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Seasonal dynamics of terrestrial vertebrate abundance between Amazonian flooded and unflooded forests

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The flood pulse is the main factor structuring and differentiating the ecological communities of Amazonian unflooded (*terra firme*) and seasonally-flooded (*várzea*) forests as they require unique adaptations to survive the prolonged annual floods. Therefore, *várzea* and *terra firme* forests hammer out a spatio-temporal mosaic of resource availability, which may result in landscape scale seasonal movements of terrestrial vertebrates between adjacent forest types. Yet the lateral movements of terrestrial vertebrates between hydrologically distinct neighbouring forest types exhibiting staggered resource availability remains poorly understood, despite the important implications of this spatial dynamic for the ecology and conservation of forest wildlife. We examined the hypothesis of terrestrial fauna seasonal movements between two adjacent forest types at two contiguous sustainable-use forest reserves in Western Brazilian Amazonia. We used camera trapping data on the overall species richness, composition, and abundance of nine major vertebrate trophic guilds to infer on terrestrial vertebrate movements as a function of seasonal changes in floodplain water level. Species richness differed in neighboring *terra firme* forests between the high-and low-water phases of the flood pulse and *terra firme* forests were more species rich than *várzea* forests. There were clear differences in species composition between both forest types and seasons. Generalized Linear Models showed that water level was the main factor explaining aggregate abundance of all species and three trophic guilds. Our results indicate that the persistence of viable populations of large terrestrial vertebrates adjacent to major Amazonian rivers requires large, well-connected forest landscapes encompassing different forest types to ensure large-scale lateral movements by forest wildlife.

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Abstract

The flood pulse is the main factor structuring and differentiating the ecological communities of Amazonian unflooded (*terra firme*) and seasonally-flooded (*várzea*) forests as they require unique adaptations to survive the prolonged annual floods. Therefore, *várzea* and *terra firme* forests hammer out a spatio-temporal mosaic of resource availability, which may result in landscape scale seasonal movements of terrestrial vertebrates between adjacent forest types. Yet the lateral movements of terrestrial vertebrates between hydrologically distinct neighbouring forest types exhibiting staggered resource availability remains poorly understood, despite the important implications of this spatial dynamic for the ecology and conservation of forest wildlife. We examined the hypothesis of terrestrial fauna seasonal movements between two adjacent forest types at two contiguous sustainable-use forest reserves in Western Brazilian Amazonia. We used camera trapping data on the overall species richness, composition, and abundance of nine major vertebrate trophic guilds to infer on terrestrial vertebrate movements as a function of seasonal changes in floodplain water level. Species richness differed in neighboring *terra firme* forests between the high-and low-water phases of the flood pulse and *terra firme* forests were more species rich than *várzea* forests. There were clear differences in species composition between both forest types and seasons. Generalized Linear Models showed that water level was the main factor explaining aggregate abundance of all species and three trophic guilds. Our results indicate that the persistence of viable populations of large terrestrial vertebrates adjacent to major Amazonian rivers requires large, well-connected forest landscapes encompassing different forest types to ensure large-scale lateral movements by forest wildlife.

Introduction

Wetland habitats are both challenging to conserve and globally important for biodiversity conservation and human wellbeing (Keddy et al., 2009). Seasonal and perennial wetlands are exceptionally productive habitats that support both high densities and a high diversity of wild species (Halls, 1997; Junk et al., 2006). They also directly underpin the livelihoods of millions of people and provide ecosystem services including productive fisheries, water purification, hydrological regulation, nutrient cycling and naturally-fertilized agricultural land (Costanza et al., 1997; François et al., 2005). The associated seasonal movements of wetland fauna are especially challenging to conserve because their spatially complex life histories require resources provided by several distinct habitats and entail diverse anthropogenic threats at multiple sites (Martin et al., 2007; Wilcove & Wikelski, 2008).

A vast proportion of the Amazon Basin is formed by natural landscape mosaics of wetlands embedded within a matrix of upland (hereafter, *terra firme*) forests on generally nutrient-poor soils well above the maximum water-level of adjacent floodplains (Tuomisto et al., 1995). Amazonian floodplains comprise a variety of habitats including swamp forests, hydromorphic savannas, coastal wetlands, tidal forests, and seasonally-flooded forests. These Amazonian wetlands are classified according to their climatic, edaphic and floristic characteristics (Junk & Piedade, 2010; Junk et al., 2011). Based on these criteria, two large groups of wetlands have been broadly distinguished: those with either (i) relatively stable or (ii) oscillating water levels (Junk et al., 2011).

Most Amazonian wetlands with oscillating water levels are subjected to a predictable, long-lasting monomodal flood pulse which alternates between the high- and low-water periods according to the Flood Pulse Concept (Prance, 1979; Junk, Bayley & Sparks, 1989). Depending on the geomorphology and geochemical profile of each watershed, these areas can be inundated by white-, black- or clear-water rivers (Sioli, 1984). White-water rivers such as the Solimões, Madeira, Japurá and Juruá have their origins in the Andes or Andean piedmonts, are nutrient-rich, and have neutral pH. These rivers deposit their alluvial sediments along wide swaths of floodplain forests of high primary productivity, which are locally known as *várzeas* (Wittmann et al., 2006; Junk et al., 2011). In contrast, Amazonian black-water rivers such as the Negro, Tefé and Jutaí rivers discharge transparent-blackish waters with low suspended sediment loads

63 and acidic pH. Forests inundated by black-water rivers are locally known as *igapós* and are
64 typically supported by low-fertility soils and their trees exhibit 50% lower diameter increment
65 compared to *várzea* forests (Junk & Piedade, 2010; Junk et al., 2011).

66 The flood pulse is the main factor structuring and differentiating the ecological communities of
67 *várzea* and *igapó* forests from adjacent *terra firme* forests (Peres, 1997; Haugaasen & Peres,
68 2005a; Haugaasen & Peres, 2005b; Hauagaasen & Peres, 2005c; Beja et al., 2009) as they
69 require unique adaptations to survive the prolonged annual floodwaters. *Terra firme* forests are
70 more species-rich, including more forest habitat specialists than *várzeas* and *igapó*, while the
71 average population biomass density is higher in seasonally-flooded forests along white-water
72 rivers (Peres, 1997). This predictable long-lasting and monomodal flood pulse triggers and
73 synchronizes critical ecological events including the availability of plant reproductive parts
74 (Nebel et al. 2001, Schöngart et al. 2002, Haugaasen & Peres 2005a, Hawes & Peres 2016),
75 dietary shifts in primates, ungulates and fishes (Bodmer 1990, Peres 1994, 1999, Saint-Paul et
76 al. 2000), human extractive activities of non-timber forest products, and the exploitation of both
77 terrestrial and aquatic prey (Newton, Endo & Peres 2011; Endo, Peres & Haugaasen 2016). As
78 they are structurally and compositionally different, Amazonian *várzeas*, *igapós* and *terra firme*
79 forests engender a spatio-temporal mosaic of resource availability which may result in
80 landscape-scale seasonal movements of terrestrial vertebrates between these often neighbouring
81 forest types (Bodmer 1990, Peres 1999, Haugaasen & Peres 2007). *Terra firme*, *várzea* and
82 *igapó* forests exhibit complementary fruit production peaks, whereby the fruiting peak in *terra*
83 *firme* forests occurs during the onset of the wet season, whereas fruit maturation in *várzeas* and
84 *igapós* begin during the late high-water season (Schöngart et al., 2002; Haugaasen & Peres,
85 2005a, 2007; Hawes & Peres, 2016).

86 This asynchrony in fruit production attracts frugivorous fish and arboreal frugivores to
87 floodplain forests during the high-water period (Saint-Paul *et al.* 2000; Beja *et al.* 2009),
88 whereas ungulates, carnivores, terrestrial insectivores and ant-following birds are attracted to
89 *várzeas* and *igapós* immediately after the water level recedes. These lateral movements are due
90 to the high abundance of fruit and seed deposited on the forest floor and higher insect abundance
91 during this period (Bodmer 1990, Peres 1994, Adis & Junk 2002, Haugaasen & Peres 2007,
92 Mendes Pontes & Chivers 2007, Beja et al. 2009).

93   We tested the hypothesis that many terrestrial vertebrates move seasonally between Amazonian

94   seasonally-flooded and unflooded forests by conducting camera-trapping surveys in both *terra*

95   *firme* and *várzea* forests along a major white-water tributary of the Amazon river during both

96   the high- and low-water phases of the flood pulse. We examined differences in vertebrate

97   abundance, species richness, and changes in species composition between these two forest types

98   and seasons. The contrast between the high- and low-water phases of the flood pulse was used

99   to indirectly infer that the terrestrial fauna most likely leave *terra firme* forest and move into

100 *várzea* forests during the low-water phase to take advantage of higher resource availability.

101 Conversely, there should be transient overcrowding of the terrestrial vertebrate fauna in adjacent

102 *terra firme* forests driven by lateral movements away from the rising floodwaters during the

103 high-water phase. We provide crucial empirical evidence supporting the notion that Amazonian

104 *terra firme* and *várzea* forests should be juxtaposed within fully functional floodplain protected

105 areas, thereby enhancing both the spatial configuration of reserve design and landscape

106 management of highly heterogeneous forest macromosaics in Amazonia for both biodiversity

107 persistence and the subsistence of local extractive communities.

