	$\chi^2$	p	Variance explained*	
					RF type	Corridor subset
All species ( $S_{obs}$ )	6.23 [2.56]	8.76 [2.22]	10.99	<b>0.0009</b>	0.345	0.173
All species ( $S_{ext}$ )	8.23 [4.68]	12.20 [5.12]	12.33	<b>0.0004</b>	0.155	0.077
Forest specialists ( $S_{obs}$ )	4.68 [2.38]	7.48 [1.83]	13.48	<b>0.0002</b>	0.423	0.212
Forest specialists ( $S_{ext}$ )	6.12 [4.08]	9.96 [3.46]	14.48	<b>0.0001</b>	0.184	0.092
$FD_{obs}$	3.80 [1.28]	5.28 [0.99]	9.65	<b>0.0019</b>	0.369	0.184
$FD_{exp}$	-0.16 [0.84]	0.17 [0.75]	1.03	0.3099	0.183	0.091

749 \*Percentage variance explained by each hierarchical site factor estimated using variance  
 750 component analysis.

751 **Figure legends**

752 Figure 1. Study area in the northern state of Mato Grosso, Brazil, showing the 43 sampling areas  
753 including 38 remnant riparian forest corridors (red circles) and five comparable riparian areas  
754 within large tracks of continuous forest (yellow triangles). Inset map (top right) shows an  
755 example of the 4 to 5 camera trapping stations (solid circles) installed within a riparian corridor,  
756 and the two forest cover classes obtained with a supervised classification of RapidEye<sup>®</sup> images  
757 (mature closed-canopy forest in green, degraded forest in light orange). White background  
758 indicates nonforest areas consisting primarily of bovine cattle pastures.

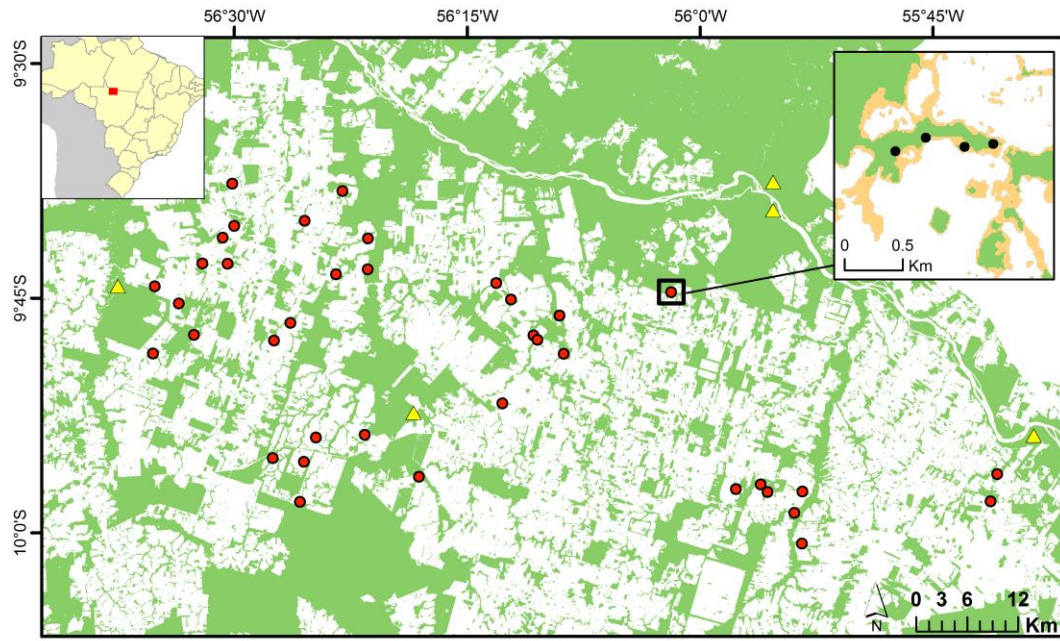
759 Figure 2. Relationships between estimated species richness (Chao1) and key predictors selected  
760 by the model averaging procedure, including: (a) mean riparian corridor width (m) (n=43), (b)  
761 proportion of degraded forest around each camera station (n=173), and (c) abundance of  
762 *Mauritia flexuosa* palms around each camera station (n=173). Blue and green solid circles  
763 represent all terrestrial mammal species and forest-specialists, respectively.

