

Igapó seed patches: a potentially key resource for terrestrial vertebrates in a seasonally flooded forest of central Amazonia

ANA CAROLINA ANTUNES^{1,2,3,4,*}, FABRÍCIO BACCARO^{1,5},
VICTOR LERY CAETANO ANDRADE⁶, JOSÉ FERREIRA RAMOS¹,
ROBERTO DA SILVA MOREIRA and ADRIAN A. BARNETT^{1,2,5,7,8}

¹Instituto Nacional de Pesquisas da Amazônia (INPA), Av. André Araújo, 69060-001 – Manaus, AM, Brazil

²Grupo de Pesquisa de Mamíferos Amazônicos, INPA, Brazil

³EcoNetLab, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103, Leipzig, Germany

⁴EcoNetLab, Friedrich Schiller University Jena, Dornburger-Str. 159, 07743, Jena, Germany

⁵Universidade Federal do Amazonas, Departamento de Biologia. Av. Rodrigo Otávio, 69077-000 – Japiim, Manaus, AM, Brasil

⁶Max Planck Institute for the Science of Human History, Department of Archaeology, 07745, Jena, Germany

⁷Department of Life Sciences, Roehampton University, London, UK

⁸Flooded Habitats Research Group, INPA, Brazil

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In Amazonian igapó forests (seasonally flooded forests on blackwater river margins), the end of the annual flood pulse results in the formation of extensive mat-like seed patches. The seeds in these patches then germinate, forming a dense, highly heterogeneous, assemblage. Animal–plant interactions in these areas, as well as the influence that the patches have on the occurrence of herbivorous vertebrates, remain almost completely unstudied. Using camera traps in areas with and without seed/seedling patches, we tested the relationship between these seed accumulation sites and the presence of bird and mammal species. At the micro-scale (between treatments), vertebrate occurrence was not related to patch presence. At the larger scale (local), distance from adjacent upland (terra firme) forest and seed patch size were correlated with vertebrate distribution. The widespread occurrence of terrestrially active birds and mammals throughout igapó forests, not just where food resource densities were high, seems to be a compromise strategy between exploring the area to select the most favourable food items, and minimizing the risk of being predated when spending extended time foraging at the concentrated food sources represented by the seed patches. Our results underline the potential importance of igapó forests as a key habitat for a variety of terrestrial terra firme taxa, as well as emphasize the dynamic nature of this forest type, and should encourage further studies of this habitat and resource availability system.

ADDITIONAL KEYWORDS: bird – Igapó forest – interaction – mammal – neotropical forest.

INTRODUCTION

The ideal free distribution (IFD) concept developed by [Fretwell & Lucas \(1970\)](#) predicts that there will be more consumers in higher-quality patches than in

lower-quality patches. Given that possible knowledge of resource availability is related to resource patch size, the predictions of the IFD model are, consequently, scale-dependent ([Ives *et al.*, 1993](#); [Cosner, 2005](#)). For example, at large spatial scales, competitors can be positively associated because a common resource is aggregated ([Giller & Doube, 1994](#); [Inouye, 2005](#);

*Corresponding author. E-mail: a.carol.antunes.88@gmail.com

Schellhorn & Andow, 2005), whereas, at smaller scales, they may use behaviour or microhabitat selection to avoid direct competition (Byers, 1989; Ziv *et al.*, 1993; Albrecht & Gotelli, 2001). Where a resource is not predictable (predator–prey interactions), models also consider that the movement of animals and the presence of refuges are important variables in determining individual distributions (Turchin, 1998; Mason & Fortin, 2017). For predators, prey movement is the main operational factor in any foraging–predation trade-off (Mitchell & Lima, 2002). Thus, predictions regarding predators and prey distributions depend on the level of predation risk, as well as the volume and type of resources available (Hammond *et al.*, 2007).

In the Amazon basin, blackwater floodplains along the Rio Negro and its tributaries cover an area of ~119 000 km² (Melack & Hess, 2010). Annual floods with a very low input of dissolved and suspended nutrients are responsible for the low level of nutrients in these habitats (hereafter igapós) (Junk *et al.*, 2015). This annual flooding may last for more than 200 days, and strongly influences the composition and zonation of plant assemblages along the flood-level gradient (Ferreira *et al.*, 2010; Barnett *et al.*, 2015; Junk *et al.*, 2015). Trees in these forests have developed a suite of anatomical, physiological, morphological and phenological adaptations that allow their survival in this stressful environment, including high seed mass to compensate for the lack of nutrients, seedlings with rapid shoot elongation (which increases the chances of non-submergence for tall seedlings), high frequency of xeromorphic leaves, and seed dispersion modes highly dependent on the annual flood pulse (Parolin *et al.*, 2004; Hawes & Peres, 2014; Parolin *et al.*, 2016). Water- and fish-dispersed species show morphological adaptations that facilitate dispersion via increased buoyancy, such as spongy tissues or large air-filled spaces (Parolin *et al.*, 2010).