108 **Materials & Methods**

109 Study Area

110 This study was carried out at two contiguous sustainable-use forest reserves within the State of

111 Amazonas, Brazil: the Médio Juruá Extractive Reserve (RESEX) spanning 253,227 ha, and the

112 Uacari Sustainable Development Reserve (RDS) spanning 632,949 ha. Both reserves border the

113 white-water Juruá River, the second largest white-water tributary of the Amazonas/Solimões

114 River. These protected areas contain large expanses of *terra firme* forests (80% of both reserves)

115 as well as an approximately 18.40 ± 5.71 km wide band of seasonally-flooded *várzea* forest

116 (17.9%) encompassing the main river channel (Hawes et al., 2012) (Fig. 1). The Juruá region

117 experiences an Af climate type (constantly humid) according to Köeppen criteria, with a mean

118 annual temperature of 27.1ºC, a mean rainfall of 3,679 mm/year, and peak water levels of 14 m

119 during a prolonged flood pulse, which is alternated by a dry phase in *várzea* between July and

120 early November (Peres, 1997). All forest sites surveyed consist of largely undisturbed primary

121 forest, although commercially valuable timber species have experienced non-mechanized

122 selective logging along the Juruá River from 1970 to 1995, especially in *várzea* forests, which

123 was banned since the formal creation of these two reserves.

124   The RESEX Médio Juruá and RDS Uacari were created in 1997 and 2005, respectively, and are

125   currently inhabited by some 4,000 legal residents, distributed across 74 local communities.

126   These communities are located on both sides of the Juruá River, adjacent to either the main river

127   channel or tributaries and oxbow lakes (Fig. S1). Residents of these reserves are variously

128   engaged in agricultural and extractive activities for both subsistence and cash income (Newton,

129   Endo & Peres, 2011; Campos-Silva & Peres, 2016).

130   Research permissions and full approval for this purely observational research were provided by

131   Centro Estadual de Unidades de Conservação do Amazonas (CEUC/SDS/AM – 020/2013) and

132   by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio – 38357-1).

133   Camera trapping

134   Data on the relative abundance of terrestrial vertebrates were collected at 279 camera-trapping

135   stations (CTS) deployed at distances of $3,100 \pm 367$ m ($\bar{x} \pm$ SD) apart, along a ~514-km nonlinear

136   section of the Juruá River (Fig. 1). We used Bushnell Trophy Cam 119436c, Reconyx Hyperfire

137   HC500 and Bushnell 8MP Trophy Cam HD camera traps. These were programmed to record

138   three and five consecutive photographs and 10-sec videos, respectively, at each trigger event

139   without intervals. A CTS consisted of one camera trap deployed 40-60 cm above ground, and

140   operated over a functional period of 38.7 ± 13.9 days ($\approx 928.8 \pm 333.6$ hours). The sensor

141   sensitivity was set to high, and all CTS were unbaited and deployed away from trails.

142   Camera-trapping stations were deployed in two complementary sample designs (Table 1; Fig.

143   1): From April 2013 to June 2014, 193 CTS were deployed at intervals of 50m, 350m, 1000m,

144   3000m and 6000m Euclidean distance along transects, arrayed in contiguous *terra firme* primary

145   forest, radiating away from local communities. This design facilitated surveys of terrestrial

146   vertebrate abundance at varying distances from the *várzea* interface and at varying intervals

147   during the receding flood pulse. In the second design, repeated over two inundation (March-

148   April 2013 and 2015) and two low-water phases (September-October 2013 and 2014), CTS were

149   deployed in both *várzea* forests and adjacent *terra firme* sites. In this arrangement, 30 *terra firme*

150   CTS were deployed during both high- and low-water phases whereas 26 *várzea* CTS were

151   surveyed only during the low-water phase, as *várzea* habitat is only available to the terrestrial

152   fauna during this time of year. All *várzea* CTS were placed in high-*várzea* forests to avoid

153 differences in plant species composition and phenology within sample sites (Wittmann et al.,

154 2006; Parolin, Wittmann & Schöngart, 2010).

155 Data management and estimates of the number of independent detections were undertaken using

156 *camtrapR* version 0.99.8 (Niedballa et al., 2016). Images of conspecifics >30 min apart were

157 defined as independent detection events. Species nomenclature followed the IUCN Red List

158 (IUCN 2018). Primates, non-terrestrial birds and rodents and marsupials smaller than 1 kg were

159 excluded from our analyses, but all other avian and mammalian taxa were considered. Congener

160 brocket deer (*Mazama* spp.), armadillos (*Dasypus* spp.), and small tinamous (*Crypturellus* spp.)

161 were each treated as single species functional group due to difficulties in differentiating them in

162 nocturnal (black and white) images.

163 All species considered here were grouped into nine trophic guilds (frugivore-insectivores,

164 granivore-frugivores, frugivores, carnivores, frugivore-carnivores, insectivore-frugivores,

165 insectivores, browsers and frugivore-browsers) based on Benchimol & Peres (2015). An

166 assemblage-wide metric of aggregate biomass was calculated by multiplying the species-

167 specific camera-trap detection rate (number of detections/100 trap-nights) by the mean adult

168 body mass per species, which could then be summed across all species detected at each CTS.

169 For group-living species, we multiplied individual body mass values by the mean observed

170 group size obtained from line-transect surveys conducted in the same study landscape

171 (Abrahams, Peres & Costa, 2017).

172 For each CTS, we extracted landscape and human disturbance covariates using ArcGIS (version

173 10.3) (Table 2). We calculated the mean water level of the Juruá River during the exposure

174 period of each CTS using daily water-level readings, recorded over 38 years (from 1st January

175 1973 to 31st December 2010; $N \approx 14,600$ daily measurements) at a nearby locality (Gavião

176 Metereological Station in Carauari-AM) (Fig. S2). As a continuous variable, mean water-level

177 during CTS sampling intervals was a far more powerful descriptor of seasonality period than

178 either categorical season (e.g. low-water vs high-water season) or time of the year (e.g. Julian

179 day) per se.

180 Data analysis

181 All analyses were conducted in R version 3.3.2 (R Core Development Team 2016). We first used

182 both Student's paired t-tests and ordinary t-tests to examine differences in species richness and

183 abundance of *terra firme* forests between the high- and low-water phases, and between *terra firme*

184 sites during the low-water phase and *várzea* forests, respectively. We estimated species richness

185 per CTS, accounting for any differences in the number of trap nights, using a rarefaction method

186 and first-order Jackknife estimator available in the *specaccum* function of the "vegan" package of

187 R. We choose this estimator because it gives the most reliable results in tropical forest camera-trap

188 studies (Tobler et al., 2008). For the abundance analyses, we considered the camera-trapping rate

189 (number of independent detections per 100 trap-nights) as our response variable. These analyses

190 were performed using CTS data from our second sample design, which targeted from both *terra*

191 *firme* forests during the high- and low-water phases of the flood pulse and *várzea* forests during

192 the low-water period.

193 Principal Coordinates Analysis (PCoA) was used to visually depict variation in vertebrate

194 assemblage structure. Differences in assemblage structure between both forest types and seasons

195 were tested using Permutational Multivariate ANOVA (PERMANOVA) (Anderson, 2001.) with

196 two factors with two levels each. Prior to these analyses, to reduce the weight of excessively

197 abundant species in the ordination space, terrestrial vertebrate abundance was standardized by

198 dividing the number of detections of each species by the total number of detections at each CTS.

199 PCoA and PERMANOVA were performed using a Bray–Curtis similarity distance matrix

200 derived from both of our sample designs. To test for seasonal effects on species composition at

201 *terra firme* CTS, we performed a Procrustes rotation analysis of the Bray-curtis ordination

202 matrices derived from CTS from our second sample design addressing both the high- and low-

203 water phases of the flood pulse.

204 We tested the hypothesis of seasonal faunal movements between adjacent forest types and

205 seasons by investigating the effects of river water level on the overall species abundance, species

206 richness, overall vertebrate biomass, and on the number of captures of the nine trophic guilds.

207 We controlled for the effects of landscape context and anthropogenic disturbance that may

208 deplete wildlife populations near human settlements across the study area (Abrahams, Peres &

209 Costa, 2017) by including these variables in the analysis. We employed Generalized Linear

210 Models (GLMs) using a Poisson distribution for count data using the combined CTS from both

211 sample designs, but a Negative Binomial distribution was chosen when overdispersion was

212   detected (Hilbe 2007). For our metric of biomass, we used a Gaussian error structure. The

213   number of camera-trapping nights per CTS was specified as an *offset* variable in all models to

214   account for difference in sampling effort (i.e. number of active days/nights) between CT

215   deployments.

