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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.

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

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11 Abstract

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14 adaptations to survive the prolonged annual floods. Therefore, *várzea* and *terra firme* forests
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16 seasonal movements of terrestrial vertebrates between adjacent forest types. Yet the lateral
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19 implications of this spatial dynamic for the ecology and conservation of forest wildlife. We
20 examined the hypothesis of terrestrial fauna seasonal movements between two adjacent forest
21 types at two contiguous sustainable-use forest reserves in Western Brazilian Amazonia. We used
22 camera trapping data on the overall species richness, composition, and abundance of nine major
23 vertebrate trophic guilds to infer on terrestrial vertebrate movements as a function of seasonal
24 changes in floodplain water level. Species richness differed in neighboring *terra firme* forests
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26 species rich than *várzea* forests. There were clear differences in species composition between both
27 forest types and seasons. Generalized Linear Models showed that water level was the main factor
28 explaining aggregate abundance of all species and three trophic guilds. Our results indicate that
29 the persistence of viable populations of large terrestrial vertebrates adjacent to major Amazonian
30 rivers requires large, well-connected forest landscapes encompassing different forest types to
31 ensure large-scale lateral movements by forest wildlife.

32

33 Introduction

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

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

53 Most Amazonian wetlands with oscillating water levels are subjected to a predictable, long-
54 lasting monomodal flood pulse which alternates between the high- and low-water periods
55 according to the Flood Pulse Concept (Prance, 1979; Junk, Bayley & Sparks, 1989). Depending
56 on the geomorphology and geochemical profile of each watershed, these areas can be inundated
57 by white-, black- or clear-water rivers (Sioli, 1984). White-water rivers such as the Solimões,
58 Madeira, Japurá and Juruá have their origins in the Andes or Andean piedmonts, are nutrient-
59 rich, and have neutral pH. These rivers deposit their alluvial sediments along wide swaths of
60 floodplain forests of high primary productivity, which are locally known as *várzeas* (Wittmann
61 et al., 2006; Junk et al., 2011). In contrast, Amazonian black-water rivers such as the Negro,
62 Tefé and Jutai 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; Haugaasen & 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 Köppen criteria, with a mean
118 annual temperature of 27.1°C , 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 Meteorological 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).

269 **Discussion**

270 Species richness, composition and seasonal movements between forest types

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

277 In general, *terra firme* forest sites were more species-rich than *várzea* forest sites, a pattern that
278 conforms with results from previous studies comparing assemblages of all mammals, primates,
279 bats, birds and small mammals in Amazonian seasonally-flooded and unflooded forests (Peres
280 1999, 1997, Haugaasen & Peres 2005b; c; Beja *et al.* 2009; Pereira *et al.* 2009, Bobrowiec *et al.*
281 2014). Salvador, Clavero & Leite Pitman (2011) reported that floodplain forests in the Peruvian
282 Amazon are more species-rich than *terra firme* forests during the dry season, which is contrary
283 to our findings. This can be explained by methodological differences between the studies once
284 they used line transects, track counts and interviews enabling the inclusion of semi-aquatic and
285 arboreal mammals such as giant otters, primates and sloths in their dataset. They also report that
286 the number of species in floodplain forest during the wet season remains the same throughout
287 the year, while in *terra firme*, a sharp increase in species richness coincided with the onset of
288 the wet season. These shifts in species richness between the two forest types are consistent with
289 our seasonal movement hypothesis, as many terrestrial vertebrate species likely exit *terra firme*
290 terrains to take advantage of seasonally abundant food resources in *várzea* forest.

291 Water level represents a physical barrier for most vertebrate species attempting to access *várzea*
292 forests during the high-water phase. This was confirmed by the positive relationship between
293 water level and aggregate community-wide abundance, and the number of detection events of
294 frugivore-insectivores, granivore-frugivores and carnivores. Bobrowiec *et al.* (2014) noted that
295 the flood pulse constituted a physical barrier even for Phyllostomid bats, whose species
296 composition differed between *terra firme* and *várzea* forests during the high-water period, but
297 this effect did not persist year-round. We found clear differences in species composition between
298 *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.

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432 (www.projetomediojuruua.org).

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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 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).