In igapó forests, ichthyochory and hydrochory are common modes of dispersion (Kubitzki & Ziburski, 1994; Correa *et al.*, 2007). However, the flood pulse also influences resource availability for fruit- and seed-eating vertebrate species. This availability is markedly seasonal, with two peaks occurring annually. The first occurs at highest water levels, when most igapó trees synchronously produce fruits (Parolin *et al.*, 2013), and the second occurs at the lowest water level, when many seeds that had been floating in the water lie exposed on the forest floor (Haugaasen & Peres, 2005, 2007). As the water level drops, floating seeds accumulate around obstacles such as floating logs and fallen trees, or in areas with low water current velocity (Barnett *et al.*, 2012), often forming floating rafts of seeds several to many square metres in extent (Supporting Information, Fig. S1A). When flood waters recede, these accumulations are deposited intact on the forest

floor, and many of the seeds within them subsequently germinate (Barnett *et al.*, 2012). The two periods of resource availability in igapó forests coincide with periods of reduced fruit availability in the adjacent upland (terra firme) forest (Haugaasen & Peres, 2005). As a result of this fruiting asynchrony, arboreal and volant animals (during the high-water season), and terrestrial animals (during the unflooded period), move annually into igapó forests to take advantage of these pulses of food resource availability (Bodmer, 1990; Renton, 2002; Haugaasen & Peres, 2007). To date, little information is available on the distribution of terrestrial vertebrates in Amazonian flooded forests in general (Alvarenga *et al.*, 2018; Costa *et al.*, 2018), and such data are even rarer for igapó forests.

Seed patches size may vary from 0.4 to 3.8 m², with densities of up to 594 seedlings per m², which contrasts strongly with the rest of the understorey vegetation, where seeds and seedlings are generally sparse (Supporting Information, Fig. S1B) (Barnett *et al.*, 2012). Although the process of seed patch formation remains largely unstudied, the patches are potentially important in explaining patterns of seasonal occupation of unflooded igapó forest by mammal and bird species. Seed patch formation, distribution and composition are hard to predict, but all appear to be related to the phenology of igapó plants, as well as their form of dispersion and the interaction between topography and water dynamics as flood levels recede. The scale of the landscape in which this phenomenon is observed is also relevant. Certainly, patch initiation depends largely on the landscape along the river, such as small altitudinal variations in the topography of the terrain, as well as the presence of local impedimenta such as floating fallen trunks and large palm fronds. As a result, the size, abundance and position of such patches varies from year to year, influencing the predictability of this resource for local frugivores.

Although the potential ecological importance of seed and seedling patches in the regeneration and long-term maintenance of igapó tree populations has been considered *em passim* (Ferreira *et al.*, 2010; Piedade *et al.*, 2010), no studies have looked at how seed patches affect the animals that inhabit the region. Here, we investigated how seed patches influence the local spatial patterning of herbivorous vertebrates in igapó forests. Our main objective was to evaluate whether areas of seed and seedling accumulation are positively related to increased presence of mammal and bird species in unflooded igapó forest. Specifically, we aimed to: (1) compare vertebrate visitation frequency at seed patches and areas of forest floor lacking such patches (control areas), (2) compare fruit and seed consumption frequencies at patches and control areas, and (3) evaluate whether (i) patch size, (ii) distance from a patch to the edge of the nearest terra

firme forest, and (iii) predator occurrence influenced vertebrate visitation frequency at such seed patches. This provides a baseline for future studies of the ecological dynamics of such seed patches: consumption and seed dispersal by animals (local-scale ecological processes), as well as the importance of floodplain forests (large-scale ecological processes) in furnishing key resources for terra firme-based vertebrates.

MATERIAL AND METHODS

STUDY AREA

The study was conducted in Jaú National Park (JNP) (01°54′–01°57′S, 61°27′–61°28′W) (Fig. 1), located between the cities of Barcelos and Novo Airão, on the southern bank of the Rio Negro, some 220 km north-west and upstream of Manaus, the capital city of Amazonas State, Brazil. Average annual temperature is 26.7 °C, and annual average rainfall is ~2400 mm. The

rainy season occurs from January to May and the lowest rainfall season is between June and October (Borges *et al.*, 2004). The hydrological regime has a monomodal flood pulse with mean amplitude of 8.17 m (peld-maua.inpa.gov.br). Flood level maxima occur during the second half of June, and minima in early November [PELD MAUA website (peld-maua.inpa.gov.br); values calculated from the Agência Nacional de Águas (ANA) hydrological station data at Moura, 70 km downstream from the Park]. JNP includes some 22 720 km² of igapó, terra firme and white sand forests, with 12% of the area occupied by igapó forest, seasonally flooded by the Rio Jaú (Fundação Vitória Amazônica, 1988). The study was conducted between September and November 2015, during the low water period.

SAMPLE DESIGN

To study the interactions between vertebrates and seed patches, we established 36 (50 × 20-m) plots on

