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 seasonal movements between two adjacent forest types at two contiguous sustainable-use forest reserves in Western Brazilian Amazonia, investigating the effects of water level, landscape and anthropogenic disturbance on the overall species richness, composition, and abundance of nine major vertebrate trophic guilds. 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. Anthropogenic disturbance and geographic setting of camera trap stations, including distance to the nearest urban center, the number of residents of the nearest community, elevation and the surrounding area of *várzea* of each camera trap station, had a variety of effects on the terrestrial vertebrate assemblage. Overall vertebrate biomass increased with distance from the nearest urban center. 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.

1 # Seasonal dynamics of terrestrial vertebrate abundance

2 # between Amazonian flooded and unflooded forests

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11 **Abstract**

12 The flood pulse is the main factor structuring and differentiating the ecological communities of

13 Amazonian unflooded (*terra firme*) and seasonally-flooded (*várzea*) forests as they require unique

14 adaptations to survive the prolonged annual floods. Therefore, *várzea* and *terra firme* forests

15 hammer out a spatio-temporal mosaic of resource availability, which may result in landscape scale

16 seasonal movements of terrestrial vertebrates between adjacent forest types. Yet the lateral

17 movements of terrestrial vertebrates between hydrologically distinct neighbouring forest types

18 exhibiting staggered resource availability remains poorly understood, despite the important

19 implications of this spatial dynamic for the ecology and conservation of forest wildlife. We

20 examined the hypothesis of seasonal movements between two adjacent forest types at two

21 contiguous sustainable-use forest reserves in Western Brazilian Amazonia, investigating the

22 effects of water level, landscape and anthropogenic disturbance on the overall species richness,

23 composition, and abundance of nine major vertebrate trophic guilds. Species richness differed in

24 neighboring *terra firme* forests between the high-and low-water phases of the flood pulse and *terra*

25 *firme* forests were more species rich than *várzea* forests. There were clear differences in species

26 composition between both forest types and seasons. Generalized Linear Models showed that water

27 level was the main factor explaining aggregate abundance of all species and three trophic guilds.

28 Anthropogenic disturbance and geographic setting of camera trap stations, including distance to

29 the nearest urban center, the number of residents of the nearest community, elevation and the

30 surrounding area of *várzea* of each camera trap station, had a variety of effects on the terrestrial

31 vertebrate assemblage. Overall vertebrate biomass increased with distance from the nearest urban

32 center. Our results indicate that the persistence of viable populations of large terrestrial vertebrates

33 adjacent to major Amazonian rivers requires large, well-connected forest landscapes

34 encompassing different forest types to ensure large-scale lateral movements by forest wildlife.

36 **Introduction**

37 Wetland habitats are both challenging to conserve and globally important for biodiversity

38 conservation and human wellbeing (Keddy et al., 2009). Seasonal and perennial wetlands are

39 globally important and exceptionally productive habitats that support both high densities and a

40 high diversity of wild species (Halls, 1997; Junk et al., 2006). They also directly underpin the

41 livelihoods of millions of people and provide ecosystem services including productive fisheries,

42 water purification, hydrological regulation, nutrient cycling and naturally-fertilized agricultural

43 land (Costanza et al., 1997; François et al., 2005). The associated seasonal movements of

44 wetland fauna are especially challenging to conserve because their spatially complex life

45 histories require resources provided by several distinct habitats and entail diverse anthropogenic

46 threats at multiple sites (Martin et al., 2007; Wilcove & Wikelski, 2008).

47 Hunted migratory species — including salmonids, bats, passerines, waterfowl and grassland

48 ungulates — often contend with severe demographic depletion due to unsustainable offtake

49 (Madsen & Fox, 1995; Dudgeon et al., 2006; Bolger et al., 2007; McCulloch, Tucker & Baillie,

50 2008; Epstein et al., 2009). Overharvesting may be exacerbated by a "tragedy of the commons"

51 whereby human harvesters have little incentive to conserve their common-pool resource stock

52 in the absence of communal resource management institutions or governance norms (Ostrom,

53 2008). Species which form large aggregations during migrations are especially attractive targets

54 to human hunters, who can maximize the return on their foraging investment by slaughtering

55 many individuals in a short period (Peres, 1996).

56 A vast proportion of the Amazon Basin is formed by natural landscape mosaics of wetlands

57 embedded within a matrix of upland (hereafter, *terra firme*) forests on generally nutrient-poor

58 soils well above the maximum water-level of adjacent floodplains (Tuomisto et al., 1995).

59 Amazonian floodplains comprise a variety of habitats including swamp forests, hydromorphic

60 savannas, coastal wetlands, tidal forests, and seasonally-flooded forests. These Amazonian

61 wetlands are classified according to their climatic, edaphic and floristic characteristics (Junk &

62 Piedade, 2010; Junk et al., 2011). Based on these criteria, two large groups of wetlands have

63 been broadly distinguished: those with either (i) relatively stable or (ii) oscillating water levels

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

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

96   during the late high-water season (Schöngart et al., 2002; Haugaasen & Peres, 2005a, 2007;
97   Hawes & Peres, 2016).

