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

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Abstract

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

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

Introduction

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

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

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

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

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

Here, we assess the role of remnant riparian forests as landscape connectors for medium to large-bodied terrestrial mammals in a fragmented landscape of southern Brazilian Amazonia. In particular, we compare mammalian use of riparian forests embedded within large tracks of continuous forest with those remaining as relict habitat in highly fragmented landscape contexts. We expect that community richness and functional diversity to be higher in continuous riparian forests than in remnant corridors, as well as a shift in community composition between these forest corridor types. Secondly, we quantitatively assess corridor use by the mammal assemblage, and relate richness, functional diversity, and composition patterns to corridor structure and quality, and landscape context. We hypothesize that both species richness and functional diversity will be lower, and species composition will be simplified in narrower and more isolated corridors of lower habitat quality, particularly those connected to distant and smaller source patches. This study focused on observed patterns of corridor use, resulting in direct conclusions on how intrinsic features of corridors affect their use by forest wildlife, and indirect conclusions on the role of riparian corridors in maintaining landscape connectivity.

Materials and Methods

1.1 Study area

This study was conducted across a 16,200-km2 landscape encompassing three municipal counties in the northern state of Mato Grosso, southern Brazilian Amazonia: Alta Floresta (09°53'S, 56°29' W), Paranaíta (09°40'S, 56°28' W), and Carlinda (09°58'S, 55°49'W). All three counties were subjected to high deforestation rates in the past four decades, and collectively represent one of the most fragmented regions of the Amazonian 'arc of deforestation'. Prior to the onset of deforestation in 1978, this entire region consisted of a similar baseline mosaic of forest formations, including mostly upland (*terra firme*) forests and to a lesser extent seasonally flooded forests. However, only ~53% of the study landscape currently retains its original forest cover. Although human settlement patterns vary among those three counties, their anthropogenic habitat matrix is similar, and consists primarily of extensively managed livestock pastures under low cattle stocking densities (Michalski et al. 2008).

1.2 Study design

We selected 43 sampling sites including 38 remnant riparian forest corridors of varying width, which were embedded into a cattle pasture matrix, and five relatively homogenous pseudo-control riparian areas embedded within relatively large tracts of continuous forest in the landscape (> 5 000 ha; Fig. 1). We defined a riparian corridor structurally, as a narrow forest remnant (relatively to its length) maintained along streams. All riparian sites were at least 1 000 m in length and spaced apart by a minimum distance of 1,500 m. At each sampling site, we installed four to five digital camera traps (Bushnell Trophy Cam and Reconyx HC500 HyperFire) along the riparian zone, which were spaced apart by 250-300 m. These two camera trap models were randomly distributed across corridors, in order to avoid model-dependent biases due to differential animal detection of cameras (Meek at al. 2014). Our observational sample size thus amounted to 199 camera-trapping stations, whereas our inferential sample size consisted of 43 independent sampling areas.

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

1.3 Environmental variables

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

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

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

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

1.4 Data Analysis

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

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

Differences in S and FD between riparian forest types (corridors vs. continuous forests) were examined with likelihood-ratio tests and variance component analyses, in which the 199 camera-trap stations were nested within the 43 riparian forests. We fitted generalized linear mixed-models (GLMM) to examine the effects of corridor quality (proportion of degraded forest, tree basal area density, understorey density, *M. flexuosa* count, and cattle intrusion rank) on total species richness, richness of forest-specialists, and FD_{exp}, with a random factor for the corridor (n=38) in which camera-trap stations were nested (n=174). To examine the effects of both patch and landscape variables (mean corridor width, mean distance to the nearest source patch, source patch area, and isolation) on the same mammal assemblage properties, we fitted generalized linear models (GLM) for riparian corridors as a whole. First, we ascertained that there was no strong multicollinearity ($r < 0.6$) between the variables entered into the global models. We then tested for residual overdispersion of the global models, and in case this was detected, overdispersion was corrected by including an observation-level random effect (Harrison 2014). GLM models that required the overdispersion correction parameter were thus transformed into GLMM models to include the random factor. All predictors included in the models were standardized to account for the different magnitudes between variables (Table 1). We identified meaningful predictors of community measures on the basis of a model selection procedure, considering all combinations of the variables included in the global models, with the Akaike Information Criterion corrected for small sample sizes (AICc, Burnham & Anderson 2002). The relative importance of each variable was compared using their regression coefficients and unconditional standard errors generated by model-averaging.