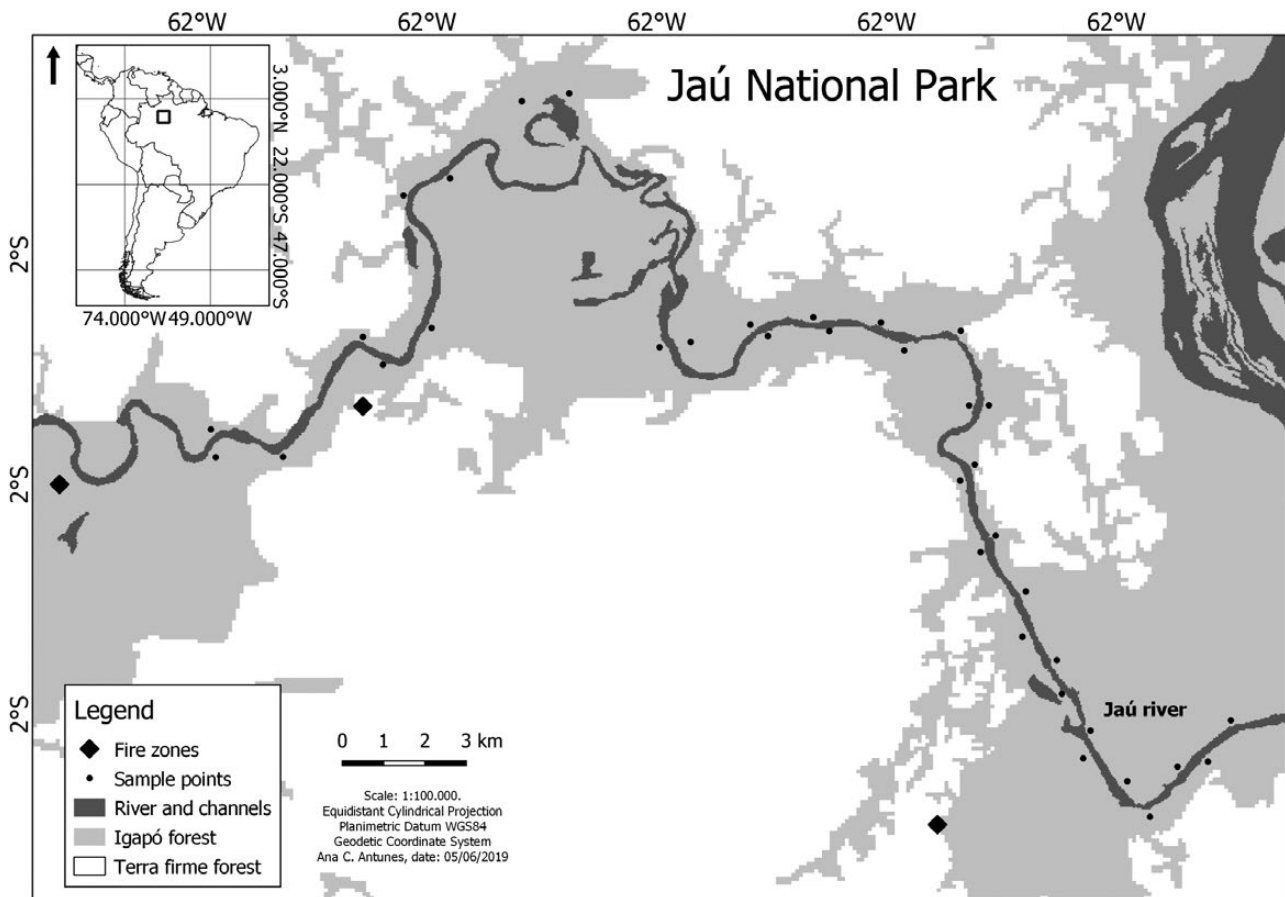


Figure 1. Map of Jaú National Park in Central Amazonia showing the locations of 36 1-ha plots in igapó forest (grey area) and three fire events (diamond) that occurred near the sampling area. We used the mask from Hess *et al.* (2015) to obtain the boundaries between flooded and non-flooded areas. Records of fires during fieldwork in the study area are from: <http://www.inpe.br/queimadas/bdqueimadas> (18 July 2018).

the floor of unflooded igapó forest. These were always parallel to the river channel and at different flood levels. Within each plot we: (1) recorded the size of all seed patches; and (2) randomly selected one seed patch per plot (through a random draw, so that patches of a range of sizes were sampled), and positioned a camera trap within it (Reconyx). To test whether animals were selectively visiting those areas of forest floor with seed patches more often than random, an equal number of camera traps were positioned to provide photographic coverage of control sites (areas where no seed patches were present inside the study plots). Control camera placement was identical to that at seed patches, at the same flood level, a determination based on highwater marks on tree trunks, but in places where seed accumulation was not observed. Camera traps were set to take five photos per event, without pause. Sequential photos from the same species within 15 min were considered a single record. We considered this time interval sufficient to record the frequency of animal visitation at patches with abundant resources, because the focus of the study was not the abundance of animals in the area, but the frequency of visitation to seed patches.

Cameras were installed in a sequence that began downstream and moved upstream as the study progressed. Fieldwork was divided into two campaigns: during the first (30 days during September and October) we sampled two sets of 12 plots (50 × 20 m) and, in the second (15 days during November), a further set of 12 plots. Site positions tracked the progressive drop of the Jaú river water level, and so moved ever closer to the middle of the river bed. However, no study plots were inundated during the study period. In each sampling, cameras remained in position, operating continuously, for 15 days. Between-plot distance was at least 1.5 km, with plots established along different elevations from the river level, so that, overall, the entire range of the flood-duration gradient was covered. Using 1 × 1-m sub-plots, we sampled the density and identified all seeds/seedlings in each seed patch and in all control areas where a camera trap was installed. We also counted those seeds/seedlings that were consumed (bite marks) within these sub-plots. Botanical material was collected in the field and seedlings and seeds were identified at the INPA Herbarium, Manaus.

The density of patches per plot was calculated by summing the area of all patches within the plot and dividing by the total plot area (1000 m²). We used the mask from Hess *et al.* (2015) that mapped wetland extent, vegetation cover and inundation state from the entire lowland Amazon at 100-m resolution using mosaics from the Japanese Earth Resources Satellite (JERS-1), and which are free for use and available on the ORNL DAAC website at <https://doi.org/10.3334/ORNLDAAC/1284>. We used these mosaics to locate

boundaries between flooded and non-flooded areas. To measure sampling point distances from the centre of each plot to the edge of the closest terra firme forest, linear measurements of distances in metres were made manually using the MEASUREMENT (Quantum GIS, v.2.10) tool.