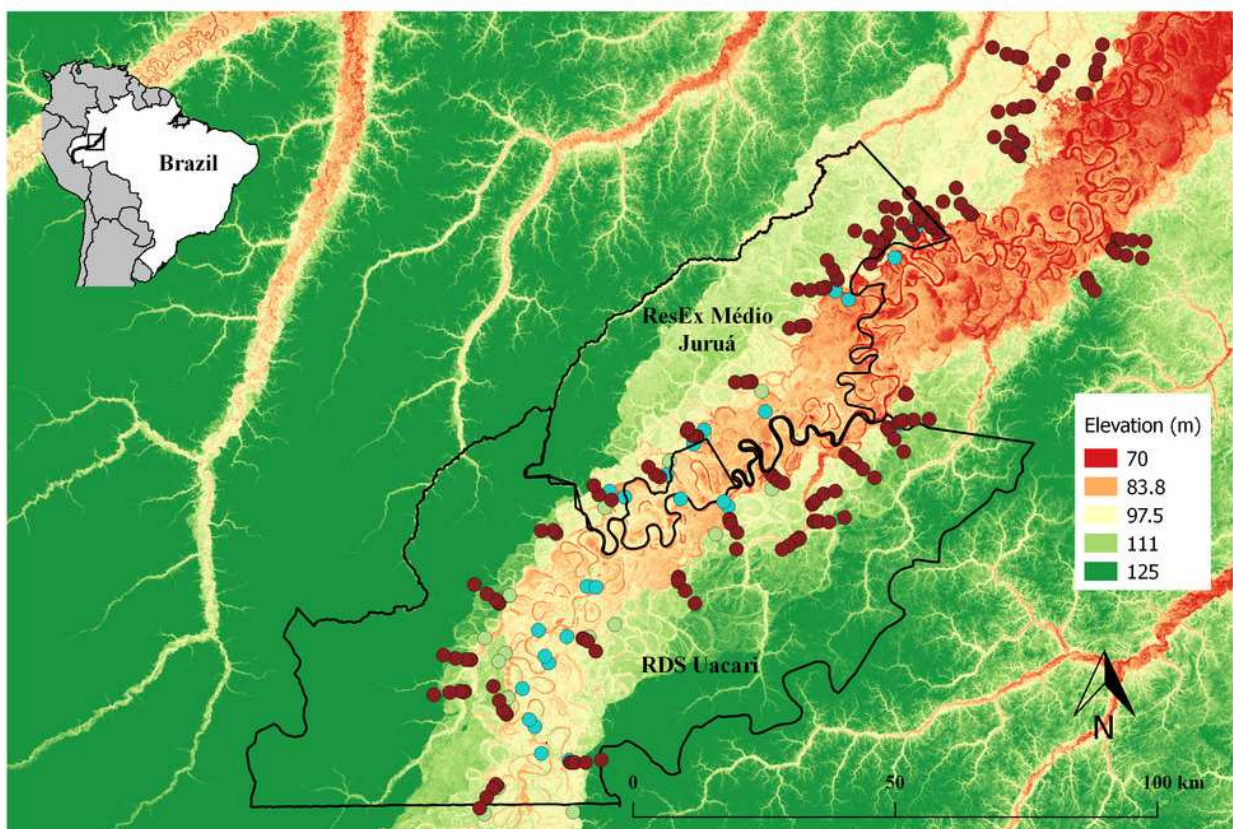
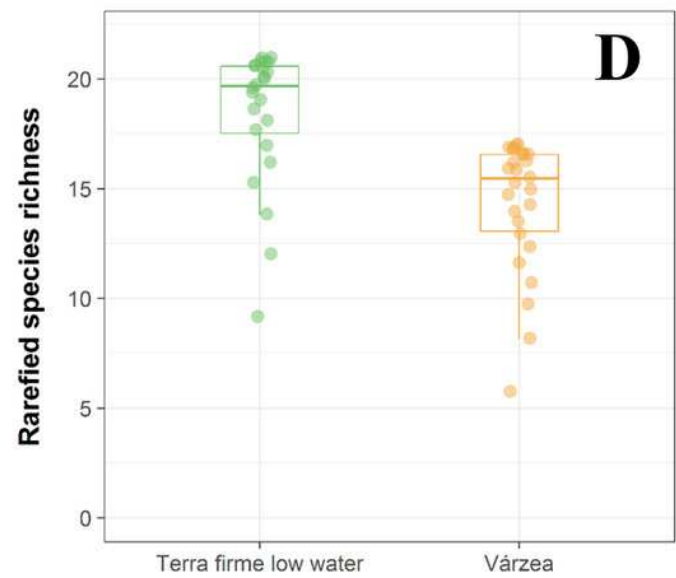
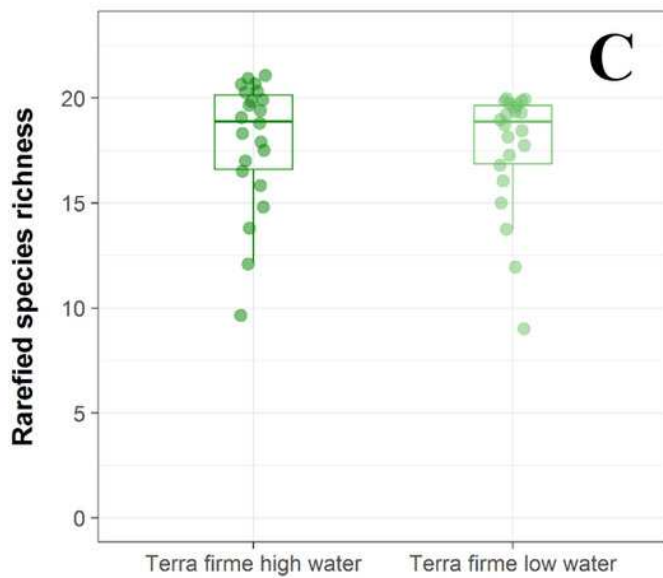