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

Results

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

2.1 Patterns of diversity

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

Models explaining estimated species richness as a function of corridor quality indicated that habitat degradation and *M. flexuosa* palm abundance were both associated with lower numbers of species for both the entire community ($\beta_{degradation}$ = –0.15 [–0.20 – –0.10], $\beta_{mauritia}$ = –0.23 [–0.29 – –0.16]) and for forest-specialists only ($\beta_{degradation}$ = –0.18 [–0.28 – –0.09], $\beta_{mauritia}$ = –0.23 [–0.40 – –0.16]) (Fig. 2 and Fig. A2). Patch structure, as measured by corridor width, however, had a positive effect on forest-specialist species richness (β_{width} = –0.17 [0.07 – 0.27]; Fig. A2), and corridors had to be at least 100-m wide to retain the same average number of forest-dependent species typical of continuous riparian areas (approx. 10 species, Table 2), although the species richness in corridors of 100 – 400 m in width was widely variable (Fig. 2). Finally, we failed to detect any effect of explanatory variables on expected functional diversity (Fig. A3).

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

2.2 Patterns of assemblage composition

Mammal assemblage composition in remnant riparian forests diverged from those in continuous forests, although they had a high degree of species overlap, suggesting that some corridors shared a similar set of species with riparian zones in continuous forests. Community composition varied strongly among camera trap stations within the same riparian forest (Fig. 3), and although there was a clear effect of overall species richness on these community-wide differences, species turnover played an even stronger role in explaining the dissimilarity (Fig. 3 and 4a). Measures of habitat quality that were significantly associated with these differences included *M. flexuosa* abundance and the proportion of surrounding degraded forest for all mammal species, for which more species-rich assemblages containing mostly forest-specialists were associated with low values of forest degradation and mauritia abundance (Fig. 4). Understorey density, cattle intrusion, and mauritia abundance also affected the composition of forest-dependent mammals, for which observed dissimilarities were best explained by community nestedness, rather than species turnover. Red-rumped agouti (*D. leporina*), collared-peccary (*Pecari tajacu*), and lesser anteater (*Tamandua tetradactyla*) were associated with higher understorey densities, lowland tapir (*T. terrestris*) occurred more frequently in areas containing denser mauritia palm clumps, while paca (*C. paca*) was negatively associated with mauritia abundance. Also, occurrence of tapir and paca were weakly related to higher levels of cattle intrusion (Fig. 4).

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

Discussion

Riparian forest remnants present a huge potential for planning and implementing connectivity networks that can not only ensure the retention of relict forest habitat but maintain the flux of many forest species across the landscape, ultimately contributing to a healthier ecosystem functioning (Crooks & Sanjayan 2006). However, the structure of these remnant features will ultimately determine whether or not they can effectively serve their full functional connectivity role for a wide range of species. In our study region in southern Amazonia, riparian forest remnants retained within private landholdings by migrant farmers less than four decades ago ranged widely in their integrity status in terms of both corridor structure and vegetation quality. Comparisons between remnant riparian strips within cattle pastures and those embedded into large continuous tracts of forest also confirmed that wide and well-preserved remnants can function as suitable habitat and/or landscape conduits for a wide range of terrestrial vertebrates present in the landscape. There were significant differences in species diversity and species composition between remnant riparian corridors and riparian zones within continuous forests, although functional diversity differences between these two classes were trait-independent. However, the high mammal community overlap between wide, high-quality riparian remnants and continuous riparian sites indicate that well-preserved corridors are the best available opportunity to maintain terrestrial mammal diversity in highly deforested landscapes. This is, however, a conservative estimate of community similarity because even our continuous "pseudo-control" sites are not exactly pristine primary forest, thereby serving as an imperfect baseline of the observed patterns. Although these continuous riparian zones were embedded within relatively large forest fragments (>5 000 ha) compared to most other forest patches remaining in the region, they do not represent the vast unbroken tracts of forests of our study region until the late 1970s, and some have been subject to selective logging thereafter. Despite an imperfect baseline, however, these large patches currently operate as source patches for mammal populations, thereby strengthening the potential of remnant riparian strips as dispersal corridors for the contemporary mammal assemblage.