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

105   Our study seeks to investigate the seasonal dynamics of terrestrial vertebrates in Amazonian
106   seasonally-flooded and unflooded forests by quantifying their relative abundance during both
107   the high- and low-water phases of the flood pulse. We predict that the species richness,
108   abundance and biomass of terrestrial vertebrates in *terra firme* forests adjacent to seasonally-
109   flooded *várzea* forests during the flood pulse will be higher than during the low-water phase.
110   This abundance contrast would indicate that the terrestrial fauna most likely leave *terra firme*
111   forest and move into *várzea* forests during the low-water phase to take advantage of higher
112   resource availability. Conversely, there should be transient overcrowding of the terrestrial
113   vertebrate fauna in adjacent *terra firme* forests driven by lateral movements away from the rising
114   floodwaters during the high-water phase.

115   To test this hypothesis we conducted camera-trapping surveys in both *terra firme* and *várzea*
116   forests along a major white-water tributary of the Amazon river during the high- and low-water
117   phases of the flood pulse. We examined differences in vertebrate abundance, species richness,
118   and changes in species composition between these two forest types and seasons and the
119   associated effects of geographic or landscape setting of camera traps in relation to anthropogenic
120   disturbance. We provide crucial empirical evidence supporting the notion that Amazonian *terra*
121   *firme* and *várzea* forests should be juxtaposed within fully functional floodplain protected areas,
122   thereby enhancing both the spatial configuration of reserve design and landscape management
123   of highly heterogeneous forest macromosaics in Amazonia for both biodiversity persistence and
124   the subsistence of local extractive communities.

125 **Materials & Methods**

126 Study Area

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

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

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

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

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

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

133 (17.9%) encompassing the main river channel (Hawes et al., 2012) (Fig. 1). The Juruá region

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

135 annual temperature of 27.1ºC, a mean rainfall of 3,679 mm/year, and peak water levels of 8 - 12

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

137 early November (Peres, 1997). The regional elevation range is 65 – 170 m above sea level. All

138 forest sites surveyed consist of largely undisturbed primary forest, although commercially

139 valuable timber species have experienced small-scale selective logging along the Juruá River

140 from 1970 to 1995, especially in *várzea* forests.

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

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

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

144 channel or tributaries and oxbow lakes. Residents of these reserves are variously engaged in

145 agricultural and extractive activities for both subsistence and cash income (Newton, Endo &

146 Peres, 2011; Campos-Silva & Peres, 2016).

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

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

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

150 Camera trapping

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

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

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

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

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

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

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

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

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

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

161 3000m and 6000m Euclidean distance along transects, arrayed in contiguous *terra firme* primary

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

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

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

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

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

167 CTS were deployed during both high- and low-water phases whereas *várzea* CTS were surveyed

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

169 this time of year.

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

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

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

173 (IUCN 2013). Primates, non-terrestrial birds and rodents and marsupials smaller than 1 kg were

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

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

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

177 nocturnal (black and white) images.

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

179 granivore-frugivores, frugivores, carnivores, frugivore-carnivores, insectivore-frugivores,

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

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

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

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

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

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

186   (Abrahams, Peres & Costa, 2017).

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

188   10.3) (Table 2). We calculated the mean water level of the Juruá River during the exposure

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

190   1973 to 31st December 2010; $N \approx$ 14,600 measurements) at a nearby locality (Gavião

191   Metereological Station in Carauari-AM). As a continuous variable, mean water-level during

192   CTS sampling intervals was a far more powerful descriptor of seasonality period than either

193   categorical season (e.g. low-water vs high-water season) or time of the year (e.g. Julian day) per

194   se.

195   Data analysis

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

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

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

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

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

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

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

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

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

205   were performed using CTS data from our second sample design.

206   To assess the effects of forest type and season on terrestrial vertebrate assemblage structure, we

207   used Principal Coordinates Analysis (PCoA) using a Bray–Curtis similarity distance matrix.

208   Prior to these analyses, to reduce the weight of abundant species in the ordination space,

209   terrestrial vertebrate abundance was standardized by dividing the number of detections of each

210   species by the total number of detections at each CTS. Differences in species composition

211   between forest types, and seasons were tested using Permutational Multivariate ANOVA

212   (PERMANOVA) (Anderson, 2001) performed using the Bray-Curtis similarity matrix. To test

213   for seasonal effects on species composition at *terra firme* CTS, we performed a Procrustes

214   rotation analysis of the ordination matrices derived from CTS that were surveyed during both

215   the high- and low-water phases of the flood pulse. In the PCoA and PERMANOVA analyses,

216   we employed all CTS, whereas the Procrustes rotation was performed using only the data from

217   the second sample design.

218   We tested the hypothesis of seasonal faunal movement between forest types and investigated

219   the effects of landscape context and anthropogenic disturbance employing Generalized Linear

220   Models (GLMs). We used a Poisson distribution for count data using CTS from both sample

221   designs, but a Negative Binomial distribution was chosen when overdispersion was detected

222   (Hilbe 2007). For the metric of biomass we used a Gaussian error structure. The number of

223   camera-trapping nights per CTS was specified as an *offset* variable in all models to account for

224   difference in sampling effort (i.e. number active nights) between CT deployments.

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

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

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

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

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

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

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

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

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

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

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

236   with the lowest AICc value.