DATA ANALYSIS

We used a paired Wilcoxon test to determine whether vertebrate occurrence was higher at seed patches than at comparable areas of forest floor lacking such patches (control areas). The sample unit of this analysis was the total number of individual herbivorous vertebrates (potential direct consumers from the seed/seedling patches) recorded per plot over 15 days at patches and in control areas. Exploratory tests were performed to analyse possible relationships between the occurrence of specific vertebrate groups and the presence of patches. Several clusters were tested (frugivores, prey, rodents, large and medium, small, herbivorous, carnivorous), but none showed a significant relationship with patches at the micro scale. We therefore focused our analyses on the herbivorous vertebrate assemblage visiting the area of study. To compare seed and seedling consumption by terrestrial vertebrates within and outside patches, we also used a paired Wilcoxon test, comparing observed percentages of consumed plants (both seeds and seedlings present inside 1 × 1-m sub-plots) in patches and control plots. Spatial dependence between neighbouring plots (seed patches and control areas) was accounted for, as we used a statistical paired test.

As preliminary analysis showed that seed patch size and patch density per plot were correlated (Pearson's $r = 0.78$), we used only seed patch size in subsequent models. We used a generalized linear mixed model (GLMM) (Bolker *et al.*, 2009) to test the effects of seed patch size, distance between patch and nearest terra firme forest edge, and occurrence of mammalian carnivores as possible influences on herbivore visitation frequency. For the last of these, we defined 'occurrence' as the total number of herbivorous vertebrates or carnivorous mammals recorded at seed patches (our dependent variable).

At the beginning of the first campaign (low water season), water level dropped rapidly during the next few days (up to 40 cm per day – our pers. obs.), depositing seed patches on the forest floor. In contrast, during the second campaign, the river was at its lowest level, and many of the seeds present in the patches were already germinating. Therefore, flood depth was strongly correlated with the field campaign. Accordingly, we applied a Poisson error distribution to account for count data, and included field campaign as

a random effect in the model to control for temporal and spatial dependence in the data.

To test the model fit, we compared Akaike's information criterion (AIC) of the full GLMM with the respective AIC value for the null model (intercept and random effect only). Full GLMMs were selected when delta AIC (the difference between the full and null models) was >2 (Zuur *et al.*, 2009). To measure the importance of the random variables in our results, we calculated the marginal and conditional R^2 for the GLMM. Marginal R^2 provides the variation explained only by the fixed variables, while the conditional R^2 gives the variation explained by fixed and random effects in the model (Nakagawa & Schielzeth, 2013). We also displayed the selected models graphically using the *visreg* package (Breheny & Burchett, 2013). The partial graphs show expected values of the dependent variable and expected values of the target independent variable if all other independent variables in the analysis are maintained at their median values. GLMMs were created with the *lme4* package (Bates *et al.*, 2015) in R (R Core Team, 2016).

RESULTS

We sampled a total area of 3.6 ha of unflooded igapó forest floor. Each 1000-m² plot had on average 2.4 seed patches (\pm SD = 1.18). Within the total area sampled we recorded 89 seed patches. Seeds and seedlings from 61 identified species were recorded from the seed patches and control areas (Table 1). A further 11 morphospecies remain unidentified. There were higher numbers of seeds in patches than in control areas ($W = 1194.5$, $P < 0.01$), demonstrating that greater seed deposition does occur in some igapó locations than in others (Supporting Information, Fig. S2). The mean number of plant species in the patches was 5.58 (\pm SD = 2.82), while in control areas on average we found 2.80 species (\pm SD = 1.5). Patch size varied widely, the smallest found being 1.34 m² and the largest around 715 m². Their distribution did not follow a discernable pattern, and the distance between them was variable (2–40 m). Also, we observed no difference between plant species composition for seed patches and control areas per camera trap station (PERMANOVA, $R = 0.01$, $P = 0.268$) (Fig. S3).

Total sampling effort was 1080 camera-trap*days. We obtained 155 photographic records of: eight rodent species (three of which remain unidentified), plus 11 other mammal and nine bird species (see Table 2 for a complete species list). However, herbivorous vertebrate visitation frequency was similar between seed patches and control areas ($V = 162.5$, $P = 0.729$) (Fig. 2). The relative number of seeds and seedlings consumed was

also similar between seed patches and control areas ($V = 102.5$, $P = 0.4723$) (Fig. 3).

The full GLMM had a better fit (AIC = 191.66) than the null model (AIC = 203.86). Seed patch size explained most of the changes in vertebrate assemblage in GLMM analyses that considered all 36 plots. Seed patch size ($P < 0.001$) (Fig. 4A) and distance to terra firme forest ($P < 0.05$) (Fig. 4B) were positively and negatively related, respectively, to vertebrate assemblage occurrence (Fig. 4). In contrast, the presence of predators failed to explain the occurrence of herbivorous vertebrates across the dry igapó forest (Fig. 4C). Thus, igapó seasonality (included in our model as a random effect) seems to be more important than the fixed factors. The full model (conditional R^2) explained around 38% of the variation in vertebrate occurrence while the fixed effects (marginal R^2) explained 9%.

DISCUSSION

At the local scale, patches with high resource density were not more attractive to potential consumers of seeds and seedlings. In addition, we found that the percentage of seed and seedling consumption did not differ within and outside the seed patches (Fig. 3). Although there was no difference in occurrence of the studied vertebrate assemblage between seed patches and control areas, a large number of vertebrate species and individuals are present in igapó forest when it is unflooded. For many vertebrate assemblages, the igapó forests provide, during the non-flooded season, not only an abundant source of food resources, but also water (because many terra firme forest streams are dry at this time: Bodmer, 1990; Haugaasen & Peres, 2007). In addition to the photographic records, other indications, such as rodent burrows, faeces, bitten seeds and paw-prints, also show this environment to be occupied or visited frequently by a variety of mammal species (Antunes *et al.*, 2017; A. C. Antunes *et al.*, unpubl. data).