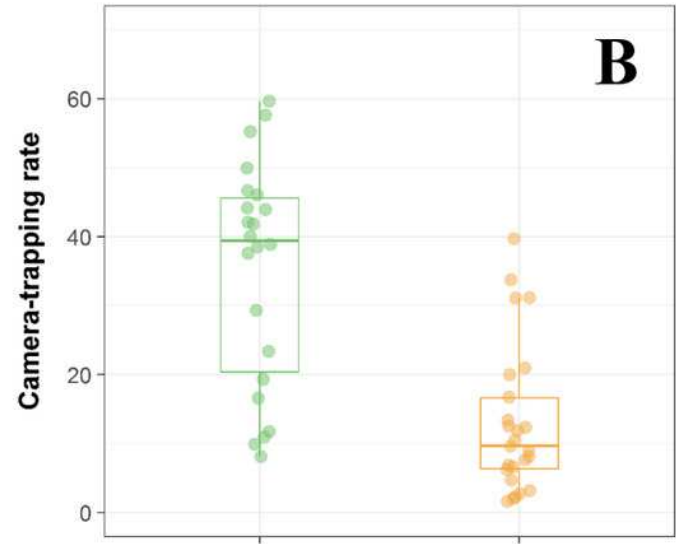
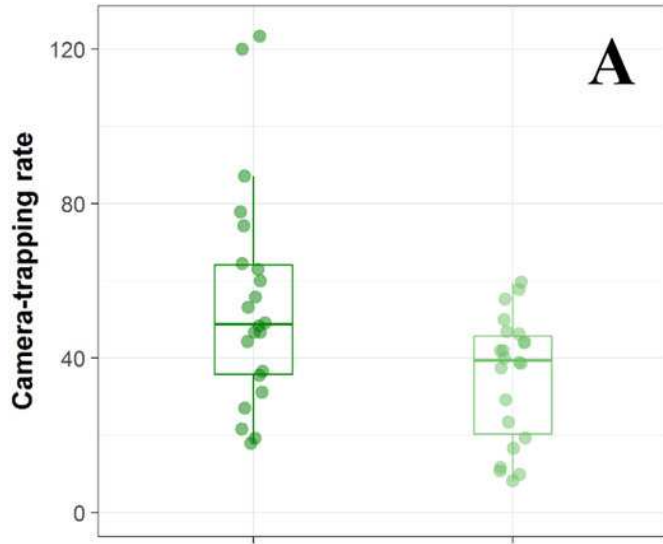