237   **Results**

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

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

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

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

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

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

244   48, p = 0.009, Fig. 2 B). Similarly, species richness was higher in *terra firme* sites (18.42 ± 3.11

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

246   D).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

273   5 E). The area of *várzea* within a 1000-m buffer around each CTS best explained insectivore

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

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

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

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

278   **Discussion**

279   Species richness and seasonal movements between forest types

280   Our camera-trapping study provides tantalizing evidence that water level governs the

281   distribution of large terrestrial vertebrates in Amazonian pristine forest mosaics. These species

282   appear to exhibit lateral seasonal movements to take advantage of periodic resource availability

283   in extremely productive floodplain forests. In our study area, the swath of floodplain forest is

284   approximately 20 km wide, thereby providing a vast area of highly productive habitat for

285   terrestrial species during the low-water phase.

286   In general, *terra firme* forest sites were more species-rich than *várzea* forest sites, a pattern that

287   conforms with results from previous studies comparing assemblages of all mammals, primates,

288   bats, birds and small mammals in Amazonian seasonally-flooded and unflooded forests (Peres

289   1999, 1997, Haugaasen & Peres 2005b; c; Beja *et al.* 2009; Pereira *et al.* 2009, Bobroweic et al.

290   2014). Salvador, Clavero & Leite Pitman (2011) reported that floodplain forests in the Peruvian

291   Amazon are more species-rich than *terra firme* forests during the dry season. They also report

292   that the number of species in floodplain forest during the wet season remains the same

293   throughout the year, while in *terra firme*, a sharp increase in species richness coincided with the

294   onset of the wet season. These shifts in the number of species between the two forest types are

295   consistent with our seasonal movement hypothesis, as the bulk of terrestrial vertebrate species

296   likely exit *terra firme* terrains to feed on the seasonally abundant *várzea* forest resources.

297   Water level represents a physical barrier for most vertebrate species attempting to access *várzea*

298   forests during the high-water phase. This was confirmed by the positive relationship between

299   water level and aggregate community-wide abundance, and the number of detection events of

300   frugivore-insectivores, granivore-frugivores and carnivores. Bobrowiec *et al.* (2014) noted that

301   the flood pulse constituted a physical barrier even for Phyllostomid bats, whose species

302   composition differed between *terra firme* and *várzea* forests during the high-water period, but

303   this effect did not persist year-round. We found clear differences in species composition between

304 *terra firme* and *várzea* forests during the low-water phase and within our *terra firme* samples

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

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

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

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

309 and forest types.

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

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

312 2004; Haugaasen & Peres, 2007). In *terra firme* forests, fruit production occurs during the early

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

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

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

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

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

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

319 277, p-value < 0.001). As water levels recede, the terrestrial fauna rapidly colonize *várzea*

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

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

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

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

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

325 period (Bodmer 1990).

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

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

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

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

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

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

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

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

334 Keuroghlian, Eaton & Desbiez, 2009). Large-bodied myrmecophages and insectivore-
335 frugivores such as giant anteaters and armadillos exhibited low detection rates in *várzea* forests,
336 likely because they are year-round residents in *terra firme* forests. They seldom move between
337 forest types because the permanently wet *várzea* soils preclude their fossorial foraging behavior.
338 We never observed giant armadillo (*P. maximus*) holes in *várzea* forests, but commonly
339 observed them in *terra firme* forests, and this is consistent with previous studies in the Araguaia
340 River (Negrões *et al.* 2011) and Peruvian floodplain forests (Salvador, Clavero & Leite Pitman
341 2011).

342 Detection rates of carnivores increased with the water level, a pattern that can be explained by
343 their swimming and climbing abilities, which allow them to both move between temporary
344 forest islands and utilize the tree canopy as floodwaters rose. Jaguars (*P. onca*) in *várzea* forests
345 in the lower Japurá River are known to spend the entire high-water season high up in the trees
346 (E.E. Ramalho, pers. comm.) and subsist upon arboreal and semi-aquatic species such as howler
347 monkeys (*Alouatta seniculus* (Linnaeus, 1766)), sloths (*Bradypus variegatus*, Schinz, 1825) and
348 spectacled and black caimans (*Caiman crocodilus* (Linnaeus, 1758), and *Melanosuchus niger*
349 (Spix, 1825)) (Ramalho 2006).

350 Conservation implications

351 Our research supports the existing body of evidence that the Médio Juruá region, and many other
352 regions of the lowland neotropics, should be viewed as an essentially interconnected multi-
353 habitat socio-ecological system. The massive long-lasting seasonal flood pulse (Junk, Bayley &
354 Sparks, 1989) and the associated phenological (Hawes & Peres, 2016), hydrological, ecological
355 (Hawes et al., 2012) and livelihood impacts this engenders (Endo, Peres & Haugaasen, 2016)
356 require conservation planning at the scale of the entire landscape, with major drainage basins
357 representing complementary management units.

358 Amazonian freshwater ecosystems such as seasonally white-water flooded forests are vulnerable
359 to anthropogenic disturbance. *Várzea* and *terra firme* forests function as ecologically integrated
360 and hydrologically interconnected habitats that are seasonally utilized by a suite of mobile
361 species, with terrestrial fauna often relying upon the temporally staggered resources of both
362 habitats. As such, they are threatened by both aquatic and terrestrial anthropogenic activities at

363   the local and regional scales. The immense fluvial transport network of the lowland Amazon

364   makes even remote forests accessible to hunters (Peres & Lake, 2003), making their faunal

365   resources non-excludable, whilst simultaneously difficult to monitor. These institutional

366   governance challenges over vast tracts of forest partly explain why terrestrial hunting

367   management has thus far proved elusive. Amazonian terrestrial fauna may be comparatively

368   robust to anthropogenic threats as they seasonally move short distances, usually do not form

369   large aggregations, and often occupy large areas of structurally intact forest. White lipped

370   peccaries, which range over vast areas and form herds of hundreds of individuals, are a notable

371   exception. Not only are they a highly preferred hunted species, vulnerable to overhunting even

372   under low-offtake scenarios (Abrahams, Peres & Costa, 2017), but they play an important

373   ecological role as natural agents of disturbance in plant community dynamics (Silman, Terborgh

374   & Kiltie, 2003) and re-distributing nutrients and fertilizing upland forests.