In comparison with studies carried out in várzea forests (white-water floodplains of the Amazon River and its tributaries) using a higher sampling effort, the total number of vertebrate records in this study was lower, although species richness was higher (Alvarenga *et al.*, 2018; Costa *et al.*, 2018). The number of records was probably affected by several fire events that happened in the JNP in 2015, some of them very close to the sampling areas of this study, and observed during the fieldwork (Fig. 1). Igapó forests have a low resilience to fire, and after a second event are unable to recover (Flores *et al.*, 2017). This only reinforces the potential ecological importance of these seed and seedling accumulations, the animal–plant interactions

Table 1. Plant species and morphotypes present in seed patches and control areas in igapó forest during the dry season, Jaú National Park (occurrence at SP = seed patches and CA = control areas)

Family	Species/ morphotypes	Occurrence
Arecaceae	<i>cf. Geonoma</i> sp.1	SP, CA
	<i>Iriartella setigera</i>	SP
	<i>Leopoldinia pulchra</i>	SP, CA
	<i>Mauritiella armata</i>	CA
	<i>Oenocarpus mapora</i>	SP, CA
Bignoniaceae	<i>Handroanthus barbatus</i>	SP
Chrysobalanaceae	<i>Couepia paraensis</i>	SP, CA
	<i>cf. Hirtella</i> sp.2	SP
Clusiaceae	<i>Licania</i> sp.1, 2, 3, 4, 5, 6, cf. 7	SP, CA
	<i>Calophyllum brasiliense</i>	SP, CA
	<i>Garcinia</i> sp.1	SP
Combretaceae	<i>Terminalia</i> sp.1, 2	SP, CA
	<i>Combretum</i> sp.1, 2, 3, cf. 4	SP
Connaraceae	<i>Connarus</i> sp.1	SP
	<i>Rourea</i> sp.1	SP
Ebenaceae	<i>Diospyros</i> sp.1	SP
Euphorbiaceae	<i>Alchornea</i> sp.1	SP, CA
	<i>Amaioua</i> sp.1, 2	SP
	<i>Hevea spruceana</i>	CA
	<i>Mabea nitida</i>	SP, CA
	<i>Mabea</i> sp.1, 2	SP
Elaeocarpaceae	<i>Sloanea</i> sp.1	CA
Fabaceae	<i>Acosmium</i> sp.1	SP
	<i>cf. Cynometra bauhiniifolia</i>	SP, CA
	<i>Cynometra</i> sp.1, cf. 2	SP
	<i>Dipteryx odorata</i>	SP
	<i>Dalbergia</i> sp. 1	SP, CA
	<i>Hydrochorea</i> sp.1, 2	SP, CA
	<i>Macrobium acaciifolium</i>	CA
	<i>Macrobium</i> sp. 1	SP, CA
	<i>Ormosia</i> sp.1, 2	SP
	<i>Swartzia polyphylla</i>	SP, CA
	<i>Swartzia</i> sp.1, 2, 3	SP, CA
	<i>Tachigali</i> sp. 1, 2, 3	SP
	<i>Gnetum</i> sp.1	CA
Gnetaceae	<i>Humiriastrum</i> sp.1, 2	SP
Humiriaceae	<i>Eschweilera tenuifolia</i>	SP, CA
Lecythidaceae	<i>Ocotea cymbarum</i>	SP, CA
Lauraceae	<i>Ocotea</i> sp.1, 2	SP, CA
	<i>Byrsonima</i> sp.1	SP
Malphigiaceae	<i>Abuta</i> sp.1	CA
Menispermaceae	<i>Abarema</i> sp.1	CA
Mimosoideae	<i>Eugenia</i> sp.1, 2	SP, CA
Myrtaceae	<i>Myrciaria</i> sp.1	SP, CA
	<i>Passiflora</i> sp.1	SP
Passifloraceae	<i>Securidaca</i> sp.1	CA
Polygalaceae	<i>Symmeria paniculata</i>	CA
	<i>Coussarea</i> sp.1	SP
Rubiaceae	<i>Allophylus</i> sp.1	SP
Sapindaceae	<i>cf. Elaeoluma</i> sp.1, 2	SP
Sapotaceae	Morphotypes 1, 2, 3, 4	SP, CA

Table 2. List of vertebrate species recorded by camera traps in igapó forest during the dry season at Jaú National Park