216   We controlled for high levels of variable inter-dependence by performing a Pearson's correlation

217   matrix, retaining non-correlated variables (r < 0.70). We retained 11 variables describing the local

218   habitat, season, landscape context, and level of human disturbance of CTS sites (vz1k, vzdist, elev,

219   waterlevel, riverdist, defor1k, defor5k, defordist, ctydist, popcomm1 and commdist1; see

220   description of these variables in Table 2). For those variables representing the same class of human

221   disturbance (e.g. deforestation area), the appropriate buffer size was determined by running all

222   models using different buffer thresholds, and then using the threshold resulting in the strongest

223   effect on our response variables. We mitigated for collinearity between the predictors using the

224   Variance Inflation Factor (VIF < 3), excluding the variables above this threshold. We used

225   Akaike's Information Criteria (AICc) to select the models that best fit the data, employing a

226   stepwise method starting with the full model and discarding predictors until we reached a model

227   with the lowest AICc value. In these models we used data from both of our sample designs

228   **Results**

229   On the basis of 10,447 trap-nights, we recorded 4,059 independent detections of 25 terrestrial

230   vertebrate species, including 21 mammals representing 12 families and eight orders and four

231   large-bodied bird species (Table 3). We found clear differences in *terra firme* forest sites in both

232   species richness and abundance between high- and low-water phases (richness: paired t = 2.552,

233   df = 21, p = 0.018; abundance: paired t = 2.950, df = 21, p = 0.007, Fig. 2A, C). During the low-

234   water season, overall abundance was higher in *terra firme* than in *várzea* sites (t = 2.709, df =

235   48, p = 0.009, Fig. 2 B). Similarly, species richness was higher in *terra firme* sites (18.42 ± 3.11

236   species) than in adjacent *várzea* sites (14.31 ± 3.00 species; t = 4.748, df = 48, p < 0.001, Fig. 2

237   D).

238   At *terra firme* sites, the black agouti (*D. fuliginosa*) was the most common species followed by

239   the brocket deer (*Mazama spp*), pale-winged trumpeter (*P. leucoptera*), razor-billed curassows

240   (*M. tuberosum*) and collared peccaries (*P. tajacu*). The detection rates of these species were

241   higher during the high-water season than during the low-water season, whereas pacas (*C. paca*),

242   jaguars (*P.onca*), giant anteaters (*M. tridactyla*), giant armadillos (*P. maximus*) and tapirs (*T.*

243   *terrestris*) were more frequently detected during the high-water phase (Fig. 3A). During the low-

244   water season, brocket deer, black agoutis, pacas, pale-winged trumpeter, razor-billed curassows

245   and collared peccaries were more abundant in *terra firme* than in adjacent *várzea* forests, while

246   tapirs, ocelots (*L. pardalis*), pumas (*Puma concolor*) and small tinamous (*Crypturellus spp*)

247   presented higher detection rates in *várzea* (Fig. 3B).

248   PCoA ordination revealed differences between sample clusters formed by all *terra firme* sites

249   between the high- and low-water phases of the flood pulse, and between *várzea* forests and *terra*

250   *firme* sites during the low-water phase (Fig. 4A), which was further confirmed by permutation

251   tests (PERMANOVA; F = 3.964, p = 0.002; F = 10.401, p = 0.001, respectively). *Terra firme*

252   sites occupied the largest area in community space during the high-water phase, with both *terra*

253   *firme* and *várzea* forest sites during the low-water phase occupying subsets of the larger group,

254   and *várzea* sites occupying the smallest area. Additionally, the Procrustes rotation performed

255   with the *terra firme* CTS from sample design two indicated significant differences in ordination

256   space in the multivariate structure of community composition between the high- and low-water

257   phases (R = 0.74, p = 0.007, Fig. 4B).

258   Generalized linear models (GLMs) revealed that water level was a significant positive predictor

259   of both overall species abundance and the detection rates for three trophic guilds: frugivore-

260   insectivores, granivore-frugivores and carnivores (Fig. 5 A, D, F, G). The size of the nearest

261   local extractive community was associated with higher detection rates for browsers (Fig. 5 J).

262   Likewise, elevation was a positive predictor of detection rates of insectivore-frugivores (Fig. 5

263   I). The best model for frugivores retained only elevation as a significant negative predictor (Fig.

264   5 E). The area of *várzea* within a 1000-m buffer around each CTS best explained insectivore

265   detection rates (Fig. 5 L), while distance to the nearest urban center had the opposite effect on

266   our metric of overall vertebrate biomass (Fig. 5 B). The best GLM model explaining overall

267   species richness and the detection rates of frugivore-carnivore and frugivore-browsers failed to

268   retain any significant predictors (Fig. 5 C, H, K).

Discussion

Species richness, composition and seasonal movements between forest types

Our camera-trapping study provides tantalizing evidence that water level governs the distribution of large terrestrial vertebrates in Amazonian pristine forest mosaics. These species appear to exhibit lateral seasonal movements to take advantage of periodic resource availability in extremely productive floodplain forests. In our study area, the swath of floodplain forest is approximately 20-km wide, thereby providing a vast area of highly productive habitat for terrestrial species during the low-water phase.

In general, *terra firme* forest sites were more species-rich than *várzea* forest sites, a pattern that conforms with results from previous studies comparing assemblages of all mammals, primates, bats, birds and small mammals in Amazonian seasonally-flooded and unflooded forests (Peres 1999, 1997, Haugaasen & Peres 2005b; c; Beja *et al.* 2009; Pereira *et al.* 2009, Bobroweic et al. 2014). Salvador, Clavero & Leite Pitman (2011) reported that floodplain forests in the Peruvian Amazon are more species-rich than *terra firme* forests during the dry season, which is contrary to our findings. This can be explained by methodological differences between the studies once they used line transects, track counts and interviews enabling the inclusion of semi-aquatic and arboreal mammals such as giant otters, primates and sloths in their dataset. They also report that the number of species in floodplain forest during the wet season remains the same throughout the year, while in *terra firme*, a sharp increase in species richness coincided with the onset of the wet season. These shifts in species richness between the two forest types are consistent with our seasonal movement hypothesis, as many terrestrial vertebrate species likely exit *terra firme* terrains to take advantage of seasonally abundant food resources in *várzea* forest.

Water level represents a physical barrier for most vertebrate species attempting to access *várzea* forests during the high-water phase. This was confirmed by the positive relationship between water level and aggregate community-wide abundance, and the number of detection events of frugivore-insectivores, granivore-frugivores and carnivores. Bobrowiec *et al.* (2014) noted that the flood pulse constituted a physical barrier even for Phyllostomid bats, whose species composition differed between *terra firme* and *várzea* forests during the high-water period, but this effect did not persist year-round. We found clear differences in species composition between *terra firme* and *várzea* forests during the low-water phase and within our *terra firme* samples

299   between the high- and low-water phases of the annual cycle. These results imply that forest

300   fauna can exhibit ephemeral occupancy of *várzea* sites during the dry season and that the rising

301   flood waters force several species to seek suitable habitats in upland forests. These seasonal

302   lateral movements drive differences in species richness and composition between both seasons

303   and forest types.

304   Food availability and its distribution within forest habitats, is the most important variable

305   explaining the occupancy and abundance of mammals in different forest types (Mendes Pontes,

306   2004; Haugaasen & Peres, 2007). In *terra firme* forests, fruit production occurs during the early

307   wet season whereas in *várzea* forests, fruit production starts during the late wet season (Hawes

308   & Peres, 2016). A substantial proportion of the large terrestrial fauna may therefore move

309   between *várzea* and *terra firme* forests to exploit seasonally available resources. For instance,

310   frugivore species in our models exhibited a negative abundance relationship with terrain

311   elevation. This predictor can be used to distinguish both forest types, as our *terra firme* CTS

312   were on average situated on terrains 14 m higher than our *várzea* CTS (t-value = 9.458, df =

313   277, p-value < 0.001). As water levels recede, the terrestrial fauna rapidly colonize *várzea*

314   forests to forage on the seasonal production of residual fruit- and seed-fall (total production

315   minus dispersal and consumption by arboreal frugivores), which can be twice as high as in

316   adjacent *terra firme* forests during this period (Bodmer, 1990). Ungulate species such as collared

317   peccaries and brocket deer exhibit a marked dietary shift following the flood pulse, consuming

318   more fruits in seasonally-flooded forests during the low-water period compared to the high water

319   period (Bodmer 1990).

320   Water level is an important determinant of species detection rates in highly heterogeneous forest

321   landscapes subjected to marked seasonal floods (Negrões et al., 2011; De Lázari et al., 2013).

322   Haugaasen & Peres (2007) reported three different strategies of landscape movements across

323   forest types, which were reflected in our results: wide-ranging species, year-round residents and

324   interface species. Large-bodied granivore-frugivores such as the large-group-living white-

325   lipped peccaries is a wide-ranging "landscape" species that, on a seasonal basis, occupies large

326   home ranges in different forest types and shift their diets and habitat use in response to both

327   seasonal flooding and resulting resource fluctuations (Bodmer, 1990; Fragoso, 1998;

328   Keuroghlian, Eaton & Desbiez, 2009). Large-bodied myrmecophages and insectivore-

329   frugivores such as giant anteaters and armadillos exhibited low detection rates in *várzea* forests,

330   likely because they are year-round residents in *terra firme* forests, which was confirmed by the

331   negative relationship in our models between terrain elevation and the detection rates of these

332   species. They are also less likely to move between forest types because the permanently wet

333   *várzea* soils preclude their fossorial foraging behavior. We never observed giant armadillo (*P.*

334   *maximus*) holes in *várzea* forests, but commonly observed them in *terra firme* forests, and this

335   is consistent with previous studies in the Araguaia River (Negrões *et al.* 2011) and Peruvian

336   floodplain forests (Salvador, Clavero & Leite Pitman 2011).

337   Detection rates of carnivores increased with the water level, a pattern that can be explained by

338   their swimming and climbing abilities, which allow them to both move between temporary

339   forest islands and utilize the tree canopy as floodwaters rose. Jaguars (*P. onca*) in *várzea* forests

340   in the lower Japurá River are known to spend the entire high-water season high up in the trees

341   (E.E. Ramalho, pers. comm.) and subsist upon arboreal and semi-aquatic species such as howler

342   monkeys (*Alouatta seniculus* (Linnaeus, 1766)), sloths (*Bradypus variegatus*, Schinz, 1825) and

343   spectacled and black caimans (*Caiman crocodilus* (Linnaeus, 1758), and *Melanosuchus niger*

344   (Spix, 1825)) (Ramalho 2006).

345   Conservation implications

346   Our research supports the existing body of evidence that the Médio Juruá region, and many other

347   regions of the lowland neotropics, should be viewed as an essentially interconnected multi-

348   habitat socio-ecological system. The massive long-lasting seasonal flood pulse (Junk, Bayley &

349   Sparks, 1989) and the associated phenological (Hawes & Peres, 2016), hydrological, ecological

350   (Hawes et al., 2012) and livelihood impacts this engenders (Endo, Peres & Haugaasen, 2016)

351   require conservation planning at the scale of the entire landscape, with major drainage basins

352   representing complementary management units.