375   The existing protected area network and management policies were created principally to protect

376   terrestrial ecosystems and are therefore not adequate to mitigate the aforementioned impacts.

377   Protected areas also suffer from design, implementation and monitoring deficiencies and their

378   delimitations does not adequately represent or protect the full suite of biotic diversity (Peres &

379   Terborgh, 1995, Albernaz *et al.* 2012, Castello *et al.* 2013). Although a protected area coverage

380   of ~25% gives the impression of extensive conservation management of floodplains, less than

381   1% of the aggregate area of Amazonian floodplains in Brazil is strictly protected (Albernaz *et*

382   *al.* 2012). Sustainable development and extractive reserves represent the majority of all

383   protected areas worldwide. Their conservation effectiveness can be compromised by high

384   human population density, the uncertain economic viability of exploiting non-timber resources

385   and a shortfall in available animal protein resulting from depleted game vertebrate populations

386   (Peres, 2011; Terborgh & Peres, 2017), but see Abrahams, Peres & Costa (2017) and Campos-

387   Silva & Peres (2016) for best-case scenarios of terrestrial subsistence hunting and local fisheries

388   management.

389   We have shown that a substantial part of the large vertebrate fauna modulates their use of

390   different forests types within a highly heterogeneous forest landscape according to the marked

391   seasonality of *várzea* floodplain forests. *Várzea* forests adjacent to major rivers are preferentially

392   settled by Amazonian extractivists seeking reliable access to transport routes, fertile soils and

393   animal protein (Endo, Peres & Haugaasen, 2016). In Amazonian extractive reserves, the forest
394   type within which villages are situated can modulate their livelihood strategies. Communities
395   with greater access to *terra firme* forests are inherently more agricultural, while communities
396   with greater access to seasonally-flooded forests rely more heavily on the seasonal extraction of
397   non-timber resources such as palm fruits (*Euterpe spp.*, Martius 1824 and *Astrocaryum*
398   *aculeatum*, Meyer), rubber (*Heavea spp.*, Aublet) and oil seeds (*Carapa guianensis*, Aublet and
399   *Astrocaryum murumuru*, Mart.) (Newton, Endo & Peres 2011).

400   Our research occupies the confluence between the issues of landscape-scale conservation
401   planning, ecological connectivity, nutrient transport and uptake, and community-based natural
402   resource management. The Médio Juruá region exemplifies these issues as it encompasses
403   extensive seasonal wetlands and a suite of hunted, seasonally-mobile species. Adequate
404   conservation strategies in this region must account for the full life-history needs of mobile
405   harvested species, ecologically interconnected habitats and the diverse livelihood portfolios of
406   local communities (Lindenmayer et al., 2008). Different Amazonian forest types exhibiting
407   staggered resource pulses must be included within the same or neighboring sustainable-use
408   protected areas. This will provide sufficiently large areas to both support large-scale ecological
409   processes (e.g. species migrations, lateral movements, persistence of apex predators) and
410   anthropogenic extractive activities in the long run (e.g. estimated sustainable harvest area for
411   tapir populations >2,000 km²) (Peres & Terborgh, 1995; Peres, 2001, 2005; Haugaasen & Peres,
412   2007). This concept can be applicable to conservation planning of other regions consisting of
413   natural forests mosaics experiencing seasonal floods such as the hyper-fragmented region of the
414   Araguaia River or at the Pantanal floodplains (Negrões et al., 2011; De Lázari et al., 2013). In
415   these different scenarios, private reserves must be situated adjacent to protected areas to ensure
416   terrestrial fauna protection during the prolonged inundation season.

417   Study limitations

418   In our study, we were unable to estimate the species richness in *várzea* forests during the high-
419   water phase of the flood pulse, because our camera trapping method focused only on terrestrial
420   species, which are more sensitive to the flood pulse than arboreal and semi-aquatic species.
421   *Várzea* forests along this section of the Juruá River are typically subjected to an annual flood
422   pulse amplitude of 8 to 12 m, which lasts for up to six months. Any camera traps deployed in

423 várzea forests during the high-water period would need to be placed almost half way up into the
424 forest canopy.