Group/Species	Common name	Seed patches	Control areas	Total
Mammals Carnivora				
<i>Leopardus pardalis</i>	Ocelot	9	2	11
<i>Leopardus wiedii</i>	Margay	3	5	8
cf. <i>Leopardus wiedii</i>		0	1	1
<i>Panthera onca</i>	Jaguar	1	3	4
<i>Pteronura brasiliensis</i>	Giant otter	2	0	2
Total carnivores		15	11	26
Rodentia				
<i>Cuniculus paca</i>	Lowland paca	3	7	10
<i>Dasyprocta leporina</i>	Red-rumped agouti	1	0	1
<i>Hydrochoerus hydrochaeris</i>	Capybara	0	1	1
<i>Isothrix</i> cf. <i>bistriata</i>	Yellow-crowned brush-tailed rat	0	1	1
cf. <i>Makalata</i> sp.		5	4	9
cf. <i>Oecomys</i> sp.		2	1	3
<i>Proechimys</i> sp.	Spiny rat	4	2	6
cf. <i>Proechimys</i> sp.		2	3	5
Didelphimorphia				
<i>Didelphis marsupialis</i>	Common ppossum	7	8	15
<i>Philander</i> sp.	Four-eyed ppossum	9	11	20
Perissodactyla				
<i>Tapirus terrestris</i>	Lowland tapir	0	1	1
Artiodactyla				
<i>Pecari tajacu</i>	Collared peccary	3	1	4
<i>Mazama guazoubira</i>	Gray brocket deer	0	1	1
<i>Mazama nemorivaga</i>	Brown brocket deer	3	2	5
Primates				
<i>Cebus albifrons</i>	White-fronted capuchin	3	4	7
Birds				
Anseriformes				
<i>Cairina moschata</i>	Muscovy duck	2	2	2
Struthioniformes				
<i>Crypturellus undulatus</i>	Undulated tinamou	1	4	5
<i>Crypturellus</i> sp.		1	1	2
Columbiformes				
<i>Geotrygon montana</i>	Ruddy quail-dove	2	0	2
<i>Leptotila rufaxilla</i>	Grey-fronted dove	4	5	9
<i>Leptotila</i> sp.		1	1	2
Galliformes				
<i>Pauxi tuberosa</i>	Razor-billed curassow	2	6	8
Gruiformes				
<i>Psophia leucoptera</i>	White-winged trumpeter	1	0	1
Pelecaniformes				
<i>Tigrisoma lineatum</i>	Rufescent tiger-heron	1	1	2
Struthioniformes				
<i>Tinamus guttatus</i>	White-throated tinamou	1	0	1
<i>Tinamus</i> cf. <i>guttatus</i>		1	0	1
<i>Tinamus major</i>	Great tinamou	3	0	3
<i>Tinamus</i> cf. <i>major</i>		0	1	1
<i>Tinamus</i> sp.		0	1	1
Total non-carnivores		62	69	129

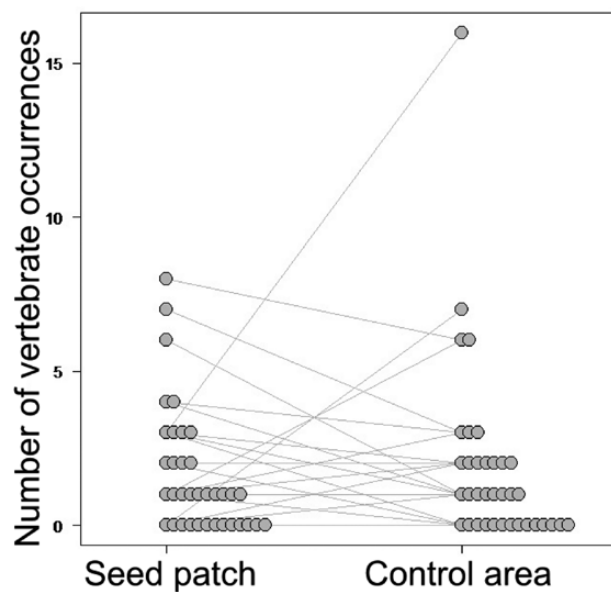


Figure 2. Number of herbivorous vertebrate occurrences, compared for seed patches and control areas (shown in paired format by the dashed lines), in igapó forest.

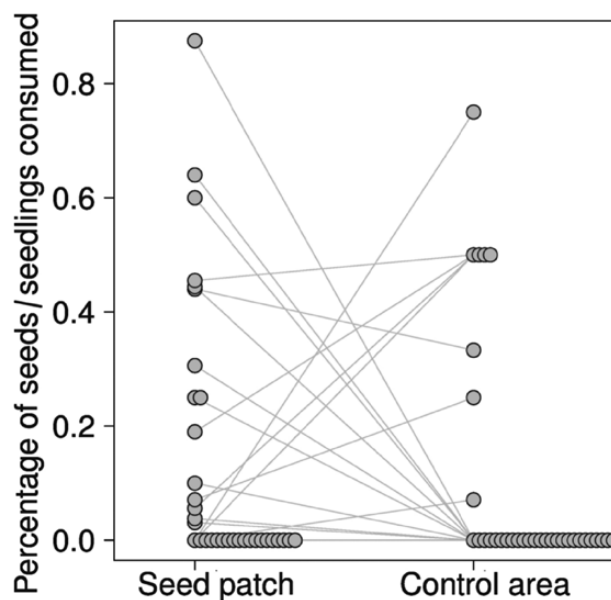


Figure 3. Percentage of seeds/seedlings consumed by vertebrates in areas with and without seed patches (shown in paired format by the dashed lines). No significant difference was observed ($P > 0.05$).

that are associated with them (including seed consumption and dispersion by animals), and which species (plant and animal) are involved, all of which are currently unknown. Haugaasen & Peres (2007) demonstrated that the increased availability of fruits and seeds deposited on the ground in igapó forests,

and new vegetative growth when water levels recede, coincide with the migration of fruit- and seed-eating vertebrates from terra firme forest. Bodmer (1990) found floodplain forests in Amazonian Peru also to be seasonally important for ungulates, and Barnett *et al.* (2012) reported seed patch use by otherwise arboreal igapó-dwelling primates that moved to the ground to exploit them.