353   *Várzea* and *terra firme* forests function as ecologically integrated and hydrologically

354   interconnected habitats that are seasonally utilized by a suite of mobile species, with terrestrial

355   fauna often relying upon the temporally staggered resources of both habitats. As such, they are

356   threatened by both aquatic and terrestrial anthropogenic activities at the local and regional

357   scales. The immense fluvial transport network of the lowland Amazon makes even remote

358   forests accessible to hunters (Peres & Lake, 2003), making their faunal resources non-
359   excludable, whilst simultaneously difficult to monitor.

360   The existing protected area network and management policies in Amazonian seasonally-flooded
361   forests were created principally to protect terrestrial ecosystems and therefore suffer from
362   design, implementation and monitoring deficiencies and their delimitations does not adequately
363   represent or protect the full suite of biotic diversity (Peres & Terborgh, 1995, Albernaz *et al.*
364   2012, Castello *et al.* 2013). Although a protected area coverage of ~25% gives the impression
365   of extensive conservation management of floodplains, less than 1% of the aggregate area of
366   Amazonian floodplains in Brazil is strictly protected (Albernaz *et al.* 2012). Sustainable
367   development and extractive reserves represent the majority of all floodplain protected areas.
368   Their conservation effectiveness can be compromised by high human population density, the
369   uncertain economic viability of exploiting non-timber resources and a shortfall in available
370   animal protein resulting from depleted game vertebrate populations (Peres, 2011; Terborgh &
371   Peres, 2017), but see Abrahams, Peres & Costa (2017) and Campos-Silva & Peres (2016) for
372   best-case scenarios of terrestrial subsistence hunting and local fisheries management.

373   We have shown that a substantial part of the large vertebrate fauna modulates their use of
374   different forests types within a highly heterogeneous forest landscape according to the marked
375   seasonality of *várzea* floodplain forests. Our study represents the confluence between the issues
376   of landscape-scale conservation planning, ecological connectivity, nutrient transport and uptake,
377   and community-based natural resource management. The Médio Juruá region exemplifies these
378   issues as it encompasses extensive seasonal wetlands and a suite of hunted, seasonally-mobile
379   species. Adequate conservation strategies in this region must account for the full life-history
380   needs of mobile harvested species, ecologically interconnected habitats and the diverse
381   livelihood portfolios of local communities (Lindenmayer et al., 2008). Different Amazonian
382   forest types exhibiting staggered resource pulses must be included within the same or
383   neighboring sustainable-use protected areas. This will provide sufficiently large areas to both
384   support large-scale ecological processes (e.g. species migrations, lateral movements, persistence
385   of apex predators) and anthropogenic extractive activities in the long run (e.g. estimated
386   sustainable harvest area for tapir populations >2,000 km²) (Peres & Terborgh, 1995; Peres, 2001,
387   2005; Haugaasen & Peres, 2007). This concept can be applicable to conservation planning of

388 other regions consisting of natural forests mosaics experiencing seasonal floods such as the
389 hyper-fragmented region of the Araguaia River or at the Pantanal floodplains (Negrões et al.,
390 2011; De Lázari et al., 2013). In these different scenarios, private reserves must be situated
391 adjacent to protected areas to ensure terrestrial fauna protection during the prolonged inundation
392 season.

393 Study limitations

394 In our study, we were unable to estimate the species richness in *várzea* forests during the high-
395 water phase of the flood pulse, because our camera trapping method focused only on terrestrial
396 species, which are more sensitive to the flood pulse than arboreal and semi-aquatic species.
397 *Várzea* forests along this section of the Juruá River are typically subjected to an annual flood
398 pulse amplitude of 8 to 12 m, which lasts for up to six months. Any camera traps deployed in
399 várzea forests during the high-water period would need to be placed almost half way up into the
400 forest canopy.

401 We acknowledge that these landscape-scale seasonal movements between forest types can only
402 be conclusively verified by either radio or GPS telemetry studies targeting multiple species. The
403 prohibitive costs of such an undertaking limit its community-wide feasibility. Our evidence is
404 based on patterns of local population abundance, species richness and biomass, particularly
405 along the *várzea* - *terra firme* interface, where temporary overcrowding is expected to occur for
406 species abandoning the wide belt of *várzea* forest during the rise of floodwaters.

407 **Conclusions**

408 The annual floodwaters along several major white-water rivers in the Amazon is the main factor
409 structuring and differentiating *várzea* floodplains from adjacent *terra firme* forests as unique
410 adaptations are required to tolerate the prolonged flood pulse. This remarkable natural
411 phenomenon drives several key ecological processes, including staggered plant phenology, high
412 plant productivity, and supports major local livelihood activities such as subsistence fishing and
413 hunting. This landscape scale seasonal dynamics between these major adjacent forest types was
414 investigated in terms of species richness, species composition and population abundance for as
415 many as 25 vertebrate species. We have shown that many upland forest terrestrial vertebrate
416 species make seasonal use of *várzea* forests to take advantage of the abundant trophic resource

417 in this forest type following the receding waters. We acknowledge that detailed movement data

418 using GPS telemetry can further clarify the magnitude and seasonal importance of *várzea* habitat

419 use by *terra firme* vertebrates. However, we highlight that this unique seasonal dynamic is a

420 critical issue in Amazonian forest reserve design and biodiversity monitoring, particularly

421 within large sustainable use reserves encompassing complex natural landscape mosaics, where

422 unimpeded lateral movements should continue to support both local extractive economies and

423 healthy wildlife populations.

424 **Acknowledgements**

433 **References**

434 Albernaz AL., Pressey RL., Costa LRF., Moreira MP., Ramos JF., Assunção PA., Franciscon

435 CH. 2012. Tree species compositional change and conservation implications in the white-water

436 flooded forests of the Brazilian Amazon. *Journal of Biogeography* 39:869–883. DOI:

437 10.1111/j.1365-2699.2011.02640.x.

438 Abrahams MI., Peres CA., Costa HCM. 2017. Measuring local depletion of terrestrial game

439 vertebrates by central-place hunters in rural Amazonia. *PLoS ONE* 12:1–25. DOI:

440 10.1371/journal.pone.0186653.

441 Adis J., Junk WJ. 2002. Terrestrial invertebrates inhabiting lowland river floodplains of Central

442 Amazonia and Central Europe: a review. *Freshwater Biology* 47:711–731. DOI:

443 10.1046/j.1365-2427.2002.00892.x.

444 Anderson MJ. 2001. A new method for non parametric multivariate analysis of variance. *Austral

445 ecology* 26:32–46. DOI: 10.1111/j.1442-9993.2001.01070.pp.x.

446 Beja P., Santos CD., Santana J., Pereira MJ., Marques JT., Queiroz HL., Palmeirim JM. 2009.

Seasonal patterns of spatial variation in understory bird assemblages across a mosaic of flooded and unflooded Amazonian forests. *Biodiversity and Conservation* 19:129–152. DOI: 10.1007/s10531-009-9711-6.

Benchimol M., Peres CA. 2015. Predicting local extinctions of Amazonian vertebrates in forest islands created by a mega dam. *Biological Conservation* 187:61–72. DOI: 10.1016/j.biocon.2015.04.005.

Bobrowiec PED., Rosa L dos S., Gazarini J., Haugaasen T. 2014. Phyllostomid Bat Assemblage Structure in Amazonian Flooded and Unflooded Forests. *Biotropica* 46:312–321. DOI: 10.1111/btp.12102.

Bodmer RE. 1990. Responses of ungulates to seasonal inundations in the Amazon floodplain. *Journal of Tropical Ecology* 6:191–201.

Campos-Silva JV., Peres CA. 2016. Community-based management induces rapid recovery of a high-value tropical freshwater fishery. *Scientific Reports* 6:1–13. DOI: 10.1038/srep34745.

Castello L., Mcgrath DG., Hess LL., Coe MT., Lefebvre PA., Petry P., Macedo MN., Renó VF., Arantes CC. 2013. The vulnerability of Amazon freshwater ecosystems. *Conservation Letters* 6:217–229. DOI: 10.1111/conl.12008.

Costanza R., Arge R., Groot R De., Farberk S., Grasso M., Hannon B., Limburg K., Naeem S., O'Neill R V., Paruelo J., Raskin RG., Suttonkk P., van den Belt M. 1997. The value of the world ' s ecosystem services and natural capital. *Nature* 387:253–260. DOI: 10.1038/387253a0.

De Lázari R., Santos-Filho M., Canale G., Graipel M. 2013. Flood-mediated use of habitat by large and midsized mammals in the Brazilian Pantanal Flood-mediated use of habitat by large and midsized mammals in the Brazilian Pantanal. *Biota Neotropica* 13:0–6.

Endo W., Peres CA., Haugaasen T. 2016. Flood pulse dynamics affects exploitation of both aquatic and terrestrial prey by Amazonian floodplain settlements. *Biological Conservation* 201:129–136. DOI: 10.1016/j.biocon.2016.07.006.

Fragoso JM V. 1998. Home Range and Movement Patterns of White-lipped Peccary (Tayassu pecari) Herds in the Northern Brazilian Amazon. *Biotropica* 30:458–469.