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

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

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

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

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

Although mauritia palm clusters (*veredas*) provide important food sources for many ungulate and rodent species, such as the tapirs (*T. terrestris*), white-lipped peccaries (*Tayassu pecari*), pacas (*Cuniculus paca*) and agoutis (*D. leporina*) (Beck 2006; Endress et al. 2013), palm density had a negative effect on mammal community structure. This can be explained by the high rates of deforestation of *veredas* in the region. *Veredas* were dominated by mauritia palms, and consisted of poorly drained, waterlogged soils even during the dry season. Although palm swamps are also legally protected, the absence of a clearly-defined water course, from which to measure the buffer strip width, may explain why many landowners feel entitled to convert a larger fraction of *veredas* than what would be required to meet their minimum APP legal compliance. This results in *veredas* becoming the most deforested vegetation formation throughout our study area, with pastures often encroaching right up to the stream (BZ and CAP, pers. obs.). *Vereda* corridors were therefore typically very narrow (<40m wide) and waterlogged throughout, so it is unsurprising that local movement rates under these conditions were apparently low for several species. This is corroborated by the fact that large herds of white-lipped peccaries as well as the pacas were virtually never observed using these narrow corridors, despite the high abundance of a preferred food resource.

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

3.1 Policy implications

Prior to legislative changes, the Brazilian Forest Act required landowners to set aside a permanent forest strip (APP) of at least 30 m on each side of rivers and perennial streams narrower than 10 m. The more lenient current legislation prevents any further clearing, but bestows amnesty to landholdings up to 400 ha that failed to comply with the legislation prior to 2008 in requiring a strip width of only 5-10 m on both sides of streams, depending on landholding size (Brazil 2012). These small non-complying landholdings represent the vast majority of private properties in the study region (Michalski et al. 2010) and elsewhere in the Brazilian Amazon (Godar et al. 2014). In terms of width, the amount of riparian forest protection currently required by law has already been shown to be insufficient (Lima & Gascon 1999; Lees & Peres 2008; De Fraga et al. 2011; Bueno et al. 2012), and most species, particularly forest specialists that are usually of highest conservation concern, rarely use very narrow corridors. In practice, the newly approved Forest Act condones past illegal deforestation, effectively increasing compliance rates. However, recent deforestation monitoring indicates a 53% increase in the overall annual deforestation rate for the Brazilian Amazon between 2014 and 2015 (Fonseca et al. 2015).

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

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

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

3.2 Conclusions

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

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Tables

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

Variable	Mean [Range]
Landscape structure	
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[a]	0.31 [0.13–0.51]
Forest quality	
Tree basal area (m^2/ha)	35.8 [1.9–145.5]
Understory density	0.54 [0.01–0.99]
Mauritia flexuosa count	5.6 [0–81]
Cattle intrusion	1 [0–4]
Degraded forest proportion[b]	20.4 [0.0–100.0]

[a] Total forest proportion refers to the proportion of forest within a 1-km buffer around the corridor, excluding the area of the corridor.

[b] Degraded forest proportion refers to the proportion of forest classified as degraded or secondary within a 50-m buffer around each camera trap station.