Our results contradict the central hypothesis proposed in this study and so raise the following question: why, given the presence of patches of abundant resources, are animals not distributed as predicted by the IFD? Ungulate herbivores and small mammals are well known to have good spatial memories with regard to aggregations of food resources (Howery & Bailey, 1999). Also, rodents detect, and prefer to forage in, larger and denser seed patches (Cabin *et al.*, 2000; Baraibar, 2011); consequently, resource distribution can strongly influence the spatial use of an area by such animals (Fagan *et al.*, 2013). However, because of how igapó seed patches form, their size and spatial distribution on the igapó forest floor is likely to vary significantly between years, decreasing the relevance of any long-term spatial memory of resource locations that an animal might deploy. Consequently, fruit- and seed-eaters visiting unflooded igapó forests are probably exploring the area extensively in search of resources that are unpredictable in size, composition and density. This characteristic violates one of the principles of the IFD, namely that individuals are aware of the resource profitabilities of each patch. In addition, as animals are unlikely to be territorial under such circumstances, the progressive depletion of patch value over time (a key element of resource use foraging: see Krebs *et al.*, 1974; Kotler & Brown, 1990) is also likely to be highly variable in nature and extent.

There may, in addition, be others factors in play. In this study, camera-traps recorded several carnivores ($n = 26$; 16% of records). The large numbers of paw-prints also attested to the frequent occurrence of such animals in the study habitat (A. C. Antunes, unpubl. data). The species present included those known to prey on small granivores (e.g. rats and mice), such as margay and ocelot, and those, such as the jaguar, that prey on larger species (e.g. paca, peccary and deer). In comparison to upland forests, an open landscape such as the unflooded igapó forest (de Almeida *et al.*, 2016; and see Supporting Information, Fig. S4) offers greater visibility and consequently has an influence on the risk of predation by these predators. For the golden-backed uacari monkey (*Cacajao ouakary*), another igapó mammal that uses these seed patches, landscape composition is one of the key factors influencing its foraging behaviour: this primate avoids seed patches close to dense ground-based vegetation (Barnett *et al.*, 2012). In addition, not all fruits and seeds available

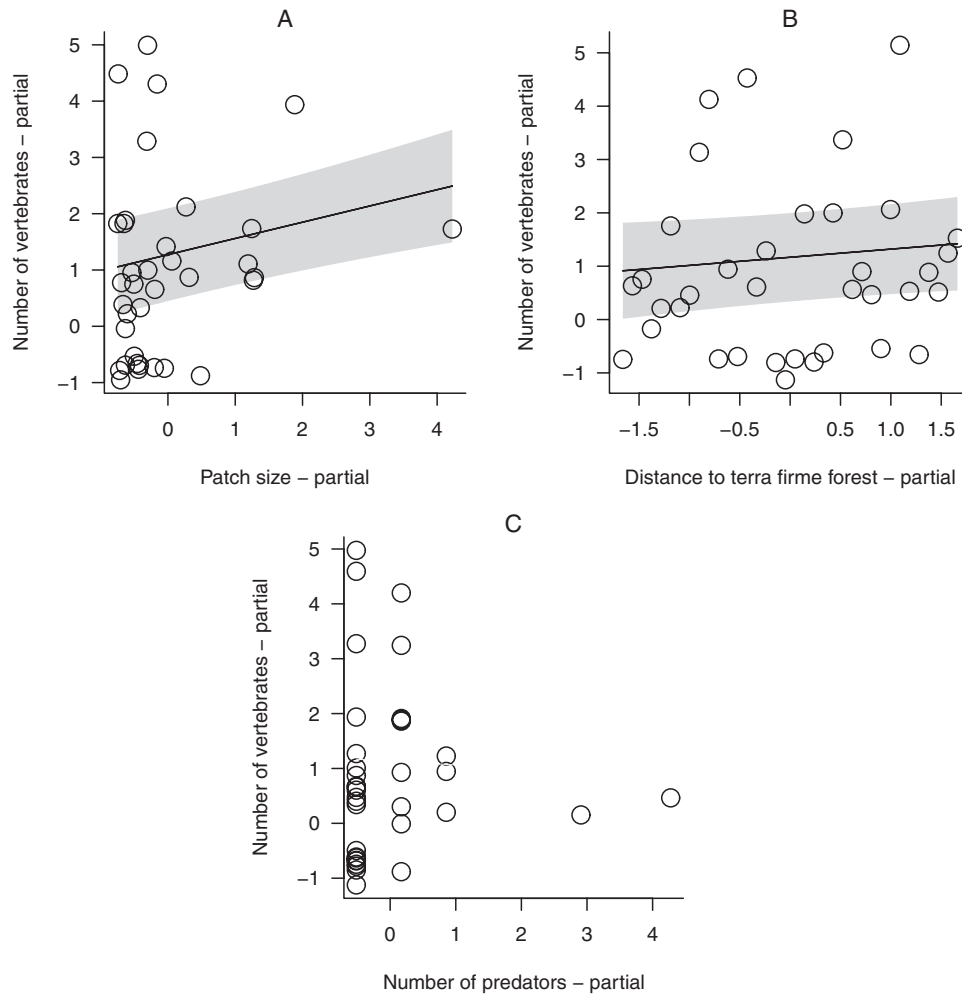


Figure 4. Relationship between vertebrate number and patch size (A), distance to terra firme forest (B) and number of predators (C). Regression lines are shown only for significant relationships (see text). The grey area represents the 95% confidence interval.

in patches are palatable, as plants may invest less in anti-herbivory defences when nutrients are plentiful (Coley, 1985). In the generally nutrient-poor study area, plants are known to invest heavily in anti-herbivory defences such as tannins and other phenolic compounds, which in turn are considered to reduce the carrying capacity for a variety of organisms, both directly (vertebrate and invertebrate herbivores) and indirectly (their predators and parasites) (Freeland & Janzen, 1974; Janzen, 1974; Marples, 2018). Also, many fruits and seeds are of a size compatible with the consumer (Antunes *et al.*, 2017), so that energy reward in each patch is unpredictable. Coupled with the random distribution of most seeds and seedlings (which consequently require extensive travel by herbivores to find them), this could influence the ways in which potential prey species are consuming and moving between the resources available at seed

patches and control areas (Mitchell & Lima, 2002; Schmitz *et al.*, 2004). In prey species known to have well-developed spatial memory capacity (e.g. scatterhoarding rodents: Smulders *et al.*, 2010; Hirsch *et al.*, 2013), it is known that they will randomize movements to decrease encounters with predators (Mitchell & Lima, 2002).