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

431 **Conclusions**

432 The annual floodwaters along several major white-water rivers in the Amazon is the main factor
433 structuring and differentiating *várzea* floodplains from adjacent *terra firme* forests as unique
434 adaptations are required to tolerate the prolonged flood pulse. This remarkable natural
435 phenomenon drives several key ecological processes, including staggered plant phenology, high
436 plant productivity, and supports major local livelihood activities such as subsistence fishing and
437 hunting. This landscape scale seasonal dynamics between these major adjacent forest types was
438 investigated in terms of species richness, species composition and population abundance for as
439 many as 23 vertebrate species. We have shown that many upland forest terrestrial vertebrate
440 species make seasonal use of *várzea* forests to take advantage of the abundant trophic resource
441 in this forest type following the receding waters. We acknowledge that detailed movement data
442 using GPS telemetry can further clarify the magnitude and seasonal importance of *várzea* habitat
443 use by *terra firme* vertebrates. However, we highlight that this unique seasonal dynamic is a
444 critical issue in Amazonian forest reserve design and biodiversity monitoring, particularly
445 within large sustainable use reserves encompassing complex natural landscape mosaics, where
446 unimpeded lateral movements should continue to support both local extractive economies and
447 healthy wildlife populations.

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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 study region (black square). The boundaries of the RESEX Médio Juruá and RDS Uacari are outlined in black. Background colors represent elevation, with blue and brownish orange 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).

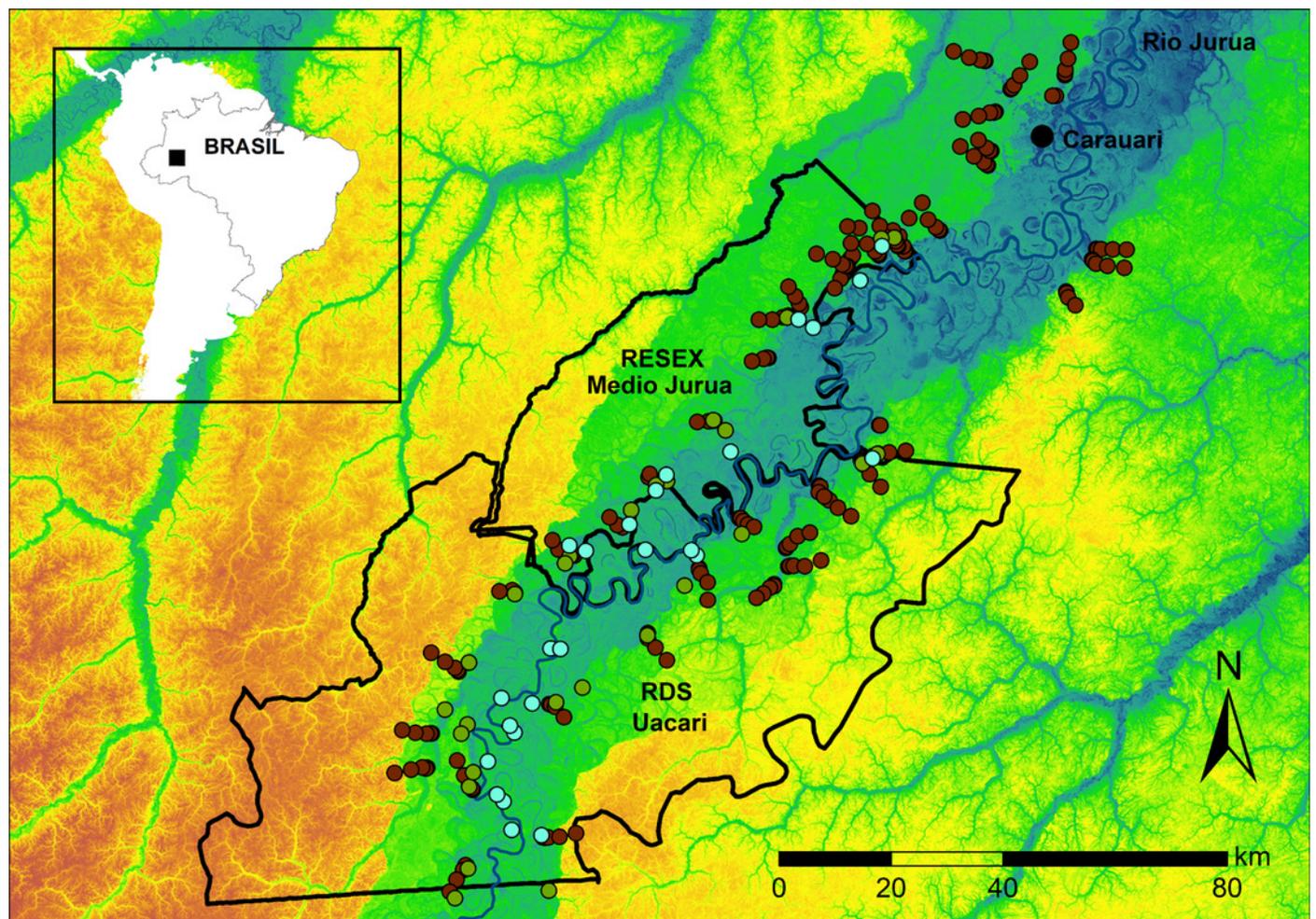



Figure 2

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).