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

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

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

Figure legends

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

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

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

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

Figures

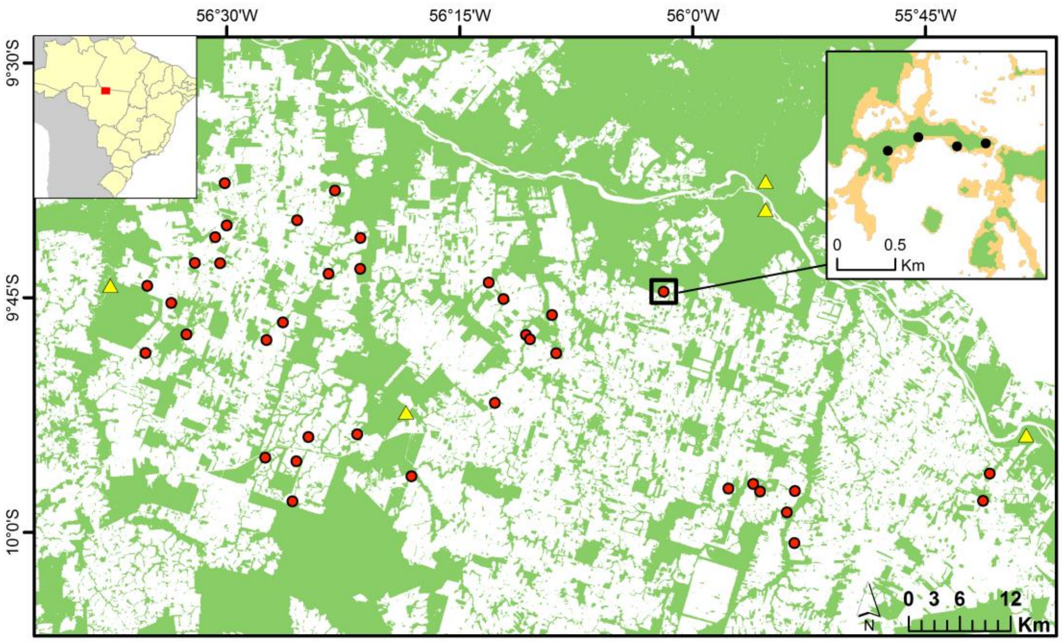
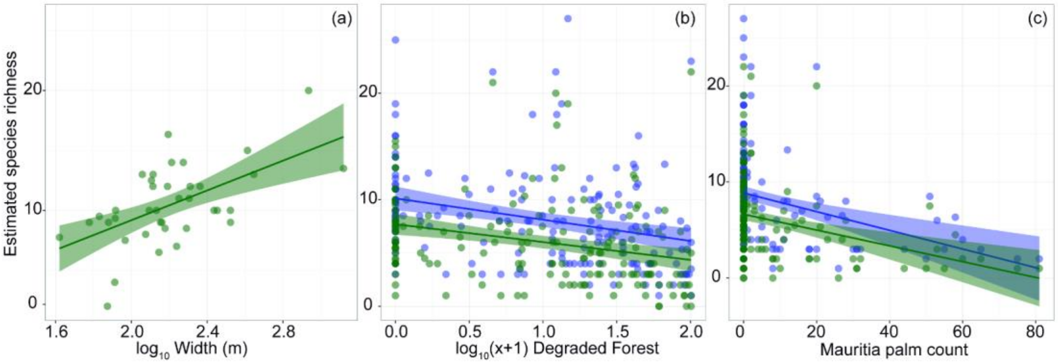


Figure 1 (1.5 column)



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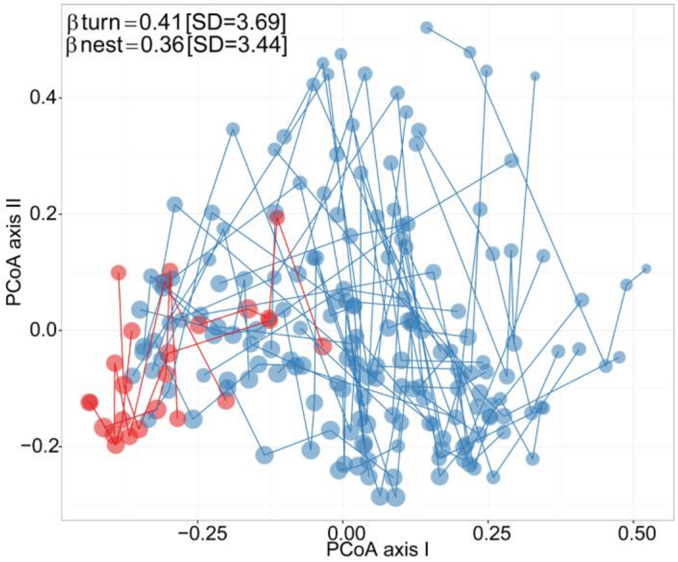

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787 Figure 3 (1 column)