764 Figure 3. Principal Coordinate Analysis (PCoA) ordination the dissimilarity of terrestrial  
765 mammal species between camera-trapping stations within remnant riparian corridors (blue  
766 circles) and continuous riparian forests (red circles) based on Bray-Curtis index. Mean [SD] of  
767 the degree to which mammal beta-diversity was accounted for by either species turnover ( $\beta_{\text{turn}}$ )  
768 or community nestedness ( $\beta_{\text{nest}}$ ) are also shown. Size of solid circles was scaled according to the  
769 species richness observed at the scale of camera-trapping stations.

770 Figure 4. Principal Coordinate Analysis (PCoA) ordination of the dissimilarity between  
771 sampling points within corridors (blue symbols) and between corridors (red symbols) on the  
772 basis of Bray-Curtis dissimilarity. Corridor quality (D: proportion of degraded forest around each  
773 camera-trap station; M: *Mauritia* palm count; C: degree of cattle intrusion; U: understorey  
774 density) or structure variables (PF: proportion of forest around the corridor; W: corridor width)  
775 that significantly affected the composition dissimilarity between mammal communities. PCoA  
776 ordination was performed considering both all terrestrial mammal species (open circles) and only  
777 species defined as forest specialists (open triangles). Beta-diversity [mean  $\pm$  SD] explained by  
778 either the species turnover ( $\beta_{\text{turn}}$ ) or community nestedness ( $\beta_{\text{nest}}$ ) are also shown. Symbol sizes  
779 are scaled according to the observed species richness.