François GGH., K GF., Marcelle GSL., Mooney HA., Cropper A., Leemans R., Arico S.,

476 Bridgewater P., Peterson G., Revenga C., Rivera M., Peter AW., Fallis A., Dubay L., Point

477 P., Aboutayeb H., Mermet L., Raphaël Billé., Maya Leroy., Poux X., Schuyt K. 2005.

478 Ecosystems AND HUMAN WELL-BEING: WETLANDS AND WATER. *Regions and*

479 *Cohesion* 13:127–137. DOI: 10.1017/CBO9781107415324.004.

480 Halls AJ. 1997. *Wetlands, Biodiversity and the Ramsar Convention: The Role of the Convention*

481 *on Wetlands in the Conservation and Wise Use of Biodiversity.*

482 Haugaasen T., Peres C. 2005a. Tree Phenology in Adjacent Amazonian Flooded and Unflooded

483 Forests1. *Biotropica* 37:620–630.

484 Haugaasen T., Peres C A. 2005b. Mammal assemblage structure in Amazonian flooded and

485 unflooded forests. *Journal of Tropical Ecology* 21:133–145. DOI:

486 10.1017/S026646740400207X.

487 Haugaasen T., Peres C A. 2005c. Primate assemblage structure in Amazonian flooded and

488 unflooded forests. *American Journal of Primatology* 67:243–58. DOI: 10.1002/ajp.20180.

489 Haugaasen T., Peres C A. 2007. Vertebrate responses to fruit production in Amazonian flooded

490 and unflooded forests. *Biodiversity and Conservation* 16:4165–4190. DOI: 10.1007/s10531-

491 007-9217-z.

492 Hawes JE., Peres CA. 2016. Patterns of plant phenology in Amazonian seasonally-flooded and

493 unflooded forests. *Biotropica* 48:465–475.

494 Hawes JE., Peres C A., Riley LB., Hess LL. 2012. Landscape-scale variation in structure and

495 biomass of Amazonian seasonally-flooded and unflooded forests. *Forest Ecology and*

496 *Management* 281:163–176. DOI: 10.1016/j.foreco.2012.06.023.

497 IUCN 2018. The IUCN Red List of Threatened Species. Version 2017-3. Avaiable at

498 *http://www.iucnredlist.org* (acessed 15 May 2018).

499 Junk WJ., Bayley PB., Sparks RE. 1989. The flood pulse concept in river -floofplain systems. In:

500 Dodge DP ed. *International Large River Symposium*. 110–127.

501 Junk WJ., Brown M., Campbell IC., Finlayson M., Gopal B., Ramberg L., Warner BG. 2006.

502 The comparative biodiversity of seven globally important wetlands: a synthesis. *Aquatic*

503 *Sciences* 68:400–414. DOI: 10.1007/s00027-006-0856-z.

504　Junk WJ., Piedade MTF. 2010. An Introduction to South American Wetland Forests:

505　　　　Distribution, Definitions and General Characterization. In: Junk WJ, Piedade MTF,

506　　　　Wittmann F, Schöngart J, Parolin P eds. *Amazonian Floodplain Forests Ecophysiology,*

507　　　　*Biodiversity and Sustainable Management*. Ecological Studies. Dordrecht: Springer

508　　　　Netherlands, 4–24. DOI: 10.1007/978-90-481-8725-6.

509　Junk WJ., Piedade MTF., Schöngart J., Cohn-Haft M., Adeney JM., Wittmann F. 2011. A

510　　　　Classification of Major Naturally-Occurring Amazonian Lowland Wetlands. *Wetlands*

511　　　　31:623–640. DOI: 10.1007/s13157-011-0190-7.

512　Keddy PA., Fraser LH., Solomeshch AI., Junk WJ., Campbell DR., Arroyo MTK., Alho CJR.

513　　　　2009. Wet and Wonderful: The World's Largest Wetlands Are Conservation Priorities.

514　　　　*BioScience* 59:39–51. DOI: 10.1525/bio.2009.59.1.8.

515　Keuroghlian A., Eaton DP., Desbiez A. 2009. The response of a landscape species, white-lipped

516　　　　peccaries, to seasonal resource fluctuations in a tropical wetland, the Brazilian Pantanal.

517　　　　*International Journal of Biodiversity and Conservation* 1:87–97.

518　Lindenmayer D., Hobbs RJ., Montague-Drake R., Alexandra J., Bennett A., Burgman M., Cale

519　　　　P., Calhoun A., Cramer V., Cullen P., Driscoll D., Fahrig L., Fischer J., Franklin J., Haila

520　　　　Y., Hunter M., Gibbons P., Lake S., Luck G., MacGregor C., McIntyre S., Mac Nally R.,

521　　　　Manning A., Miller J., Mooney H., Noss R., Possingham H., Saunders D., Schmiegelow F.,

522　　　　Scott M., Simberloff D., Sisk T., Tabor G., Walker B., Wiens J., Woinarski J., Zavaleta E.

523　　　　2008. A checklist for ecological management of landscapes for conservation. *Ecology*

524　　　　*Letters* 11:78–91. DOI: 10.1111/j.1461-0248.2007.01114.x.

525　Martin TG., Chadès I., Arcese P., Marra PP., Possingham HP., Norris DR. 2007. Optimal

526　　　　conservation of migratory species. *PLoS ONE* 2:3–7. DOI: 10.1371/journal.pone.0000751.

527　Mendes Pontes A. 2004. Ecology of a community of mammals in a seasonailly dry forest in

528　　　　Roraima, Brazilian Amazon. *Mammalian Biology-Zeitschrift für Säugetierkunde* 69:319–

529　　　　336.

530　Mendes Pontes A. R., Chivers DJ. 2007. Peccary movements as determinants of the movements

531　　　　of large cats in Brazilian Amazonia. *Journal of Zoology* 273:257–265. DOI:

532　　　　10.1111/j.1469-7998.2007.00323.x.

533   Nebel G., Dragsted J., Vega AS. 2001. Litter fall , biomass and net primary production in
534   floodplain forests in the Peruvian Amazon. *Forest Ecology and Management* 150:93–102.

535   Negrões N., Revilla E., Fonseca C., Soares AMVM., Jácomo AT a., Silveira L. 2011. Private
536   forest reserves can aid in preserving the community of medium and large-sized vertebrates
537   in the Amazon arc of deforestation. *Biodiversity and Conservation* 20:505–518. DOI:
538   10.1007/s10531-010-9961-3.

539   Newton P., Endo W., Peres CA. 2011. Determinants of livelihood strategy variation in two
540   extractive reserves in Amazonian flooded and unflooded forests. *Environmental*
541   *Conservation* 39:97–110. DOI: 10.1017/S0376892911000580.

542   Niedballa J., Sollmann R., Courtiol A., Wilting A. 2016. camtrapR : an R package for efficient
543   camera trap data management. *Methods in Ecology and Evolution* 7:1457–1462. DOI:
544   10.1111/2041-210X.12600.

545   Parolin P., Wittmann F., Schöngart J. 2010. Tree Phenology in Amazonian Floodplain Forests.
546   In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin eds. *Amazonian Floodplain*
547   *Forests: Ecophysiology, Biodiversity and Sustainable Management*. Springer-Verlag New
548   York, 105–126. DOI: 10.1007/978-90-481-8725-6.

549   Pereira MJR., Marques JT., Santana J., Santos CD., Valsecchi J., de Queiroz HL., Beja P.,
550   Palmeirim JM. 2009. Structuring of Amazonian bat assemblages: the roles of flooding
551   patterns and floodwater nutrient load. *The Journal of animal ecology* 78:1163–71. DOI:
552   10.1111/j.1365-2656.2009.01591.x.

553   Peres C. A. 1994. Primate responses to phenological changes in amazonian terra firme forest.
554   *Biotropica* 26:98–112.

555   Peres C.A. 1997. Primate community structure at twenty western Amazonian flooded and
556   unflooded forests. *Journal of Tropical Ecology* 13:381–405.

557   Peres C. A. 2001. Synergistic Effects of Subsistence Hunting and Habitat Fragmentation on
558   Amazonian Forest Vertebrates. *Conservation Biology* 15:1490–1505. DOI: 10.1046/j.1523-
559   1739.2001.01089.x.

560   Peres C.A. 2005. Why We Need Megareserves in Amazonia. *Conservation Biology* 19:728–733.
561   DOI: 10.1111/j.1523-1739.2005.00691.x.

562 Peres C. A. 2011. Conservation in sustainable-use tropical forest reserves. *Conservation biology*
563   25:1124–9. DOI: 10.1111/j.1523-1739.2011.01770.x.

564 Peres C.A., Lake I. 2003. Extent of nontimber resource extraction in tropical forests:
565   accessibility to game vertebrates by hunters in the Amazon basin. *Conservation Biology*
566   17:521–535. DOI: 10.1046/j.1523-1739.2003.01413.x.

567 Peres C.A., Terborgh J. 1995. Amazonian nature reserves: an analysis of the defensibility status
568   of existing conservation units and design criteria for the future. *Conservation Biology* 9.

569 Prance G. 1979. Notes on the vegetation of Amazonia III. The terminology of Amazonian forest
570   types subject to inundation. *Brittonia* 31:26–38.

571 R Development Core Team. 2016. *R: a language and environment for statistical computing*
572   (Version 3.3.2). Vienna: R Foundation for Statistical Computing.

573 Ramalho E E. 2006. Uso do habitat e dieta da onça pintada *Panthera onca* em uma área de várzea,
574   reserva de desenvolvimento sustentável mamirauá, amazônia central Brasil. MSc. Thesis,
575   Instituto Nacional de Pesquisas da Amazônia.

576 Saint-paul U., Zuanon J., Villacorta Correa MA., Garcia M., Fabré NN., Berger U., Junk WJ.
577   2000. Fish communities in central Amazonian white- and blackwater floodplains.
578   *Environmental Biology of Fishes* 57:235–250.