Figure 2

Comparison between *terra firme* 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).



Season

Forest type

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 firme* 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); * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

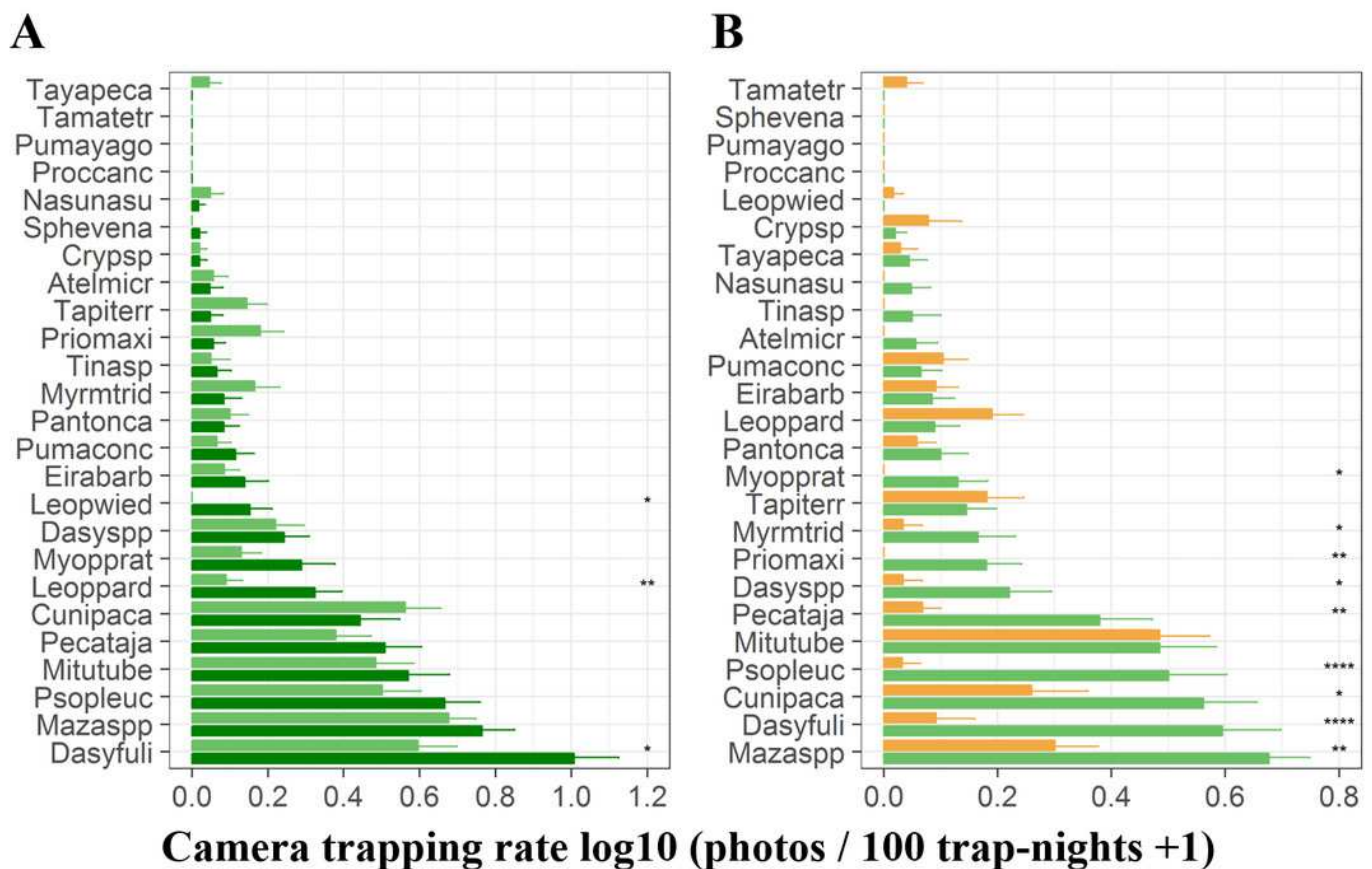


Figure 4

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.