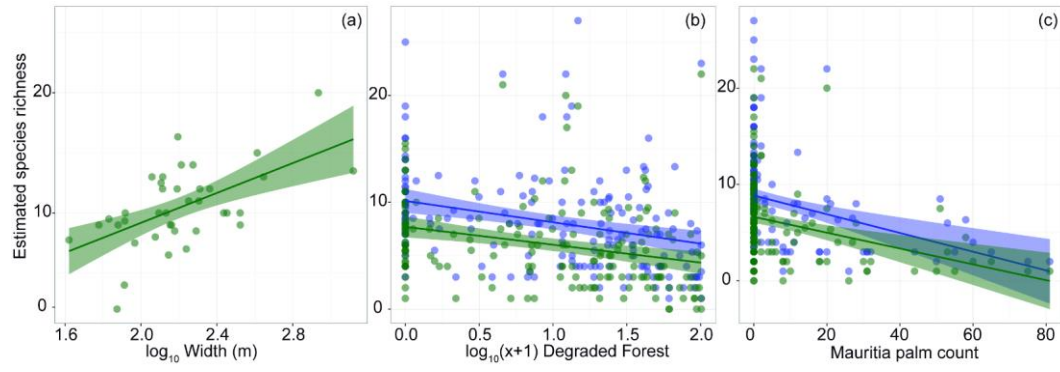
780 **Figures**

781



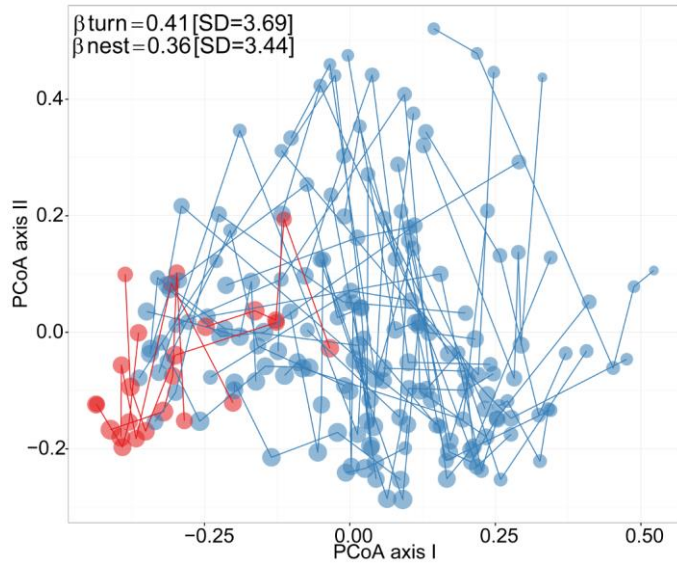
782

783 Figure 1 (1.5 column)



784

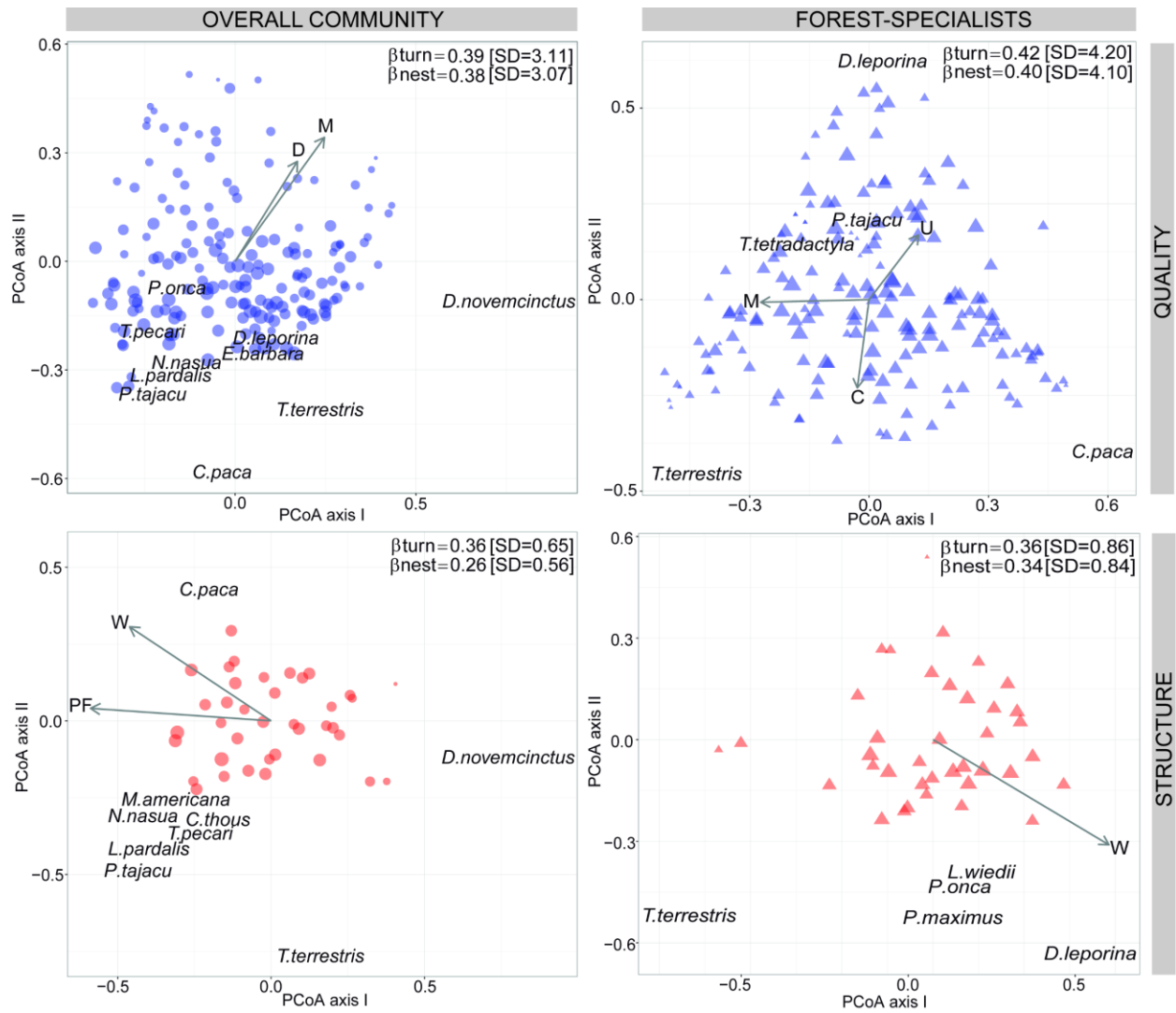
785 Figure 2 (1.5 column)