579 Salvador S., Clavero M., Leite Pitman R. 2011. Large mammal species richness and habitat use
580   in an upper Amazonian forest used for ecotourism. *Mammalian Biology - Zeitschrift für*
581   *Säugetierkunde* 76:115–123. DOI: 10.1016/j.mambio.2010.04.007.

582 Schöngart J., Piedade MTF., Ludwigshausen S., Horna V., Worbes M. 2002. Phenology and
583   stem-growth periodicity of tree species in Amazonian floodplain forests. *Journal of*
584   *Tropical Ecology* 18:581–597. DOI: 10.1017/S0266467402002389.

585 Sioli H. 1984. The Amazon and its main afluents: Hydrography, morphology of the river courses
586   and river types. In: Sioli H ed. *The Amazon Liminology and landscape ecology of a mighty*
587   *tropical river and its basin*. 127–165.

588 Terborgh J., Peres CA. 2017. Do community-managed forests work? a biodiversity perspective.
589   *Land* 6:22. DOI: 10.3390/land6020022.

590   Tobler MW., Carrillo-Percastegui SE., Leite Pitman R., Mares R., Powell G. 2008. An
591   evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest
592   mammals. *Animal Conservation* 11:169–178. DOI: 10.1111/j.1469-1795.2008.00169.x.

593   Tuomisto H., Ruokolainen K., Kalliola R., Linna A., Danjoy W., Rodriguez Z. 1995. Dissecting
594   amazonian biodiversity. *Science* 269:63–66.

595   Wilcove DS., Wikelski M. 2008. Going, going, gone: Is animal migration disappearing? *PLoS*
596   *Biology* 6:1361–1364. DOI: 10.1371/journal.pbio.0060188.

597   Wittmann F., Schongart J., Montero JC., Motzer T., Junk WJ., Piedade MTF., Queiroz HL.,
598   Worbes M. 2006. Tree species composition and diversity gradients in white-water forests
599   across the Amazon Basin. *Journal of Biogeography* 33:1334–1347. DOI: 10.1111/j.1365-
600   2699.2006.01495.x.

601

Figure 1

Map of the study area in the central Rio Juruá region of western Brazilian Amazonia, Amazonas, Brazil.

Map inset shows the geographic location of the Juruá River and the study region. The boundaries of the RESEX Médio Juruá and RDS Uacari are outlined in black. Background colors represent elevation, with reddish and green shades indicating low and high elevation, respectively. Solid red circles represent camera trap stations (CTS) deployed radiating inland into *terra firme* forest (sample design 1). Green and aqua circles represent CTS deployed at *terra firme* forest sites near forest habitat boundaries along the *várzea* interface and far into *várzea* forest, respectively (sample design 2).
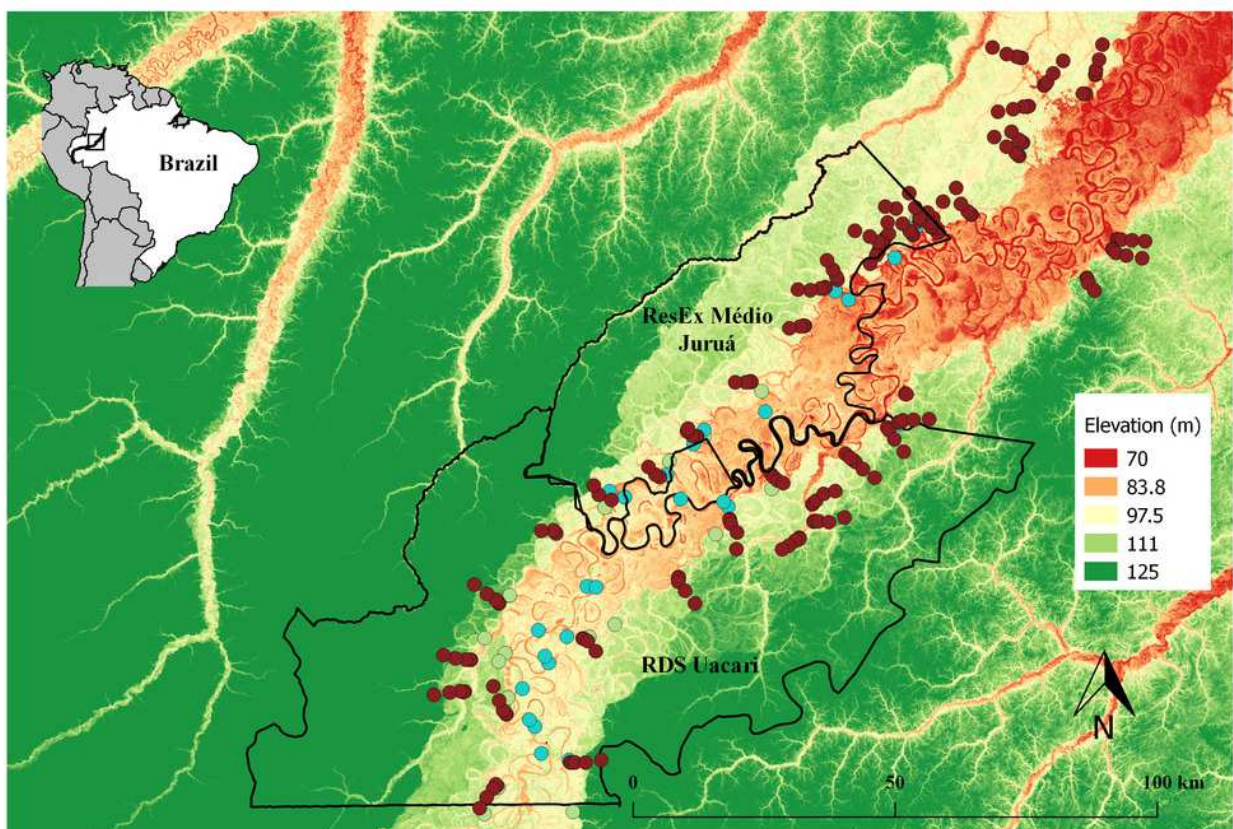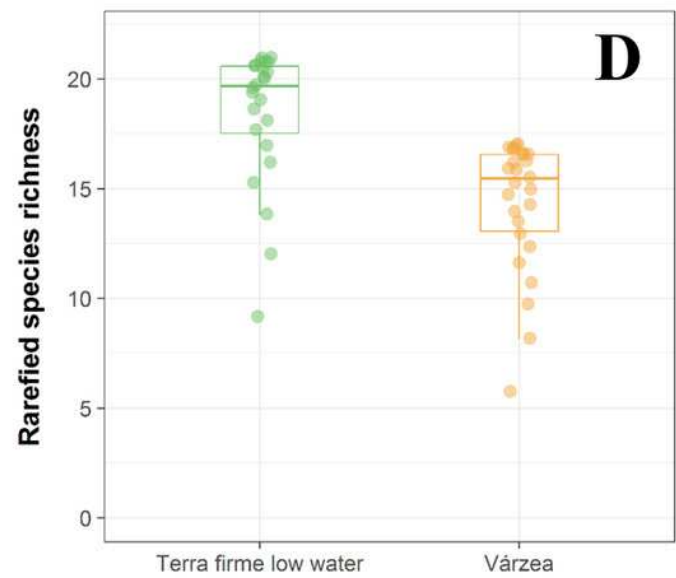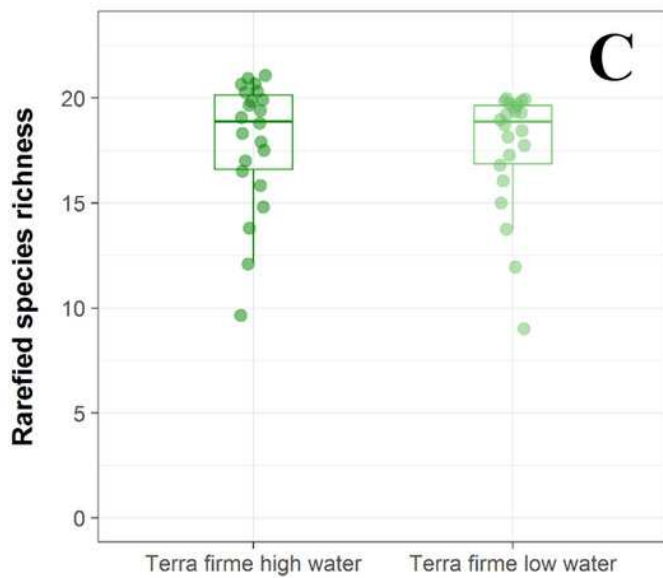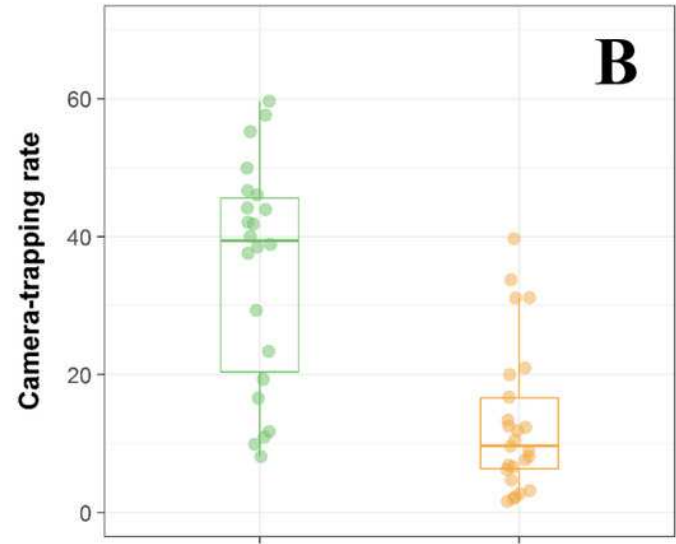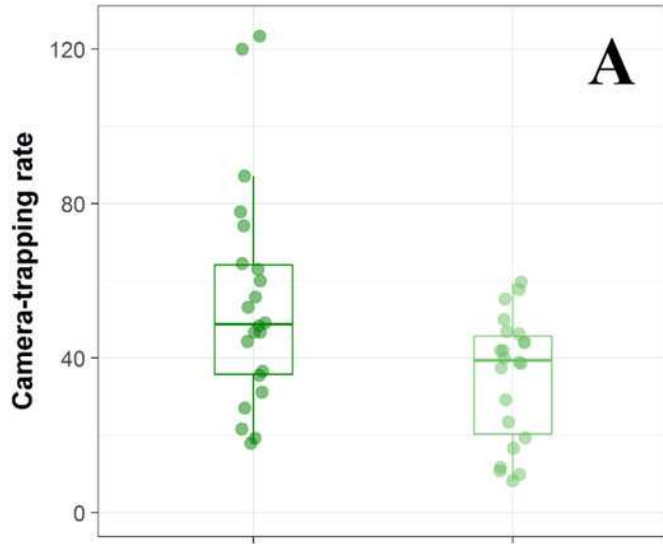
Figure 2