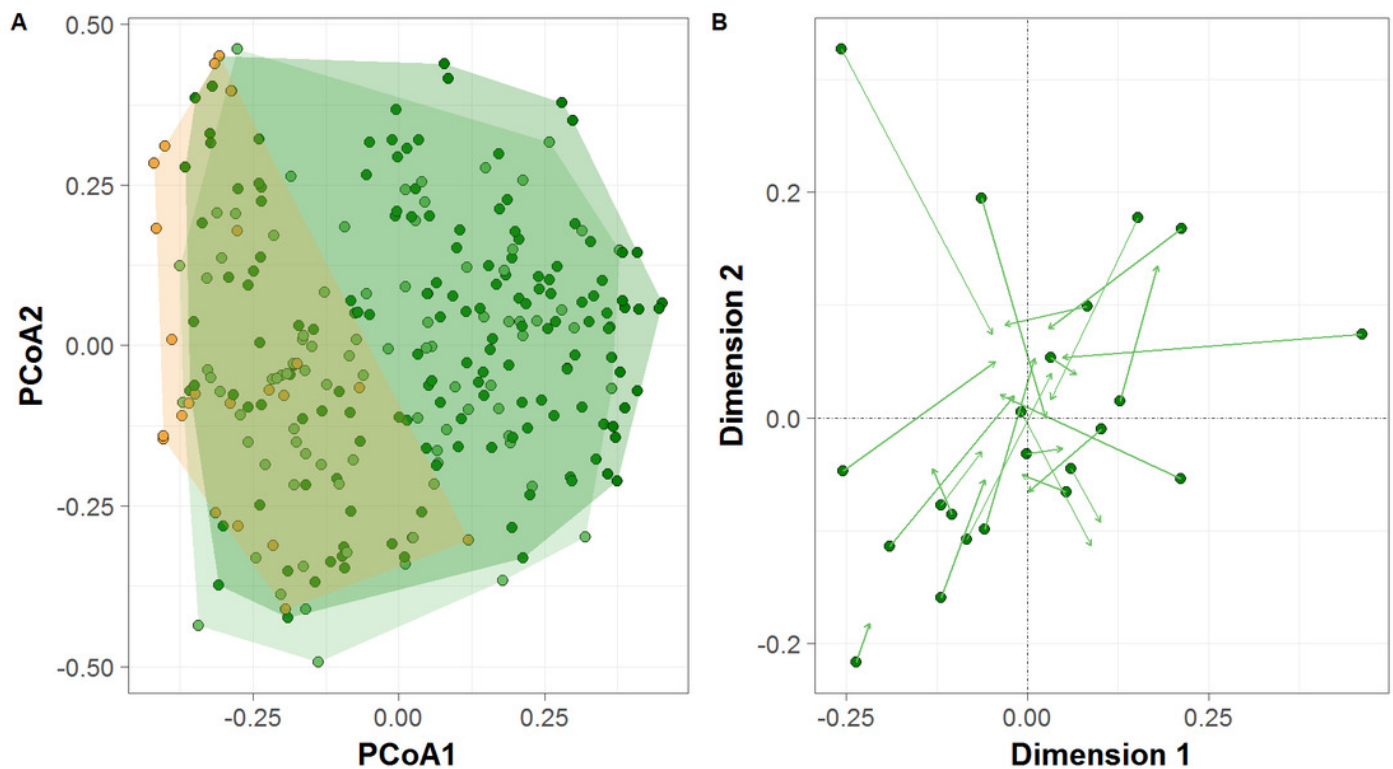
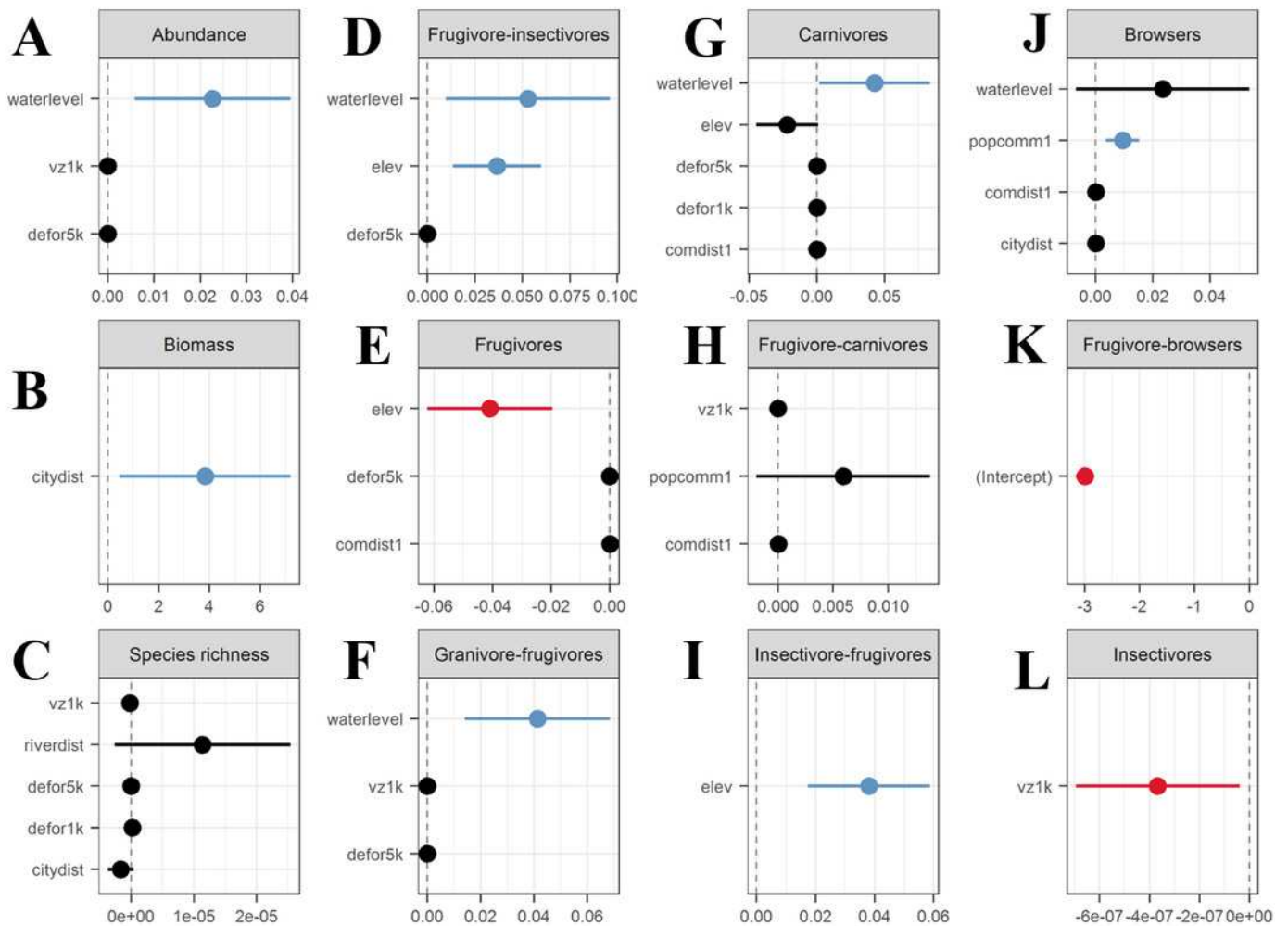


Figure 5

Coefficient estimates (\pm 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 \pm 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	
		<i>Terra Firme</i>	<i>Várzea</i>
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 <i>várzea</i> forest	vz0.5k	Area (m ²) of seasonally flooded forest within a 500m circular buffer centered at each CTS
	vz1k	Area (m ²) of seasonally flooded forest within a 1000m circular buffer centered at each CTS
	vz5k	Area (m ²) of seasonally flooded forest within a 5000m circular buffer centered at each CTS
Distance to <i>várzea</i> forest	vzdist	Euclidean distance from each CTS to the nearest <i>várzea</i> forest
Deforestation area	defor0.5k	Total area (m ²) of deforestation within a 500m circular buffer centered at each CTS
	defor1k	Total area (m ²) of deforestation within a 1000m circular buffer centered at each CTS
	defor5k	Total area (m ²) 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
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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

2

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

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