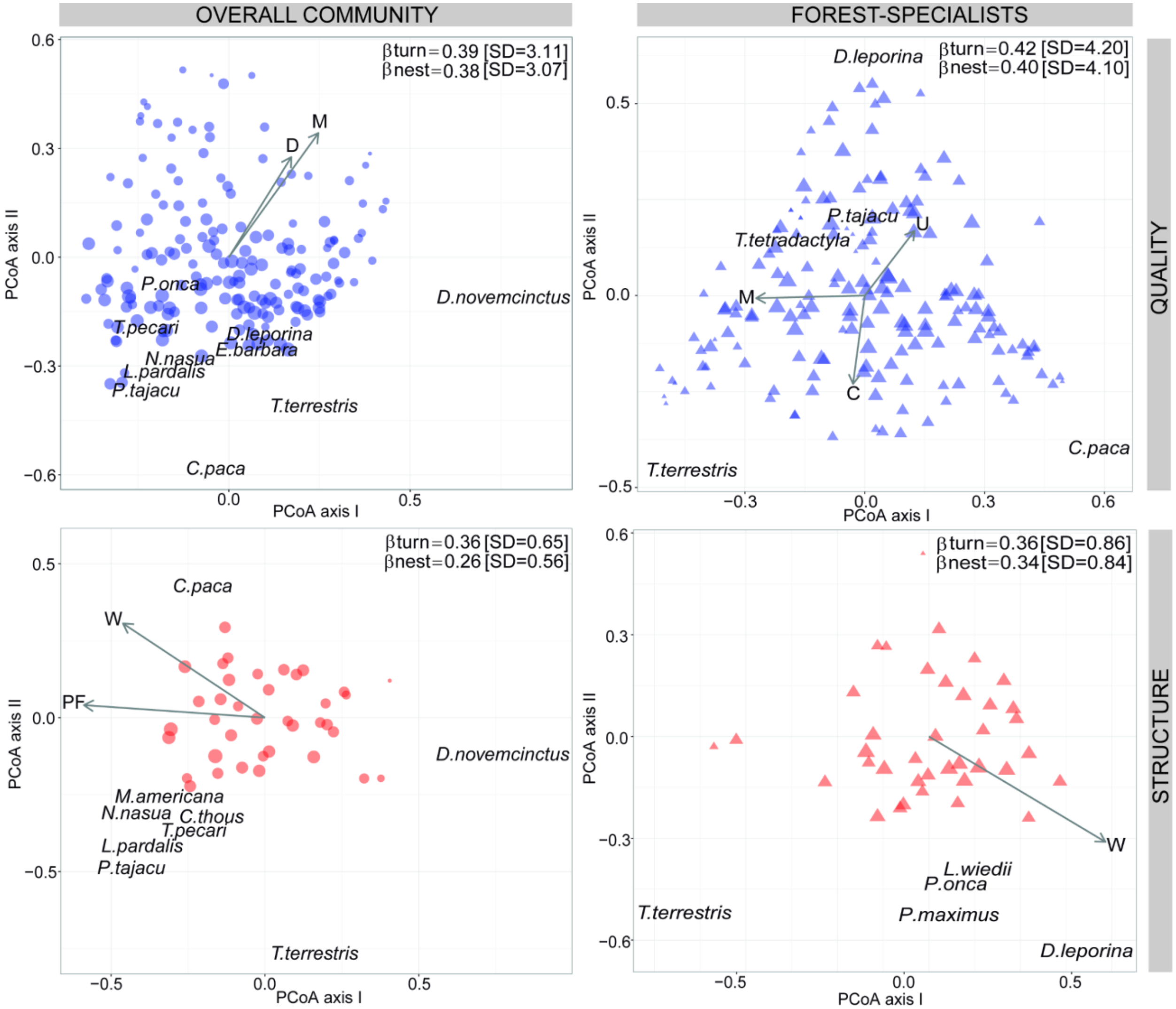

Figure 4 (2 columns)

Supplementary material

Table A1. Species trait compilation to generate the functional diversity (FD) metric: 1) group biomass was estimated by multiplying mean body mass by the mean group size; 2) forest specificity, subjectively categorized from 1 (frequently occurring in open habitats such as the pasture matrix) to 3 (restricted to forested areas, and strongly avoiding open habitats); 3) trophic index, generated as a 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) home range size (in hectares); 5) and a categorical measure of the main mode of locomotion and/or vegetation stratum (terrestrial, scansorial or arboreal).