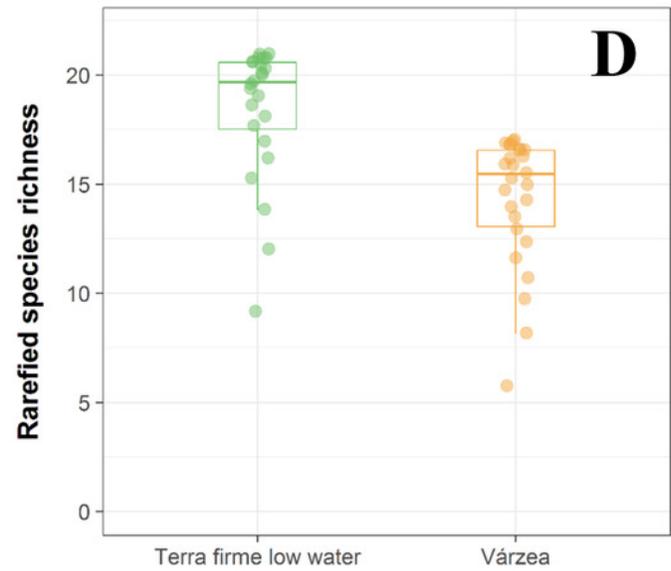
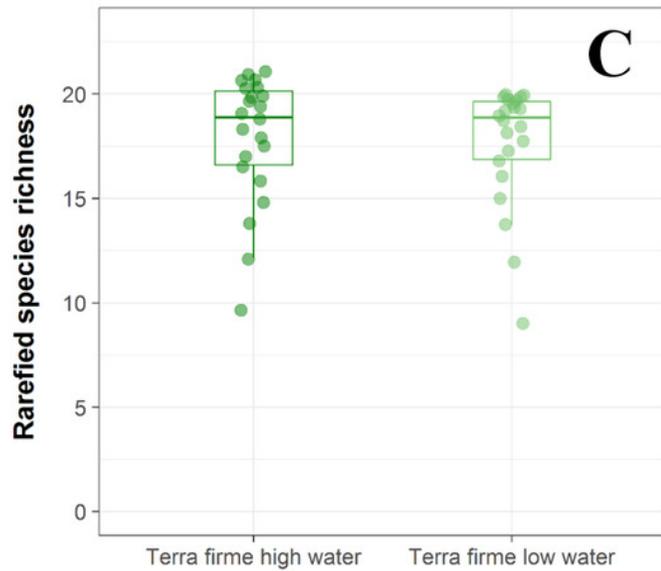
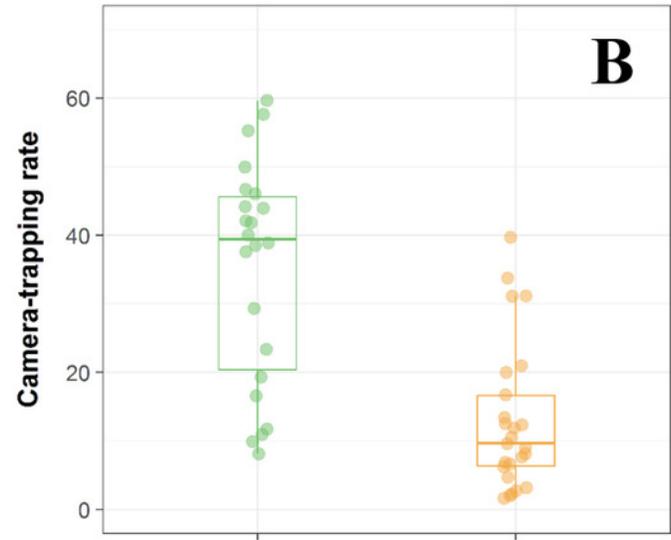
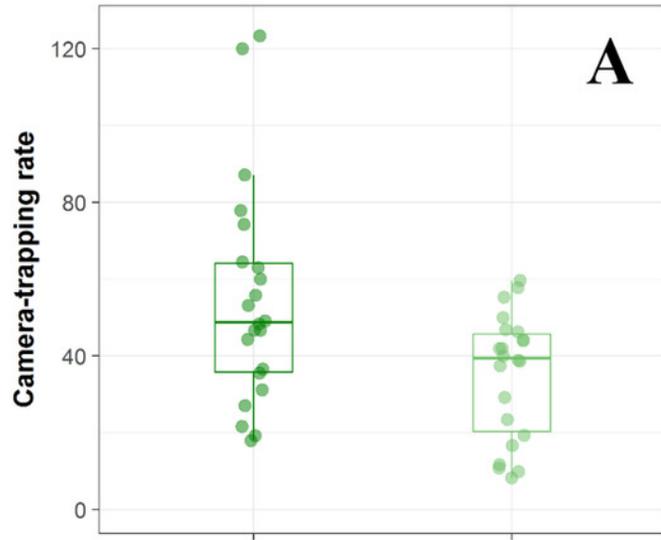



Figure 3

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 *várzea* 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.