Comparison between *terra fime* and *várzea* forests during both the high- and low-water phases of the flood pulse considering both the total abundance and species richness of terrestrial forest vertebrates.

Boxplots comparing abundance and rarefied species richness between *terra firme* forests during both high- (dark green) and low-water (light green) phases of the flood pulse (A and C) and between *várzea* (orange) and *terra firme* forests (light green) during the low-water phase (B and D).

Figure 3

Camera trapping rate of terrestrial vertebrates recorded in *terra firme* and *várzea* forests.

(A) Camera trapping rates in *terra firme* forests during both high- (dark green bars) and low-water phase of the flood pulse (light green bars). (B) Camera trapping rates in both *terra fime* and in v*árzea* forests during the low-water phase of the flood pulse. Light green and orange bars represent *terra firme* and *várzea* forests, respectively. Species are represented by the first four letters of each genus and first four letters of each species and ordered from least to most abundant top to bottom. Asterisks indicate significant differences according to paired (A) and unpaired t-tests (B); *p ⩽ 0.05, **p ⩽ 0.01, *** p ⩽ 0.001.
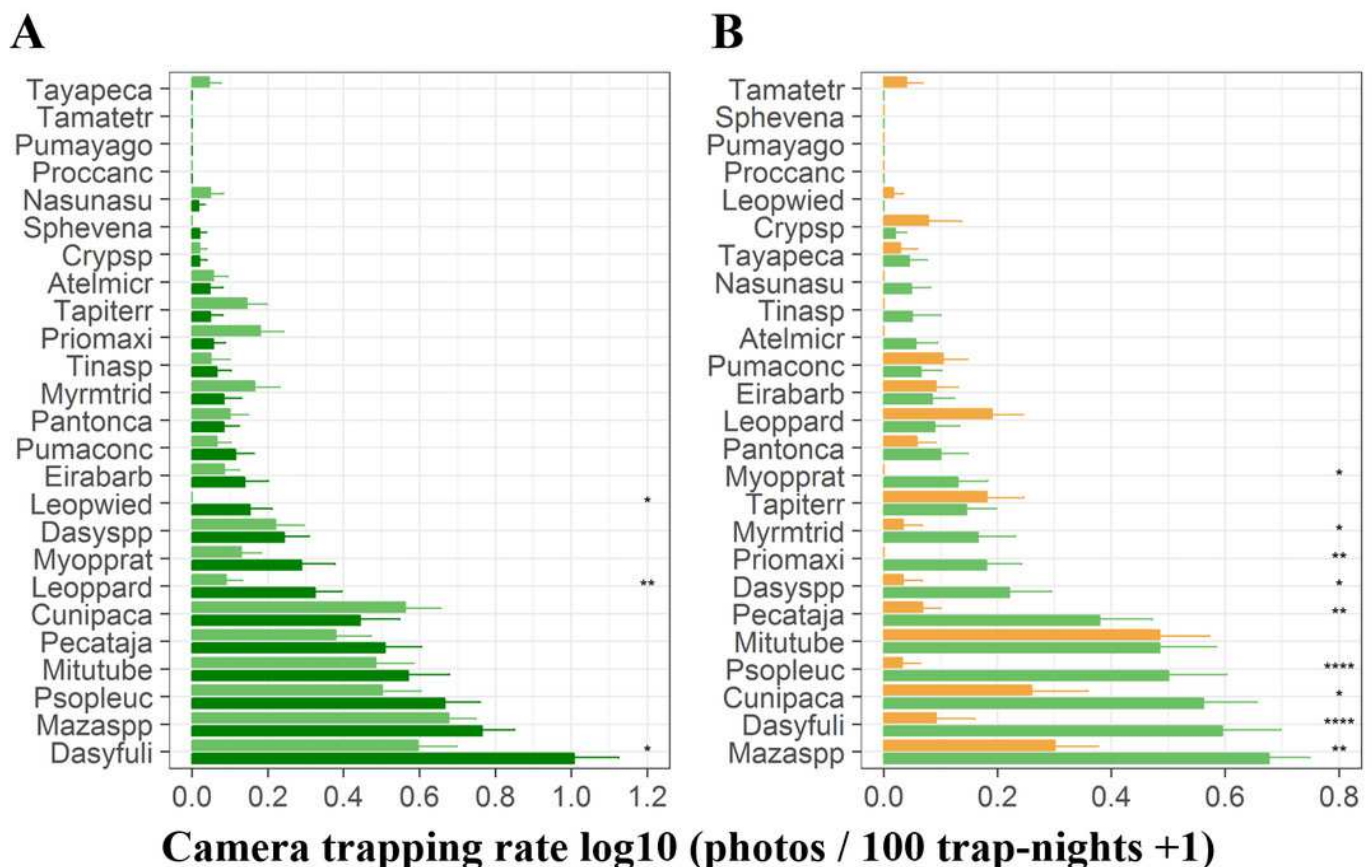
Figure 4

Terrestrial vertebrate species composition in Amazonian seasonally-flooded and unflooded forests during both high- and low-water phases of the flood pulse.