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

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

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

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

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

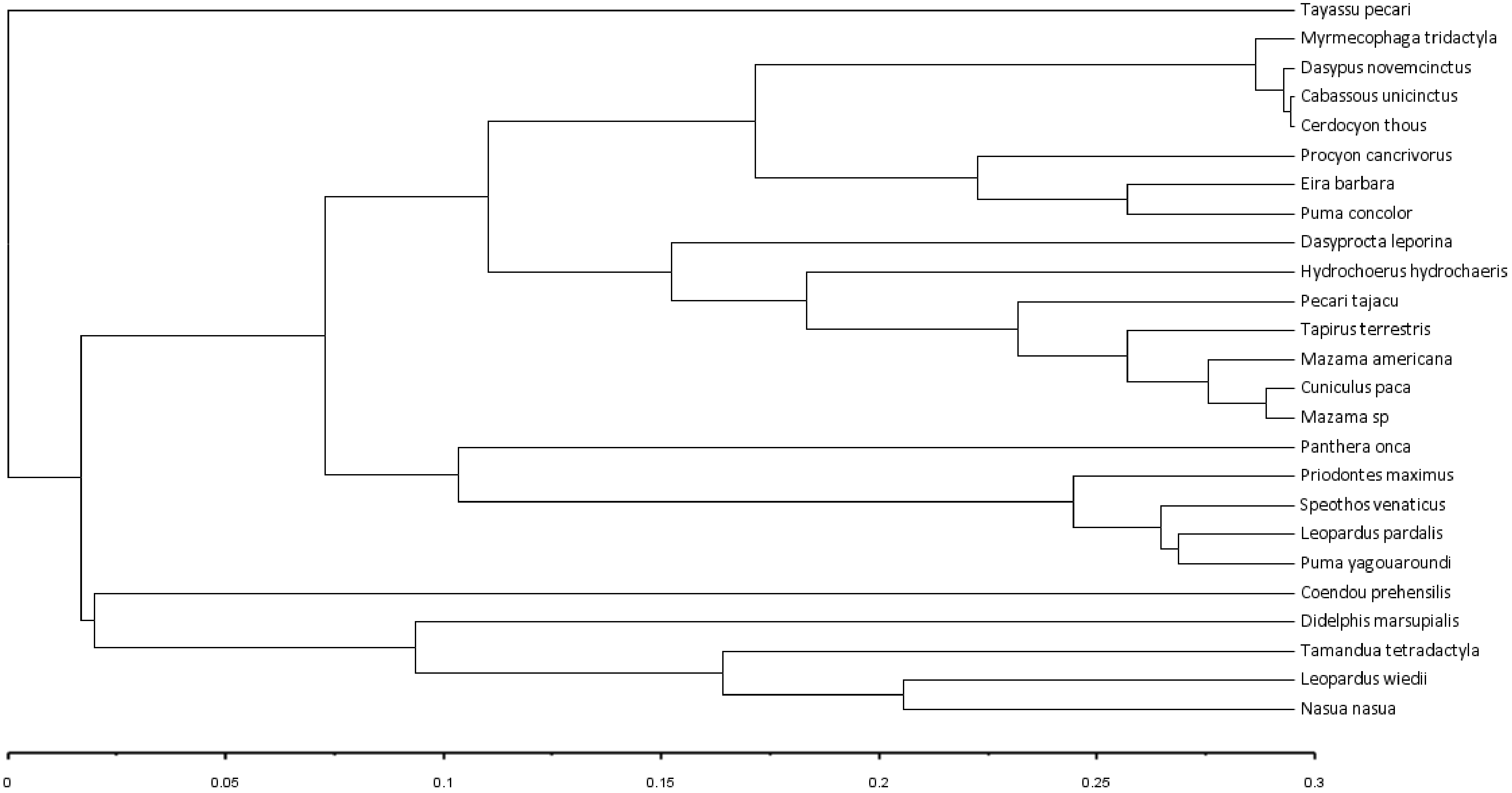

Figure A2. Regression coefficient values and confidence intervals for all variables included in the global models, and obtained by the model averaging procedure. Models generated for: (a) riparian corridor quality predictors of total estimated species richness (Chao1); (b) corridor quality predictors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