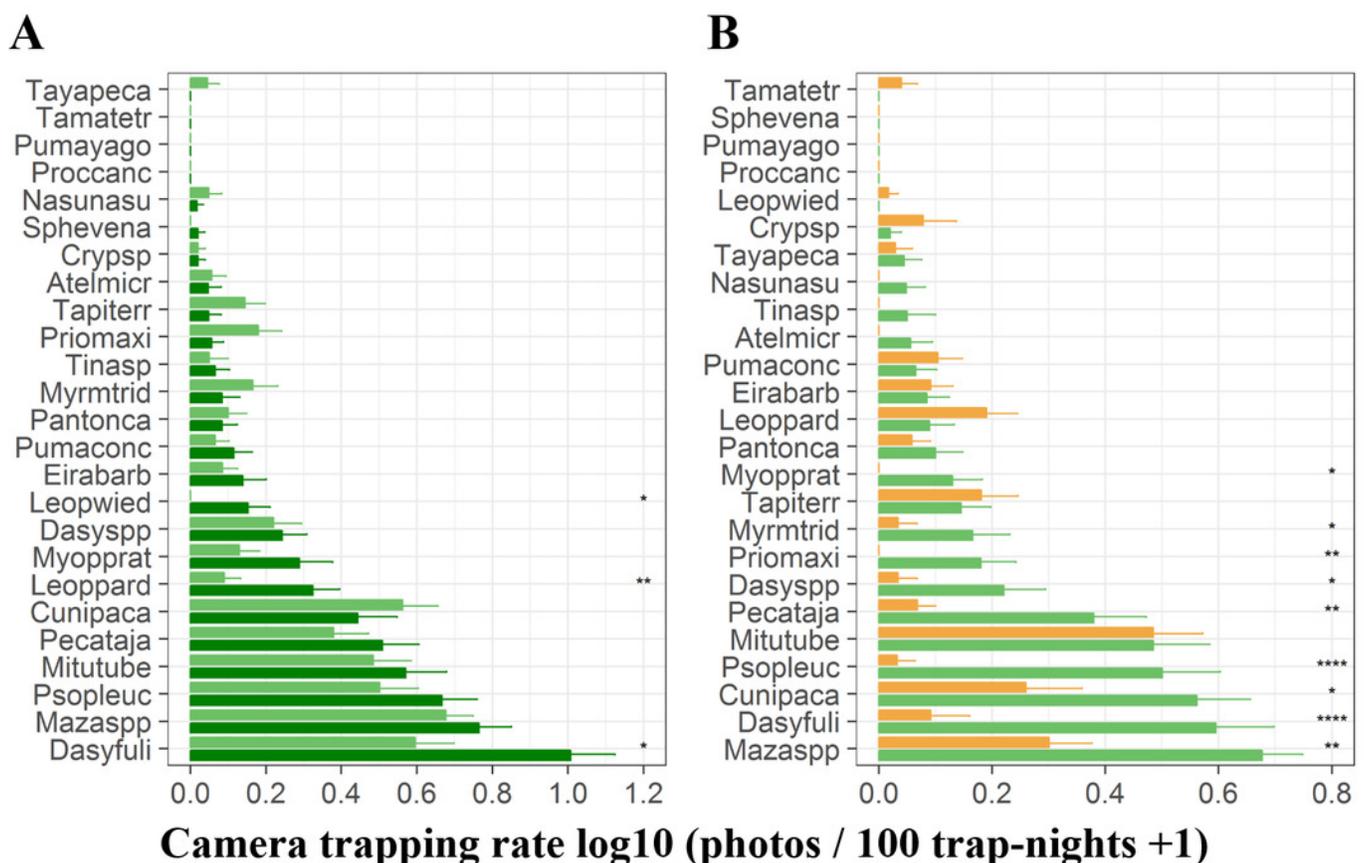



Figure 4

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.