786

787 Figure 3 (1 column)





788

789 Figure 4 (2 columns)

790 **Supplementary material**

791

792 Table A1. Species trait compilation to generate the functional diversity (FD) metric: 1) group biomass was estimated by multiplying  
 793 mean body mass by the mean group size; 2) forest specificity, subjectively categorized from 1 (frequently occurring in open habitats  
 794 such as the pasture matrix) to 3 (restricted to forested areas, and strongly avoiding open habitats); 3) trophic index, generated as a  
 795 weighted mean of the energetic level of a species diet by the proportion of items found on that diet (following Wilman et al. 2014); 4)  
 796 home range size (in hectares); 5) and a categorical measure of the main mode of locomotion and/or vegetation stratum (terrestrial,  
 797 scansorial or arboreal).

Species	Group mass	Forest specificity	Trophic index*	Home range size	Stratum	References
<i>Cabassous unicinctus</i>	4.80	1	80	101.60	G	Reis et al. 2011, Wilman et al. 2014
<i>Cerdocyon thous</i>	5.24	1	80	75.00	G	Bertha, A. 1982, Eisenberg & Redford 1999, Nowak 1999, Wilman et al. 2014
<i>Coendou prehensilis</i>	4.40	2	26	17.50	Ar	Eisenberg & Redford 1999, Nowak 1999, Wilman et al. 2014
<i>Cuniculus paca</i>	8.17	2	36	3.44	G	Nowak 1999, Pérez 1992, Wilman et al. 2014
<i>Dasyprocta leporina</i>	3.02	3	34	3.00	G	Nowak 1999, Wilman et al. 2014
<i>Dasybus novemcinctus</i>	4.20	1	80	7.70	G	Eisenberg & Redford 1999, McBee & Baker 1982, Nowak 1999, Wilman et al. 2014
<i>Didelphis</i>	1.09	1	50	69.50	S	Eisenberg & Redford 1999, Nowak 1999, Wilman et al. 2014

<i>marsupialis</i>						
<i>Eira barbara</i>	3.91	3	94	2000.00	G	Eisenberg & Redford 1999, Nowak 1999, Wilman et al. 2014
<i>Hydrochoerus hydrochaeris</i>	962.90	1	22	10.40	G	Eisenberg & Redford 1999, Mones & Ojasti 1986, Nowak 1999, Wilman et al. 2014
<i>Leopardus pardalis</i>	11.90	3	100	1815.00	G	Eisenberg & Redford 1999, Murray & Gardner 1997, Oliveira & Cassaro 2006, Reis et al. 2011, Wilman et al. 2014
<i>Leopardus wiedii</i>	3.25	3	88	500.00	S	Eisenberg & Redford 1999, Oliveira & Cassaro 2006, Oliveira 1998, Reis et al. 2011, Wilman et al. 2014
<i>Mazama americana</i>	22.80	3	28	100.00	G	Nowak 1999, Tobler et al. 2009, Wilman et al. 2014
<i>Mazama sp</i>	16.63	2	34	100.00	G	Nowak 1999, Tobler et al. 2009, Wilman et al. 2014
<i>Myrmecophaga tridactyla</i>	22.33	1	80	370.00	G	Eisenberg & Redford 1999, Nowak 1999, Wilman et al. 2014
<i>Nasua nasua</i>	94.85	3	56	445.00	S	Eisenberg & Redford 1999, Gompper & Decker 1998, Reis et al. 2011, Wilman et al. 2014
<i>Panthera onca</i>	100.00	3	100	7825.00	G	Eisenberg & Redford 1999, Nowak 1999, Oliveira & Cassaro 2006, Wilman et al. 2014
<i>Pecari tajacu</i>	638.00	2	44	113.00	G	Eisenberg & Redford 1999, Nowak 1999, Wilman et al. 2014
<i>Priodontes maximus</i>	45.36	3	80	1000.00	G	Reis et al. 2011, Wilman et al. 2014
<i>Procyon cancrivorus</i>	6.95	2	80	695.00	G	Reis et al. 2011, Wilman et al. 2014
<i>Puma concolor</i>	51.60	2	100	3200.00	G	Currier, M.J.P. 1983, Nowak 1999, Oliveira & Cassaro 2006, Wilman et al. 2014