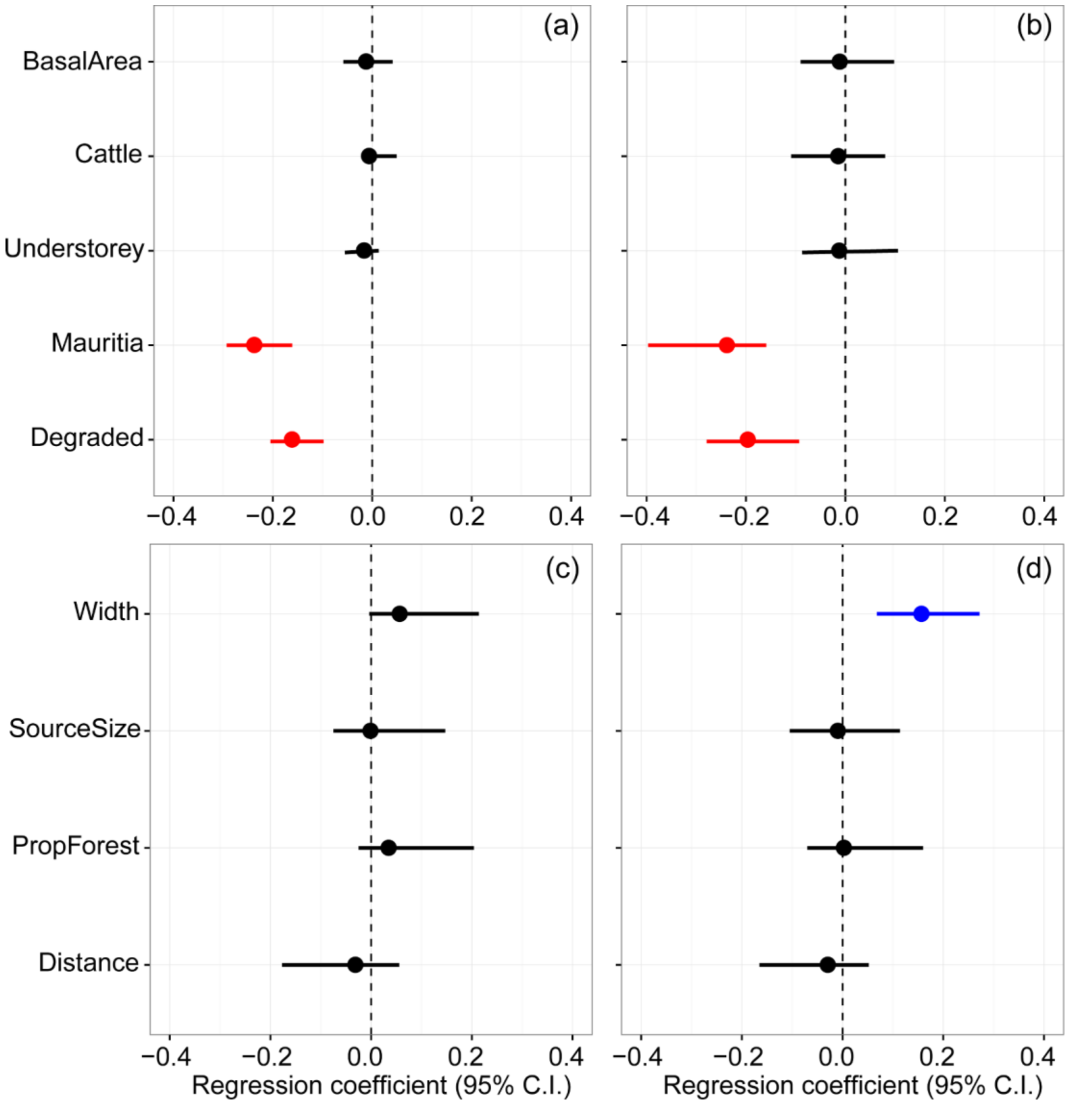

Figure A3. Regression coefficient values (and 95% confidence intervals) for all predictors included in the global models, and obtained by the model averaging procedure. Models generated for: (a) riparian corridor quality predictors of expected functional diversity (FD_{exp}); and (b) landscape structure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