(A) Principal Coordinates Analysis (PCoA) ordination of the terrestrial vertebrate assemblage structure detected by camera traps in Amazonian *terra firme* forests during both high- and low-water phases of the flood pulse (green and light-green circles, respectively) and in *várzea* forests (orange circles). (B) Procrustes rotation plot of *terra firme* sites sampled during both high- and low-water phase of the flood pulse. Arrows (vectors) indicate the species migration in community space from the high- to the low-water season.
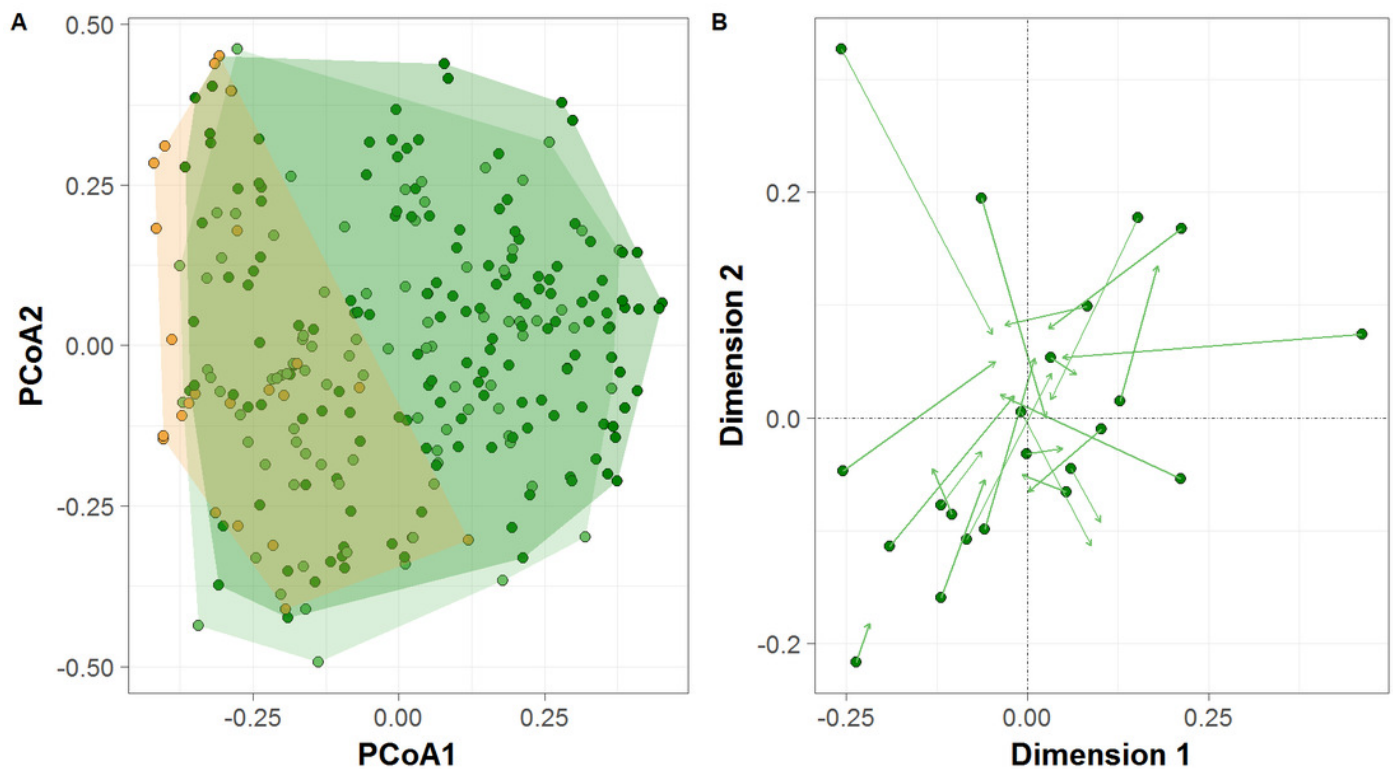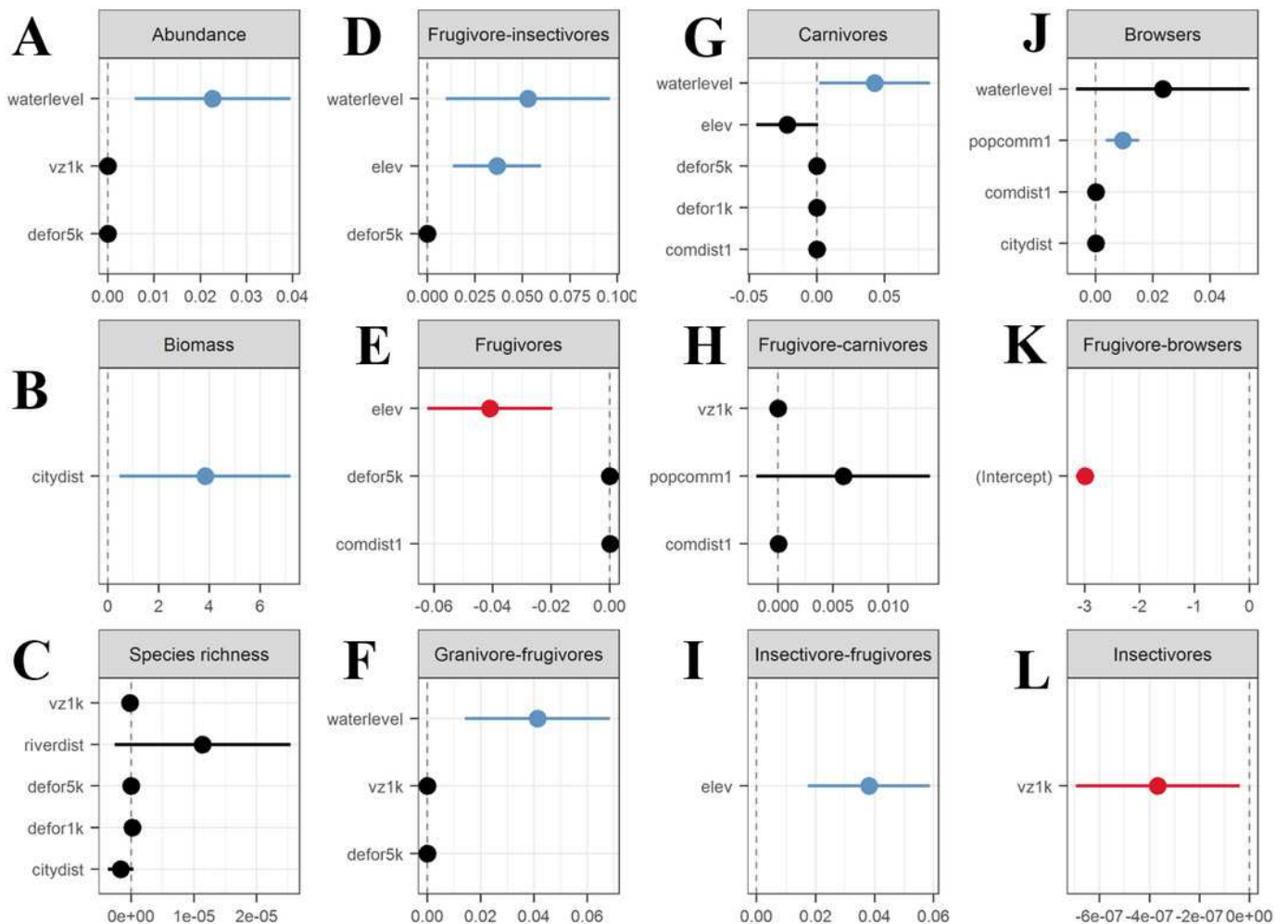
Figure 5

Coefficient estimates (± 95% confidence intervals) showing the magnitude and direction of effects of different explanatory variables retained in the best performing GLMs.

(A) aggregate abundance, (B) aggregate biomass of all species, (C) species richness (D-L) numbers of detections of each trophic guild.

Regression coefficients ± 95% CI

Table 1 **(on next page)**

Camera trapping effort at Amazonian flooded and unflooded forests, along the Juruá River, Amazonas, Brazil (see Fig. 1).

Sample Design	Flood pulse phase	Number of active CTS	
		Terra Firme	*Várzea*
Sample design 1	From high to low water	193	
Sample design 2	High-water	30	-
Sample design 2	Low-water	30	26
Total		**253**	**26**

1

Table 2(on next page)

Covariates used to investigate the seasonal dynamics of terrestrial vertebrates in Amazonian flooded and unflooded forests, along the Juruá River region, western Brazilian Amazonia

1

Covariate	Abbreviation	Description
Area of *várzea* forest	vz0.5k	Area (m²) of seasonally flooded forest within a 500m circular buffer centered at each CTS
	vz1k	Area (m²) of seasonally flooded forest within a 1000m circular buffer centered at each CTS
	vz5k	Area (m²) of seasonally flooded forest within a 5000m circular buffer centered at each CTS
Distance to *várzea* forest	vzdist	Euclidean distance from each CTS to the nearest várzea forest
Deforestation area	defor0.5k	Total area (m²) of deforestation within a 500m circular buffer centered at each CTS
	defor1k	Total area (m²) of deforestation within a 1000m circular buffer centered at each CTS
	defor5k	Total area (m²) of deforestation within a 5000m circular buffer centered at each CTS
Distance to nearest deforestation	defordist	Euclidean distance from each CTS to the nearest deforestation patch
Community size	popcomm1	Number of residents of the local community nearest each CTS

Table 2 continued

Distance to local	commdist1	Euclidean distance from each CTS to the nearest local community

community		
Distance to urban center	citydist	Euclidean distance from each CTS to the nearest urban center
Elevation	elev	Elevation (m) of the CTS above the main channel of the Juruá river.
River distance	riverdist	Distance from each CTS to the midpoint of Juruá river
Water level	waterlevel	Mean daily water level of the Juruá river during the deployment period of each CTS

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Table 3(on next page)

Terrestrial vertebrate species detected by camera trapping stations (CTS) deployed in this study in Amazonian flooded and unflooded forests, along Juruá river, Amazonas, Brazil.

Class	Order	Species	English vernacular name	Trophic guild
AVES	GRUIFORMES	*Psophia leucoptera* (Spix, 1825)	Pale-winged trumpeter	Frugivore-Insectivore
	STRUTHIONIFORMES	*Crypturellus spp* (Brabourne & Chubb, 1914)	Small tinamous	Granivore-frugivore
	GALLIFORMES	*Tinamus sp* (Hermann, 1783)	Great tinamous	Granivore-frugivore
		Mitu tuberosum (Spix, 1825)	Razor billed curassow	Frugivore
MAMMALIA	CARNIVORA	*Panthera onca* (Linnaeus, 1758)	Jaguar	Carnivore
		Procyon cancrivorus (G.[Baron] Cuvier, 1798)	Crab-eating-racoon	Frugivore-insectivore
		Puma concolor (Linnaeus, 1771)	Puma	Carnivore
		Herpailurus yagouaroundi (É. Geoffroy Saint-Hilaire, 1803)	Jaguarundi	Carnivore
		Leopardus wiedii (Schinz, 1821)	Margay	Carnivore
		Leopardus pardalis (Linnaeus, 1758)	Ocelot	Carnivore
		Speothos venaticus (Lund, 1842)	Bush dog	Carnivore
		Eira barbara (Linnaeus, 1758)	Tayra	Frugivore-Carnivore
		Atelocynus microtis (Sclater, 1883)	Small-eared-dog	Frugivore-Carnivore
		Nasua nasua (Linnaeus, 1766)	Coati	Frugivore-insectivore
	CINGULATA	*Priodontes maximus* (Kerr, 1792)	Giant armadillo	Insectivore-Frugivore
		Dasypus spp (Linnaeus, 1758)	Armadillo	Insectivore-Frugivore
Class	**Order**	**Species**	**English vernacular name**	**Trophic guild**

	CETARTIODACTYLA	*Tayassu pecari* (Link, 1795)	White lipped peccary	Granivore-Frugivore
		Pecari tajacu (Linnaeus, 1758)	Collared peccary	Granivore-Frugivore
		Mazama spp (Rafinesque, 1817)	Brocked deer	Browser
MAMMALIA	PERISSODACTYLA	*Tapirus terrestris* (Linnaeus, 1758)	Tapir	Browser
	PILOSA	*Tamandua tetradactyla* (Linnaeus, 1758)	Southern tamandua	Insectivore
		Myrmecophaga tridactyla (Linnaeus, 1758)	Giant anteater	Insectivore
	RODENTIA	*Myoprocta pratti* (Pocock, 1913)	Green acouchy	Granivore-frugivore
		Dasyprocta fuliginosa Wagler, 1832	Black agouti	Granivore-frugivore
		Cuniculus paca (Linnaeus, 1766)	Paca	Frugivore-browser

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