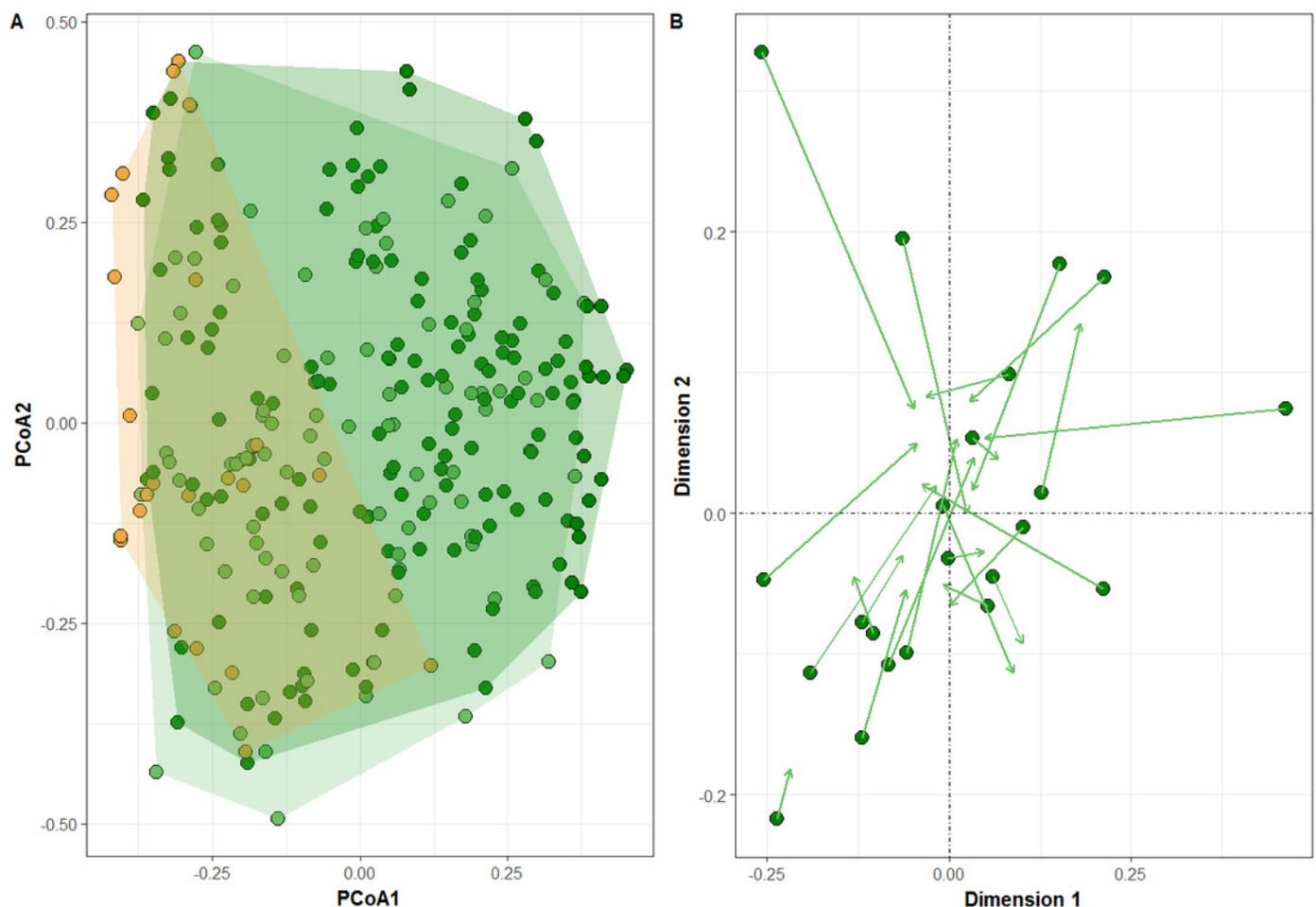
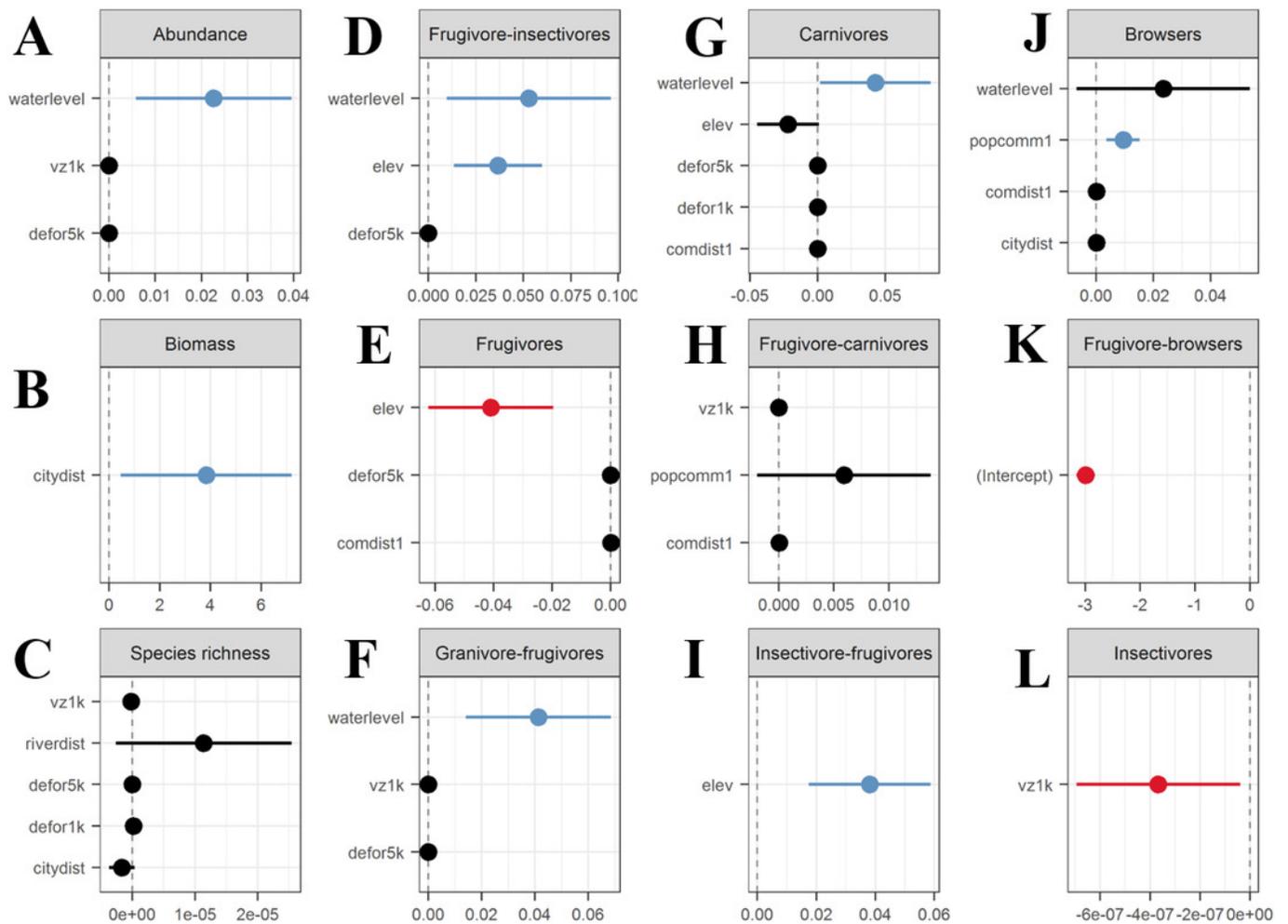



Figure 5

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.

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**

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

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

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

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