<i>Puma yagouaroundi</i>	6.88	3	92	1330.00	G	Eisenberg & Redford 1999, Oliveira & Cassaro 2006, Oliveira 1998, Wilson & Mittermier 2009, Wilman et al. 2014
<i>Speothos venaticus</i>	12.00	3	100	690.00	G	Reis et al. 2011, Wilman et al. 2014
<i>Tamandua tetradactyla</i>	5.52	2	80	380.00	S	Reis et al. 2011, Wilman et al. 2014
<i>Tapirus terrestris</i>	207.50	2	20	200.00	G	Padilla & Dowler 1994, Reis et al. 2011, Wilman et al. 2014
<i>Tayassu pecari</i>	3223.37	3	44	1100.00	G	Eisenberg & Redford 1999, Mayer & Wetzel 1987, Nowak 1999, Wilman et al. 2014

798 \*The energy levels considered for each diet category were assigned to a rank order including 1 (foliage), 2 (fruits), 3 (seeds), 3  
799 (invertebrates), and 4 (vertebrates or carrion).

800

801

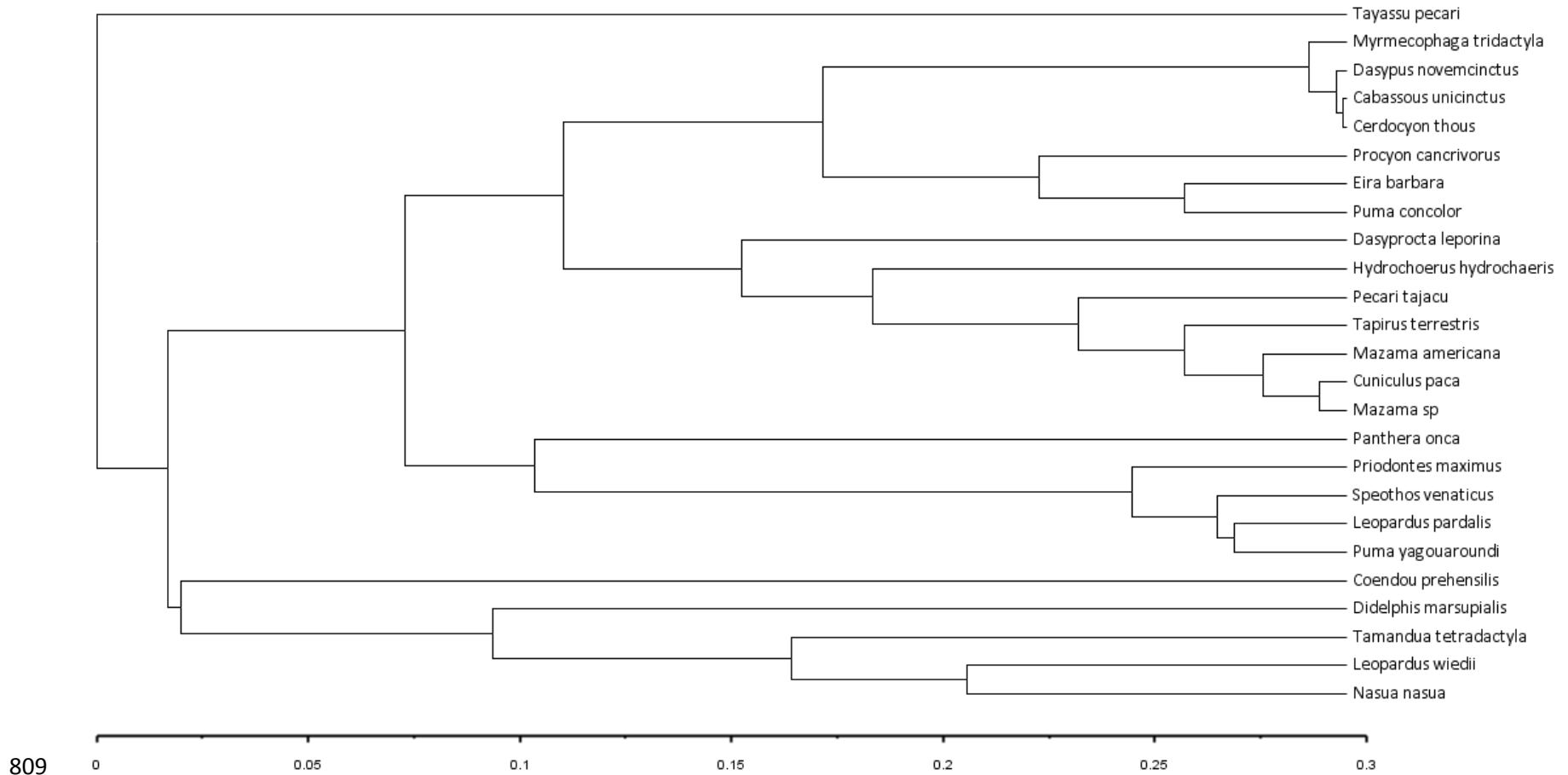
802

803

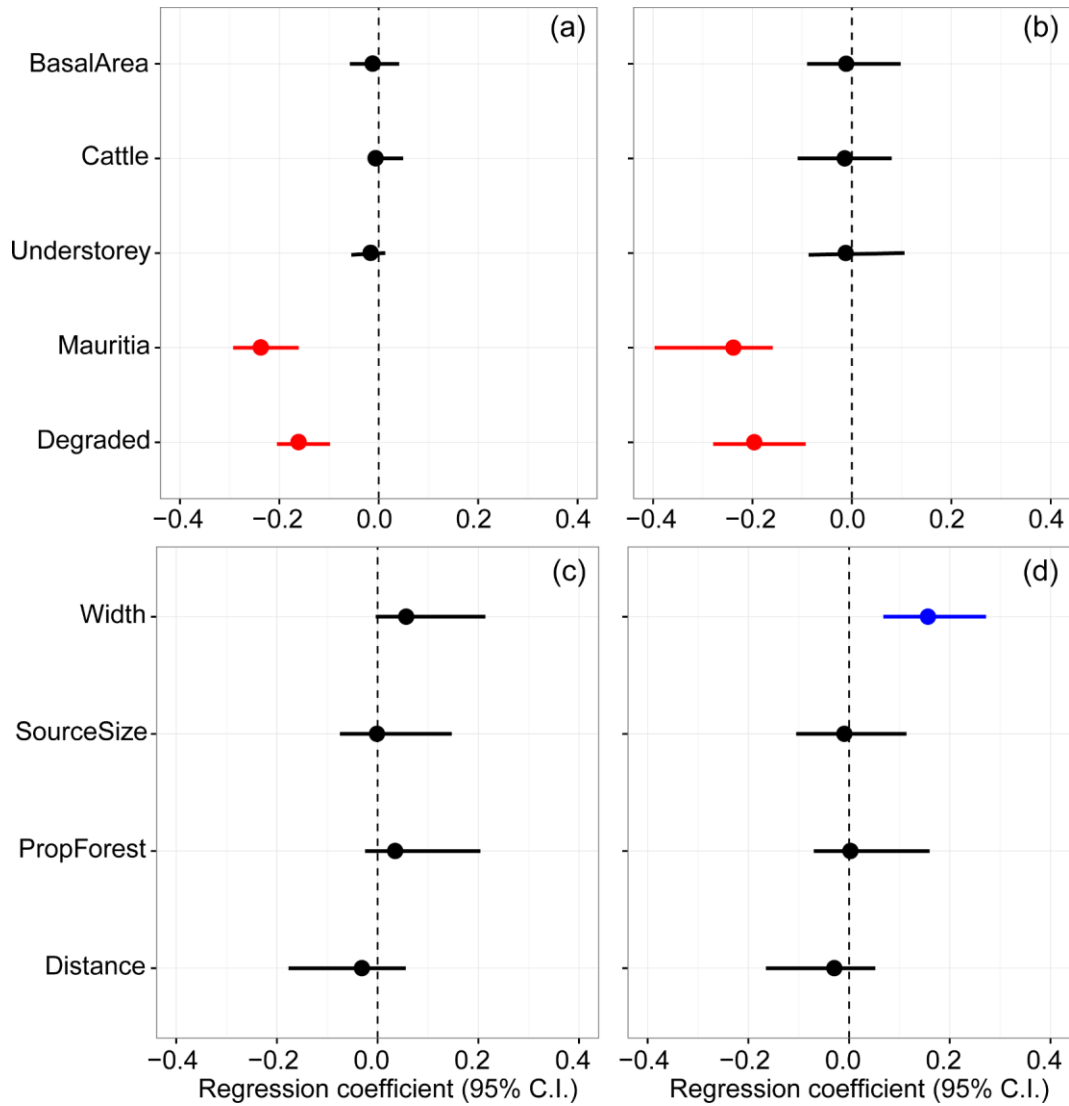
804

805

806 Figure A1. Functional dendrogram generated with the Euclidean distance and the unweighted paired-group clustering method by  
807 arithmetic averages (UPGMA) of trait values. Branch length was standardized from the root to the tips of the tree. Traits used to  
808 calculate distances between species are presented in Appendix S1.



810 Figure A2. Regression coefficient values and confidence intervals for all variables included in  
 811 the global models, and obtained by the model averaging procedure. Models generated for: (a)  
 812 riparian corridor quality predictors of total estimated species richness (Chao1); (b) corridor  