Although patch formation is unpredictable at the small scale (between treatments), it is likely that at larger scales (e.g. along the river) there are more suitable sites for floating patches to be deposited, depending on topography and other landscape features, which makes the deposition of patches somewhat more predictable for the vertebrates that are present in these areas, especially those with larger home-ranges. Despite frugivorous vertebrate occurrences not being related to seed patches locally, they are positively related to seed patches sizes at larger scales. Other

studies have also shown that species responses are scale-dependent (Garmendia, 2013; Quesnelle, 2014; Alvarenga *et al.*, 2018). For várzea forests, mammal assemblage composition varies according to scale, which reinforces the importance of considering scale in ecological landscape studies (Alvarenga *et al.*, 2018). In our study, the larger the size of patches, the greater the number of occurrences of vertebrates associated with them. According to the IFD, animals tend to forage in the highest quality patches, and therefore larger patches would be more attractive. Even though patch compositions are unpredictable, larger patches are more likely to have a greater energy reward for animals that feed on them than smaller patches.

Distance to terra firme forests was an additional explanatory factor in frugivorous vertebrate occurrence at large scales within JNP igapó forests: the closer to the terra firme forest, the greater the number of recorded occurrences. During the driest months of the year, water availability is known to affect the distribution of terra firme-dwelling animals very intensely (Paredes *et al.*, 2017), so that animals move through igapó forests in search of water. Because all plots were established near the Rio Jaú main channel, the distance from study plots to terra firme forest was linked to the distance from the main remaining free-standing water source (Supporting Information, Fig. S5), once most small streams dry up (R. S. Moreira, pers. comm.). Accordingly, patches closer to terra firme forest represent the smallest distances to be travelled from the edge of the terra firme to the igapó forest during the search for resources and water, and consequently this equates to less time of exposure and lower risk of predation.

The occurrence of this frugivore assemblage in the forest is independent of the presence of predators, probably due to prey avoidance of open or exposed areas, while seeking rapid access to water and valuable food resources in the larger patches. In várzea forests, some predators (such as the margay) use the habitat homogeneously, with no precise association with their prey, probably due to the large variety of prey that occur in these forests (Alvarenga *et al.*, 2018). A similar process seems to occur in the igapó forest during the dry season, a period in which there is large-scale lateral movement of animals from terra firme to adjacent igapó forest in search of resources and water. The absence of a correlation between predator and prey occurrences on this scale may also be linked to refuge availability, because the igapó forest floor is very open compared with other tropical forest habitats, and the absence of cover is known to explain a lack of correlation in the spatial distribution of predators and prey (Sih, 1984; Formanowicz & Bobka, 1989).

CONCLUSION

Information on vertebrates in igapó forests remains very limited. River flood-pulse dynamics directly influence the distribution and composition of plant assemblages and, consequently, those of animals. Differences in water levels between field campaigns explained most of the variation in vertebrate occurrence we found. The lateral movement of frugivorous vertebrates between terra firme and igapó forests reinforces the importance of these floodplains as a source of food and water during the dry season (Haugaasen & Peres, 2007; Costa *et al.*, 2018). At the large scale, the formation of seed and seedling aggregates on the forest floor appears to be important to the herbivorous guild that feed on them during this period, but this also highlights other little-known ecological aspects, such as seedling establishment and recruitment in the area, dispersal/predation of seeds by small mammals, and infestation of these seeds by insects, among others. A better understanding of these processes is needed for igapó forests, which must be understood as functionally linked mosaics of ecologically integrated habitats, which include upland forests and white-sand scrub-forest (campina). This is important for vertebrate conservation in Amazonia, because such a dual-habitat greatly enhances the vulnerability of species that use this seasonal resource utilization strategy (Flores *et al.*, 2017). Consequently, this study contributes to understanding the dynamic nature of frugivorous animals on the igapó forest floor, as well as paving the way for future studies.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Fig. S1. A, seed patch accumulating and floating during the flooded season in igapó forest. The arrow shows the seed patch limit. B, high density of deposited seedlings (arrow), contrasting with the rest of the forest floor during the unflooded season.

Fig. S2. There are significantly higher numbers of seeds and seedlings in patches than in control areas ($P < 0.01$), confirming the formation of seed patches in contrast to control areas (shown in paired form by dashed lines).

Fig. S3. Multidimensional scaling ordination of plant species composition at seed patches and control areas.

Fig. S4. Image of igapó forest within the Jaú National Park during the dry season. The open nature of the understorey allows high visibility within the forest.

Fig. S5. During the dry season, it is common for streams to dry-up, so that the main channel of the Jaú River, accessible only by crossing igapó forest, becomes the main source of water for many vertebrates. The figure shows a stream in the year that the sampling was performed (the entire open area is water-filled in the high-water season).