 813 quality predictors of estimated richness of forest-specialists (Chao1); (c) landscape structure  
 814 predictors of total estimated species richness (Chao1); and (d) landscape structure predictors of  
 815 richness of forest-specialists (Chao1).



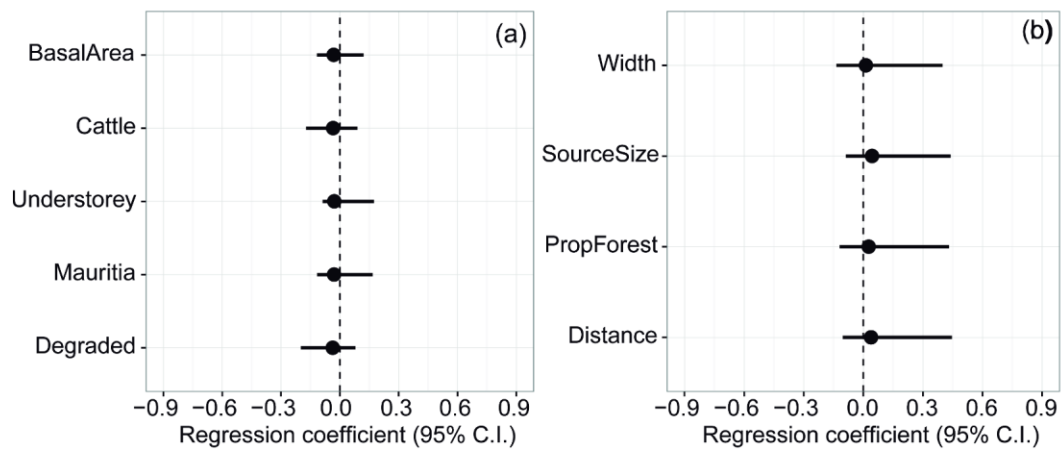
816

817

818

819

820 Figure A3. Regression coefficient values (and 95% confidence intervals) for all predictors  
821 included in the global models, and obtained by the model averaging procedure. Models  
822 generated for: (a) riparian corridor quality predictors of expected functional diversity ( $FD_{exp}$ );  
823 and (b) landscape structure predictors of  $FD_{exp}$ .



824